Foraging behavior and diet of lined seedeaters (Sporophila lineola) in the breeding and wintering grounds

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Abstract

Migratory animals face seasonal variations in energetic and nutritional demands, especially between breeding and wintering grounds. In this study, we investigated the foraging behavior and diet of lined seedeaters (*Sporophila lineola*) between their breeding grounds in southeastern Brazil and wintering grounds in the Amazonia. The habitat used is a disturbed dry grassland in the breeding grounds and a natural wetland in the wintering grounds. Thus, we hypothesized that attack maneuvers would vary between habitats and that food items taken would also shift seasonally, with higher arthropod intake when breeding and higher seed intake when wintering. For that we recorded 135 and 147 foraging events in the breeding and wintering grounds, respectively, also analyzing the contents of 11 stomachs of museum specimens. Lined seedeaters were more likely to use Glean and Hang-up attack maneuvers in both grounds studied, but the proportion between them differed, likely reflecting differences in grass morphology between areas. Food category composition did not differ between grounds, with seeds being the dominant item in both areas. The diet included mainly seeds of *Urochloa brizantha* (an introduced African grass) in the breeding grounds, and seeds of *Echinochloa polystachya* and *Paspalum repens* (two native grasses from the Amazonia wetlands) in the wintering grounds. The stomach content analysis also confirmed the predominance of grass seeds in the diet of the species. We concluded that the lined seedeater is a generalist granivore capable of exploiting both native and invasive grasses. This flexibility may offer advantages over more specialized species in a changing world.

Introduction

Temporal variations in foraging behavior and diet are commonly observed in migratory animals. This is because in addition to phenological variations in their nutritional and energy demands (e.g. territorial defense, gamete production, and parental provisioning), those animals also need to cope with the challenges faced during migration, such as adverse environmental conditions, structurally distinct habitats, and different biotic interactions (Dingle 2014; Hurlbert and Haskell 2003). For example, female green sea turtles (*Chelonia mydas*) accumulate large fat reserves before migrating to the breeding grounds, where they face high energy demands associated with reproduction (Seminoff and Nichols 2002; Taquet 2006). Humpback whale (*Megaptera novaeangliae*) populations from the Southern Hemisphere seasonally migrate between wintering grounds in polar regions and breeding grounds in tropical waters. In the wintering grounds, they primarily feed on krill (Euphausiidae), accumulating energy reserves for migrating and reproducing, while in the breeding grounds they feed little or not at all (Clapham et al. 1999; Danilewicz et al. 2009). Some Nearctic migratory birds, such as the Swainson's thrush (*Catharus ustulatus*) and the Tennessee warbler (*Leiothlypis peregrina*), also exhibit seasonal changes in diet. In the breeding grounds, both species primarily feed on arthropods, whereas in the wintering grounds, the Swainson's thrush becomes more frugivorous, while the Tennessee warbler adopts a mixed diet of fruits and arthropods (Blanc-Benigeri et al. 2024; Salewski et al. 2002; Baker 1973; Lovette and Holmes 1995).

Numerous studies have demonstrated marked differences in foraging behavior and diet in animals between their breeding and wintering grounds, providing valuable insights into the evolution of different foraging strategies in migratory species (Rabol 1987). However, such studies are rarely conducted using standardized methodologies, as the geographic distance between breeding and wintering grounds imposes logistical and financial challenges that are difficult to overcome. This is especially true in tropical regions, which chronically lack financial resources (Tydecks et al. 2018), creating an important knowledge gap about the life history strategies of tropical migratory species.

Within this context, the lined seedeater (*Sporophila lineola*) represents an interesting model for studying potential variations in foraging behavior and diet between breeding and wintering grounds. This granivorous songbird is widely distributed in South America, occupying various types of open natural and, more often, disturbed landscapes (Ridgely and Tudor 2009; Ferreira et al. 2025). The lined seedeater is an intra-tropical migrant bird, with populations in southeastern Brazil breeding in human-made habitats from December to April (Cunha and Lopes 2022). After breeding, individuals migrate to northern South America, where they winter in open natural habitats along the Amazon floodplains, savannas, and seasonally dry shrublands (Cunha and Lopes 2022). The main goal of this study was to investigate the foraging behavior and diet of lined seedeaters in the breeding and wintering grounds.

Given the likely differences in vegetation structure and food resources availability between their wintering and breeding ground, we hypothesized that the lined seedeater attack maneuvers and food items taken would differ between the breeding and the wintering grounds, a pattern already described for other bird species (Lovette and Holmes 1995; Gómez et al. 2018). Given the distinct nutritional demands exhibited during the breeding season (e.g. mate guarding, egg production, nest provisioning), we hypothesized that there would be a higher consumption of arthropods (i.e., protein-rich items items), in the breeding grounds when compared to the wintering grounds (Díaz 1996). Finally, we characterized the species' diet based on data from field observations, stomach content analysis, and literature.

