

Social dominance facilitates, and social network centrality hinders, the expression of spatial feeding preferences

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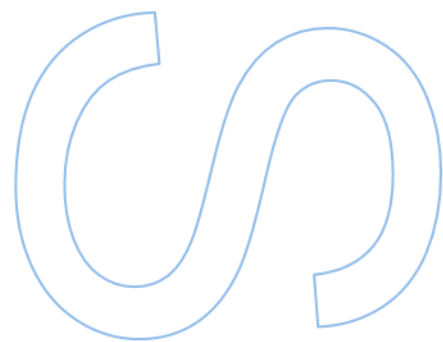
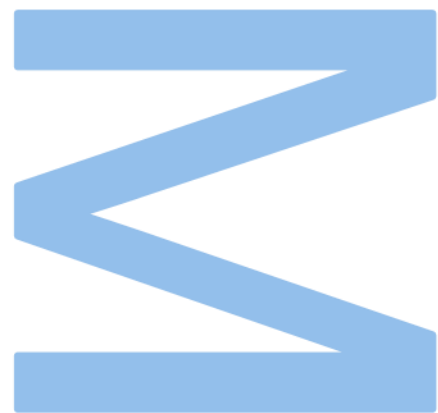
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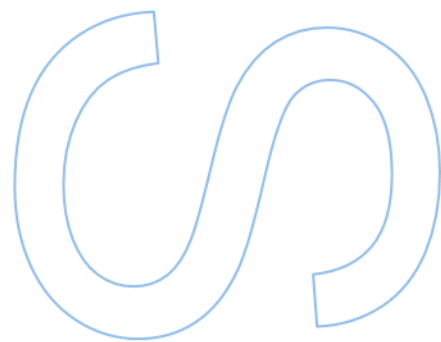
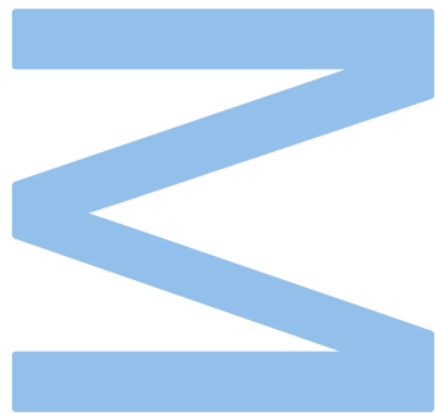
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Resumo

Viver em grupo pode fornecer vários benefícios aos animais, como maior frequência e diversidade de recursos encontrados e diminuição do risco de predação. A posição espacial de um indivíduo no seu grupo pode ser influenciada pelos benefícios proporcionados. A estrutura espacial de um grupo também pode ser influenciada pela hierarquia de dominância dos indivíduos. Estudos que testam as preferências espaciais de indivíduos dentro do grupo com base na sua posição na hierarquia de dominância são comuns, especialmente em espécies de mamíferos. Porém, trabalhos com outros fenótipos, tal como a posição de um indivíduo na rede social, são escassos. As redes sociais são uma ferramenta valiosa para compreender as conexões entre animais e a sua inclusão nos estudos pode ajudar a compreender como outros tipos de relações entre indivíduos podem influenciar a sua posição dentro do grupo. As preferências espaciais também podem ser confundidas por diferenças de qualidade nas áreas alimentares. Neste trabalho pretendi compreender as preferências espaciais numa área de alimentação. Para isso, utilizei bicos-de-lacre (*Estrilda astrild*) a viver num ambiente de cativeiro seminatural onde a qualidade e quantidade dos alimentos são homogêneas dentro da área de alimentação. Também testei relações entre as suas preferências espaciais e diferenças individuais em fenótipos. Descobri que os comedouros mais preferidos pela população ficavam perto do centro da área alimentar e que havia maior agressividade nos comedouros mais preferidos. Embora a maioria dos indivíduos tivesse uma preferência semelhante à preferência média da população, houve diferenças significativas entre os indivíduos no tipo e força das preferências espaciais. As diferenças individuais nos fenótipos (por exemplo, tipo de personalidade, sexo, dominância social, centralidade da rede social) não explicaram a diversidade no seu tipo de preferências espaciais. As diferenças na força das suas preferências espaciais, no entanto, foram previstas por diferenças individuais na posição na hierarquia de dominância e na centralidade da rede social. Indivíduos mais dominantes e indivíduos que ocupam posições menos centrais na rede social expressaram preferências espaciais mais fortes. Este trabalho ajuda a compreender como as preferências espaciais de uma ave gregária são influenciadas pelas suas interações e ligações com outros indivíduos.

