



Territorial behavior of the migratory Lined Seedeater during the breeding season

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Abstract

Most bird species will defend a territory during the breeding period to assure the availability of resources for their reproductive success. Migratory birds abdicate their territory ownership during the non-breeding period, posing a challenge for the following breeding season. Here we investigated the territorial behavior of male Lined Seedeaters *Sporophila lineola*, an intra-tropical migrant, during the breeding season (December–May) 2018/2019 in south-eastern Brazil. The Lined Seedeater is a sexually color-dimorphic species that inhabits open areas and feeds on seeds. We followed 18 color-banded individuals, during the period in which they had an active nest. For each individual, we recorded the locations in which they exhibited any potential territorial behavior, with the aid of a handheld GPS. We then estimated the size and shape of the territories using a Kernel Density Estimator. The breeding territories had on average 0.59 ± 0.24 ha, ranging from 0.21 to 0.91 ha in area. Males exhibited agonistic behavior whenever another male intrudes on their territories, especially if in the vicinity of their nests. Our observations indicate that male Lined Seedeaters defend small territories of exclusive use during the breeding season, but forage over a wider home range shared with other conspecifics. Therefore, Lined Seedeaters and other members of *Sporophila* seem to exhibit home ranges that are much larger than their breeding territories. Empirical studies are needed to understand the influence of territory size and quality on reproductive fitness.

Keywords Birds · Breeding biology · Neotropics · Kernel Density Estimator

Introduction

Territorial behavior is one of the most elementary aspects of a species' natural history, with most bird species defending some type of territory during at least part of their lives (Alcock 2016). The comparatively few studies on territoriality ever conducted in tropical zones were mostly performed with year-round resident species (Greenberg and Gradwohl

1997; Lopes and Marini 2006; Duca and Marini 2014), and almost nothing is known about the territorial behavior of migratory species, especially the intra-tropical migrants. Here, we investigated the territorial behavior and estimated the breeding territory size of the Lined Seedeater *Sporophila lineola* (Thraupidae).

The Lined Seedeater is a small granivorous songbird with a diagnostic sexually color-dimorphic plumage with adult males exhibiting a distinctive black-and-white plumage that strongly contrasts with the dull brownish plumage of females; young males exhibit a female-like brownish plumage (Ridgely and Tudor 2009). The species is widespread throughout much of South America, where it inhabits a variety of open habitats (Ridgely and Tudor 2009). This is an intra-tropical migratory species, with the studied population breeding in south-eastern Brazil from December to April (Oliveira et al. 2010; Ferreira and Lopes 2017), then migrating to the northern part of South America, where it winters (Silva 1995). However, to this day little is known about its migratory habits and pathways.

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A territory is of crucial importance for the reproductive fitness of an individual since it can comprise the necessary resources to successfully raise offspring (Verner 1977; Lobato et al. 2010). Migratory birds face a particular challenge since they abdicate of territory ownership between breeding seasons; therefore, it is assumed that as soon as the males are refueled from their migratory journey, they would then start to claim and/or re-claim their territories (Greenberg 1986). In Lined Seedeaters, the territory plays an important role in mating. Females build the nest alone and assume the main role over incubation and feeding (Ferreira and Lopes 2017); thus, it is assumed that territory is a valuable resource to which males would then compete over it. Little is known about territorial behavior of Lined Seedeaters; thus, in this study, we analyzed territory size and investigate territorial behaviors displayed by males. In this study, we cover a gap in the knowledge of the natural history of the species shedding new light for future empirical studies on the function and mechanism of territorial behavior and fitness interplay.

Methods

We conducted our field observations in the Campus Florestal of the Universidade Federal de Viçosa, municipality of Florestal, state of Minas Gerais, south-eastern Brazil. The study area lies in the transition zone between the Cerrado savannas and the Atlantic Forest biogeographic provinces (IBGE 2004). Climate in Florestal is subtropical with a dry, mild winter, and a humid, hot summer (Lopes and Marçal 2016). The Campus Florestal is about 1500 ha, covered by fragments of secondary semideciduous forests and by several types of man-made open habitats, including extensive pastures of African grasses, cultivated areas, extensive gardens around the main buildings, and several small ponds (Ferreira and Lopes 2017).

