ALÉXIA PAULA RODRIGUES SANDIM GUIMARÃES

BREEDING SITE FIDELITY AND SEASONAL VARIATION IN BREEDING EFFORT IN A TROPICAL MIGRANT SONGBIRD

Dissertation submitted to the Management and Conservation of Natural and Agrarian Ecosystems Graduate Program of the Universidade Federal de Viçosa – Florestal Campus in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

Adviser: Leonardo Esteves Lopes

FLORESTAL - MINAS GERAIS
2023

Ficha catalográfica elaborada pela Biblioteca da Universidade Federal de Viçosa - Campus Florestal

T

G963b
2023

Guimarães, Aléxia Paula Rodrigues Sandim, 1996-

Breeding site fidelity and seasonal variation in breeding effort in a tropical migrant songbird / Aléxia Paula Rodrigues Sandim Guimarães. – Florestal, MG, 2023.

1 dissertação eletrônica (43 f.): il. (algumas color.).

Orientador: Leonardo Esteves Lopes.

Dissertação (mestrado) - Universidade Federal de Viçosa, Departamento de Biologia Animal, 2023.

Inclui bibliografia.

DOI: https://doi.org/10.47328/ufvcaf.2023.007

Modo de acesso: World Wide Web.

1. Pássaros. 2. Reprodução. 3. Migração. 4. Habitat. I. Lopes, Leonardo Esteves, 1979-. II. Universidade Federal de Viçosa. Departamento de Biologia Animal. Mestrado em Manejo e Conservação de Ecossistemas Naturais e Agrários. III. Título.

CDD 23. ed. 598

Bibliotecário(a) responsável: Kellen dos Santos Silva Barbosa CRB-6/ES 548

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APPROVED: August 18, 2023.

Assent:

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Leonardo Esteves Lopes
Adviser

ACKNOWLEDGEMENTS

I would like to express my heartfelt gratitude to the following individuals and entities who have played a significant role in my journey during this master's program.

First and foremost, I am grateful to God for providing me with strength, guidance, and faith throughout this academic journey.

To my loving family - Maria, Celso, Jordana, Prislla, and João Gabriel for supporting me at all times, especially this one, understanding my dreams and loving me unconditionally always. Special thanks to my fiancé, Henrique Simplício, for motivating me from the beginning to the end, always supporting me and encouraging me to improve. I also thank my parents-in-law, Maria Helena e Afonso Timão, for all the love and attention during this journey. A heartfelt acknowledgment goes to all my friends from university and life who have stood by me, providing encouragement and support in countless ways.

To my laboratory team - Alexa, Ana, Bárbara, Dalila, Érica, Femke, Gabriela, Gustavo, Guido, Júlia, Lívia, Lucas, Malavika, Mayllin, Mellindy, Robert, Sjoerd, Tessa, Tarso, Vinicius, Yvone, your collaboration, friendship, and contributions to the research have made this journey even more meaningful. A special mention to my dear friend Dalila Ferreira, who accompanied me throughout my academic journey, always guiding and supporting me, both professionally and personally.

I am very grateful to the Federal University of Viçosa for granting me the opportunity to continue and complete this postgraduate degree. This experience was very important for both my academic knowledge and my personal growth. Thanks to my advisor, Leonardo Lopes, for his thoughtful guidance, support, and constructive corrections, which have guided me since graduation. I also thank my co-advisor, Filipe Cunha, for his contributions to my research. Thank you in advance, Dr Pedro Diniz, and Dr Raphael Dias, for agreeing to be the evaluators for my master's defence Your contributions were valuable for my dissertation.

Finally, this study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. I would like to express my gratitude to the CAPES for the financial support that made this study possible. Your help was essential to fulfil my academic activities. Thank you all for being a part of this remarkable chapter in my life, I am truly grateful for each and every one of you.

“Success is not final; failure is not fatal: It is the courage to continue that counts."

(Winston Churchill)

ABSTRACT

GUIMARÃES, Aléxia Paula Rodrigues Sandim, M.Sc, Universidade Federal de Viçosa, August 2023. **Breeding site fidelity and seasonal variation in breeding effort in a tropical migrant songbird.** Adviser: Leonardo Esteves Lopes.

This dissertation investigates two intriguing aspects of birds' reproductive ecology: breeding site fidelity and seasonal variation in breeding effort. For that, we used the lined seedeater (*Sporophila lineola*), a tropical migrant songbird, as a model species. The first chapter explores breeding site fidelity, a common strategy among migratory birds, and its potential association with prior breeding success. Utilizing data from a monitored population of lined seedeaters during seven breeding seasons, we tested the hypothesis of a "win-stay, lose-change" by measuring the distance between nests built in subsequent seasons and the success of the last nest in the previous season. We found no significant difference in nest distances based on reproductive success, suggesting that breeding site fidelity in lined seedeaters is not primarily determined by prior breeding success but rather by other factors, such as habitat quality and predictability. The second chapter focuses on seasonal variation in breeding effort, an aspect of a species' life history influenced by multiple factors. We observed a significant reduction in both clutch size and mean egg volume per clutch as the breeding season progressed. Notably, female body size did not influence the reproductive variables tested. These findings provide insights into the strategies migratory birds employ to optimize reproductive success within a breeding season. Overall, this research emphasizes the importance of considering habitat characteristics in the study of breeding site fidelity in migratory birds. Additionally, the investigation contributes to our broader knowledge of bird life history strategies and the ecological factors influencing reproductive output within a breeding season.

Keywords: Breeding site fidelity. Migratory birds. Reproductive success. Habitat quality. Seasonal variation. Reproductive effort.

RESUMO

GUIMARÃES, Aléxia Paula Rodrigues Sandim, M.Sc, Universidade Federal de Viçosa, agosto de 2023. **Fidelidade ao local de reprodução e variação sazonal no esforço reprodutivo em uma ave migratória tropical.** Orientador: Leonardo Esteves Lopes.