Palavras-chave: bico-de-lacre, *Estrilda astrild*, centralidade da rede social, hierarquia de dominância, preferência alimentar espacial

Abstract

There are many benefits animals can have by living in a group, such as higher frequency and diversity of resources encountered and decrease in predation risk. The spatial position of an individual within their group can be influenced by the benefits provided. The spatial structure of a group can also be influenced by the dominance hierarchy of the individuals. Studies that test for individual within-group spatial preferences based on their dominance rank are common, especially in mammalian species. However, works with other phenotypes, such as the position of an individual in their social structure, are scarce. Social networks are a valuable tool for understanding animal connections and their inclusion in the studies can help understand how other type of relationships between individuals might influence their within-group position. Spatial preferences may also be confounded by differences in quality within food patches. That is why, in this work I aimed to understand spatial preferences in a food patch, using common waxbills (*Estrilda astrild*) living in a semi-natural captive environment where food quality and quantity are homogeneous within the foraging area. I also assessed relations between their spatial preferences and individual differences in phenotypes. I discovered that most population-wide preferred feeders were close to the centre of the food patch, and that there were more aggressive displacements in the most preferred feeders. Although most individuals had a similar preference to the mean population preference, there were significant differences among individuals in the type and strength of spatial preferences. Individual differences in phenotypes (e.g., personality type, sex, social dominance, social network centrality) did not explain the diversity in their type of spatial preferences. Differences in the strength of their spatial preferences, however, were predicted by individual differences in social dominance rank and social network centrality. More dominant individuals and individuals occupying less central positions in the social network expressed stronger spatial preferences. This study helps to understand how spatial preferences of a gregarious bird are influenced by their interactions and connections with their peers.

Keywords: common waxbill, *Estrilda astrild*, social network centrality, dominance hierarchy, spatial feeding preference

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List of Abbreviations

ANOVA	ANALYSIS OF VARIANCE
CI	CENTRALITY INDEX
GLMM	GENERALIZED LINEAR MIXED MODEL
IGI	INDIVIDUAL/GLOBAL INDEX
LM	LINEAR MODEL
PIT	PASSIVE INTEGRATED TRANSPONDERS
PCA	PRINCIPAL COMPONENT ANALYSIS
PC	PRINCIPAL COMPONENT
RFID	RADIO FREQUENCY IDENTIFICATION
SPI	STRENGTH PREFERENCE INDEX
SE	STANDARD ERROR

1. Introduction

A wide variety of animals live and forage in groups, and predation is often considered a reason for this behaviour (Krause & Ruxton, 2002). Living in a group can provide many benefits such as an increase in the frequency (Pitcher et al., 1982) and array of resources encountered (Creel & Creel, 1995), as well as a reduction in the antipredator vigilance that each individual needs to do, due to risk dilution and enhanced threat detection in groups (Roberts, 1996). The risk that each individual experiences may also be different due to within-group spatial factors, such whether the individual is nearer the centre or the periphery of a group (Elgar, 1989; Heesen et al., 2015; Janson, 1990a, 1990b).

Hamilton's "selfish herd" theory (Hamilton, 1971) predicted that individuals on the spatial periphery of groups have higher risks of predation due to having fewer adjacent individuals. They can often provide a layer of protection to those in more central positions considering that the periphery makes the first contact with an approaching predator and still has a higher chance of being attacked by a predator moving in a 3 dimensional space (Romey et al., 2008). When food is dispersed and not monopolized, individuals in central positions are more likely to have a reduced food intake due to increased feeding interference (i.e., the behavioural interactions between individuals decrease the time they spend acquiring food or the quantity of food they consume; Janson, 1990b; Krause, 1994; Krause & Ruxton, 2002). Furthermore, those at the edges may often have access to resources first, since they have first contact with new resources, and may face less competition than those in central positions, increasing their foraging efficiency (Blanchard et al., 2008). When food patches are limited and defendable, however, it is more likely they will be accessed by individuals in the centre of the group (Hirsch, 2007).

The different spatial positions individuals can occupy may not only be influenced by the trade-off between the risks of predation and the benefits of feeding, but by other social factors such as dominance. Individuals with higher social status may use their rank to obtain privileged access to, and prevent lower-ranking individuals from occupying, preferred positions, such as in situations when food patches are defendable. In this case, high-ranking individuals occupy and defend food patches while maintaining their position in the centre of the group (Hirsch, 2007). The occupation of preferred positions by high-ranking individuals can also happen in a passive way, in which lower-ranking individuals will occupy less preferred positions to avoid competition with higher-ranking individuals (Hall & Fedigan, 1997; Hirsch, 2011). High-ranking individuals can also exploit food (scroungers) made available by lower-ranking individuals in the peripheries (producers;

Di Bitetti & Janson, 2001; King et al., 2009). In species that follow this model, the most advantageous spatial position in the group distribution should be centre-front (Hirsch, 2007). The correlation between dominance rank and spatial position has been observed in a series of taxa, including mammals (Di Bitetti & Janson, 2001; Hall & Fedigan, 1997; Heesen et al., 2015; Hirsch, 2007, 2011; Janson, 1990b; Naud et al., 2016; Teichroeb et al., 2015), birds and fish (reviewed in Krause, 1994) and spiders (Rayor & Uetz, 1990).