This study is part of the Lined Seedeater Project, which monitors a breeding population of the species since 2014. After the arrival of the first migratory birds in the study area in the first week of November 2018, we began to search for territorial males and mist-netting those males that have not been banded during previous breeding seasons. Unmarked males were then banded with a numbered metallic band and a unique combination of three colored plastic bands, which allowed individual identification with the aid of binoculars (Fig. 1). Our fieldwork extended until May 2019, when birds migrated to their wintering grounds, marking the end of the breeding season.

We defined breeding territories as the defended area around the nest location (Welty and Baptista 1988; Maher and Lott 1995). Once we discovered a nest during the construction stage or early incubation, we followed the males collecting



Fig. 1 Male of Lined Seedeater *Sporophila lineola* color-banded in the study area, southeastern Brazil

the data points on their geographical locations of the territorial male until nest failure or success. With a handheld GPS device (Garmin™ eTrex 30×, 3–5 m precision), we marked the locations where the male was observed singing, fighting other males, and/or copulating. We marked a new location for every displacement, but only after the male spontaneously left the perch, to interfere as less as possible on its behavior. We sampled each territory for the duration of a single reproductive event, during at least 6 different days. We assume this is the minimum amount necessary for sampling the territory, so as not to bias the results due to the constant human presence. This decision was made based on our experience obtained from monitoring previous seasons with the species.

To estimate territory size, we used the Kernel Density Estimator, implemented in the ‘rhr’ package (Signer and Balkenhol 2015) in R software (R Core Team 2016). The Kernel Density Estimation was calculated for a contour value of 95% and using the reference bandwidth, since this method is appropriate when the locations are arranged as a single tight cluster (Signer and Balkenhol 2015). We also investigated site fidelity using the mean square distance from the center of activity and verified if the territories reached an asymptote (e.g., Laver and Kelly 2010; Signer and Balkenhol 2015). Territories with less than 30 locations were discarded (e.g., Seaman et al. 1999). The software QGIS and Google Earth Satellite images were used to prepare the map depicting the home ranges.

Results

Overall, we assessed and monitored 19 breeding territories belonging to 18 males. For one male (*Male number* 8, Fig. 2), we estimated the size of the two territories this

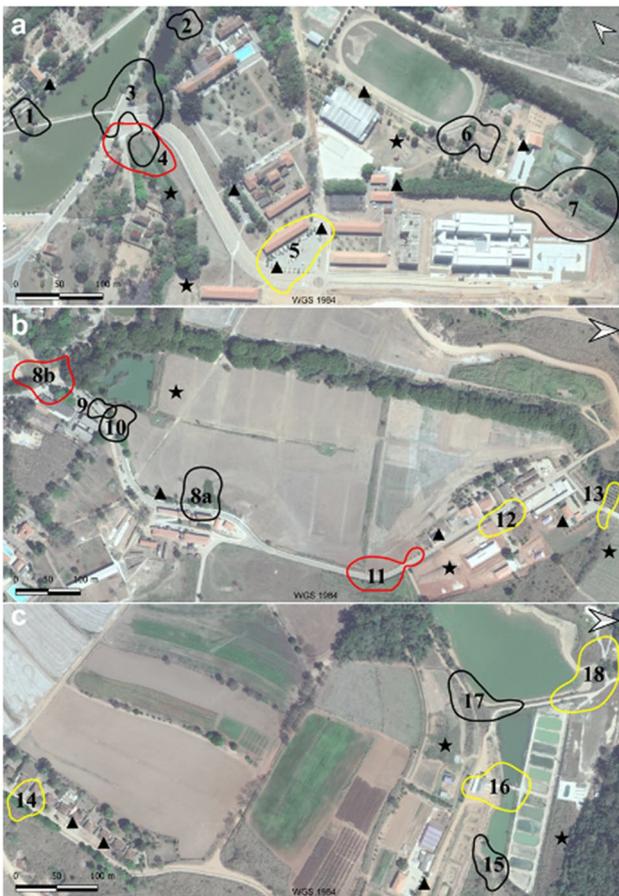


Fig. 2 Breeding territory size of eighteen males of Lined Seedeaters *Sporophila lineola* monitored in southeastern Brazil. Black areas are territories held by males in relation to the previous breeding season; red areas represent males that have changed the location of their territories between seasons or during a same season; yellow areas represent males color-banded in the 2018–2019 season and for which we have no previous information. Note that the *Male 8* held two distinct territories (8a and 8b) estimated during two distinct nesting attempts. Black triangles indicate the approximate location of the center of the territory of other territorial males that have not been sampled during this study. Black stars indicate shared feeding zones where at least one banded male was observed side by side with other individuals during a nesting attempt

individual held during the breeding season. This male paired with two distinct females, the first paired female was not observed in the study area after the first nesting attempt. Six males were captured between November and March 2019. The other 12 males were banded during previous breeding seasons.

