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Tarso Natividade Ciolete

PROTANDRIA E SEU IMPACTO SOBRE A REPRODUÇÃO DE UMA AVE MIGRANTE INTRA-TROPICAL

Belo Horizonte

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Dissertação apresentada ao programa de Pós-Graduação em Zoologia da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Zoologia

Orientador: Prof. Dr. Leonardo Esteves Lopes

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Protandria e seu impacto sobre a reprodução de uma ave migrante intra-tropical

TARSO NATIVIDADE CIOLETE

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*A minha mãe, Elaíze, que me
incentivou a seguir meus
sonhos e objetivos.*

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Resumo

Introdução: aves migratórias enfrentam anualmente uma jornada custosa durante a temporada reprodutiva. O momento de chegada nos territórios reprodutivos está associado com esses custos e também com importantes consequências no fitness individual. Trabalhos anteriores apontam que os momentos ótimos de chegada nos territórios variam de acordo com o sexo, idade e fatores morfológicos, indivíduos que conseguem adiantar a data de chegada tem um maior investimento e sucesso reprodutivo na temporada. Entretanto pouco se sabe sobre a influência da data de chegada em aves migratórias intra-tropicais que estão submetidas a um ambiente diferente e, portanto, tem um estilo de vida diferente de aves de clima temperado a qual a maioria dos estudos foi conduzido.

Métodos: Nos monitoramos a data de chegada de um passeriforme migratório intra-tropical, Bigodinho *Sporophila lineola*, para os territórios reprodutivos no sudeste do Brasil, no qual uma população anilhada da espécie é monitorada desde 2014. Foi realizado amostragens diárias em uma rota pré-determinada de novembro de 2019 até fevereiro de 2020, registrando a data de chegada, comprimento da asa, cauda e tarso, sexo e a combinação única de anilhas coloridas de cada ave observada. Usamos um modelo linear generalizado para analisar a influência de fatores morfológicos e um wilcoxon rank sum test para analisar a influência de idade e sexo na data de chegada. Para avaliar a influência da data de chegada nas características reprodutivas procuramos ninhos de novembro de 2019 até março de 2020. Usamos um modelo linear generalizado para avaliar a influência da data de chegada no acasalamento seletivo, sucesso reprodutivo, número de tentativas de reprodução e investimento na ninhada na primeira tentativa e durante toda a temporada

Resultados: Conseguimos determinar a data de chegada de 125 indivíduos e encontrar 137 ninhos. Nossos resultados indicam que machos mais velhos chegam antes dos mais novos e que machos, irrespectivamente da idade, chegam antes de fêmeas (protandria). Indivíduos com caudas e tarsos mais longos também chegaram antes, independente do sexo. O investimento em cada ninhada parece estar inversamente correlacionado a data de chegada, porem está diretamente relacionado ao início da temporada e com número de tentativas reprodutivas, o que gerou um aumento no fitness dos machos, para as fêmeas o aumento do fitness

parece estar relacionado à data de chegada de seus parceiros.

Conclusão: O presente trabalho mostrou a primeira evidência de protandria e uma data de chegada dependente da idade e do fenótipo para o bigodinho. Também aponta que a chegada precoce aumenta a duração da estação reprodutiva e permite uma estratégia em que o investimento reprodutivo é diluído em um maior número de tentativas de reprodução.

Palavras-chave: migração, data de chegada, tamanho corporal, idade, aves tropicais

Abstract

Introduction: Migratory birds annually face a costly journey during the breeding season. The arrival time in breeding grounds is associated with these costs and also with important consequences for individual fitness. Previous works show that the optimal moments of arrival in breeding ground vary according to sex, age and morphological traits, individuals who manage to advance the arrival date tend to have a greater investment and reproductive success in the season. However, little is known about the influence of the arrival date on intratropical migratory birds that are subjected to a different environment and therefore have a different pace of life than the temperate climate birds which most studies have been conducted.

Methods: We monitored the arrival date of an intra-tropical migratory passerine, Lined Seedeater *Sporophila lineola*, to breeding grounds in southeastern Brazil, where a ringed population has been monitored since 2014. We conducted daily samplings in a predetermined path from 1 November 2019, till 13 February 2020, recording the arrival date, wing, tail and tarsus length, sex and the unique combination of colored rings of each bird observed. We use a generalized linear model to analyse the influence of morphological traits and a wilcoxon rank sum test to analyse the influence of age and sex on the arrival date. To assess the influence of arrival date on reproductive traits we looked for nests from November 2019 to March 2020. We used a generalized linear model to assess the influence of arrival date on assortative mating, reproductive success, number of breeding attempts and investment in broods on first attempt and throughout the full season.

Results: We were able to determine the arrival date of 125 individuals and find 137 nests. Our results indicate that older males arrive before younger ones and that males, regardless of age, arrive before females (protandry). Individuals with longer tails and tarsus also arrived earlier, regardless of sex. The investment in each brood seems to be inversely correlated with the arrival date, however it is directly related to the start of the season and the number of reproductive attempts, which generated an increase in male fitness, for females the increase in fitness seems to be correlated to arrival date of her partners.

Conclusion: The present work showed the first evidence of protandry and an age and phenotype-dependent arrival date for the Lined Seedeater. It also points out that early arrival increases the duration of the breeding season and allows for a

strategy in which the reproductive investment is diluted in a greater number of breeding attempts.

Keywords: migration, arrival date, body size, age, tropical birds

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Chapter 1. Large males arrive first: protandry in an intra-tropical migratory bird

Abstract

Background: Individual and environmental constraints play important role on the duration of the costly journey that migratory bird species face every year. In most migratory bird species males arrive first at breeding grounds, and experience (e.g. age) and morphometric traits that presumably optimize flight (e.g. wing length) seem to also predict individual's migratory schedules. However, little is known on how those factors influence breeding ground's arrival dates in intra-tropical migrants.

Methods: To investigate this, we monitored the arrival date of an intra-tropical migratory songbird, the Lined Seedeater *Sporophila lineola*, to a breeding ground in south-eastern Brazil in which a ringed population of the species is monitored since 2014. Lined Seedeater is a small sexually colour-dimorphic species in which males are territorial and can use the same territory across seasons. We conducted daily samplings in a predetermined path from 1 November 2019, till 13 February 2020, recording the arrival date, sex, date, geographical coordinates, and the individual identification.

Results: Overall, we were able to determine the arrival date of 125 individuals. Our findings indicate that males arrived before females in the breeding ground (i.e. protandry). Moreover, amongst males, those older and with longer tarsus, and longer tails arrived earlier, similar pattern was also observed amongst females.

Conclusions: Those morphometric traits may be related to an increase on flight performance during the migratory journey. The present work showed first evidence of protandry and a phenotype dependent arrival date for Lined Seedeater.

Keywords: migration, arrival date, body size, age, tropical birds

Introduction

Migratory birds face, every year, a costly journey to and from their breeding grounds (Rappole 2013). Environmental (Both 2010), social (Kokko 1999), and morphological traits (Goymann et al. 2010) may affect the costs and duration of the travel from the breeding grounds to the wintering grounds and vice versa. The journey's schedule also have additional fitness consequences (Rappole 2013). An early arrival to the breeding grounds can yield benefits like better territories, more opportunities for extra-pair mating, and replacement broods (Newton, 2008). However, there are also costs for an early arrival, such as facing suboptimal weather conditions, low food availability (Møller, 1994; Newton, 2008; Rotics *et al.*, 2018) and greater chances of getting involved in territorial disputes (Kokko 1999) at the beginning of the breeding season.

The costs and benefits of advancing the arrival are not the same for all individuals within a population, with some individuals experiencing a higher cost or lower benefits to arrive at the same time as others. Therefore, each individual has an optimal arrival date (Kokko 1999; Kokko et al. 2006), which is determined by the balance between the benefits and the costs of an early arrival (Alerstam and Lindström 1990; Kokko 1999; Espmark 2003). This differential trade-off can cause variation on migratory schedule, thus a spectrum of arrival dates to the reproductive site is expected.

The most common phenomena of differential arrival to the breeding grounds based on sex is protandry, in which males arrive before females. This phenomenon can be observed among many species of fishes (Morbey 2000), mammals (Michener 1984), birds (Francis and Cooke 1986; Stewart et al. 2002), and even insects (Thornhill and Alcock 1983). Protandry is the norm among territorial migratory birds species in which males defend territories (Coppack and Pulido 2009), like Wood Warblers *Phylloscopus sibilatrix* (Francis and Cooke 1986), European Pied Flycatchers *Ficedula hypoleuca* (Canal et al. 2012) and Eastern Kingbirds *Tyrannus tyrannus* (Cooper et al. 2009), but is less prevalent among female territorial species like Sanderlings *Calidris* spp. (Parmelee 1970) or non-territorial species like Red Phalaropes *Phalaropus fulicarius* (Connors et al. 1979). Females invest heavily in egg production and incubation therefore, the advantage of arriving much earlier may not offset the costs of low body reserves and suboptimal environment at the time of arrival (Morbey and Ydenberg 2001; Rappole 2013). However, an early arrival can also benefit females, because a late arrival would lead to pairing with less attractive males that also arrived later (Bensch and Hasselquist 1991).