Esta dissertação investiga dois aspectos intrigantes da ecologia reprodutiva das aves: fidelidade ao sítio reprodutivo e variação sazonal no esforço reprodutivo. Para isso, nós utilizamos *Sporophila lineola*, uma ave migratória tropical, como modelo de estudos. O primeiro capítulo explora a fidelidade ao sítio reprodutivo, uma estratégia comum entre as aves migratórias, e sua potencial associação com o sucesso reprodutivo anterior. Utilizando dados de uma população monitorada de *Sporophila lineola* durante sete temporadas reprodutivas, testamos a hipótese de "ganha-fica, perde-troca" medindo a distância entre os ninhos construídos nas temporadas subsequentes e o sucesso do último ninho na temporada anterior. Não encontramos nenhuma diferença significativa nas distâncias dos ninhos com base no sucesso reprodutivo anterior, sugerindo que a fidelidade ao sítio reprodutivo da espécie não é determinada diretamente pelo sucesso reprodutivo anterior, mas sim por outros fatores, como qualidade e previsibilidade do habitat. O segundo capítulo enfoca a variação sazonal no esforço reprodutivo, um aspecto da história de vida de uma espécie influenciado por múltiplos fatores. Observamos uma redução significativa no tamanho da ninhada e no volume médio de ovos por ninhada à medida que a estação reprodutiva avançava. Notavelmente, o tamanho do corpo da fêmea não influenciou as variáveis reprodutivas testadas. Essas descobertas fornecem informações sobre as estratégias que as aves migratórias empregam para otimizar o sucesso reprodutivo durante a estação reprodutiva. No geral, esta pesquisa enfatiza a importância de considerar as características do habitat no estudo da fidelidade ao sítio reprodutivo em aves migratórias. Além disso, a investigação contribui para nosso conhecimento mais amplo das estratégias de história de vida das aves e dos fatores ecológicos que influenciam a produção reprodutiva durante a estação reprodutiva.

Palavras-chave: Fidelidade ao sítio de reprodução. Aves migratórias. Sucesso reprodutivo. Qualidade do habitat. Variação sazonal. Esforço reprodutivo.

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SUMMARY

GENERAL INTRODUCTION

Breeding site fidelity and seasonal variation in reproductive effort are interesting aspects of the reproductive ecology of birds, reflecting possible strategies that birds employ to ensure reproductive success. These phenomena are common in migratory birds, which face challenges in selecting suitable breeding sites and optimizing their reproductive efforts in a restricted period of time.

The first chapter of this dissertation explores the phenomenon of reproductive site fidelity in the tropical migratory songbird *Sporophila lineola* (Figure 1). Breeding site fidelity refers to the remarkable tendency of migratory birds to return to previously occupied breeding grounds after migration, displaying extraordinary orientation skills (PIPER, 2011). This adaptive behaviour allows birds to choose breeding sites based on previous environmental information, such as habitat quality and the presence of individuals of the same species (DOLIGEZ *et al.*, 2003; ROBERT *et al*., 2014). Breeding site fidelity is a common feature observed in several groups of birds, including Anseriformes, Ciconiiformes, Procellariiformes and Passeriformes (BLUMS *et a*l., 2002; CEZILLY *et al.,* 2000; Procellariiformes; BRIED *et al*., 2003; SHITIKOV *et al.,* 2012).

The decision to return to the same reproductive site involves benefits and costs, but generally males find it advantageous to remain in territories with high quality nesting resources, which provides them with access to mates and greater chances of reproductive success (GREENWOOD, 1980). On the other hand, females tend to explore new territories, investing more in reproductive efforts and offspring care (SEDGWICK, 2004). Consequently, fidelity to the reproductive site tends to be more prevalent in males than in females. In addition, several factors influence the decision to remain or disperse, including individual experience, competition for resources, predation risk and previous reproductive success (SERRANO *et al*., 2001; BORRMANN *et al*., 2019; PAREJO; AVILÉS, 2011; HOOVER, 2003).

In this chapter 1, we had the specific focus on analysing reproduction data from a monitored population of lined seedeaters over seven breeding seasons, our objective was to reveal the relationship between reproductive site fidelity and previous reproductive success, investigating the "win-stay, lose-change strategy". Surprisingly, our results revealed that reproductive site fidelity in lined seedeaters is not determined by previous reproductive success. Other factors, such as habitat quality and

predictability, may exert a more significant influence on breeding site fidelity in this population.

Birds, being one of the most diverse groups of animals, exhibit a wide variety of reproductive strategies and behaviours. Another important strategy is the size of the clutch, which is related to the quantity and quality of the offspring that is produced (LACK, 1947). Factors such as food availability and predation pressure influence clutch size throughout the breeding season, resulting in a decrease in clutch size as the season progresses (LACK, 1968; KLOMP, 1970). The timing of egg laying is another important factor that influences bird reproduction, with early breeders benefiting from favourable conditions and greater reproductive success (SOCKMAN; SHARP; SCHWABL, 2006). Furthermore, female body size plays a crucial role, as larger females tend to produce larger clutches and larger eggs (WINKLER; WALTERS, 1983; GLADBACH; QUILLFELDT, 2010).

The second chapter of this dissertation examines this seasonal variation in reproductive effort observed in lined seedeaters. Reproductive effort plays a key role in the life history of a species and is influenced by many factors that shape reproductive output within a breeding season. We analysed long-term data from a Lined Seedeater population, focusing on clutch size and mean egg volume. We investigated how these variables change as the breeding season progresses. The models built to analyse the data revealed a significant reduction in clutch size and in the average volume of eggs per clutch throughout the reproductive season, but female body size did not influence the two reproductive variables tested. These findings are important because they give us insights into how these migratory birds handle reproduction over time. And this helps us better understand the birds' reproductive strategies and the environmental factors that affect breeding site fidelity and variation in reproduction across the season.