The first Lined Seedeaters arrived in the study area on 06 November 2018, when we observed five males in the adult black-and-white plumage foraging. Even though these males eventually sang, we observed no sign of aggressiveness between them. On 11 November, we observed four other males foraging side by side, but no aggressive behavior

was recorded during the 5 days these birds shared a grass patch, in which *Male 4* established his territory for the season (Fig. 2).

The number of individuals recorded in the study area increased over the days with the arrival of new males. The first female, however, was only recorded in the study area on 17 November, 11 days after the arrival of the first males. During the first 2 weeks, individuals shared feeding areas, and even though they eventually sang, they were mostly tolerant with one another. On 28 November, the first two territories were established, as evidenced by the observation of the first territorial disputes and an increase in song output. For example, *Male 4* chased and evicted another male that invaded its territory on three occasions on the same day, on 01 December. *Male 7*, who has previously been seen twice sharing a feeding area with other conspecifics, chased away a brownish male that sang within its territory on 02 December.

Only one of males monitored, *Male 12* (Fig. 2), was in the brownish plumage, while all other males were in the adult plumage. We obtained 1260 geographical locations, in an average of 66.3 ± 19.2 locations per territory, ranging from 39 to 99 locations. Males from all territories studied exhibited site fidelity, but four of the 19 territories monitored did not reach an asymptote (Supplementary Material S1). Breeding territories were on average 0.59 ± 0.24 ha in area, ranging from 0.21 to 0.91 ha (Table 1).

At the present study, 10 out of the 18 males occupied roughly the same territories where they have bred during the previous season, as evidenced by the location of their nests monitored 1 year before (Table 1). However, one of these individuals, *Male 8*, had another reproductive attempt in a distinct territory. After breeding successfully during the 2017–2018 breeding season, this individual returned to the same site in the 2018–2019 breeding season, but after succeeding in a first attempt, this same individual moved about 300 m southwestward, where it established a distinct territory (see Fig. 2b). Two other males banded during previous breeding seasons changed the location of their territories, with *Male 11* moving about 850 m (in relation to the border of his current territory) from the place where his nest was monitored the year before. *Male 4* moved about 300 m from the place where it was captured during the previous breeding season. The remaining six males were banded during this study, but three of which established territories in areas that were occupied by other banded males whose nests were monitored during the previous breeding seasons. Therefore, *Males 12, 14, and 16* occupied their territories for the first time.

Even though in Lined Seedeaters nest construction and incubation are performed exclusively by females, males usually stay close to females during nest construction. In four occasions, we observed the male chasing the female briefly after she added new material on the nest, returning

Table 1 Breeding territory size of 18 males of Lined Seedeaters *Sporophila lineola*. Estimates were obtained with the Kernel Density Estimator using the reference bandwidth and a 95% contour value. The table indicates if the birds exhibited site fidelity and if their territories reached an asymptote, as well as whether the individuals maintained their territories from the previous season, except those that were captured during the present study (–)

Male	Number of points	Area (ha)	Site fidelity	Asymptote	Kept territory
1	50	0.25	Yes	Yes	Yes
2	45	0.21	Yes	Yes	Yes
3	50	0.80	Yes	Yes	Yes
4	98	0.72	Yes	Yes	No
5	63	0.84	Yes	No	–
6	83	0.41	Yes	Yes	Yes
7	59	0.91	Yes	No	Yes
8a	85	0.88	Yes	Yes	Yes
8b	71	0.81	Yes	No	No*
9	39	0.20	Yes	Yes	Yes
10	45	0.48	Yes	Yes	Yes
11	56	0.60	Yes	Yes	No
12	68	0.49	Yes	Yes	–
13	98	0.44	Yes	Yes	–
14	52	0.34	Yes	Yes	–
15	99	0.31	Yes	Yes	Yes
16	54	0.73	Yes	No	–
17	64	0.55	Yes	Yes	Yes
18	81	0.85	Yes	Yes	–
Mean ± SD	66.3 ± 19.2	0.59 ± 0.24			