Methods

Study Areas

In the breeding grounds, we studied lined seedeaters between December 2023 and April 2024 at the Universidade Federal de Viçosa – Campus Florestal (19°53'S, 44°25'W), in the municipality of Florestal, state of Minas Gerais, southeastern Brazil. This area lies in the transitional zone between the Cerrado savannas and the Atlantic Forest, consisting of fragments of semideciduous forest embedded in an open matrix of artificial pastures, active and abandoned crops, and gardens around the university's buildings (Lopes and Marçal 2016). Local vegetation used by lined seedeaters is completely anthropogenic and is dominated by planted pastures with scattered shrubs, palms, exotic trees, and small forest groves. The species usually forage on disturbed areas, such as wastelands, and roadsides dominated by exotic grasses from the genus *Urochloa*, and exotic and native species of *Echinochloa*. The height and density of the herbaceous layer is highly dynamic during the breeding season due to frequent grazing, mowing, and herbicide application.

In the wintering grounds, we studied lined seedeaters in August 2024 at Marchantaria Island (03°13’S, 59°54’W), municipality of Iranduba, state of Amazonas, northern Brazil. This river island, located in the Amazon floodplain, is influenced by the seasonal flood pulse of the Solimões and Negro rivers (Remsen and Parker 1983). The habitat used by lined seedeaters is dominated by “floating meadows” — herbaceous mats dominated by flood-adapted grasses of the genera *Paspalum* and *Echinochloa* (Junk 1970; Piedade 1991). There are few woody elements and almost no vertical stratification. When we visited the region, during the dry season, large expanses of floating meadows were available, providing an abundant seed supply that was easily accessible to granivorous birds. However, during the flooding season, most of this meadow is submerged, radically reducing the amount of food available to granivorous birds.

The two study areas are separated by approximately 2,500 km and are both subjected to recurrent disturbances (Fig. 1). However, while the breeding grounds are shaped by persistent anthropogenic disturbances, the wintering grounds are shaped by the natural dynamics of the floodplain, resulting in distinct temporal patterns of habitat and food availability.

Data Collection

We concentrated our observations in the morning period, from 06:00 to 09:00 am, with occasional observations made in the afternoon, from 03:00 to 05:00 pm. We made observations of the foraging behavior of lined seedeaters using binoculars, thus ensuring minimal interference with the birds' natural behaviors. To describe the foraging behavior of lined seedeaters, we followed the classification scheme of Remsen and Robinson (1990), which consists of sequential components of foraging behavior. It is important to note that a single foraging event could include more than one attack maneuver. Individuals often adjusted their position on the same grass panicle as it bent under their body weight. Thus, each maneuver was recorded independently, even when performed within the same event.

To investigate our hypotheses, we quantified two of these sequential components, namely the attack maneuvers used (Fig. 2) and the type of food items taken. Whenever possible, the arthropods caught were identified in the field with the help of binoculars to the taxonomic level of Orders. Plants consumed were photographed in the field and, whenever necessary, collected in plastic bags with proper labeling for later preparation and identification by a plant taxonomist (PLV). Plant specimens (stems with attached leaves, flowers and/or fruits) were then pressed and prepared as herbarium vouchers. After identification, these vouchers were deposited in the herbarium of the National Institute of the Atlantic Forest (INMA), in Santa Teresa, Brazil (See supplementary material).

In addition to field observations, we conducted stomach content analysis of museum specimens to characterize the species’ diet. The stomach contents from 11 birds were removed from carcasses deposited in the ornithological collection at the Universidade Federal de Viçosa – Campus Florestal (UFV-CAF). These carcasses were saved during the taxidermy of birds found dead or that have been collected for other purposes. Carcasses were fixed in 10% formalin and later preserved in 70% ethanol. The stomach contents (including also crop contents, whenever available) were removed from carcasses and stored in labeled vials with 70% ethanol. Stomach content analysis was conducted under a stereomicroscope, following the procedures described by Lopes et al. (2005). Finally, to characterize the species diet, we performed a literature review with the help of three searching engines (Google Scholar, Scopus, and Web of Science), using the following keywords and their combinations: "*Sporophila lineola*", "diet", "foraging behavior", "feeding ecology", and "granivorous". We also searched for the equivalent keywords in Portuguese and Spanish (search performed in December 2024).

Data Analysis

To test whether proportions of attack maneuver differed between sites (breeding vs. wintering grounds), we used a Pearson's Chi-squared test performed in R version 4.4.1 (R Core Team 2024), using the RStudio environment (Posit Team, 2025). To classify the diet type of lined seedeaters, we followed the scheme proposed by Lopes et al. (2016), which is based on the proportion of each food category consumed, as verified after stomach content analysis. This scheme considers the volumetric proportion of each food category observed in the diet, such as fruits, seeds, and insects, allowing for the determination of the species' diet type.