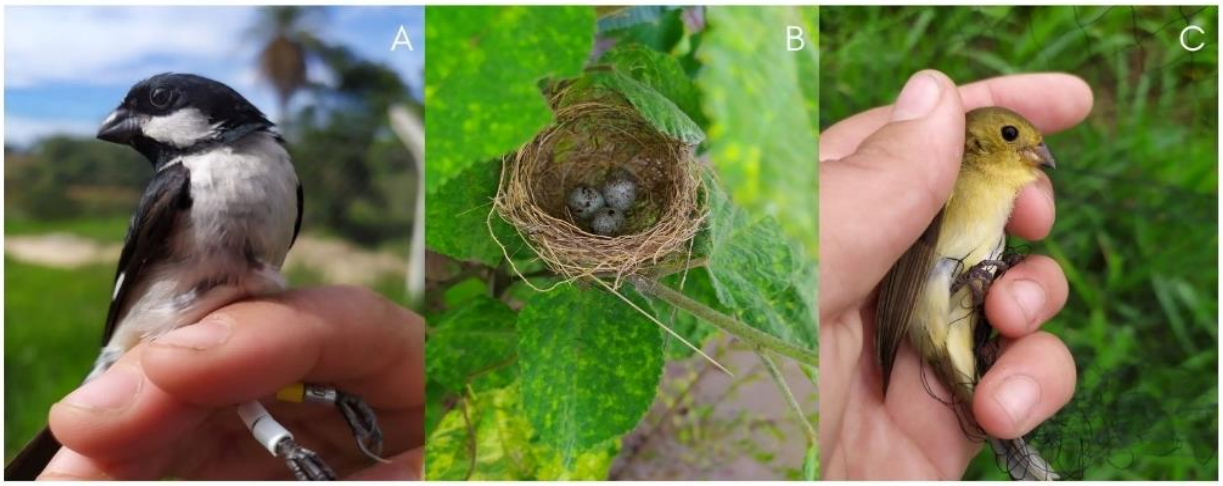

Figure 1 - Observations of the Lined Seedeater: A: Male Lined Seedeater ringed in December 2020 in Florestal, Minas Gerais. B: Nest of the Lined Seedeater recorded in February 2020. C: Female Lined Seedeater captured ringed in December 2019.

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CHAPTER 1 - Breeding site fidelity is not explained by prior breeding success in an intra-tropical migrant songbird

Abstract

Breeding site fidelity is a common strategy among migratory birds and may be related to breeding success in the previous season. To investigate the hypothesis that breeding site fidelity is associated with prior breeding success ("win-stay, lose-change

strategy"), we used breeding data from a ringed population of lined seedeater, an intra-tropical migrant songbird, that was monitored during seven breeding seasons. To test our hypothesis, we measured the distance between the last nest of the previous season of each individual and the first nest of the subsequent season. We analysed the relationship between the distance between nests built in subsequent seasons and the success of the last nest in the previous season. After analysing data from 116 nests, we found no significant difference in the distance between nests in relation to the reproductive success between seasons. This suggests that breeding site fidelity in lined seedeaters is not primarily determined by prior breeding success. Instead, other factors, such as habitat quality and its predictability may play a more important role in determining fidelity to breeding sites in this population. Our findings highlight the importance of considering habitat quality and predictability when studying breeding site fidelity in migratory birds. Understanding the behind reproductive site fidelity can provide valuable insights into adaptive and evolutionary strategies in animal species.
Keywords: reproductive biology, territorial fidelity, migration, tropics.

INTRODUCTION

Migratory birds generally exhibit strong breeding site fidelity (GREENWOOD, 1980; MARINÉ; BERNARD, 2020), a phenomenon that can be defined as the tendency of individuals to return, after a migration, to an area previously occupied by them (GAUTHREAUX, 1982). The precise return of migratory birds from the wintering grounds to exactly the same breeding territories of previous years is remarkable, revealing extraordinary orientation skills (PIPER, 2011). Breeding site fidelity is an adaptive strategy, allowing individuals to select breeding sites based on prior environmental information, such as the presence of other conspecifics, environmental features, and habitat quality (DOLIGEZ *et al.*, 2003; ROBERT *et al*., 2014). This strategy is found in several groups of birds, such as Anseriformes (BLUMS *et al*., 2002), Ciconiiformes (CEZILLY *et al.*, 2000), Procellariiformes (BRIED *et al*., 2003), and Passeriformes (SHITIKOV *et al*., 2012), being an important determinant of demography and genetic variability (HOOVER, 2003).

Returning to the same breeding site involves both costs and benefits. For males, it is usually more advantageous to return to territories that offer high-quality nesting resources rather than attempting to establish a new territory in an area of uncertain

quality (GREENWOOD, 1980). This decision allows males to capitalize on the available resources, such as gaining preferential access to mates and increasing their chances of reproductive success. Thus, dispersal from the previously occupied territory may have substantial costs for males. On the other hand, females typically do not establish and defend territories, thus facing lower costs associated with dispersal when compared to males (SEDGWICK, 2004). Thus, it is usually more advantageous for females to explore new territories, enabling them to invest more in reproductive efforts and offspring care. Consequently, it is usually more advantageous for males to exhibit breeding site fidelity than females.

The decision to return or disperse is influenced by several factors, such as individual experience (SERRANO *et al.*, 2001), competition for resources (BORRMANN *et al.*, 2019), risk of predation (PAREJO; AVILÉS, 2011), or breeding success in the previous season (HOOVER, 2003). Among these factors, prior breeding success seems to be the main determinant of breeding site fidelity, a relationship known in the literature as the "win-stay, lose-change strategy" (BONNET-LEBRUN *et al.*, 2021). According to this hypothesis, successful individuals would stay in the same breeding site, while less successful individuals would seek new breeding sites in the following breeding season (KAMIL, 1983; PATRICK; WEIMERSKIRCH, 2017; FREUND; BAHAT; MOTRO, 2017; BONNET-LEBRUN; COLLET; PHILLIPS, 2021).

This study seeks to investigate the relationship between breeding site fidelity and prior breeding success in lined seedeaters (*Sporophila lineola*), a tropical songbird widely distributed in South America (RIDGELY; TUDOR, 2009).We used the lined seedeater as a model species because it is an intra-tropical migrant bird (RIDGELY; TUDOR, 2009) that in recent decades expanded its range throughout the southeast and south of Brazil, where it inhabit degraded and peri-urban open areas (FERREIRA, 2022). The study of breeding site fidelity in lined seedeaters may help us understand how and why the species expanded its range into human-transformed environments in such a remarkable way.