*Male 8 had two distinct territories estimated during distinct nesting attempts

afterward to a singing perch close to the nest. Males are the main responsible for nest guarding and territorial defense, singing on high perches close to the nest, usually facing it, for most of the day, even under apparently adverse weather conditions (e.g., when drizzling or in the hottest hours of the day). Only on rare occasions, we observed females engaged in agonistic interactions with other Lined Seedeaters, including attacks to other males ($n=3$) and to a brown individual of undermined sex that has approached on the nests.

Males did not tolerate the invasion of their territories by other males, especially if close to their nests. When this occurred, the resident male often evicted the intruder. During this study, we observed 17 agonistic encounters between males, most of them during the nest construction period ($n=9$). Territorial disputes were frequent throughout the breeding season, eventually leading to adjustments in the territory borders or even to the replacement of the territory owned by another male. For example, the territory of *Male 5* was delimited at the beginning of the breeding seasons, before the arrival of the two other males indicated in Fig. 2a and whose territories have not been sampled. Later in the season, these three males stayed in the same area, occupying very small territories with apparently no or only negligible overlap between them.

The purported overlap between the territories of *Males 3* and *4*, as well as between *Males 9* and *10* (Fig. 2) did not occur

temporally, with each male occupying the area of overlap only during a distinct period of the breeding season. *Males 17* and *18* were observed disputing a territory on 18 November, during the early breeding season. We observed at least four agonistic encounters between them, until *Male 17* eventually won the territory dispute, with *Male 18* being forced to occupy an adjacent territory. *Male 5* took the territory of another unbanded male that occupied the same area at the beginning of the breeding season.

Males and females of the Lined Seedeater frequently feed in grassland patches out of their territories. These feeding areas were used by several individuals of the species, sometimes simultaneously (e.g., two black-and-white males and two brown unsexed birds were observed foraging side by side in grassland between *Males 16* and *17*; Fig. 2c). *Male 5*, for example, has established its territory in a parking lot with no food sources available in there. This male usually foraged in a grassland patch about 150 m from the borders of its territory, in a feeding area that was also used by his neighbor males and other conspecifics. These feeding areas were also shared with other granivorous species, such as the Yellow-bellied Seedeater *Sporophila nigricollis*, the Saffron Finch *Sicalis flaveola*, and the Blue-black Grassquit *Volatinia jacarina*, with intra or interspecific agonistic encounters seldom occurring.

Discussion

As soon as Lined Seedeaters arrive on their breeding grounds, males exhibit a tolerant social behavior toward other males, similarly to what is observed on their wintering grounds in the savannas of Surinam and Venezuela, where small flocks of the species are commonly seen, with several males foraging side by side (Haverschmidt 1968; Thomas 1979). This behavior persisted in the study area for about 2 weeks, while males foraged in a small corn plantation with some invasive African grasses and other seed-bearing weeds. This plantation, which was located at the central upper portion of Fig. 2c, was subsequently not used for breeding by any male.

Territories of Lined Seedeaters and other congeneric species are defended by the males (Areta et al. 2013; Franz and Fontana 2013; Ferreira and Lopes 2017; Rosoni et al. 2019), which usually sing on high and exposed perches close to the nest (Rovedder and Fontana 2012; Franz and Fontana 2013; Repenning and Fontana 2016). Concerning territory size, our findings suggest that territories of Lined Seedeater are smaller than those of some other species of the genus, such as the Rusty-collared Seedeater (*S. collaris*; 3.22 ha, Rosoni et al. 2019) and the Tropeiro Seedeater (*S. beltoni*; 1.60 ha, Repenning 2012), but slightly larger than that found for the Black-bellied Seedeater (*S. melanogaster*; 0.27 ha, Rovedder 2011).