While it is known that a larger group size can lead to higher levels of resource competition, there are cases in which social bonds between individuals can positively influence resource acquisition. Animals with more central positions in social networks should have access to more social information, resulting in a higher probability of finding and using novel foraging patches than those with limited social connections (Aplin et al., 2012). However, cooperation is more likely to be beneficial if individuals of groups with a certain size interact in relatively small subgroups (Santos et al., 2006), especially with familiar neighbours (Croft et al., 2006). It is also worth considering the possibility that an individual with more social relationships and connections, corresponding to a more central position in the social network of the group, could have higher difficulty occupying its preferred position, due to increased interference from its peers.

Under field conditions, the investigation of the causes for within-group spatial positioning may be hindered by several factors. For instance, food quantity or quality throughout a patch may not be homogeneous, and a higher vigilance rate among peripheral individuals can be a consequence of central individuals having a higher rate of food intake (Krause, 1994). Moreover, it is hard to precisely define “central” and “peripheral” individuals, considering that the shape of the group changes, particularly for vagrant groups (Mooring et al., 2004; Stankowich, 2003). To the extent of my knowledge, studies on spatial position have been mostly done on mammals (Blanchard et al., 2008; Di Bitetti & Janson, 2001; Di Blanco & Hirsch, 2006; Gall & Manser, 2018; Heesen et al., 2015; Hirsch, 2011; Janson, 1990a, 1990b; Robinson, 1981; Tamar et al., 1996; Teichroeb et al., 2015), and a few on captive environments (Naud et al., 2016). Works done with free range birds focus on the association of the spatial positioning of the individuals with foraging types such as scrounger vs producer (Barta & Giraldeau, 1998; Flynn & Giraldeau, 2001; Mónus & Barta, 2008) and foraging modes such as risky vs less risky (Beauchamp, 2013), and do not investigate how phenotypes, social dominance rank or social network position influence spatial preferences (except Barta & Giraldeau, 1998). Thus, these studies do not attribute individual birds to a within-group spatial position based on their characteristics but rather attribute a way of foraging to within-group spatial positions. However, Barta & Giraldeau (1998) suggested that in small foraging groups,

strong differences in competitive ability can influence the use of scrounger-producer tactics, with dominant individuals using scrounger strategies and subordinates using more producer strategies.

In this work, I aim to understand spatial preferences of individuals within a homogeneous food patch in a highly gregarious bird species, and to assess the relation between spatial preferences and individual phenotypes. To do so, I used a population of common waxbills (*Estrilda astrild*) living in a semi-natural captive environment. These individuals are continuously monitored through a Radio Frequency Identification (RFID) system (Gomes et al., 2021), being their social structure stable through time (Gomes et al., 2022), and their phenotypes extensively quantified and studied, namely morphology and behaviour (Gomes et al., 2020). Given that the spatial distribution of the individuals can be influenced by many factors, it can be hard to understand which are at play in an individual's spatial preference. With this study system, factors such as feeding interference, patch heterogeneity and first contact of the peripheral individuals with food were eliminated. This was possible due to the placement of feeders on a wall, evenly separated from each other, all with *ad libitum* food of the same quality. This permitted the focus of the study to be on spatial preference, not confounded by spatial differences in food quantity or quality.

To develop this study, I first tested for a population-wide spatial preference in feeder use. Considering current theory, I expected a preference for the central feeders. I then tried to understand individual differences in spatial preferences, comparing the different individual preferences to the population-wide mean preference, and the strength of those preferences (i.e., if the birds used their preferred feeders very often or instead visited the feeders more homogeneously). Here, I expected differences in the strength of expression of the individual's preferred feeders considering that individuals on higher social rank might have less difficulty accessing their preferred feeders than ones of lower social rank. I also evaluated the aggression rate at the different feeders and whether they differed between the most and less preferred feeder locations. Higher aggression rates in the population-preferred feeders were expected. Finally, I tested which phenotypic traits (e.g., personality type, social dominance, position in the social network) predicted individual differences in spatial preferences or in the preference strength. I expected more dominant birds to use their preferred feeders more often, and perhaps individuals with less central positions in the social network to have facilitated access to their preferred feeders. However, to my knowledge, there is no work that studies the relationship between social network centrality and spatial feeding preferences.