Results

We recorded 135 attack maneuvers at the breeding grounds and 147 at the wintering grounds. Our findings confirmed that individuals employed different attack maneuvers depending on the seasonal grounds ($\chi^2 = 11.748$, df = 3, p-value = 0.008). The Glean was the predominant attach maneuver in both the breeding (55.1%) and wintering (49.7%) grounds. In contrast, Hang-up was more common at the wintering grounds (38.2%) compared to the breeding site (25.3%), whereas Hang-down was relatively rare in the wintering grounds (1.3%) when compared to the breeding grounds (7.9%) (Fig. 3).

At the breeding grounds, the most frequently consumed food item was seeds of *Urochloa brizantha* (93 occurrences). At the wintering grounds, the most consumed food items were seeds of *Echinochloa polystachya* (85 occurrences) and *Paspalum repens* (61 occurrences) (Fig. 4).

Field observations combined with stomach content analyses (Appendix 1), and literature data (Table 1) revealed a predominant consumption of grass seeds by lined seedeaters in both breeding and wintering grounds. Field observations showed that 99.4% of the food items consumed by lined seedeaters consisted of seeds, while only 0.6% were arthropods. Similarly, the analysis of 22 stomach contents (Appendix 1) revealed an average volumetric composition per stomach of 98.6 ± 5.5% seeds and 1.4 ± 5.5% arthropods. Specifically, 20 individuals from different regions and periods showed diets exclusively composed of seeds, mostly Poaceae. Arthropods were only found in two out of 22 stomach contents analyzed. These findings further confirmed the species' granivorous diet across its range, according to the scheme proposed by Lopes et al. (2016).

Discussion

In this study, we investigated potential differences in the foraging behavior and diet of lined seedeaters between the breeding and wintering grounds. We found statistically significant differences between the frequency of Glean and Hang-down attack maneuvers between the two study areas. Additionally, the consumption of arthropods was low or nonexistent on both sites, with no important differences between them. Finally, the species of grass seeds consumed differed notably between the two study areas.

In both study areas, the Glean and Hang-up attack maneuvers predominated, with lined seedeaters capturing seeds directly from the grass panicles while perched on the stalks, never foraging on the ground. The frequency of Glean, however, was lower in the wintering grounds than in the breeding grounds. This can be attributed to significant differences in plant species composition and structure between the two sites. The greater robustness of the grasses most frequently consumed in the wintering grounds, such as *Echinochloa polystachya* (stalk diameter ~ 2 mm) and *Paspalum repens* (~ 1.7 mm), may hinder certain attack maneuvers. The stalk of those grasses is, for example, nearly three times thicker than the stalk of *U. brizantha*, the grass predominantly consumed in the breeding grounds, suggesting that structural features of the vegetation may constrain maneuverability and influence foraging strategies. The greater robustness of the grasses consumed in the wintering grounds hindered the bending of the stalk when the bird perched, preventing it from adopting the horizontal position necessary for executing the Glean maneuver. Differences in stalk robustness also explain why the Hang-down maneuver was more frequent in the breeding grounds, as in some cases, the stalk bent in such a way that the lined seedeaters were forced to adopt an upside-down position to forage.

Lined seedeaters took seeds directly from the grass panicle, a foraging strategy that is recurrent among members of the genus *Sporophila* (Remsen and Hunn 1979; Schwartz 1975; Silva 1999), reflecting a likely adaptation to the relatively homogeneous environment and the type of resource exploited, which is abundant, static, and readily accessible. Thus, the birds adopt simple, low-energy attack maneuvers (Remsen and Robinson 1990), which maximize energy gain by reducing the physical effort required to obtain food (Moreno and Carrascal 1993).

Lined seedeaters are granivorous birds, with a diet almost exclusively composed of grass seeds at both breeding and wintering grounds. This characteristic is already highlighted by the English name of the genus representatives, which are collectively known as “seedeaters" (in Brazil, several species are known as "papa-capim", which means “grass seed eaters”). Lined seedeaters do not consume arthropods in an important way during reproduction, unlike other bird species that undergo significant seasonal dietary changes (Savory 1989; Carey 1996). For instance, studies on other passerine species, such as blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*), revealed important seasonal dietary changes, alternating between a mixed diet of plant and animal food items during winter and a diet predominantly composed of arthropods during the breeding season (Pollock et al. 2017; Serrano-Davies and Sanz 2017). It is worth noting that the occasional observation of lined seedeaters capturing arthropods in the breeding grounds does not necessarily imply their consumption by adults. They could have been merely carrying these arthropods to the nest to meet the nutritional needs of growing nestlings, which require higher protein intake (Siriwardena et al. 2000). Therefore, the actual extent of arthropod consumption by adult lined seedeaters may be even lower than reported here.