The breeding territories of Lined Seedeaters are very small, with most territories studied covering a radius of only a few dozen meters around the nest. There was, however, great variation in territory size between the eighteen males studied, with the largest territory (0.91 ha) exhibiting an area four and a half times larger than the smallest territory (0.20 ha) studied. There are several explanations for such large variation in territory size, including differences in the previous breeding experience of males, differential abundance of resources, or even the presence of physical barriers (e.g., high buildings and ponds, Fig. 2) that can impose limits to the size and shape of territories (Hinde 1956; Powell 2000; Barg et al. 2005).

Our observations also suggest that territorial defense is probably not related to the defense of food resources in Lined Seedeaters, since birds frequently feed out of their territories (i.e., the home range, even though not measured, are much larger than their territories). Given that most of the agonistic encounters recorded during this study occurred during the nest construction period (i.e., when females are supposed to be fertile), we suggest that territorial defense in Lined Seedeaters may have an important role in avoiding extra-pair paternity (Rovedder and Fontana 2012). On the few occasions that we observed an intruder male perched in the same tree where the nest of

the territory owner was located, the intruder was chased by the resident pair, who evicted it. This behavior was observed five times during nest building and three times when the nest contained nestlings. Similar behavior was reported for the Double-collared Seedeater *Sporophila caerulea* (Francisco 2006).

After egg laying and the onset of incubation, males of the Lined Seedeater apparently expanded their home ranges, exploring feeding areas more distant from their nests and territories. The use of feeding areas far apart from the breeding territory has also been reported for other species of *Sporophila*, such as the Rusty-collared Seedeater (Rosoni et al. 2019) and the Black-bellied Seedeater (Rovedder 2011), which have been recorded using feeding areas as far as 1.4 km from its breeding territory. Therefore, Lined Seedeaters and other members of *Sporophila* seem to exhibit home ranges that are much larger than their breeding territories.

The defense of year-round multi-purpose territories is a common strategy among resident tropical birds, with migratory species usually defending territories only during the breeding season (Stutchbury and Morton 2001). The territorial behavior of Lined Seedeaters has already been highlighted by Sick (1997) and Ferreira and Lopes (2017), who reported frequent vocal disputes and agonistic encounters between males of the species. Agonistic interactions between males consisted of single, isolated events (e.g., attempts of extra-pair copulations) or could last for days (e.g., true territorial disputes), as observed in one of the territories monitored, where a black-and-white plumaged bird (*Male 5*) disputed its territory with an unbanded brownish male during 3 consecutive days. Frequent disputes, especially at the beginning of the breeding season, have also been reported for the Tropeiro Seedeater (Repenning 2012). The Black-bellied Seedeater, on the other hand, did not present a high frequency of territorial intrusions (Rovedder 2011).

The only brownish male we monitored was banded in its breeding territory in the 2018–2019 breeding season. Lined Seedeaters, as many other species of *Sporophila*, exhibit delayed plumage maturation (Hawkins et al. 2012), with the black-and-white adult plumage being acquired only during the second cycle (Ferreira 2019). These young brownish males were already known to successfully breed (Oliveira et al. 2010; Ferreira and Lopes 2017), but this is the first time its territorial behavior was studied. This brownish male defended a 0.49-ha territory, which was slightly smaller than the mean 0.59 ha territory size recorded in this study, but larger than the territory of eight black-and-white males monitored in this study (Table 1).

Our findings reported here represent an advance to our understanding of the behavioral ecology of Lined Seedeaters, raising some additional questions that deserve further empirical investigation such as the traits that define the quality of a territory that is tangible with reproductive fitness.

Given the migratory nature of Lined Seedeater, it is unclear if migratory schedule influence territory quality, size, and/or occupancy. The present work sheds new light on the natural history of Lined Seedeater and opens new venues for the study of long-standing evolutionary puzzles.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s43388-021-00065-y>.

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Availability of data and material The raw data with all localities are available at a separate file (.xlsx).

Declarations

Ethics approval Permits for this project were granted by Instituto Chico Mendes da Conservação da Biodiversidade (61078-1) and animal procedures were approved by the Comissão de Ética no Uso de Animais—Universidade Federal de Viçosa (03/2018).

Consent to participate All the authors consent to participate in this study.

Consent for publication All the authors consent to publish this study.

Conflict of interest The authors declare no competing interests.

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