Several factors are known to influence the arrival date. Age is an important factor, because older individuals are more likely to have greater migratory experience (Whitmore et al. 1977; Francis and Cooke 1986), thus arriving on the breeding grounds before younger individuals (Lozano et al. 1996;

Stewart et al. 2002; Smith and Moore 2005a). A delayed arrival, on the other hand, could benefit young individuals, as the competition with older territorial males would be reduced (Sherry and Holmes 1989).

Arrival date can also be related to morphometric traits, with larger individuals of both sexes arriving earlier on the breeding grounds (Francis and Cooke 1986; Choi et al. 2010). Certain morphometric traits play an important role in the ability to fly long-distances during migration, which larger individuals arriving first and with lower energy costs (Forstmeier 2002; Choi et al. 2010). Larger size can also help birds to endure sub-optimal conditions at the beginning of the breeding season (e.g. cold, low food supply), making the early arrival date less costly than it would be for smaller birds (Francis and Cooke 1986). Larger individuals also present better competitive advantage (Petrie 1988), usually dominating the resource access hierarchy at stopover sites (Lindström et al. 1990; Arizaga et al. 2011) and winning fights (Petrie 1988).

Although migration patterns have been extensively studied for numerous temperate zone bird species, little is known about migratory schedules for intra-tropical migrants (Bejarano and Jahn 2018) which have a pace of life quite distinct from that exhibited by temperate zone birds (Wiersma et al. 2007). Consequently, little has been published about protandry in the southern hemisphere, what raises the question about the prevalence of such phenomenon in the tropics (Bejarano and Jahn 2018). Investigating differential arrival to the reproductive site in tropical birds is an interesting research question, because tropical climate is characterized by comparatively high and constant temperatures, without significant seasonal variation in day length (Schnitzer and Carson 1999). Therefore, an intra-tropical migrant bird travels comparatively short-distances in a comparatively benign habitat, and, consequently, the risks of advancing arrival are lower than that faced by temperate zone intercontinental migrants (Rappole 2013). Other factors such as a longer breeding season can also impact migratory dynamics in tropical birds (Jahn and Cueto 2012) decreasing competition for mates or territories (Goymann et al. 2010).

To investigate differential arrival to the breeding grounds in an intra-tropical migratory species, we conducted a field study of a ringed population of Lined Seedeaters (*Sporophila lineola*). This is a small granivorous songbird that breeds in south-eastern Brazil from December to April (Ferreira and Lopes 2017) and winters in an unspecified region in northern South America, performing a journey of over 3,000 km one way. Breeding males of the species can exhibit two plumage types: (i) a common black-and-white plumage exhibited by adult birds, and (ii) a less common (10.7% of breeding males in the studied population, unpub. data) brownish plumage exhibited by males in the first reproductive season (Ferreira 2019). Brownish males, which are remarkably similar to females, can only be sexed in the field through behavioural cues, such as singing and territory defence

(Ferreira 2019).

In this paper, we investigated if sex, age, and morphometric traits influence the arrival date to the breeding grounds in the Lined Seedeater. Given that Lined Seedeaters are a male territorial species (Martins, et al. in press.), we predict that the early arrival is more advantageous for males, that will arrive before females. We also predict that black-and-white males, which are older, will arrive before brownish males. Finally, we predict that larger individuals, which have greater flight surface, will arrive in the breeding territories before smaller individuals.

Methods

Study area

We conducted the field work in the *campus* Florestal of the Universidade Federal de Viçosa, municipality of Florestal, Minas Gerais, south-eastern Brazil (19°53'S, 44°25'W). The campus encompasses 1500ha covered by fragments of semideciduous forests and man-made habitats (e.g. gardens, orchards, active and abandoned crops, and pastures) (Lopes and Marçal 2016).

Previous observations of the studied population suggest that the first individuals usually arrive at the breeding ground during the second half of November (Ferreira and Lopes 2017). Therefore, we conducted daily censuses starting on 1 November 2019 to determine the arrival date of each individual. The observer (TNC) walked a predefined route of 9.87 kilometres covering the entire study area from 05:00 to 11:00 am, at ~1.6 km/h. The direction travelled were alternated daily. We scanned the area for Lined Seedeaters visually and acoustically (males are extremely vocal and sing during all day long). Playbacks of the male song were used as an aid to attract territorial birds that were heard or seen away from the route, allowing the identification of the colour ring combination (see below). The audio used for the playbacks was 12 sec long and contained three songs of the same individual (<http://www.wikiaves.com/1981768>). The observer remained stationary during the playback, which was repeated every minute for a maximum of six times. Daily censuses were conducted for 105 days (1 November 2019 to 13 February 2020), until the arrival of new individuals became indistinguishable from internal movements (see below). The Lined Seedeater Project, from which this study is part, is a long-term project that monitors the studied population since 2014, resulting that 497 individuals have already been ringed when we started this study. When a non-ringed individual was detected, we tried to capture it with mist-nets and ring it on the same in subsequent days. Each bird received a uniquely numbered metallic ring and a unique combination of three coloured rings. We also measured tarsus length using a digital calliper (0.1 mm), and wing and tail lengths using a ruler (0.5 cm) (see Eck *et al.*, 2011).

During censuses, we recorded the colour ring combination, sex, plumage colour (black-and-white or brownish), date, and the geographic coordinates (with a handheld GPS) of the point where every bird was observed in the field. The arrival date was considered as the first day when a ringed individual was seen in its breeding territory, which we defined as the defended area where it bred. For unringed birds we considered the ringing date as the arrival date (see below). Records obtained in areas temporarily used for feeding before territory establishment, such as a corn plantation where we observed small flocks of birds foraging side by side in middle November, were discarded, because those records were not obtained within a breeding territory and could be fuelling stations for birds on their migratory journey to further south and/or that breed in other breeding grounds.

Due to the COVID-19 pandemic we were forced to stop the fieldwork on 19 March 2020, 46 days before the end of the previous season and 39 days before the mean end of all seasons since 2014.

Data analysis

All statistical analyses were conducted using the software R version 4.0.2 (R Core Team 2020) and the interface RStudio (RStudio Team 2020). To follow the arrival of new individuals of each sex we used the number of days after 1st November as the arrival date variable. We build a rarefaction curve to follow the arrivals and to decide when stop the daily censuses, (Gotelli and Colwell 2011) (Fig. 2) using the “specaccum” function from the R package “Vegan” (Oksanen et al. 2019). We stopped the census on 13 February 2020, when the curve approached an asymptote for males, but not for females. We decided to end it before the curve for females reached an asymptote because the arrival date records were beginning to be confused with internal rearrangements of previously occupied territories. This is because females could be moving from one territory to another, what would be undistinguishable from recently arrived females.

Because we cannot be sure if a given unringed bird that we captured is the same bird that we have observed previously in the same territory, we considered the ringing date as the arrival date for these birds. To reduce biases caused by the long time-lag between the purported first detection and ringing of some of these birds, we arbitrarily excluded from the analyses those birds that took more than 10 days between the first purported sighting and the ringing day. We used the Wilcoxon rank sum test to test for differences in arrival dates between the sexes and age classes (Wilcoxon 1945), using the function “wilcox.test”.

To test if the morphometric traits influenced individuals’ arrival date, we fitted for each sex a Generalized Linear Model assuming a Poisson distribution with arrival date as a response variable and the three morphometric traits (wing length, tarsus length, and tail length) as predictor variables.

For that we used the “glm” function from the R package “lme4” (Bates et al. 2015), after evaluating for multicollinearity using the “vif” function from R (R Core Team 2020) stipulating a cut-off point in variance inflation factors greater than 2 (Craney and Surles 2002).

Results

Overall, we registered the arrival date for 125 individuals, being 60 females, 58 black-and-white males, and 7 brownish males. We also registered additional 11 individuals that we were unable to sex and were not included in any analysis. We registered 97 individuals (77,6%) that have been ringed during previous seasons. The median number of days from the date an unringed bird was first detected in a given territory to the date of its purported capture was 9 ± 13.1 days (ranging from 0 to 56 days) (Fig.2). We excluded from the analysis three brownish males, 10 black-and-white males and 11 females as it took more than 10 days between their purported arrival date and ringing.

At the second half of February, at least nine males recorded defending territories during censuses at the beginning of the breeding season have left their former territories and were seen defending new territories. For example, one bird recorded defending a territory on 29 November 2019 (19°52'32"S, 44°24'51"W) was observed defending another territory 475 m southwest on 28 February 2020 (19°52'40"S, 44°25'03"W).