In terms of the number of species consumed, grasses predominated in both the breeding and wintering grounds. Among the most consumed species, those from the genera *Paspalum*, *Echinochloa*, and *Panicum* stand out, not only for our study species, but also for other Neotropical seedeaters (Ilha and Ragusa-Netto 2023; Sales Jr. and Major 2001; Bencke,2010; Olifiers et al. 2001). The genus *Paspalum* seems to be particularly important due to its abundance in various habitat types and the high number of seeds produced (Maciel et al. 2009). Other members of *Sporophila*, such as the double-collared seedeater (*S. caerulescens*), the rusty-collared seedeater (*S. collaris*), and the tawny-bellied seedeater (*S. hypoxantha*) have also been reported consuming *Paspalum* seeds, highlighting the importance of this food resource (Ilha and Ragusa-Netto 2023; Areta and Almirón 2009; Rosoni et al. 2019).

Seeds from *Urochloa* predominated in the diet of lined seedeaters in the breeding grounds, while seeds from *Echinochloa* and *Paspalum* predominated in the wintering grounds. Thus, the species of grass consumed seems to reflect the ecological conditions and resources availability at each study area. Grasses such as *Echinochloa* and *Paspalum* are widely found in both floodplain areas as well as on non-flooded areas. However, some species from these genera have specific preferences for flooded habitats, such as *Echinochloa polystachya* and *Paspalum repens*, which are abundant in floodplain habitats across much of Amazonia (Lopes and Piedade 2009; Piedade 1993). On the other hand, species like *Megathyrsus maximus*, *Panicum fasciculatum*, and *U. brizantha* are more frequently found in non-flooded disturbed habitats (Viciedo et al. 2019; Baptistella et al. 2020; Sales Jr. and Major 2001). This ecological differentiation of the consumed grass species is good indication of the feeding plasticity of lined seedeaters, which use different habitat types and food resources throughout its life cycle.

The diet of lined seedeaters includes both native and invasive African grasses. Genera such as *Paspalum*, *Setaria*, and *Echinochloa* are widely distributed across tropical and temperate habitats worldwide, with many native species found across the distinct habitat types (Conserva and Piedade 2001; Viana and Filgueiras 2008; Filgueiras 2021) used by lined seedeaters across their migratory journey in South America. Thus, the migration of lined seedeater is likely associated to the distinct phenology of grasses at the breeding and wintering grounds (Areta et al. 2012; Cunha et al. 2022). This is because the lined seedeater, like other *Sporophila* species, generally does not exploit seed stocks accumulated on the ground (Remsen and Hunn 1979). Thus, lined seedeaters would leave the breeding grounds in search for abundant food in the floating meadows along the Amazonian floodplains, which provide abundant resources during the species' wintering period.

Invasive African grasses, such as *U. brizantha* and *U. plantaginea*, are widely consumed by lined seedeaters and other farmland birds in disturbed habitats such as man-made pastures, wastelands, vacant lots, and roadsides (Baptistella et al. 2020; Ferreira et al. 2025; Sales Jr. and Major 2001). This preference for invasive grasses in man-made habitats aligns with the theory of biotic homogenization, where species like the lined seedeater benefit from changes induced by habitat disturbance, while species specialized in native, undisturbed habitats tend to decline (McKinney 2002; Smart et al. 2006; Callaghan et al. 2019; Santos et al. 2024). Therefore, the high consumption of invasive grasses associated with man-made habitats is a key component explaining why the lined seedeater have expanded its range so dramatically in southeastern and southern Brazil during the last century (Ferreira et al. 2025).

The high dietary adaptability of lined seedeaters seems to contribute to its wide distribution and large population size, factors that justify its classification as "Least Concern" by the IUCN (2025). In contrast, *Sporophila* species more specialized in native grasses have faced significant population declines during the last decades due to habitat degradation (Franz 2012; IUCN 2025). This scenario highlights the resilience of lined seedeaters and the vulnerability of its congeners less adapted to environmental changes.

Declarations

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Author contributions AML: Conceptualization, Methodology Data collection, Formal analysis, Writing-original draft (lead); TNC: Methodology, Formal analysis, Writing-review and editing; PLV: Botanic identification, Writing-review and editing; FCRC: Supervision, Formal analysis, Writing-review and editing; LEL: Conceptualization, Methodology, Supervision, Writing-review and editing.

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Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information.

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Competing interests The authors declare no competing interest

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Table 1

Table I. Food items consumed by lined seedeaters (*Sporophila lineola*) based on literature data and field observations. The food items were marked as having been consumed at the breeding or wintering grounds, which also included individuals observed foraging along migratory pathways (i.e., transient birds).