2. Methods

2.1. Study System

In this work, I studied spatial feeding patterns in a waxbill flock from April 2018 to November 2020. I used waxbills housed in an outdoor mesocosm (ca. 235m², ca. 1.30 to 2.70 m high) in a quiet rural setting in the northwest of Portugal. The mesocosm was covered with fine net and provided the waxbills with semi-natural living conditions, exposing them to the natural climate and allowing them to move freely, with abundant vegetation (grass, bushes, brambles, small trees) used during the breeding seasons as nesting areas (Beltrão et al., 2021a). Although the birds in the mesocosm were protected from predation, they still exhibit appropriate behavioural responses when potential predators like jays or raptors are occasionally heard or seen in the surrounding area (P. Beltrão & A. C. R. Gomes, personal observation). Birds had *ad libitum* access to seeds (Versele-Laga Prestige Tropical Finch), mostly in an array of 12 feeders placed near each other on a wall ca. 0.90 to 1.55m high (Figure 1). Each of these feeders was equipped with an RFID antenna that recorded arrival times and departure times, and allowed individual identification of birds based on the identification of the PIT (Passive Integrated Transponders) tag that each bird had in a leg-ring. There were also 8 long perches located in the feeding area with 4 small antennae each (Figure 1). Elsewhere in the mesocosm, the birds had access to water from two large dispensers (three during dry and hot months) and three long and shallow water containers for bathing. Two to three times a week, water from the water containers was replaced, feeders were checked, and seeds replenished when necessary. A multi-vitamin supplement, mixed together with a small amount of the usual seeds and with unpeeled white millet, was added twice a week to all feeders. Every two months, the feeders and water containers were cleaned, sterilized and replaced. One day each year, in autumn, all birds were captured to check PIT tags and replace them in case of loss or malfunction, before returning birds to the mesocosm.



Figure 1. Placement of the 12 feeders in the mesocosm.

This mesocosm population started with 30 birds captured in October 2016, and other 30 in September 2017, in agricultural areas in the northwest of Portugal, near Póvoa de Varzim. These birds were released in the mesocosm in December 2016 and November 2017, respectively (details in Guerra et al., 2020). After this, a stable flock size of ca. 60 individuals was maintained throughout the years, with births of new birds in the mesocosm and the occasional addition of wild-captured individuals in some autumns (total 17 birds across 7 years) offsetting natural mortality or rare escapes. Offspring were given a PIT tag during the annual autumn captures in the mesocosm. For this study, the data of a total of 78 individuals was used.

2.2. Phenotypes

Genetic Sexing

The sex of each bird was assessed molecularly, as described in Gomes et al. (2020). With a small puncture in the branchial vein, a small blood sample (< 100 µL) was obtained and immediately stored at -20°C until DNA extraction. A set of primers (P2 and P8) were used to amplify the CHD-W and CHDZ genes, as described in Griffiths et al. (1998). Individuals showing double (ZW) or single (ZZ) bands were identified as females or males, respectively.

Mirror Test

In waxbills, the mirror test can be used as a way of evaluating an individual's personality along a proactive-reactive axis, with more proactive individuals displaying more activity and exploring more in open-field tests but being less attentive towards a mirror image, and the reverse for more reactive individuals (Carvalho et al., 2013).

Mirror tests were performed by Gomes et al. (2020) for the birds captured in 2016 and 2017. They were conducted twice for each bird, ca. 6 weeks apart in the non-breeding season, during the period between capture from the wild and release in the mesocosm. The tests consisted of video recorded sessions of 10 minutes, 5 minutes with the mirror covered with a cardboard and 5 minutes with the mirror exposed, in a small bird cage placed in an isolated room. For the period with the mirror exposed, 4 behaviours reflecting an increased response to the stimulus were quantified: (1) time facing the mirror; (2) time in fast movement; (3) activity; and (4) number of vocalizations. These behaviours were summarized into a PCA, with high values of the first PC indicating more

proactive individuals (a greater number of fast movements, more activity, and vocalizations), and lower values of this PC indicating more reactive individuals (more attention to the mirror image; Gomes et al., 2020). This measure is highly repeatable between the two tests (Gomes et al., 2020) and even between seasons or a year apart (Guerra et al., 2020). Thus, the mean value of the two tests were used as the mirror test scores for each individual. This phenotype was available for 54 individuals out of the 78 that were present in the mesocosm during the period of my study.