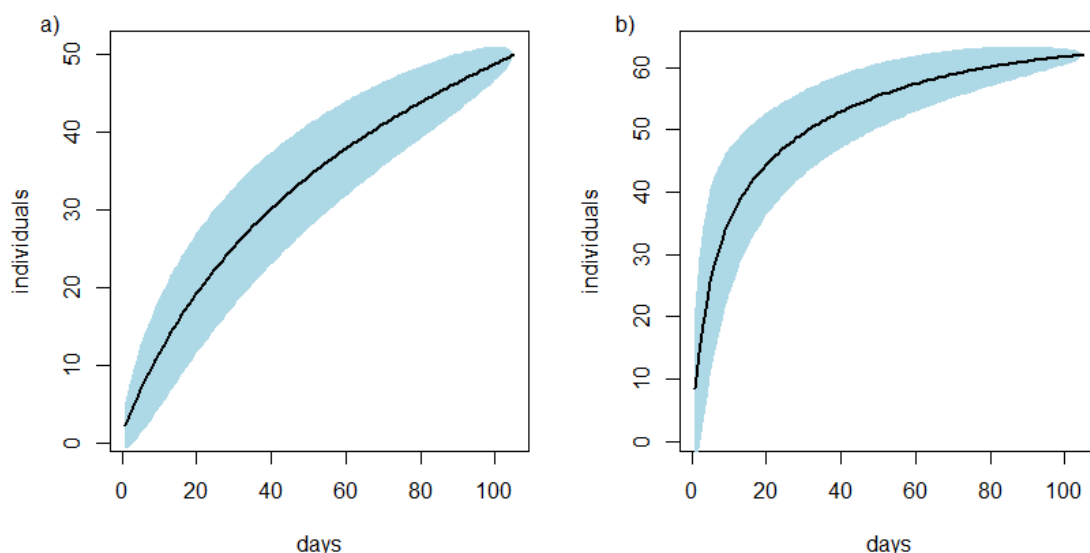


Fig. 1 Rarefaction curve for the arrival of new a) females and b) males of Lined Seedeaters *Sporophila lineola* during the 2019–2020 breeding season in Florestal, south-eastern Brazil.

Males, irrespective of plumage colouration, arrived significantly before females ($W = 7063$, p -value < 0.001), with the first female arriving 19 days after the first male (Fig. 2). Black-and-white

males arrived significantly before brownish males ($W = 589$, p -value = 0.012), with the first brownish male arriving 25 days after the first black-and-white male, even though the number of brownish males in the analyses ($n = 4$) was rather small for a definitive conclusion (Fig. 3). We found no significant difference in morphometric traits between black-and-white and brownish males (Table 1).

Table 1: Wilcoxon rank sum test of male plumage colours and morphometric traits of Lined Seedeater *Sporophila lineola* during the 2019–2020 breeding season in Florestal, south-eastern Brazil.

Character	Black-and-white males				Brownish males				W	P value
	Mean	SD	N	Min–Max	Mean	SD	N	Min–Max		
Wing length	60.1	1.37	48	57.0–62.5	61.0	1.00	4	60.0–62.0	112	0.645
Tarsus length	15.4	0.73	48	13.9–17.2	15.1	0.79	4	14.2–15.7	95	0.986
Tail length	46.5	1.47	48	44.0–50.0	47.0	1.73	4	46.0–49.0	90	0.849

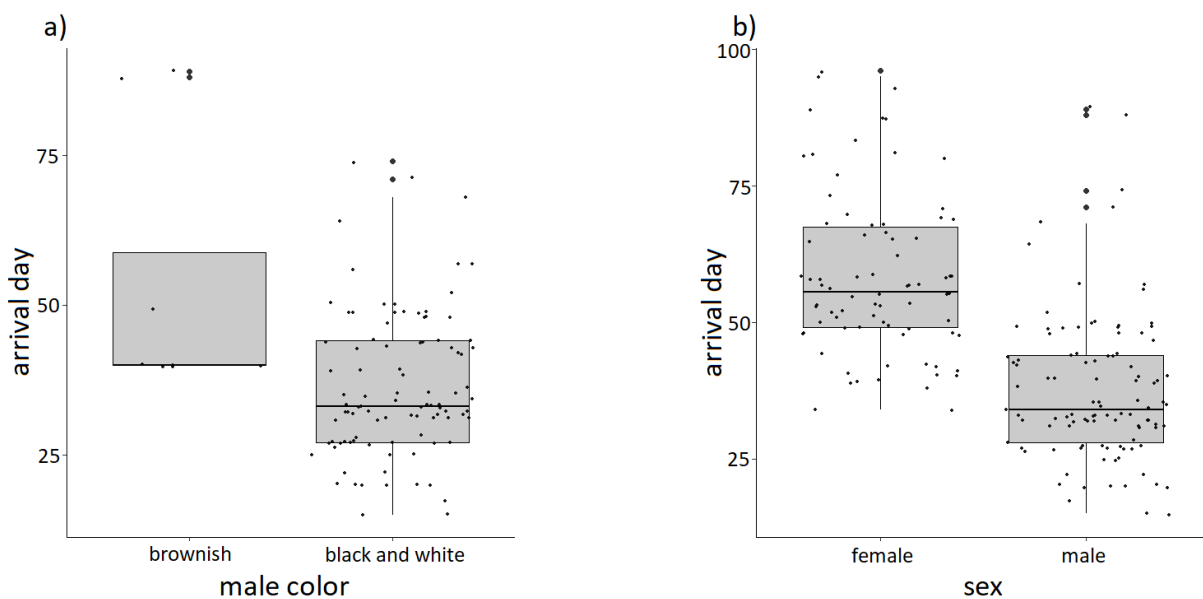


Fig. 2 Arrival dates of Lined Seedeaters *Sporophila lineola* during the 2019–2020 breeding season in Florestal, south-eastern Brazil. Black-and-white males arrived earlier than brownish males, and males arrived earlier than females. Arrival day assume that day 1 is the 1 November 2019. The box range represents the interquartile range (IQR) (Q1 to Q3) and the whiskers represent the 1.5 times the interquartile range. The large dots represent outliers and the small dots represent individual observations.

When considering the morphometric trait, we found that longer tarsus and longer tails predicted early arrival for males and females (table 2, Fig. 3). Wing length did not significantly influence the arrival date of either sex. Overall, the predictors showed variance inflation below two, rejecting the influence of collinearity in our findings.

Table 2: Generalized Linear Model of morphometric traits of Lined Seedeaters *Sporophila lineola* in relation to the arrival date in breeding grounds during the 2019–2020 breeding season in Florestal, south-eastern Brazil.

Variables	Males				Females			
	Estimate	Std. Error	z value	P value	Estimate	Std. Error	z value	P value
Intercept	6.265	1.222	5.123	<0.001	6.170	1.069	5.769	<0.001
Wing length	-0.009	0.016	-0.582	0.560	0.021	0.012	1.649	0.099
Tarsus length	-0.069	0.029	-2.406	0.016	-0.067	0.027	-2.483	0.013
Tail length	-0.041	0.013	-3.137	0.001	-0.031	0.008	-3.548	<0.001

Discussion

In this paper we investigated the existence of differential arrival to the breeding grounds if an intra-tropical songbird. Our findings revealed that males of the species arrive before females (i.e. protandry), as predicted. However, some males only arrived after the arrival of the first females, showing that the optimal arrival date of some males may be later than the optimal arrival date of some females. Older males also arrived earlier than younger males, as predicted. Longer tarsus and tail length also predicted an early arrival to the breeding grounds but, contrary to our predictions, wing size did not affect the arrival date.

Lined Seedeaters exhibit high sexual dichromatism (Ridgely and Tudor 2009), what is in line with previous studies that found a relationship between the degree of protandry during spring migration and sexual dichromatism. Birds species exhibiting low sexual dichromatism, such as European Nightjars *Caprimulgus europaeus*, European Bee-eaters *Merops apiaster*, and Common Cuckoo *Cuculus canorus* do not show protandry, whereas birds with high sexual dichromatism, such as Common Rock Thrushes *Monticola saxatilis*, Woodchat Shrikes *Lanius senator*, and European Pied Flycatchers, exhibit protandric migration (Rubolini 2004).