FOOD ITEM	BREEDING	WINTERING	SOURCES
VEGETABLE MATTER			
Poaceae Seeds			
Andropogon bicornis		X	Ilha and Ragusa-Neto (2023)
Axonopus argentinus		X	Ilha and Ragusa-Neto (2023)
Digitaria horizontalis	X		This study
Digitaria insularis		X	Ilha and Ragusa-Neto (2023)
Echinochloa colona	X		This study; Sales Jr. and Major (2001)
Echinochloa crus-pavonis	X		Bencke (2010)
Echinochloa polystachya	X	X	This study; Olifiers et al. (2001); Areta and Almirón (2009); Bencke (2010)
Eleusine indica	X		This study
Hymenachne amplexicaulis	X	X	This study
Megathyrsus maximus	X		This study
Panicum cf. *aquaticum*	X		This study
Panicum fasciculatum	X		Sales Jr. and Major (2001)
Paspalum hydrophilum		X	Ilha and Ragusa-Neto (2023)
Paspalum intermedium	X		Di Giacomo (2005)
Paspalum notatum	X		This study; Areta and Almirón (2009)
Paspalum plicatulum	X		This study
Paspalum repens		X	This study; Olifiers et al. (2001)
Paspalum urvillei		X	Di Giacomo (2005); Areta and Almirón (2009)
Setaria parviflora		X	Ilha and Ragusa-Neto (2023)
Setaria verticillata		X	Sales Jr. and Major (2001)
Steinchisma laxum		X	Ilha and Ragusa-Neto (2023)
Urochloa arrecta	X		This study
Urochloa brizantha	X		This study
Urochloa plantaginea	X		Sales Jr. and Major (2001)

Amaranthaceae Seeds			
Amaranthus viridis	X		This study
Astereacae Seeds			
Unidentified species	X		This study
Cyperaceae Seeds			
Cyperus sp.	X		Sales Jr. and Major (2001)
ANIMAL MATTER			
Unidentified spiders	X		This study
Unidentified arthropods		X	Ilha and Ragusa-Neto (2023)