Dominance Hierarchies

Aggression was studied following methods in Beltrão et al. (2021b), by identifying aggressive displacements in the feeders' RFID datastream as cases when the time interval between one bird leaving a feeder and another bird arriving was less than 2 seconds, with both individuals staying at least 3 seconds in the feeder. This criterion was earlier validated as a reliable indicator of aggressive displacements based on analyses of video recordings (Beltrão et al., 2021b). To compute the dominance rank of each individual, I used the randomized Elo-rating method (Sánchez-Tójar et al., 2018) based on the aggressive displacements at the feeders. The randomized Elo-rating method infers dominance scores based on the outcome of aggressive interactions irrespective of their order in time, which is appropriate for study systems like mine where the outcome of aggressive interactions does not show temporal autocorrelation and the slope of the dominance hierarchy is not very steep (Beltrão et al., 2021b; Beltrão et al., 2021c; Funghi et al., 2015). To identify aggressive displacements, I used RFID data from every Sunday from April 2018 to November 2020, because there were never disturbances in the mesocosm on Sundays (e.g., changing water or replenished seeds). In addition to computing randomized Elo-ratings for this entire period, I also analysed separately the RFID data from Sundays in each of 3 separate periods: (1) 11-04-2018 to 31-01-2019; (2) 01-02-2019 to 31-01-2020; (3) 01-02-2020 to 09-11-2020 (see below).

Social Network Centrality

Social networks were inferred using a proximity-based criterion to identify associations between individuals. I used the synchronous time overlaps between individuals up to 40cm of distance in the array of RFID antennae to identify associations between them. I chose this proximity-based criterion because, in this study system and compared to alternative proximity criteria, this criterion has been repeatedly found to better uncover

the non-random structure in the social network (Beltrão et al., 2023; Gomes et al., 2021, 2022, 2023). The strength of association between two individuals was computed as the total time each dyad of individuals were detected at less than 40 cm from each other divided by the sum of times that each of those was present in the RFID system; this index is akin to the Simple Ratio Index, but varies between 0, if individuals in a dyad were never associated at less than 40cm, and 0.5, if they were always together at less than 40 cm. To assess the position of individuals within social networks, the weighted eigenvector centrality metric (Bonacich, 1987) was calculated. It quantifies the centrality of an individual based on its associations and the associations of its associates, weighted by their strengths of association. High eigenvector centrality indicates that the focal individual is strongly connected to multiple other individuals and/or is associated with individuals who themselves have strong connections (Farine & Whitehead, 2015; Whitehead, 2008). Eigenvector centrality was calculated separately with RFID data from every Sunday in 3 separate periods: (1) 11-04-2018 to 31-01-2019; (2) 01-02-2019 to 31-01-2020; (3) 01-02-2020 to 09-11-2020 (see below).

2.3. Statistical Analysis

Differences among feeders in usage and in aggressive displacements

To test if there were differences in the use of the feeders, I used the entire dataset from every Sunday between April 2018 to November 2020 and performed a Linear Mixed Model with the total time (min) spent each day per feeder as the response variable, feeder identity as a categorical, non-ordered predictor, and date as a categorical, non-ordered random factor.

To test if aggression rates differed between feeders, a non-parametric test was performed (Friedman test), since the data did not meet the assumption of homogeneity of variances. Aggression rate for each feeder was computed as the total number of aggressive displacements in that feeder divided by the time spent at that feeder by all birds, per day. I included feeder's identity as group, and date as a block.

To test if the time spent on each feeder by the individuals correlated to the aggression rates suffered at the different feeders, I performed a non-parametric Spearman correlation since the sample size is small.

Individual differences in within-patch spatial preferences

I tested if feeder location, from left to right within the feeding patch, influenced their usage, and if these left-to-right spatial preferences differed between individuals. For this, I computed a Linear Model with the standardized time spent on each feeder per bird as response variable, 'feeder position' from left to right (feeders were ordered numerically from left to right; Figure 2A) as the main predictor, 'bird identity' as an additional predictor, and the interaction term between these two predictors. Time spent at the different feeders was standardized per individual (i.e., for each individual I divided the time spent in a particular feeder by the overall time in all 12 feeders) in order to render preferences comparable between individuals, since not all individuals spent the same total time on the feeders or lived for the same duration in the mesocosm. The effect of the predictor 'feeder position' tests if, on average, there is a preference for feeders more towards the left (significant effect and negative slope of the regression coefficient) or more towards the right (significant effect and positive slope of the coefficient). The effect of the predictor 'bird identity' would test if individuals differ in the total time spent on feeder, which here is by definition non-significant and with a zero slope because, as explained above, we used standardized values per individual. Instead, the result of interest is the interaction between 'bird identity' and 'feeder position', which tests if individuals differ in their spatial preference from left to right within the feeding patch.