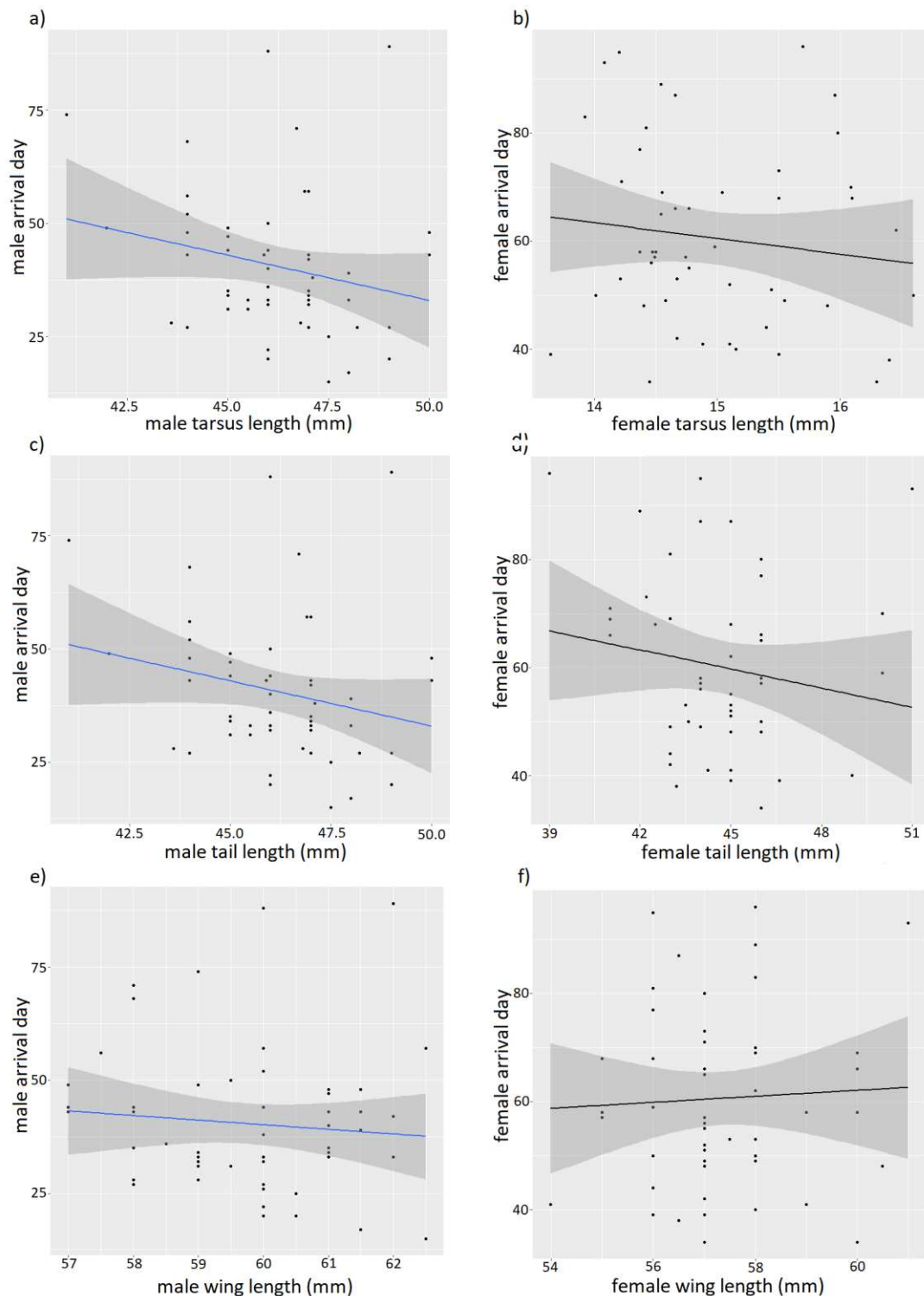


Fig. 3 A Generalized Linear Model with Poisson distribution comparing Lined Seedeaters a) male (p value = 0.016) and b) female (p value = 0.013) tarsus length, c) male (p value = 0.001) and d) female (p value < 0.001) tail length and e) male (p value = 0.56) and e) female (p value = 0.099) wing length to the arrival date in the breeding grounds during the 2019–2020 breeding season in Florestal, south-eastern Brazil (shaded area indicates 95% confidence interval of the regression).

Males of protandric bird species can use several strategies to reach the breeding grounds

earlier. Sanderlings *Calidris alba* males, for example, can winter nearer to the breeding grounds (Myers 1981), Eastern Great Reed Warbler *Acrocephalus orientalis* males can start their migratory journey earlier than females (Nisbet and Medway 1972), Northern Wheatear *Oenanthe oenanthe* males have morphometric traits, as a more angular wing, that allow them to migrate faster than females (Corman et al. 2014). We do not know the proximal cause of protandry in Lined Seedeaters, and future studies showing how this happens are important to understand migratory dynamics in intratropical migrants.

Individuals who arrive earlier can invest more in each egg as demonstrated in American Redstarts *Setophaga ruticilla* (Smith and Moore 2003), achieve better territories as in Northern Wheatears (Brooke 1979), and this reflects in an advantage in fitness as in Field Sparrows *Spizella pusilla* (Smith et al. 2020). Field observations suggest that Lined Seedeater males can hold ownership of territories across breeding seasons (Martins et al. in press), thus the inherent value of a potential resource rich and/or safety of a territory may motivate an early arrival, but it remains unclear what drives the migratory schedule in the studied species.

We also found that, among males, older individuals arrived earlier to the breeding grounds than younger individuals, what is a widespread phenomenon among birds (Cristol, 1995; Ketterson & Nolan Jr., 1983; Stewart et al., 2002). Older individuals are more likely to have greater migratory experience (Oring and Lank 1982). Asymmetrical competition with older males may also explain why younger males are less likely to arrive earlier to the breeding grounds, especially if older males, even when arriving later, are dominant or able to win territorial disputes, evicting the younger ones from their territories (Morse 1973; Howe 1974; Holmes et al. 1989; Moore et al. 2003). Therefore, we hypothesize that brownish males could obtain benefits by delaying their arrival, thus avoiding the energy costs of competition and aggression from older males (Hill 1989; Møller 1994; Smith and Moore 2005a). This hypothesis remains to be tested.

Our results showed that individuals of both sexes with larger tarsus arrived first, as observed in other studies (Aebischer et al. 1996). Tarsus length has been pointed as a good predictor of body size in passerines (Senar and Pascual 1997) and has been used as such in other works (Garnett 1981; Alatalo et al. 1990). A larger body size usually improves an individual's intraspecific competitive ability, because larger animals tend to win fights or to be dominant in competition for food at the stopover sites, having shorter stopping times and, therefore, a higher overall migration speed (Petrie 1988; Stolt and Fransson 1995; Yong et al. 1998; Arizaga et al. 2011). Furthermore, the beginning of the season is marked by suboptimal environmental conditions, with less food availability (Canal et al. 2012), as larger individuals have a smaller area / volume ratio, larger individuals may have better metabolic efficiency and suffer less from suboptimal environmental

conditions (Kissner et al. 2003; Rubolini 2004; Rappole 2013).

Tail length was also relevant on both sexes' arrival date but, surprisingly, wing length was not. The importance of longer flight surfaces (wing and tail) may be due to the possible advantage they confer in flight speed and efficiency, playing an important role in the ability to perform movements during long-distance migration reflecting in arrival date (Gosler et al. 1998). Flight surface area may be under selection for optimal flight performance (Gosler et al. 1998) and correlates with the arrival date was found in other studies (Nam et al. 2011). The length and quality of the feathers also in part reflect the body condition of the individual at the time of feather growth, with disadvantageous environmental conditions leading to small feather length and quality (Dawson et al. 2000; Benowitz-Fredericks et al. 2006; Vagasi et al. 2012).

Conclusion

The present work demonstrated the occurrence of differential arrival in breeding grounds in Lined Seedeaters, being one of the first studies to demonstrate that this widespread phenomenon in the temperate zone also occur in the tropical zone, where birds exhibit a quite distinct pace of life. Differential arrival in the studied species was related to sex, age and morphometric traits, showing that this phenomenon occurs in an intratropical migrant in a similar way to that already reported for temperate zone birds. Further studies are needed to demonstrate the generality of our findings.

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Chapter 2. First birds to arrive invest in more breeding attempts: fitness influence of arrival date in a protandric intra-tropical migratory bird

Abstract

Background: Migratory birds face a costly journey to their breeding ground during their breeding season. The early arrival in the breeding territories has important fitness consequences and other works have already shown that it influences the partners choice, increases the number and investment on eggs, the number of breeding attempts, advances the beginning of the first breeding attempt and is consequently associated with a higher reproductive success.

Methods: To test this idea, we monitored the arrival date of a migratory songbird, Lined Seedeater *Sporophila lineola*, to a breeding ground in south-eastern Brazil in which the species has been monitored since 2014. Lined Seedeaters are a small sexually dimorphic species. We conducted daily samplings in a predetermined route from Nov 2019, till Feb 2020, recording the arrival date, sex, date and the unique combination of coloured rings of each bird observed. To assess reproductive traits we searched for nests from Nov 2019, till Mar 2020 based on behavioural observations of adult birds and we checked them in intervals of 1 to 5 days. We use generalized linear model to evaluate the arrival date influence in assortative mating, reproductive success, number of breeding attempts and brood investment in first attempt and throughout the all season.