Figures

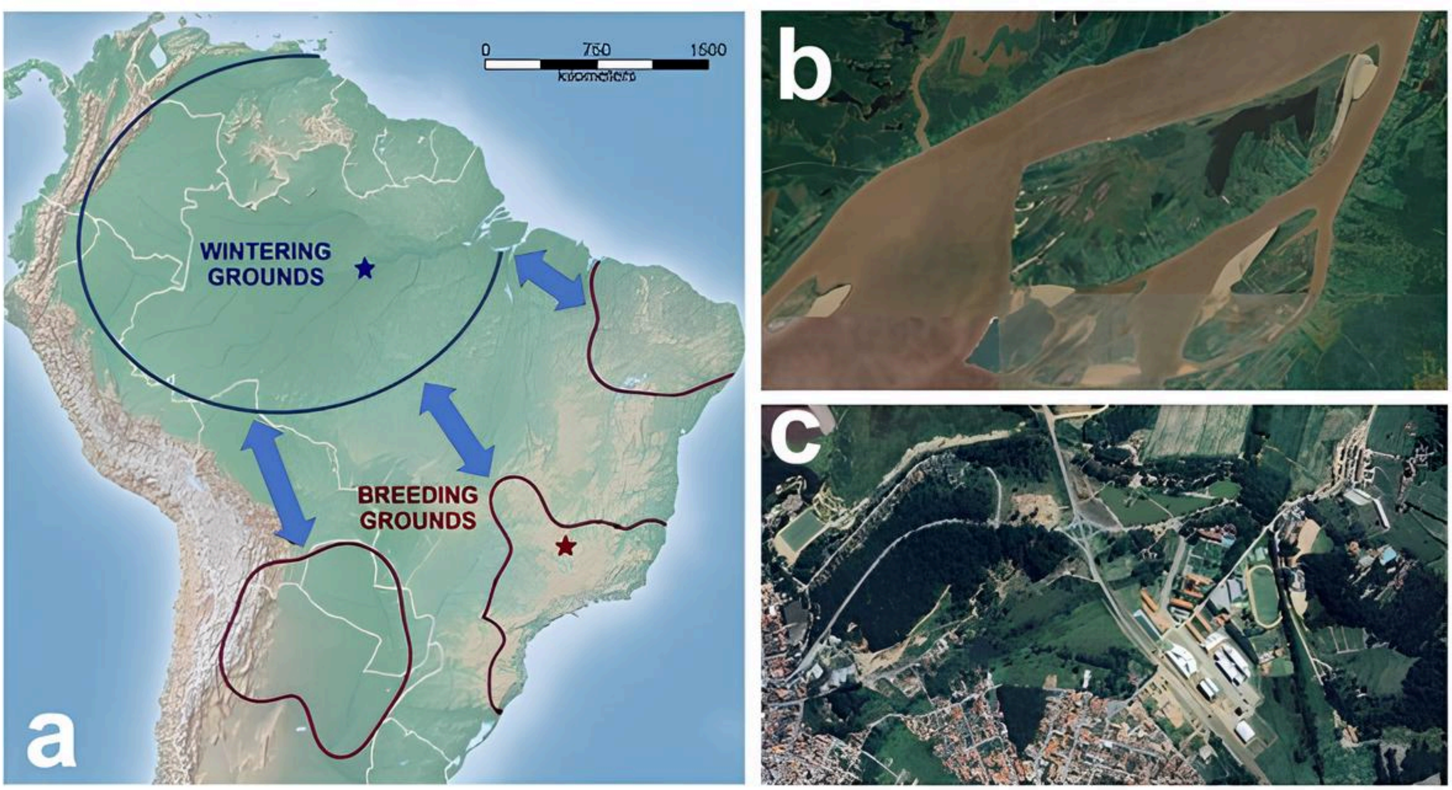

Figure 1

a) Map of South America showing the approximate location of the wintering (blue line) and breeding grounds (red lines) of lined seedeaters (*Sporophila lineola*), according to Cunha et al. (2022). The study areas are indicated by the blue star (Ilha da Marchantaria, Iranbuba, Amazonas) and the red star (Campus Florestal – Universidade Federal de Viçosa, Florestal, Minas Gerais). Satellite images of the study areas are presented for the wintering grounds (b) and for the breeding grounds (c). Satellite images obtained from Google Earth™.