Our research focused on the males of the species, as this is usually the sex with highest breeding site fidelity (FRIEDRICH *et al.*, 2014). In lined seedeaters, males establish and defend territories (MARTINS; CUNHA; LOPES, 2021), whereas females build the nests and incubate the eggs (MARCONDES-MACHADO, 1997; FERREIRA; LOPES, 2017). In addition, lined seedeater males are the main responsible for nesting site selection, suggesting to the females the exact place where the nest should be built

(FERREIRA; CUNHA; LOPES, 2022). We investigated the hypothesis that breeding site fidelity in males of lined seedeater is influenced by the prior breeding success. According to the "win-stay, lose-change strategy", we predicted that males that were successful in the last nest of the previous breeding season will be more likely to return to the same territory previously occupied.

METHODS

Study area. The study was conducted at the Universidade Federal de Viçosa, Campus Florestal (centred at 19º52'51"S and 44º24'49"W, 750 m alt.), in the municipality of Florestal, Minas Gerais, Brazil. The area is located in a transition zone between the Cerrado and the Atlantic Forest (IBGE, 2004). Local climate has two well-marked seasons: a hot and rainy season from October to March and a mild and dry season from April to September; the mean precipitation is ~1450 mm and the mean annual temperature is ~20 °C (LOPES; MARÇAL, 2016).

The study area is approximately 1500ha, half of which is covered by semi-deciduous forests and the other half covered by open areas. Field work was carried out in the open areas, which comprise planted pastures of African grasses, active and abandoned cultivated areas, as well as several ponds and buildings surrounded by gardens.

Species studied. Lined seedeater is a granivorous species widely distributed in South America (RIDGELY; TUDOR, 2009). The population found in southeastern Brazil reproduces between November and April, migrating through central Brazil to northern South America, where it winters (SILVA, 1995; CUNHA; LOPES; SELEZNEVA, 2022). This species is socially monogamous and has marked sexual dimorphism when in the adult plumage, with brownish females and black-and-white males (FERREIRA; LOPES, 2017). Only the females build the nests and incubate, while both sexes feed the nestlings (MARCONDES-MACHADO, 1997; OLIVEIRA *et al.*, 2010; FERREIRA; LOPES, 2017). The mean clutch size is 2.4 eggs, which are incubated for 11 days, and the nestlings remain on mean 10 days in the nest after hatching; multiple reproductive attempts are common (FERREIRA; LOPES, 2017).

Capture and ring of individuals. Data were collected over seven breeding seasons (2014–2022) from November to April, therefore, coinciding with the presence of the species in the study area (FERREIRA; LOPES, 2017). As soon as the first

individuals were detected, capture attempts with mist nets began, with individuals ringed with a numbered metallic ring and a unique combination of three coloured rings. When necessary, we used audio playbacks to attract males during capture attempts, as they actively defend the surroundings of the nests.

Nest search and monitoring. Nests were located based on observation of couples of the species and their behaviour, such as transporting material for nest building, transporting food for the nestlings, and chasing of females (a common behaviour exhibited by males during nest building and egg laying). Nest searching was carried out concomitantly with the bird ringing. Each nest received a unique number and had its coordinates recorded with the aid of a handheld GPS device. Nests were systematically monitored at intervals of 2–3 days, until their inactivity, allowing the definition of their fate (success or failure).

Reproductive success. Nests in which at least one nestling fledged were considered successful. Those nests in which all eggs or nestlings were predated or disappeared before the minimum period of 10 days expected for fledging were considered unsuccessful (FERREIRA; LOPES 2017). Nests were considered abandoned when their construction, incubation of eggs or care for the nestlings ceased within the normal time frame for no apparent reason.

Breeding site fidelity. To estimate males' fidelity to the breeding site, we first verified if those ringed males returned to the breeding grounds in a subsequent season. For that we used data on field observation and mist-net recapture in the study area. Since the search for nests, monitoring of adult birds and bird ringing was intensive and occurred on a daily basis, we assumed that the probability of detecting birds that have been ringed during previous seasons was high, and that individuals not detected within the study area had dispersed to other locations or died (MARTIN *et al*., 1995).

For individuals that returned to the breeding grounds and reproduced again, we evaluated the distance between nests built in subsequent seasons. To measure the distance between these nests, the geographic coordinate data of each one of them was exported in a shapefile format file and then converted into a GeoDataFrame object using a Geopandas library (JORDAHL, 2017) in the Jupyter Notebook computational environment (https://jupyter.org). The geographic coordinates were represented in the decimal degree format, and the system of reference used was the WGS 84 (World Geodetic System 1984), which is a commonly used coordinate reference system for geographic data. From this GeoDataFrame, we calculated the distances between

nests using the "distance" function of the Geopandas library, by computing great-circle distances on the Earth's surface.

Data analysis. To assess whether males that had success in their last nests of the previous breeding season were more faithful to the breeding site than those that were unsuccessful, we analysed data in two ways. First, we used a Generalized Linear Model (GLM), considering prior nesting success as the explanatory variable (coded as 1 = success and 0 = failure) and distance (in meters) between the last nest of the previous season and the first nest of the studied season as the response variable. Ring number of males was included in the model as a random effect, as some males were observed in more than one breeding season, thus avoiding potential biases caused by repeated observations of the same individuals. The analyses were performed using the R software (R CORE TEAM, 2020) and the gamma distribution was used for the analysis, since this distribution is suitable for continuous variables with positive values ($Y > 0$). The model was fitted using the "lmer" function from the "lme4" package (BATES *et al.*, 2015). To verify the model's assumptions, we tested for residuals normality and variance homogeneity using the Shapiro-Wilk and the Levene tests, respectively.

Second, we used the Fisher's Exact Test to assess whether there were a significant association between two categorical variables, which were breeding site fidelity ("faithful" and "unfaithful") and prior breeding success ("success" and "failure"). We considered as faithful to the breeding site those individuals that reproduced within a radius equal to or less than 45 meters from the last nest of the prior breeding season, a value that represents the mean radius of the territory of a pair of the species (MARTINS *et al.*, 2021).

Ethical and legal aspects. The study had permits for bird capture and ringing issued by SISBio (No. 61078) and by the Commission for Ethics in the Use of Animals of the Federal University of Viçosa (No. 03/2018).

RESULTS

We analysed data from 116 nests belonging to 30 males of the species. Of these, 58 nests were used to determine whether there was success in the previous season or not (14 were successful and 44 were unsuccessful, 24.1% success). The GLM revealed no significant differences in the distance between nests in subsequent

seasons and prior breeding success (Figure 1, Table 1). The effect size was also very small (r = 0.03). In a similar way, the Fisher's Exact Test indicated no statistically significant association between nest site fidelity and prior breeding success (Figure 2).