Results: Overall, we were able to determine the arrival date of 125 individuals and find 137 nests. Our results show that an early arrival means a decrease in the investment during each breeding attempt in both sexes. However, early arrived individuals started the season earlier, and had more reproductive attempts, which generated an increase in the male's fitness related to the date of arrival, for females, the increase in fitness seems to be related to the arrival date of their partners.

Conclusions: Early arrival increases the duration of the breeding season and allows for a strategy in which the reproductive investment is diluted into a greater number of breeding attempts.

Introduction

Annual migration to breeding grounds is one of the most important and costly phenomena in a bird's life and it has important fitness consequences (Rappole 2013). Early arrival ensures a range of benefits for individuals, like replacement clutches, more opportunities for extra-pair mating, less inter-sexual competition for mates, and better territories (Newton 2008). However, there are also a number of associated disadvantages with arriving early in the breeding season, such as a greater likelihood of getting involved in territorial disputes (Kokko 1999), suboptimal weather conditions, and lower food availability (Møller, 1994; Newton, 2008; Rotics *et al.*, 2018).

The costs and benefits of early arrival vary between individuals from the same population, and each individual would have their own optimal arrival date. Therefore only individuals able to afford the costs would advance their arrival and take advantage of the fitness benefits (Kokko 1999; Kokko *et al.* 2006). In addition to the afore-mentioned individual differences in cost and benefits of early arrival, there are also differences between sexes, as males tend to arrive earlier than females at the breeding grounds, a phenomenon known as protandry (Kokko *et al.* 2006).

Many hypotheses have been proposed to explain the phenomenon of protandry and the advantages of an early arrival at breeding grounds for each sex. For birds, the two most relevant are the rank advantage hypothesis (Myers 1981; Oring and Lank 1982; Francis and Cooke 1986) and the mate opportunity hypothesis (Reynolds *et al.* 1986). The rank advantage hypothesis predicts that, in male territorial species, early arriving males have an advantage in the competition for the best territories in comparison to late arriving males (Ketterson and Nolan 1976; Myers 1981). Under this hypothesis, males' arrival dates can be seen as an evolutionary game, where the quality of the territory and/or the chances of holding it depend on the number of other males that have already arrived (Kokko 1999). Under this hypothesis, early arrival is advantageous regardless of sex and the acquisition of a better territory will confer advantages during each breeding attempt (Morbey and Ydenberg 2001). Earlier studies support this hypothesis, showing that the fitness of individuals arriving early increases because the number of eggs produced is higher (Smith and Moore 2005b) and are of larger volume (Smith and Moore 2003). Other studies have found that the first breeding attempts tend to have a higher egg's volume, which in turn is linked to larger nestlings with more steep growth (Hipfner and Gaston 1999; Barkowska and Pinowski 2004).

The mate opportunity hypothesis was originally formulated to explain insect emergence (Bulmer 1983), where arriving early increases the number of females mated to a polygynous male (Wiklund and Fagerström 1977). However, there is evidence that this hypothesis also applies to birds, as in Rose-breasted Grosbeaks *Pheucticus ludovicianus*, for which an early arrival increases the male's

chances of finding a mate (Francis and Cooke 1990) or the number of extra-pair nestlings, as in Common Reed Bunting *Emberiza schoeniclus* (Coppack et al. 2006). In socially monogamous birds, this hypothesis is more important in an extra-pair paternity context (Coppack et al. 2006; Kokko et al. 2006) or in a situation where the opportunities for new breeding attempts are more relevant to the reproductive success (Morbey and Ydenberg 2001; Coppack et al. 2006). Early arrival may be related to the number of replacement clutches (Morrison et al. 2019), and the increased opportunity for new breeding attempts (Møller 1990), as the number of attempts can be one of the most important factors for increasing reproductive success in birds (Møller 1990).

The early arrival date is also important for the reproductive success of females (Kokko et al. 2006), since arriving early guarantee that the best males will still be available. By delaying the arrival, the female will be forced to choose the mate between the remaining males and/or territories (Smith and Moore 2005b). Therefore, assortative mating based on arrival day to the breeding grounds is an important reproductive selection process in birds (Bearhop et al. 2005) and has been observed in other species such as Swainson's Thrush *Catharus ustulatus* (Ruegg et al. 2012).

Most studies have focused on temperate zone birds extensively (Bejarano and Jahn 2018). However, little information is known about the migration dynamics of tropical birds, which have a distinct pace of life (Wiersma et al. 2007). Intra-tropical migrant birds travel shorter distances (Rappole 2013) and have longer, less synchronized breeding seasons (Jahn and Cueto 2012). Consequently, tropical birds face less competition for mates and/or territories and have more breeding opportunities during the same breeding season when compared to temperate zone birds (Goymann et al. 2004). Considering higher nest predation rates usually observed in the tropics (Oniki 1979), a greater investment in replacement clutches and brood attempts seems to be a decisive factor in the reproductive success of tropical birds (Roper 2005).

The present study aims to assess the reproductive consequences of the order of arrival at the breeding grounds in a population of Lined Seedeaters (*Sporophila lineola*) and better understand what drives the phenomenon of protandry in the specie. The Lined Seedeater, a protandric intratropical migrant (Chapter 1), is a small granivorous songbird that inhabits a variety of open areas, including man-made habitats (Ridgely and Tudor 2009). The species has multiple breeding attempts with a clutch size ranging from one to three eggs (Ferreira and Lopes 2017). It is a socially monogamous species that overwinters in northern South America, with the studied population breeding in south-eastern Brazil from December to April (Ferreira and Lopes 2017). We investigated whether the arrival date influences in 1) assortative mating (i.e. early females mate with early males); 2) onset of breeding, and 3) breeding investment.

We predict that 1) females that arrive early will prefer males that also arrived early because the

arrival date is an indicator of mate value (Kokko 1999); 2) individuals who arrive earlier will start to breed earlier; 3) early individuals will invest in more breeding attempts (Morrison et al. 2019) 4) and invest more in each attempt with larger eggs and larger clutches, 5) which is reflected in early individuals have higher breeding success.

Material and methods

Study area

We conducted our field observations at the campus Florestal of the Universidade Federal de Viçosa, municipality of Florestal, Minas Gerais, south-eastern Brazil (19°53'S, 44°25'W). The campus is 1500ha in area and consists of fragments of semi deciduous forests and man-made habitats (e.g. plantations, gardens, abandoned crops, orchards, and planted pastures). Local climate is subtropical and has two well-marked seasons: a dry one, from April to September, and a wet one, from October to March (Lopes and Marçal 2016).

Determination of arrival date

The first individuals usually arrive in the breeding grounds in mid-November (Ferreira and Lopes 2017). To determine the arrival date of each individual, we conducted daily censuses starting on 1 Nov 2019. I walked from 05:00 to 11:00 am, at ~1.6 km/h, in two directions (north-east or south-west), which were alternated daily in a predefined route of 9.87 kilometres covering the whole study area.

Lined Seedeaters were sought visually and acoustically (males sing throughout the whole day). To attract territorial birds that were heard or seen away from the route we used playbacks of a male song, enabling individual identification based on unique ring colour combination (see below). For the playback we used a 12 sec long audio recording comprised of three songs of the same individual (<http://www.wikiaves.com/1981768>), which was repeated every minute for a maximum of six times. During playbacks the observer remained stationary. Census were conducted for 105 days (1 November 2019 to 13 February 2020), when the new individuals' arrival became indistinguishable from internal movements of birds changing territory (see Chapter 1 for details).

This study is part of the Lined Seedeater Project, which monitors the study population since 2014. The database has six years' worth of data and currently has 497 previously ringed individuals in the study area. When a non-ringed individual was detected, we tried to capture it with mist-nets

and ring it during the same or subsequent days. Each bird received a uniquely numbered metallic ring and a unique combination of three coloured rings.

Researchers wrote down relevant information such as sex, date, colour ring combination, and geographic coordinates (using a handheld GPS) of the location where we observed each individual during the census. The arrival date was considered the first day when we saw a ringed individual in its breeding territory, defined as the area the male defended during the season. We dismissed birds recorded before territory establishment in areas temporarily used for feeding, such as a corn plantation where small flocks of birds were observed foraging together in mid-November. Given that no bird bred in this particular area, we considered this plantation as a fuelling station for birds on their migratory journey further south and/or that breed in other sites in the study area.

Due to the COVID-19 pandemic, we were forced to stop the field study suddenly on 19 March 2020, 39 days before the last nest in the previous season became inactive and 20 days before the mean end of all seasons since 2014. Considering data from previous seasons, we found that until the date we interrupted fieldwork, on average, 90.8% of the nests of the season had been found. Therefore, we expect that the loss of those later nests would not significantly impact the conclusions presented here.

Investigating the influence of arrival date on breeding traits

Nests were located based on behavioural observations of adult birds, looking for evidence of reproduction, such as transport of nest material, food for nestlings or males chasing females, we consider the first attempt as the first nest found for an individual. After the nests were found, they were monitored at intervals of 1 to 5 days, with smaller intervals being adopted close to the laying date, hatching, or fledging. The length and width of eggs were measured with a calliper (precision 0.1 mm).