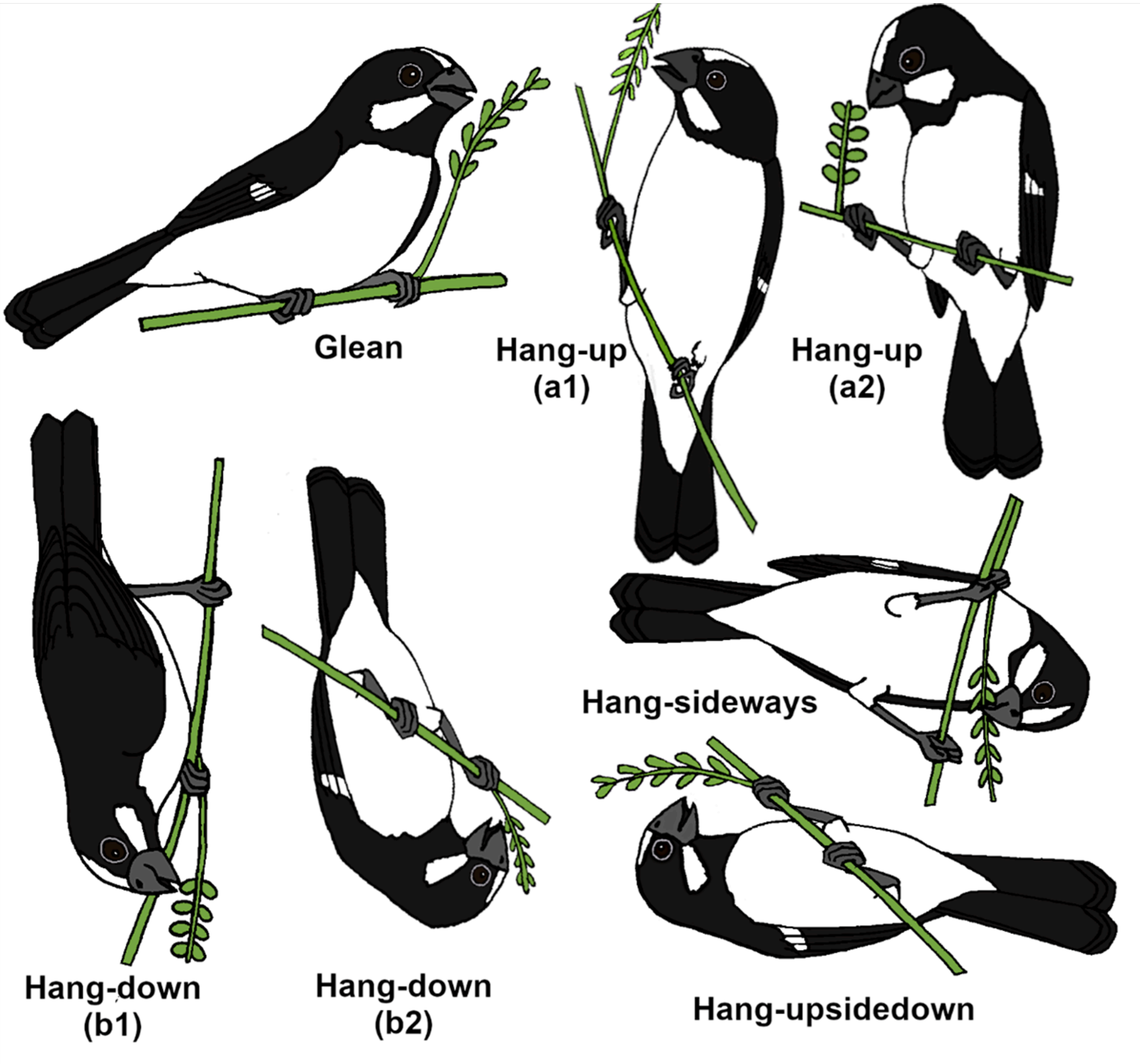

Figure 2

Surface attack maneuvers used by the lined seedeater (*Sporophila lineola*), according to the classification scheme for foraging behavior developed by Remsen and Robinson (1990). Glean consists of picking up food items from a nearby substrate, without involving acrobatic movements; Hang-up consists of using the legs and toes to suspend the body, which remains hanging, with the head upwards, and can be performed on vertical (a1) or horizontal (a2) perches; Hang down consists of hanging the body head-down, and can be performed clinging on vertical (b1) or horizontal (b2) perches; Hangsideways consists of hanging on the side of a substrate, with the body axis parallel to the ground and the bird's side oriented upwards; Hang-upside down consists of hanging, belly-up, on underside of horizontal or diagonal perches. In addition to the attack maneuvers illustrated, the "Reach" is also recognized by Remsen and Robinson (1990). This attack maneuver is similar to Glean but involves extending completely the legs or neck to reach food. Due to the strong similarity between the two maneuvers and the difficulty of separating them in the field, both were considered synonymous in this study. Artwork by Leonardo Lopes.

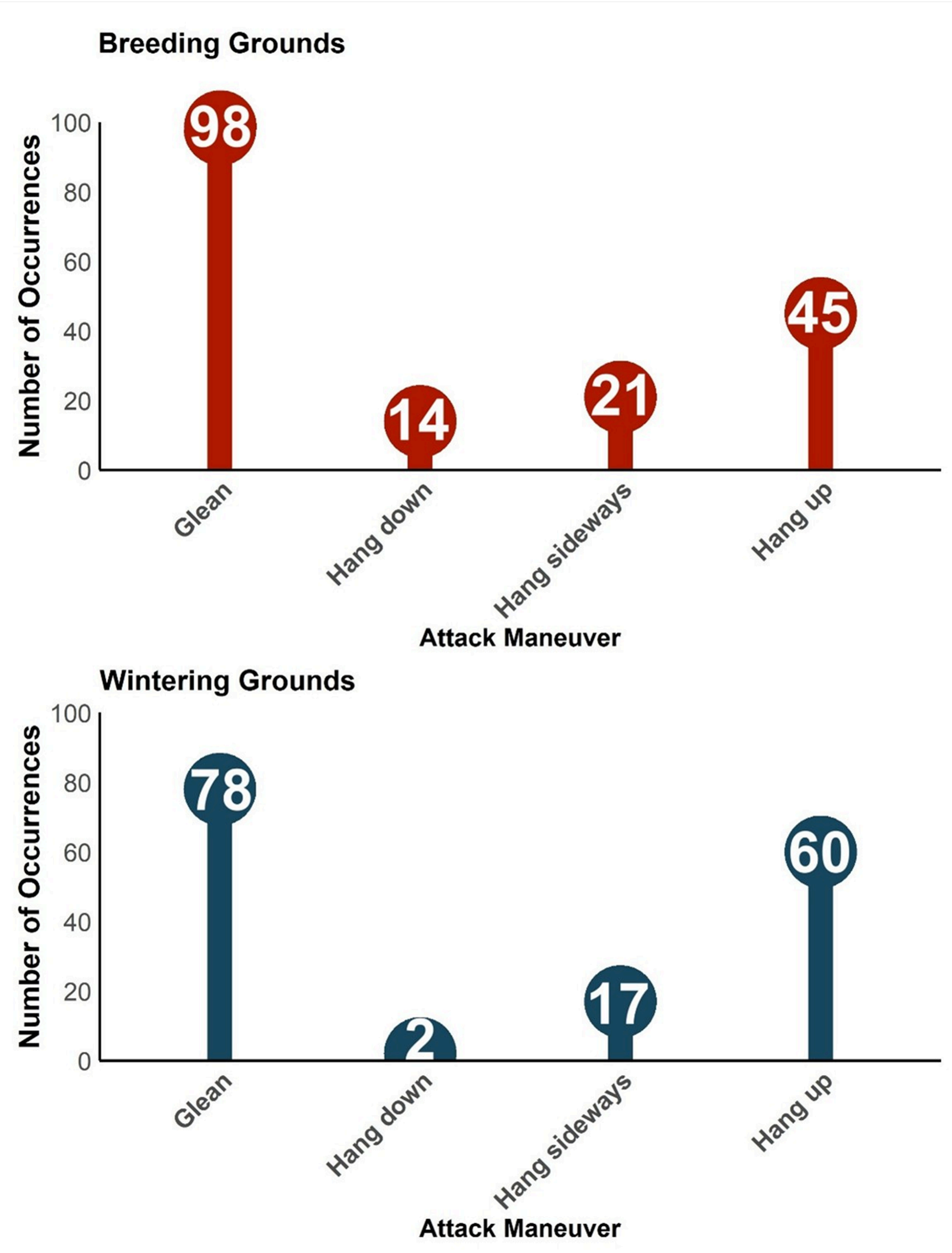

Figure 3

Different attack maneuvers exhibited by lined seedeaters (*Sporophila lineola*) at the breeding (above) and wintering grounds (below).