Table 01 – GLM Results. Results of the generalized linear model constructed based on data from the monitoring of lined seedeater nests in southeastern Brazil during the period (2014–2022).

	Estimate	**t value**	**p value**
Intercept	29.392	10.397	1.39e-11
Breeding success	0.295	0.063	0.950
Random effect	**Variance**	**Std. Dev**	
Male ID	5.933	2.436	

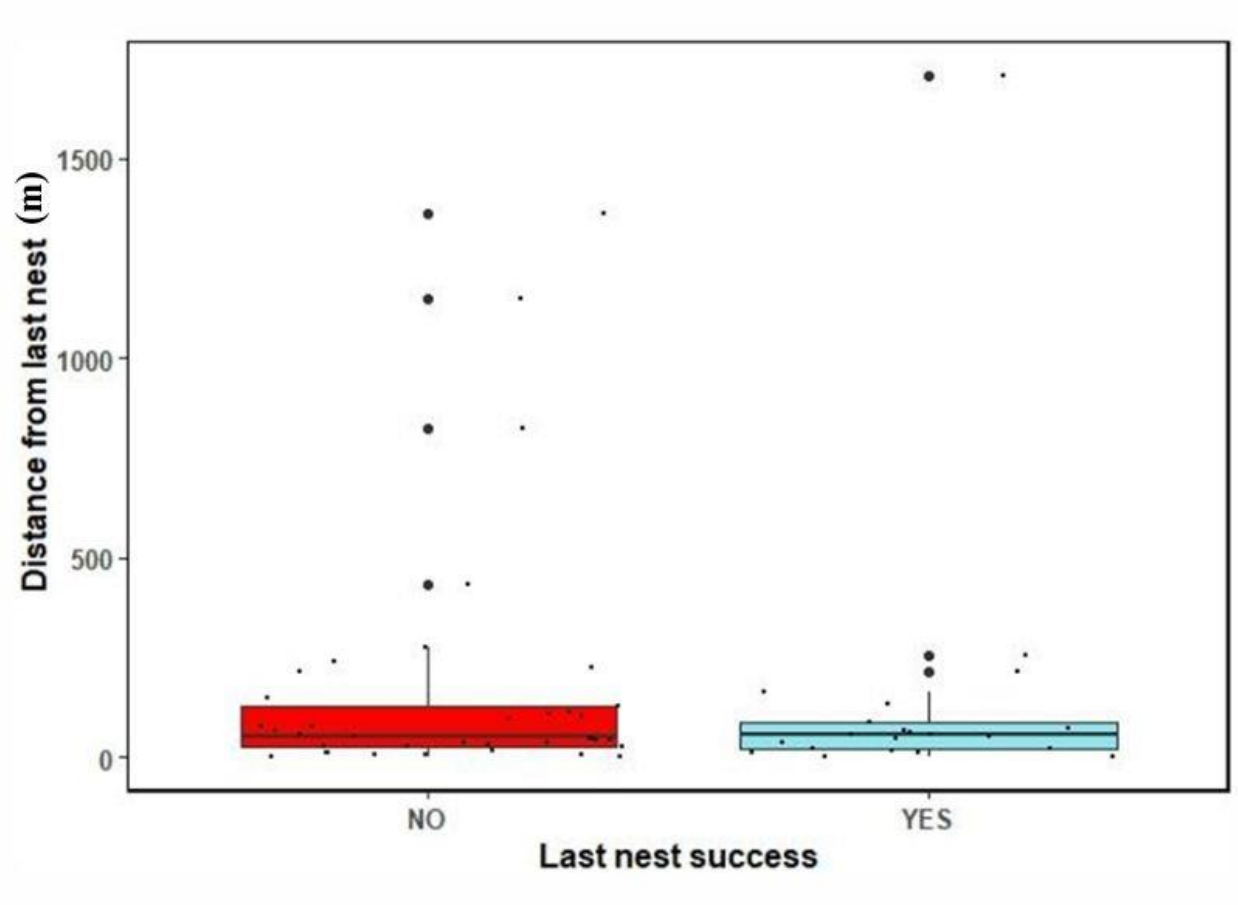

Figure 2. Boxplot of distance between nests and reproductive success in lined Seedeaters. Values were obtained by the generalized linear mixed effects model. The points on the graph represent the raw values of distance between nests. Nests centred on the left (aligned with "No") correspond to nests without reproductive success in the previous season, while nests centred on the right (aligned with "Yes") represent successful nests. Data collected in southeastern Brazil between 2014 and 2022.

Figure 3. Bar Chart with Fisher's Exact Test. Counting of fidelity and reproductive success data in lined Seedeaters. The figure shows the count of nests considered faithful (in the column 'Faithful') and unfaithful (in the column 'Unfaithful'), as well as the count of nests that were successful (in blue) and unsuccessful (in red). This table was used to perform Fisher's exact test to verify the association between fidelity and reproductive success. Data collected in southeastern Brazil between 2014 and 2022.

Figure 4 - Satellite images of the study are: located in the Universidade Federal de Viçosa, Campus Florestal, southeast Brazil. Each column shows a distinct area of the campus in three different years, illustrating how dramatically the landscape changed.

DISCUSSION

In this paper, we demonstrated that breeding site fidelity is not explained by prior breeding success in lined seedeaters. Therefore, our results go against the findings of

several previous studies who have found support for the “win-stay, lose-change strategy” (HAAS, 1998; HOOVER, 2003; VERGARA *et al.,* 2006). In this way, breeding site fidelity in lined seedeaters may be more related to other factors, such as age (HARVEY *et al*., 1984), individual quality (SERRANO *et al*., 2001), or territory quality (BENSCH; HASSELQUIST, 1991).