I also tested if feeder centrality within the patch influenced their usage, and if these spatial preferences differed between individuals. For this, I computed a Linear Model as the previous one with only one difference: 'feeder position' is now replaced by 'feeder centrality', and, in this variable, feeders were ordered numerically from the periphery to the centre (Figure 2B). Similarly to the previous model, the interaction term between 'bird identity' and 'feeder centrality' tests if individuals differ in their spatial preference for central vs. peripheral feeders. Moreover, I ran, separately for each individual, a simplified version of this model with the standardized time spent on each feeder as response variable and 'feeder centrality' as the single predictor, to obtain a regression slope to be used as a measure of each individual's preference for more central feeders (centrality index, CI): steep positive slopes indicate individual preferences more towards the central feeders, and steep negative slopes indicate preferences more towards the peripheral feeders.

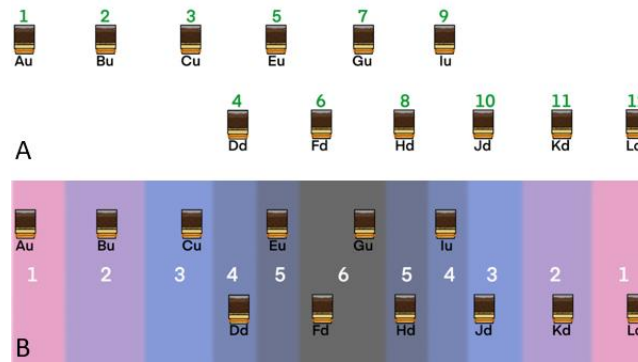


Figure 2. Feeders were named alphabetically (with a second letter indicating the row; ‘u’ for upper row and ‘d’ for lower row), and were given a number (A) from 1 to 12 according to their position from left to right, or (B) from 1 to 6 according to their position from the periphery to the centre.

I tested if individual preferences differed in how similar they were to the population-level spatial preference in feeder usage. For this, I ran a model similar to the two previous with only one difference: instead of quantifying feeder position from the left to the right of the patch or from the periphery to the centre, I now assigned to each feeder the mean time (min) across all studied days that all birds spent at the feeders (values in Figure 3B). The interaction term between ‘bird identity’ and this predictor (‘population preference’) now tests if some individuals express spatial preferences more similar, and other more dissimilar, to the mean population preference. I again also ran, separately for each individual, a simplified version of this model, only with the standardized time on each feeder as response variable and ‘population preference’ as single predictor, to obtain a regression slope to be used as a measure of similarity between the individual and population preferences (individual/global index, IGI): steep positive slopes indicate individual preferences similar to the population mean preference, and steep negative slopes indicate preferences opposed to the population mean preference.

Finally, I tested if individuals differed in the strength of their spatial preferences, irrespective of the direction or type of their preferences. For this, I again computed a model similar to the previous, but now the main predictor is the within-individual order of feeders’ usage. In other words, separately for each individual, I assigned to each feeder the ordinal numbers 1 to 12, from the least used to the most used feeder for that individual. For individuals with strong spatial preferences there will be steeper positive slopes between their standardized time spent at the feeders (dependent variable) and this main predictor, and for individuals with weak spatial preferences there will be less steep positive slopes. The interaction term between ‘bird identity’ and this predictor (‘strength of preference’) now tests if individuals differ in the strength of their spatial preferences, irrespective of the actual direction or type of special preference. I also ran,

separately for each individual, a simplified version of this model, only with the standardized time on each feeder as response variable and 'strength of preference' as predictor, to obtain a regression slope that measures the strength of individual preferences (strength preference index, SPI): steep positive slopes indicate strong spatial preferences, and slopes close to zero indicate weak spatial preferences.

Phenotypic predictors of individual differences in spatial preferences

To test if phenotypic differences between individuals predict their usage of the feeders I divided the data into 3 periods, representing each year of study: (1) 11-04-2018 to 31-01-2019; (2) 01-02-2019 to 31-01-2020; (3) 01-02-2020 to 09-11-2020. The periods end in January because the start of the following breeding season is typically from February onwards (Beltrão et al., 2021a). Data was separated by year because social dominance and the social network may change with time, while also preventing directly comparing the phenotypes of birds that were not in the mesocosm in the same year.

The different indexes of spatial preference (CI, IGI and SPI) were calculated for each of these three periods, as were the dominance hierarchies and social networks. Because the mirror test was only performed in 2016 and 2017, data from individuals born or added to the population afterwards was not used. I conducted Generalized Linear Mixed Models with one of the indexes of spatial preference as the dependent variable and, as predictors, each individual's social dominance score in that year, social network centrality in that year, mirror test score and sex. An additional predictor was the total time that each individual spent at the feeders in that year, used here as a control since the computation of social dominance and social network variables may be affected by it, and the times spent in the feeders are not the same for all individuals. Including this predictor is advised by Hart et al. (2022), in order to make statistical models robust to test the significance of hypothesis using social network data (see also Gomes et al., 2022, 2023 for similar model in the system I am studying here). Bird identity and year were also included in the model as random factors.