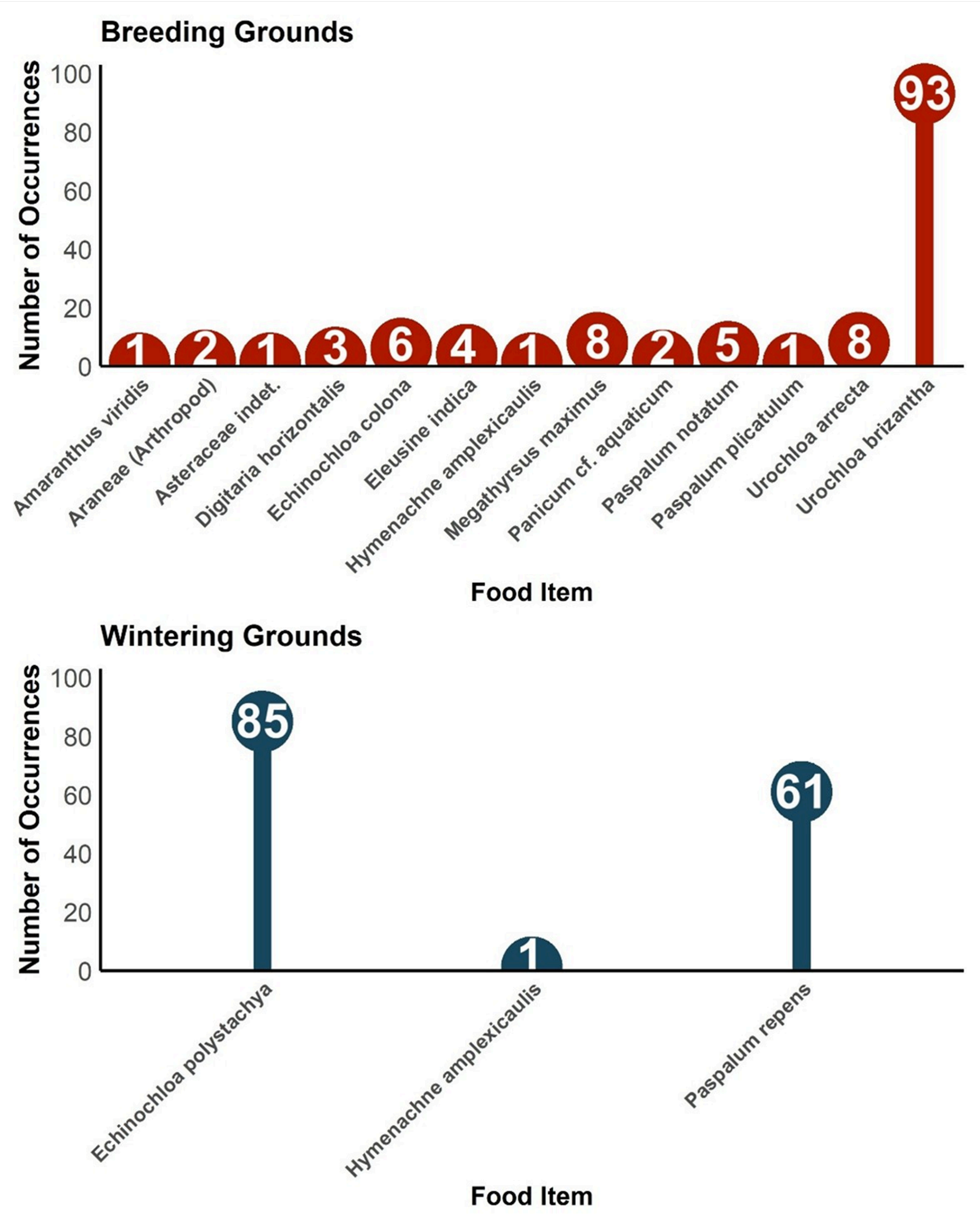

Figure 4

Comparison between the types of food items consumed by lined seedeaters (*Sporophila lineola*) at the breeding grounds (top) and the wintering grounds (bottom).

Supplementary Files

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- LaTex.rar
- APPENDIX.docx