Understanding the factors that influence dispersal between alternative breeding sites is important to understand the survival and reproductive strategies of individuals of a given species. Among the various factors already listed as determinants of breeding site fidelity in birds, the territory quality has been repeatedly demonstrated as an important decision criterion (HOLMES *et al*., 1996; DOLIGEZ *et al*., 1999). For example, return rates to the breeding site in bobolinks (*Dolichonyx oryzivorus*) were similar between successful and unsuccessful individuals at a high-quality habitat, but at low-quality habitat unsuccessful individuals were less faithful e (BOLLINGER; GAVIN, 1989). On the other hand, in common goldeneye (*Bucephala clangula*), birds that dispersed exhibited lower reproductive success, suggesting that there are other costs involved in changing the nest location, such as the difficulty of locating alternative nesting cavities, as the availability of nest boxes are irregular and unpredictable (DOW; FREDGA, 1983).

Predicting territory quality between seasons, however, may be challenging in habitats that are highly dynamic between seasons. For example, in highly dynamic open grassland areas with frequent and unpredictable wildfires, the species does not maintain territories throughout the year, instead, they wait until the breeding season to establish new territories (LOPES *et al*., 2023). However, in intensively managed human-made habitats, such as the study area (which constantly suffers from grass cutting, use of herbicides, planting/harvesting of crops, construction of new buildings etc.), habitat quality can vary dramatically between seasons or even throughout the season (Appendix 1). Thus, in situations where the distribution of high-quality territories is unpredictable over space and time, being faithful to a specific territory may not be the better adaptive strategy (SWITZER, 1993). Thus, each season, individuals may face a very distinct situation, and they will need to reassess territory-quality and make decisions on a case-by-case basis. In other words, returning to a breeding site that has been previously used does may not pay when there is a low probability of finding a high-quality habitat there (EDWARDS *et al*., 2009).

Despite reproductive site fidelity being commonly observed in several other

animal groups, including terrestrial and aquatic mammals, reptiles and even some invertebrates (ARONSSON; PERSSON, 2018; POMEROY *et al*., 2000; SHERIDAN *et al.*, 2010; HOEFLER *et al.*, 2006), understanding their motivations is a great challenge, as each species has its idiosyncrasies. In lined seedeaters, males have a behaviour of exploring various sites when they arrive from the migration, roaming the study area for several days before settling in a specific territory (personal obs.). This possibly represents a period of exploration, where males evaluate different areas before taking the decision to establish their territory. Thus, factors other than reproductive success seem to play an important role in the individual's decision to be faithful to the previous breeding site or to disperse. Habitat quality and its predictability may be more relevant elements than previous reproductive success in determining the site fidelity of individuals in this population. As a suggestion for future studies, we recommend further investigating the influence of habitat quality and its predictability in determining fidelity to the breeding site of this bird population. This would help determine if the strategy exhibited by the lined seedeater in the study area also applies to other less managed locations with more predictable habitats.

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CHAPTER 2- Seasonal variation in the reproductive effort of a tropical songbird

ABSTRACT

Reproductive effort plays an important role in a species' life history, influenced by a multitude of factors that shape reproductive output within seasons. In bird species with well-defined breeding seasons, an optimal breeding period exists, determined by factors such as resource availability, low predation, favourable climate conditions, and more. Additionally, migratory species face the challenge of resource exhaustion upon arrival and the need to accumulate resources before embarking on their wintering journey. To explore the within-season variation in reproductive effort among migratory birds, we analysed long-term data from a population of lined seedeaters (*Sporophila lineola*), a small passerine intra-tropical migrant. Our investigation focused on examining the variation in clutch size and egg volume during the breeding season, utilizing data from 335 nests collected between December and April over six breeding seasons from 2014 to 2022. Clutch size ranged from 2 to 3 eggs (mean 2.37 ± standard deviation 0.48). As predicted, the models revealed significant reduction in clutch size and in mean egg volume per clutch throughout the breeding season. Female body size did not influence the two reproductive variables tested. This study enhances our understanding of within-season dynamics in the reproductive effort of migratory birds, providing insights into their strategies for optimizing reproductive success. It contributes to our broader knowledge of avian life history strategies and the ecological factors influencing them.

Key words: breeding biology, clutch size, egg volume; life history.

INTRODUCTION

Clutch size is an important adaptive strategy that reflects the relationship between the quantity and quality of offspring produced (LACK, 1947). Clutch size is not fixed, as it can be adjusted according to changes in habitat features, such as forest fragmentation in the Eurasian Treecreeper (*Certhia familiaris*) (SUORSA *et al.,* 2003), and an ecological trap in Urban Great Tits (*Parus major*) (DEMEYRIER *et al*., 2016). Such adjustments have already been reported for members of several animal groups, including birds, mammals, reptiles, and amphibians (MCINROY; BROUSMICHE; WYNNE EDWARDS, 2000). In birds, for example, clutch size often decreases at a populational level throughout the breeding season, usually due to seasonal variations in habitat features such as food availability, predation pressure, and weather severity (LACK, 1968; KLOMP, 1970; HOCHACHKA, 1990; NORRIS; MARRA, 2007; CHALFOUN; MARTIN, 2010).

Timing of egg laying can, therefore, influence clutch size, since the number of nestlings that can be raised depends on the breeding season period and the availability of resources (KLOMP, 1970; EJSMOND *et al*., 2021; DEME *et al.,* 2023). In birds, females that reproduce at the beginning of the breeding season are more likely to achieve reproductive success because they benefit from warmer temperatures, which reduce the energy costs associated with reproduction (SOCKMAN; SHARP; SCHWABL, 2006).

In addition to the timing of egg laying, female body size can also influence clutch size. Larger females tend to initiate breeding earlier in the season, lay larger clutches and larger eggs (WINKLER; WALTERS, 1983; GLADBACH; QUILLFELDT, 2010). Larger eggs have higher hatching success rates (PERRINS, 1966) and produce larger and faster-growing nestlings, which positively influence their survival prospects, especially in the early days after hatching (AMUNDSEN; STOKLAND, 1990; RUTKOWSKA; CICHON, 2005).

Understanding how the timing of egg laying and female body size influence clutch size and egg size is important to unravel the life history strategies of birds. In this study, we investigated these relationships in lined seedeaters *Sporophila lineola*, a small intra-tropical migratory songbird with multiple breeding attempts per season and a small variation in clutch size (2 or 3 eggs). We sought to fill a knowledge gap by

examining the relationship between egg laying date, female body size, clutch size, and egg size. We investigated the hypothesis that lined seedeaters exhibit a seasonal decrease in reproductive effort at a population level along the breeding season. Thus, we predicted a decrease in clutch size and mean egg volume throughout the breeding season. We also predicted a positive relationship between female wing size and clutch size and mean egg volume per nest. This research contributes to a deeper understanding of the factors that shape reproductive effort in an intra-tropical migratory songbird.