To assess the impact of arrival date on reproductive traits throughout the season, we used data from 137 nests from 31 females and 28 males. As divorces followed by new matings occurred, each sex was analysed separately for all analyses.

We measured the total and average clutch size, brood size, number of fledglings, and clutch volume. We also estimated the number of breeding attempts in the season and the number of successful breeding attempts. Average values were obtained by dividing the total value of each variable by the number of breeding attempts recorded for each individual. The volume of the eggs was calculated using the formula $0.51 \times \text{length} \times \text{width}^2$ (Hoyt 1979).

The influence of arrival date on the reproductive traits of the first attempt was tested using the

first 42 nests of 31 females and 28 males. We measured different variables for the first attempt of each individual. The variables included clutch size, brood size, number of fledglings, first egg laying date, clutch total volume, and clutch average volume. First egg laying date was considered as the first egg in the first nest found of an individual and first attempt clutch average volume was considered as the sum of the volume of eggs in the first nest found divided by the number of eggs in that nest.

Data analysis

To test whether the early females mated preferably with early males, we used a linear mixed-effects model assuming a Poisson distribution using female arrival date as a response variable and her partner's arrival date as a predictor variable. If a female had two or more partners throughout the season, we include only the first mate. For this test, only 30 females were included, excluding those females for which we could not establish their partner's arrival date.

To test the influence of arrival date on reproductive traits throughout the season, we used two generalized linear models assuming a Poisson distribution for each sex, one using arrival date as the predictor variable and the total clutch size, total brood size, total number of fledglings, total clutch volume, number of breeding attempts, and number of successful breeding attempts as response variables. In the second model we used arrival date as the predictor variable and the average clutch size, average brood size, average number of fledglings, and average clutch volume as response variables.

To test the influence of the arrival date on the reproductive traits during the individual's first attempt, we used a generalized linear model assuming a Poisson distribution for each sex, using arrival date as the predictor variable and the first attempt clutch size, first attempt brood size, first attempt number of fledglings, first egg laying date, first attempt total clutch volume, and first attempt average clutch volume average as response variables. All statistical analysis used the "glm" function from the R package "lme4" (Bates et al. 2015), and assume as a significant P-value of 0.05 and were performed using the R software version 3.6.3. (R Core Team 2020) and the interface RStudio (RStudio Team 2020).

After evaluating for multicollinearity using the "vif" function from R (R Core Team 2020) stipulating a cut-off point in variance inflation factors greater than 2 (Craney and Surles 2002) we decided to carry out the analyses independently for each variable, due to the high inflation rates of the model when carried out together.

Results

Overall, we were able to record the arrival date of 125 individuals, 60 females and 65 males. Of those, 97 individuals (71%) were ringed during previous seasons. The median number of days from the date an unringed bird was first detected in a given territory to the date of its purported capture was 9 ± 13.1 days (ranging from 0 to 56 days). We excluded 13 males and 11 females from the analysis as it took more than 10 days between their arrival date and ringing (see chapter 1). Of the individuals we were able to track the arrival date we found 137 nests of 30 females and 28 males during the season, of which 42 were considered the first nest of an individual. We find that the number of breeding attempts by individuals during the breeding season searched ranged from 1 to 6 to males and 1 to 4 to females, with a mean of 2.0 to females and 2.6 to males.

We did not find evidence of assortative mating in females (Estimate = 0.0036, p-value = 0.458). This may indicate that earlier females did not choose the first males to arrive in the season. When investigating the influence of the arrival date on reproductive traits during the entire breeding season (table 1), we found that nests of birds (irrespective of sex) arriving earlier had larger total clutch volume, and smaller average clutch volume (Fig 1). These early arriving birds also had larger number of breeding attempts and larger number of successful breeding attempts (Fig 2). Early males had a larger total number of fledglings, and early females had smaller average clutch size and average number of fledglings. We found no significant effect on arrival date on male and female total clutch size, total brood size, and average brood size (Fig 3).

Table 1: Generalized Linear Model of reproductive traits (considering the total number of breeding attempts in the season) of Lined Seedeaters *Sporophila lineola* in relation to the arrival date in breeding grounds during the 2019–2020 breeding season in south-eastern Brazil.

Variables	Males				Females			
	Estimate	Std. Error	z value	P value	Estimate	Std. Error	z value	P value
Total clutch volume	-4.410 ⁻⁰⁵	8.787 ⁻⁰⁶	-5.019	<0.001	-3.029 ⁻⁰⁵	7.960 ⁻⁰⁶	-3.805	<0.001
Average clutch volume	0.0004	0.0001	4.468	<0.001	2.903 ⁻⁰⁴	7.078 ⁻⁰⁵	4.102	<0.001
Total clutch size	-0.0032	0.0101	-0.323	0.746	-0.0099	0.0124	-0.804	0.422
Average clutch size	0.0277	0.0304	0.910	0.363	0.1208	0.0430	2.811	0.004
Total brood size	-0.0025	0.0160	-0.161	0.872	-0.0140	0.0138	-1.015	0.310
Average brood size	0.0548	0.0369	1.483	0.138	0.0385	0.0310	1.239	0.215
Total number of fledglings	-0.0584	0.0286	-2.042	0.041	0.0044	0.0244	0.181	0.856
Average number of fledglings	0.0089	0.0472	0.190	0.849	0.0962	0.0384	2.507	0.012
Number of breeding attempts	-0.1187	0.0224	-5.293	<0.001	-0.1430	0.0241	-5.925	<0.001
Number of successful breeding attempts	-0.1106	0.0480	-2.304	0.0212	-0.1538	0.0384	-3.998	<0.001

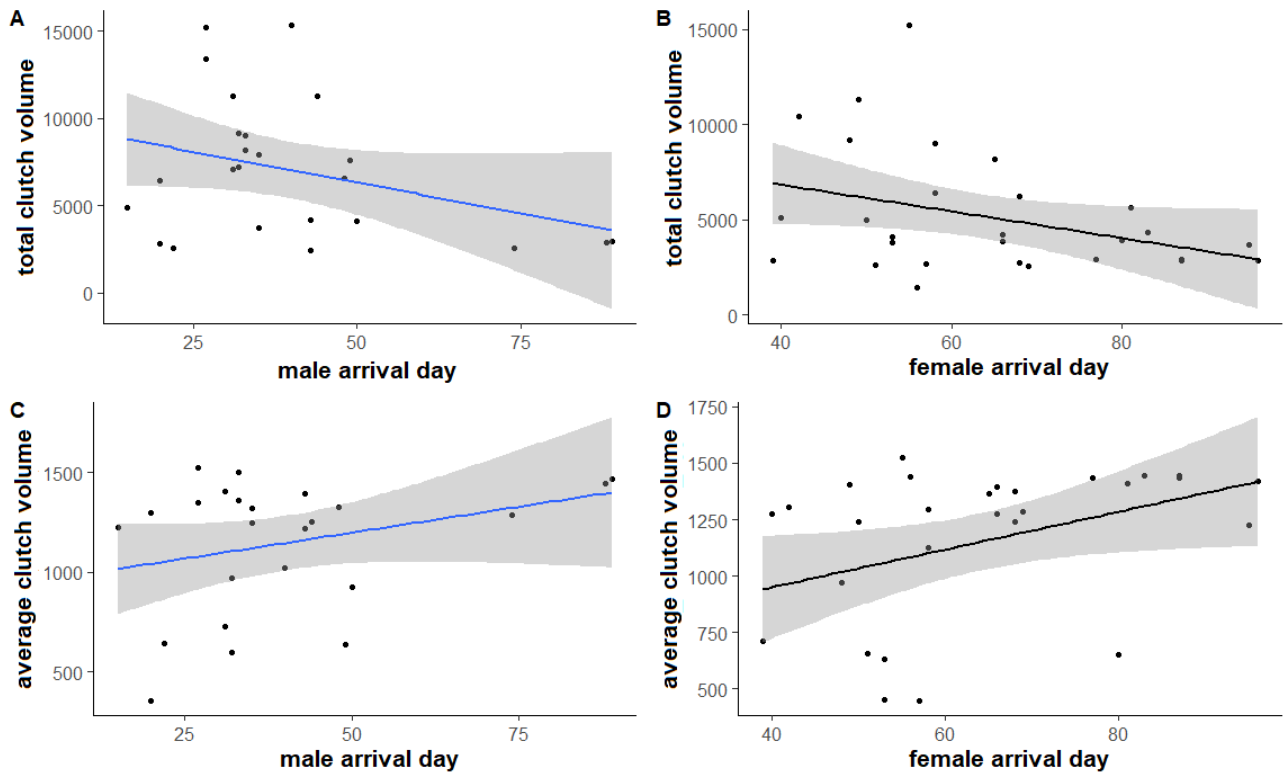


Fig 1: A Generalized Linear Model with Poisson distribution comparing A) male (p -value = <0.001) and B) female (p -value = <0.001) total clutch volume and C) male and D) female average clutch volume to the arrival date in breeding grounds during the 2019–2020 breeding season in south-eastern Brazil. Total clutch volume is positively correlated and the average clutch volume is negatively correlated with the arrival date regardless of sex (shaded area indicates 95% confidence interval of the regression).