For all statistical models, assumptions were checked graphically with the R package 'performance'. Most models were followed by an analysis of variance (ANOVA) to determine the influence that each independent variable has on the dependent variable, except those for studying the effects of individual phenotypes in spatial preferences (see earlier in section) because their null hypothesis did not meet the required assumptions for an ANOVA.

3. Results

3.1. Differences among feeders in usage and in aggressive displacements

Figure 3A shows the amount of time spent on each feeder by all individuals on every Sunday from April 2018 to November 2020. When testing population-level differences in feeder usage, I found significant differences in the time spent at each feeder ($F_{11,1440} = 125.94$; $P < 0.001$; Figure 3B).

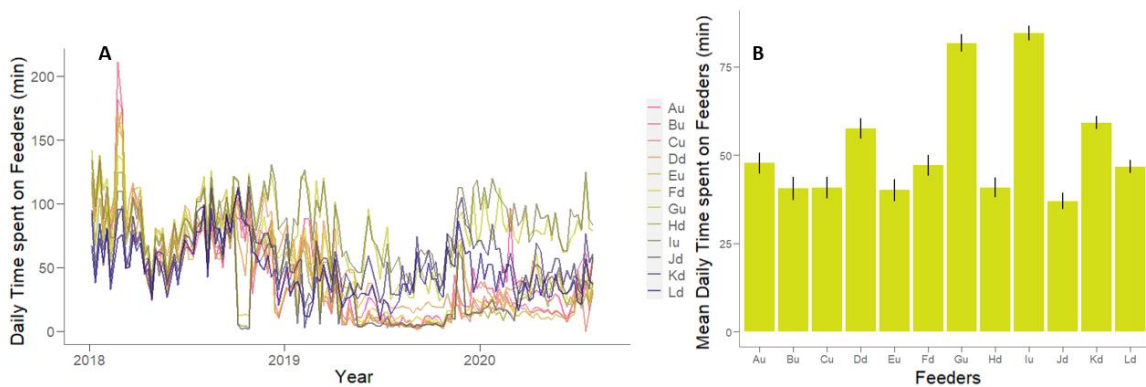


Figure 3. **A:** Daily time in minutes spent on each feeder from 2018 to 2020 by all individuals, in which each line represents one feeder and are coloured according to a gradient, with pink lines representing feeders with a position more to the left, blue lines representing feeders more to the right and green representing feeders located in a more central position. **B:** Mean daily usage in minutes of each feeder by all individuals, with respective standard error.

There were also differences among feeders in the rate of aggressive displacements ($\chi^2 = 450,38$; $df = 11$; $p < 0.001$; Figure 4). There was a strong positive correlation between the population-wise time spent at each feeder and the aggression rate at each feeder ($r_s = 0.75$; $P = 0.0074$; Figure 5), meaning that individuals were more likely to suffer an aggressive displacement when using the population-wise preferred feeders.

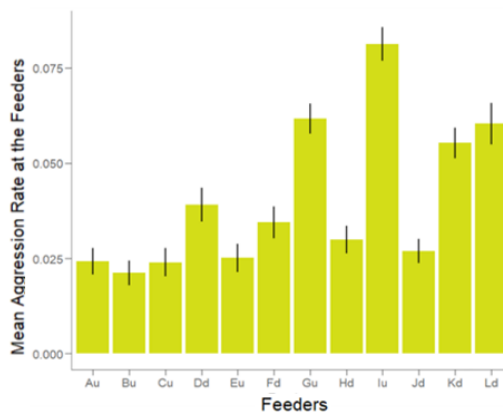


Figure 4. Mean aggression rates suffered on each feeder, with respective standard error.

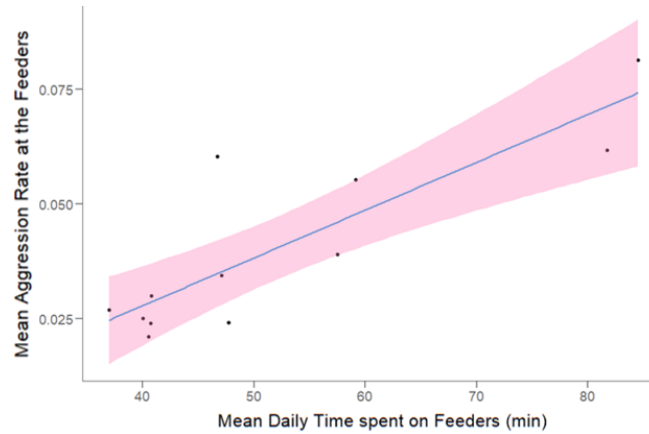


Figure 5. Correlation between the mean daily time in minutes all individuals spent on each feeder and the mean aggression rate suffered on each feeder, with the black dots representing each feeder and the blue line representing the trend line with the confidence interval shaded in pink.