METHODS

Study area. The study was conducted at the Universidade Federal de Viçosa (19º52'51''S and 44º24'49''W, 750 m alt.), municipality of Florestal, Minas Gerais, Brazil. The area is located in a transition zone between the Cerrado and the Atlantic Forest (IBGE, 2004). The climate is subtropical, with a well-marked hot and rainy season (LOPES; MARÇAL, 2016). Lined seedeater inhabits open areas comprising artificial pastures of introduced African grasses, active and abandoned cultivated areas, and several small ponds surrounded by grassy gardens.

Model species. The lined seedeater is a small granivorous passerine, widely distributed across South America, where it inhabits several types of open formations, including disturbed areas (SICK, 1997; RIDGELY; TUDOR, 2009). The population studied reproduces between December and April (FERREIRA & LOPES, 2017), migrating through central Brazil to northern South America, where it winters (SILVA, 1995; CUNHA *et al,* 2022).

The species is socially monogamous (FERREIRA; LOPES, 2017) with marked sexual dimorphism: females are brownish and adult males have black plumage with white badges (RIDGELY; TUDOR, 2009). During the reproductive period males sing actively throughout the day, defending the vicinity of their territories (FERREIRA; LOPES, 2017; MARTINS *et al*, 2021). Only females build the nests and incubate the eggs, while both sexes feed the nestlings (MARCONDES-MACHADO, 1997; OLIVEIRA *et al.* 2010; FERREIRA; LOPES, 2017). Mean clutch size is 2.4 eggs, which are incubated for 11 days, and the nestlings remain in the nest for 10 days after hatching (FERREIRA; LOPES, 2017).

Capture and ringing of individuals. Fieldwork was carried out over six breeding seasons (2014/2015, 2017/2018, 2018/2019, 2019/2020, 2020/2021, and 2021/2022). Individuals were captured with mist nets and ringed with a numbered metal ring and a unique colour combination. For each captured individual, we measured the length of the right wing (WMAX, ECK *et al.,* 2011) with a metal ruler (accuracy of 0.5 mm). We used wing length as an indication of female body size, which is usual in passerines (GOSLER *et al*. 1998; FIEDLER *et al.* 2011) and presents greater reproducibility compared to other linear measurements (GOSLER *et al*., 1998).

Nest search and monitoring. Nests were located by observing the behaviour of couples within the territories. Once found, the nests were monitored to determine the clutch size and the mean egg volume per nest. The length and width of the eggs were measured with a calliper (accuracy of 0.1 mm) and the volume of each egg was calculated using the formula 0.51 x length x width^2 (HOYT, 1979).

Data analysis. The data analysis was conducted in the R software (R CORE TEAM, 2020). We utilized the 'lme4' package (BATES *et al.* 2015) to construct linear mixed (LMM) and generalized mixed (GLMM) models. The 'lmerTest' package (KUZNETSOVA *et al.,* 2017) was employed to check the p-value for each model, and the “RVAideMemoire” package (HERVÉ, 2020) was used to examine the distribution of model residuals.

The focus of the analysis was to test the predictions of the hypothesis by exploring the effect of explanatory variables, such as the laying date of the first egg in the clutch and female body size, on the response variables related to female reproductive effort (clutch size and mean egg volume per clutch). To account for individual variations, female ring number and breeding season were included as random effects, considering that some females were monitored in multiple breeding attempts or breeding seasons.

For the mean egg volume data (normal distribution), LMMs were constructed, while for clutch size data, a GLMM with a Poisson distribution was used. Throughout the analysis, aimed to understand how these variables change over season, taking into consideration the random effects of individual females (Ring number of females) and breeding seasons.

RESULTS

A total of 335 nests were used for the analysis during the six breeding seasons sampled. Clutch size ranged from 2 to 3 eggs (mean 2.37 ± standard deviation 0.48). The models revealed significant reduction in clutch size and in mean egg volume per clutch throughout the breeding season (Figure 1, Table 1). Female body size did not influence the two reproductive variables tested (Table 1).

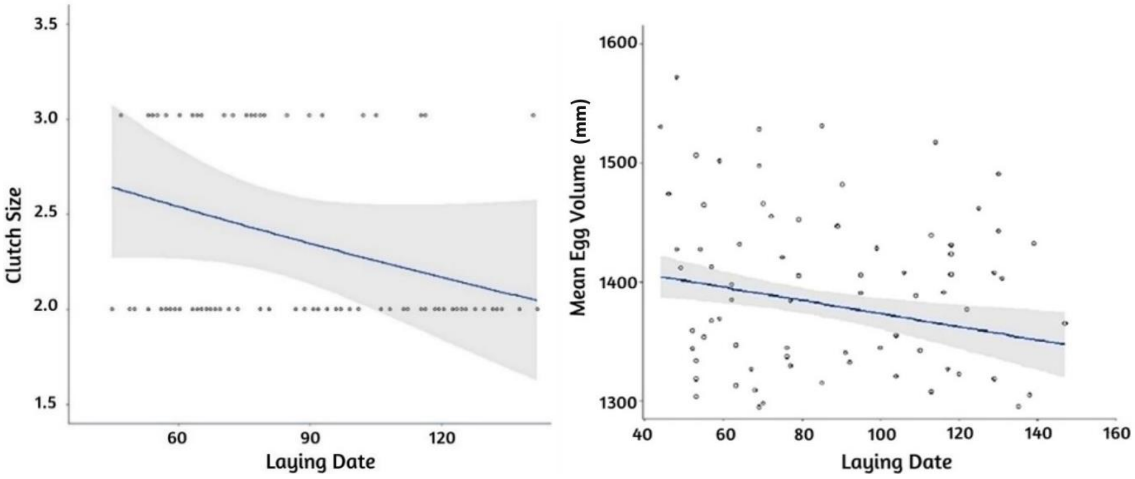

Figure 5. Scatter Plot of Seasonal Variation in Reproductive Effort. Seasonal variation in the reproductive effort of lined seedeaters in southeastern Brazil. Left: Clutch size according to the egg laying date. Right: Mean egg volume according to the egg laying date. Lines represent the fitted model, grey areas represent the 95% confidence interval, and the empty circles represent the observed values. Day 0 corresponds to November 1st, and Day 160 corresponds to March 16th.