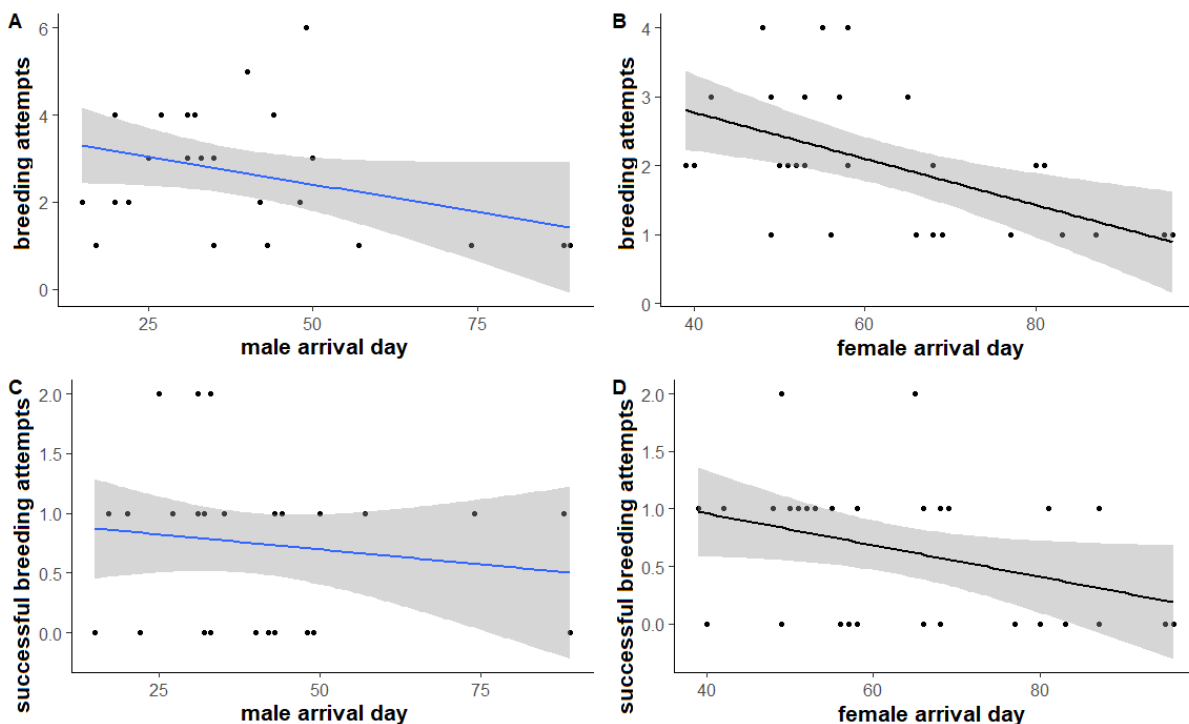


Fig 2: A Generalized Linear Model with Poisson distribution comparing A) male (p -value = <0.001) and B) female (p -value = <0.001) number of breeding attempts and C) male (p -value = 0.021) and D) female number (p -value = <0.001) of successful breeding attempts to the arrival date in breeding grounds during the 2019–2020 breeding season in south-eastern Brazil. Both number of breeding attempts and number of successful breeding attempts is positively correlated with the arrival date regardless of sex (shaded area indicates 95% confidence interval of the regression).

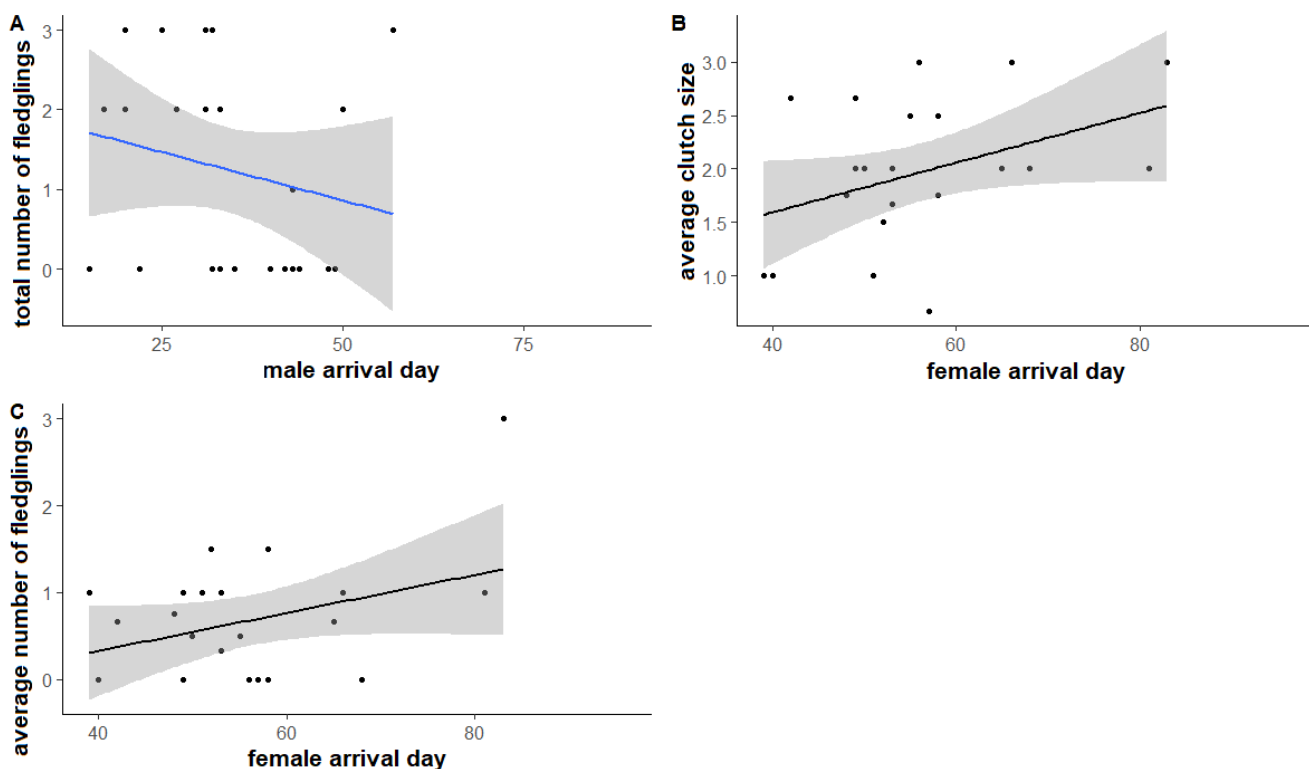


Fig 3: A Generalized Linear Model with Poisson distribution comparing A) male total number of fledglings (p -value = 0.041), B) female average clutch size (p -value = 0.004) and C) female average number of fledglings (p -value = 0.012) to the arrival date in breeding grounds during the 2019–2020 breeding season in south-eastern Brazil. Total number of fledglings volume is positively correlated to males and the average clutch size and average number of fledglings is negatively correlated with the arrival date to females (shaded area indicates 95% confidence interval of the regression).

When evaluating the arrival date influence on the first breeding attempt (table 2), nests of early individuals (regardless of sex) had eggs earlier (p -value = >0.001) (Fig 4). However, arriving early in the breeding grounds was not relevant for any other variable studied, regardless of sex.

Table 2: Generalized Linear Model of reproductive traits (considering only the first breeding attempt) of Lined Seedeaters *Sporophila lineola* in relation to the arrival date in breeding grounds during the 2019–2020 breeding season in south-eastern Brazil.

Variables	Males				Females			
	Estimate	Std. Error	z value	P value	Estimate	Std. Error	z value	P value
Clutch volume sum	-3.892 ⁻⁰⁵	6.506 ⁻⁰⁵	-0.598	0.549	7.967 ⁻⁰⁵	5.520 ⁻⁰⁵	1.443	0.148
Average clutch volume	5.052 ⁻⁰⁴	4.437 ⁻⁰⁴	1.139	0.254	5.932 ⁻⁰⁵	3.290 ⁻⁰⁴	0.180	0.856
Clutch size	3.846 ⁻⁰²	1.10 ⁻⁰¹	0.350	0.726	-1.394 ⁰¹	8.590 ⁻⁰²	-1.623	0.104
Brood size	6.086 ⁻⁰²	4.344 ⁻⁰²	1.401	0.161	6.908 ⁻⁰²	3.529 ⁻⁰²	1.958	0.050
Fledgling number	1.765 ⁻⁰²	5.271 ⁻⁰²	0.335	0.737	-5.344 ⁻⁰²	4.47 ⁻⁰²	-1.195	0.2321
First egg laying date	2.618 ⁻⁰²	7.831 ⁻⁰³	3.343	<0.001	1.841 ⁻⁰²	2.642 ⁻⁰³	6.968	<0.001

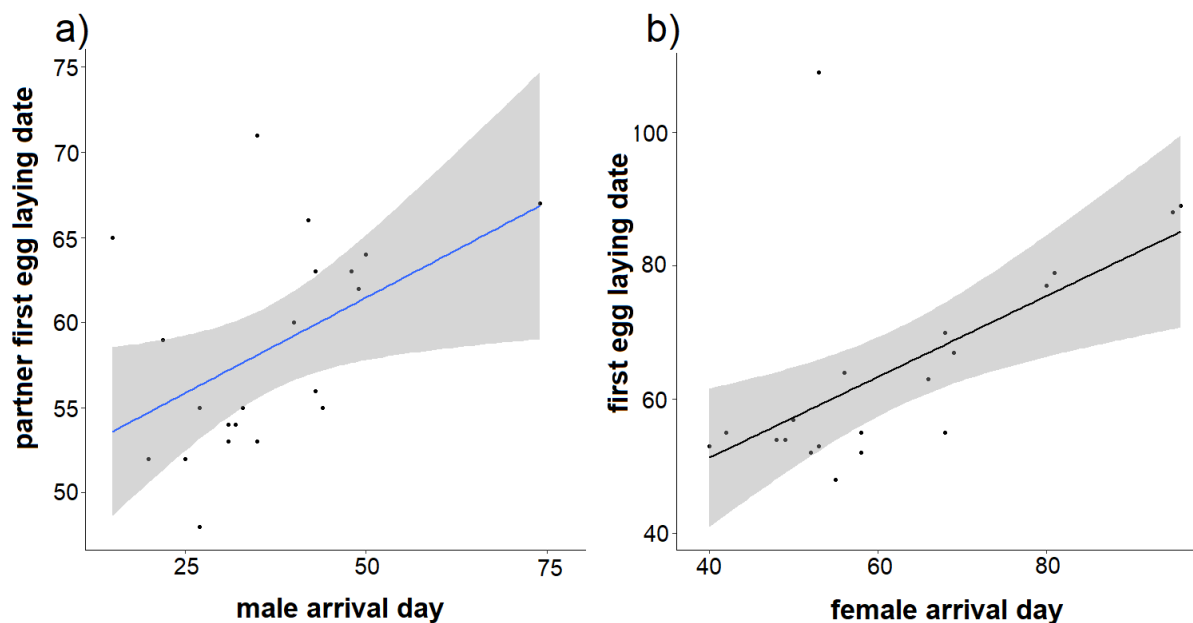


Fig 4: A Generalized Linear Model with Poisson distribution comparing a) male (p -value = <0.001) and b) female (p -value = <0.001) first egg laying date to the arrival date in breeding grounds during the 2019–2020 breeding season in south-eastern Brazil. The first egg laying day is positively correlated with the arrival date regardless of sex (shaded area indicates 95% confidence interval of the regression).

Discussion

An early arrival in the territories is not related to a greater investment in each individual brood as we predicted, but an early arrival predicted for both sexes an early start of the breeding activity and, consequently, a dilution of the reproductive effort in a higher number of breeding attempts with

a smaller average clutch volume. Arriving earlier resulted in a higher number of successful breeding attempts for both sexes. However, this mean increase in the total number of fledglings was observed for males but not for females. An increase in the reproductive output of females seems to be linked to identifying and mating with an early arrive male, which makes the low rates of assortative mating found even more intriguing.

We did not find a clear relationship between arriving first and a possible benefit in the reproductive traits that a better territory could provide. Arriving early and choosing territories in advance did not increase average brood size, average clutch volume or the average number of fledglings in each breeding attempt, which makes the rank advantage hypothesis less suitable for Lined Seedeaters. Male Lined Seedeaters are territorial birds, they defend small territories (mean 0.59 ± 0.24 ha), smaller than average for the genus (Martins et al. in press). Additionally, most feeding occurs outside the territory, in common foraging areas where the food resource are shared without obvious agonistic interactions (Martins et al. in press). Perhaps, in this species, the main function of the territory is not to increase the number of resources available to the offspring, but to ensure a suitable nesting site and, especially, to protect the female against extra-pair mating (Hinde 1956). This hypothesis is reinforced by the observation that the majority of agonistic encounters occurred during the nest building period, when females were fertile (Martins et al. in press). Thus, studies correlating territory size and quality with extra-pair mating rates still need to be carried out to fully understand the role of territory in the Lined Seedeater.

The mate opportunity hypothesis predicts a direct selection for protandry because males that arrive first have access to more females and/or mate more often. This hypothesis is also suitable in a situation where arriving early means an increase in the chances of a larger number of extra-pair nestlings (Coppack et al. 2006) or a situation where the opportunity for replacement clutches and new breeding attempts is relevant to the reproductive success (Morbey and Ydenberg 2001; Coppack et al. 2006). Our data shows that the main advantage of arriving early in Lined Seedeater is an increase in the opportunity for multiple breeding attempts. Earlier individuals of both sexes who had significantly more successful breeding attempts than late individuals, evidence that the mate opportunity hypothesis can be relevant in our population (Coppack et al. 2006). We also found a correlation between arriving early at breeding grounds and having more opportunities for replacement clutches. This correlation has already been found in other passerine birds, such as in the Eastern Kingbird *Tyrannus tyrannus* (Cooper et al. 2011) and the relationship between the date of the first attempt and multiple breeding attempts has also been found in Eurasian Hoopoes *Upupa epops* (Hoffmann et al. 2015).

Other studies with intra-tropical migratory passerines have found that early males, when

compared to late males, had their eggs laid earlier (Smith and Moore 2005b), had greater reproductive success (Bejarano and Jahn 2018), and had a larger number of breeding attempts (Lozano et al. 1996; Smith and Moore 2005b). The reproductive success of the females seems to be closely linked to the success of the males. Females of Fork-tailed Flycatchers *Tyrannus savana* that mated with early males laid eggs earlier and had larger clutches than late females at the breeding grounds (Bejarano and Jahn 2018), as predicted by Kokko et al. (2006). Our data corroborate this idea, because early males had greater reproductive success, started breeding before, and had more breeding attempts than later males. Consequently, they fathered a greater number of fledglings. Early females also started the breeding season before and had more breeding attempts than later females, but their arrival date did not influence the total number of fledglings.

Other studies have already shown that early arrival in the territory is associated with larger clutches (Lozano et al. 1996; Smith and Moore 2005b) and the laying of bulkier clutches (Lourenço et al. 2011), so it was expected that early individuals would invest more in their broods. However, when evaluating the performance in the first attempt, we found that, regardless of sex, the nests had no breeding trait measure differing between the first attempt and the general attempts in the season. On the average, the volume of the clutches was inversely correlated to the arrival date, indicating that birds that arrive first invest less in each egg. This may be due to the energy expenditure of advancing arrival and suboptimal feeding conditions at the beginning of the season, since it is well established that the pre-breeding nutritional condition of parents affects reproductive success (Sandberg and Moore 1996).

When evaluating the performance throughout the entire season, our results showed a similar pattern. The early arrival of males resulted in clutches of smaller volume but did not interfere with brood sizes. In addition, the arrival day was a predictor of reproductive success, with a greater number of total fledglings for early males.

Although early males did not have more fledglings per nest than late males, and the number of breeding attempts was more determinant for reproductive success than the number of fledglings in each attempt, as predicted in the literature for tropical birds (Roper 2005).

For the females, early arrival was not advantageous. Early females had nests that, on average, had smaller eggs, smaller clutch size and a smaller number of fledglings per nest, but the increase in the number of breeding attempts was not enough to compensate for the low performance in individual nests and there was no difference in the total sum of fledglings between females that arrived early or late.

Earlier individuals, regardless of sex, seem to dilute the investment in several breeding attempts,

which means that each individual attempt has a small investment, but, for male, this strategy makes up for the greater number of fledglings. The female's success seems to be more related to her partner's arrival date than her own arrival date, which has been found in other researches (Bejarano and Jahn 2018).

This is one of the first studies to evaluate the fitness impacts of the arrival date of an intra-tropical migratory bird, but we still do not know the long-term impact of the dilution of the reproductive effort in more breeding attempts, if by decreasing individual investment in each egg the fledglings have less chance of surviving and returning as reproductive individuals in the next season, or if the increased reproductive effort to arrive earlier and do more breeding attempts can negatively affect the life-long reproductive output, long-term studies following the arrival impact on fitness are important to understand the reproductive dynamics of tropical birds more deeply.

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