Table 2 – **LMM and GLMM Results**. Result of the linear mixed (LMM) and generalized linear mixed (GLMM) models built with data from monitoring nests over six breeding seasons of lined seedeaters in southeastern Brazil.

Breeding variables	**Laying Date**			**Body Size**		
LMMs	**Estimate**	**t value**	**p value**	**Estimate**	**t value**	**p value**
Mean egg volume	-0.5717	-2.853	**0.005**	7.103	1.117	0.266
Random effect	**Variance**	**Std. Dev**				
Female ID	5817.2	76.27				
Season	104.1	10.20				
GLMMS	**Estimate**	**z value**	**p value**	**Estimate**	**z value**	**p value**
Clutch size	-0.0032	-2.495	**0.013**	0.023	0.782	0.434
Random effect	**Variance**	**Std. Dev**				
Female ID	7634.1	87.37				

Season	254.1	15.94

DISCUSSION

Our study's results align with previous research on bird reproduction. We observed a seasonal variation pattern in clutch size and mean egg volume. As the laying date advanced, both clutch size and egg volume showed a significant decline, indicating that females tend to produce smaller clutches and eggs as the breeding season progresses. Similar patterns of reduced clutch size have been observed in temperate (GLADBACK *et al.,* 2010) and tropical regions (DYRCZ, 2002; MASSONI, 2007). This highlights the importance of considering egg size when investigating the decline in seasonal variation of reproductive effort in the studied population. Larger eggs are known to increase the chances of offspring survival and growth, potentially leading to higher reproductive success for individuals and the entire population. Therefore, the lined seedeater may employ a strategy of investing more at the beginning of the season by producing larger eggs precisely when it arrives, because this timing aligns with the ideal moment of higher reproductive effort, as it needs to conserve energy toward the end of the season. By utilizing this strategy, the bird ensures a greater potential for reproductive success for its offspring, at the time that is most ideal for the female expend energy.

There is a great influence of egg size in the first days of the nestling's life, because the nestling that hatch from larger eggs, containing more nutrients and water reserves, tend to be larger (BRYANT, 1978; CROXALL *et al*., 1992, WILLIAMS, 1994), increasing their chances of survival as they are more resistant to hunger and cold (AMUNDSEN; STOKLAND, 1990; RUTKOWSKA; CICHON, 2005). Based on this information, it can be inferred that the females in the present study employed this reproductive strategy of laying larger eggs at the beginning of the season, increasing the mean size of the eggs, in order to achieve successful results. Furthermore, during the breeding season, environmental factors such as predation and food availability change over time. Studies have shown seasonal increases in the risk of nest predation (MULLER *et al*., 2005; WIEBE, 2003; GRANT *et al.*, 2005; KROLL; HAUFLER, 2009). Given this, it is possible that for lined seedeater females it is more strategic to invest

in larger eggs earlier in the season, where perhaps there is a lower risk of predation, in order to achieve greater reproductive success.

In this study, we did not find any correlation between female size and mean egg volume or clutch size in the lined seedeater population. This contrasts with findings in other bird species (GLADBACK *et al.,* 2010) and other egg-laying animals, such as lizards (STEWART, 1979; RAMÍREZ-BAUTISTA *et al.,* 2022), sea turtles (MCGINLEY, 1989; LE GOUVELLO *et al*., 2020), alligators (MEJÍA-REYES *et al.,* 2023), and amphibians (HÖBEL *et al.,* 2021). Despite, factors like food availability, habitat quality, and geographic and climatic variations can influence the relationship between body condition and reproductive parameters, birds, unlike other organisms mentioned, stop growing after their first reproductive event, leading to relatively small differences in size among female birds. Moreover, the lined seedeater, exhibits multiple breeding attempts per season and faces high predation rates. Therefore, spreading their reproductive efforts across multiple attempts might be a better strategy for increasing the chances of successful reproduction, rather than concentrating all efforts in a single attempt. The absence of a significant relationship between female body size and reproductive parameters in the lined seedeater population can be better understood by considering the unique reproductive strategies of birds and how they differ from other organisms mentioned. These species-specific characteristics, along with environmental factors and individual reproductive strategies, likely interact to shape the observed patterns in this study.

Lined seedeaters have multiple reproductive attempts per season, with up to five or six attempts recorded. This contrasts sharply with most species from temperate zones, which generally have only a single reproductive attempt or, at most, a second clutch. For example, a decrease in clutch size was observed in the Upland Goose *Chloephaga picta*, a species from the temperate zone, where seasonality is marked and the reproductive period is short (GLADBACK *et al.,* 2010). However, the lined seedeater has a relatively long reproductive period of five months (FERREIRA; LOPES, 2017), compared to species from temperate zones, which generally have a reproductive period of two to three months (STUTBURRY; MORTON, 2001). It is interesting to note that both the lined seedeater and other species from temperate regions show a reduction in reproductive effort at the end of the season, which may be related to the migratory period. Considering that the lined seedeater is a long-distance migratory bird (SILVA, 1995), we hypothesize that this reduction in reproductive effort

may be associated with preparations for migration. This observation highlights the reproductive strategy of the species and raises questions about trade-offs and adaptations related to multiple reproductive attempts and long-distance migration. In addition, it is important to highlight that the decrease in the reproductive effort of this research is related to the effort at the population level, as well as the studies cited throughout the text. In view of the research, it is possible to suggest that apparently, at an individual level, this topic has not yet been investigated in tropical birds.

In conclusion, our study reveals a significant reduction in clutch size and egg volume during the breeding season for the lined seedeater. This suggests an adaptive reproductive strategy in response to environmental changes. However, female body size did not influence the two reproductive variables tested, probably other unexplored factors, such as specific climatic variables, individual characteristics and quality and individual habitat quality, may also influence these variations. This research contributes to our understanding of the reproductive strategies of the lined seedeater species. Further research into these factors is needed to gain a comprehensive understanding of the specie reproductive strategies. It also encourages further investigation into different bird species, to expand scientific knowledge in this field.

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