3.2. Individual differences in within-patch spatial preferences

Individuals differed significantly in their left-to-right spatial preferences (interaction effect between feeder position and individual ID: $F_{77,780} = 1.90$, $P < 0.001$; Table 1). There were no significant differences in the individuals' peripheral-central spatial preferences (interaction effect between feeder centrality and individual ID: $F_{77,780} = 0.93$, $P = 0.65$; Table 1; Figure 6B), and there was a non-significant trend for individual preferences differing in their similarity to the population-wise preference (interaction effect between population preference and individual ID: $F_{77,780} = 1.26$, $P = 0.08$; Table 1; Figure 6A). Irrespective of the type of individual preferences, individuals differed significantly in the strength of their spatial preferences (interaction effect between strength of preference and individual ID: $F_{77,780} = 3.87$, $P < 0.001$; Table 1; Figure 6C).

Table 1. Results from four LMs performed with the predictors 'Feeder Trait' and 'Bird Identity' and their interaction, with the total time spent on each feeder per bird standardized per individual as the response variable. The predictor 'Feeder Trait' represents the predictor relative to the feeder characteristic of each LM. The Degrees of Freedom of 'Feeder Trait' are (1,780), and of 'Bird Identity' and the interaction 'Feeder Trait' * 'Bird Identity' are (77,780). F represents the F values and P represents the P values.

	LEFT-TO-RIGHT FEEDER POSITION	PERYPHERY-TO- CENTRE FEEDER POSITION	POPULATION- WIDE FEEDER USAGE	WITHIN- INDIVIDUAL FEEDER PREFERENCE
FEEDER TRAIT	F = 6.75 (P = 0.01)*	F = 8.91 (P = 0.003)*	F = 96.89 (P < 0.001)*	F = 1518.30 (P < 0.001)*
BIRD IDENTITY	F = 0.00 (P = 1.00)	F = 0.00 (P = 1.00)	F = 0.00 (P = 1.00)	F = 0.00 (P = 1.00)
FEEDER TRAIT * BIRD IDENTITY	F = 1.90 (P < 0.001)*	F = 0.93 (P = 0.65)	F = 1.26 (P = 0.08)	F = 3.87 (P < 0.001)*

* Significant values, $P < 0.05$

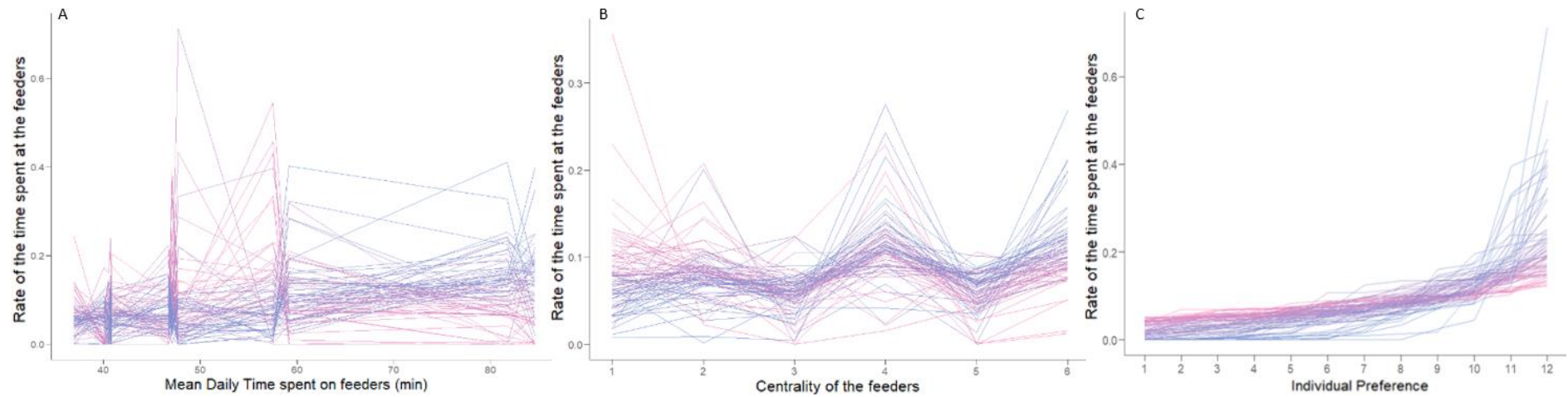


Figure 6. A: Time, standardized for each individual, that they spent at the feeders, ordered by least to most used in general by the population (data collected from Figure 3B). Each line represents an individual and they are coloured according to a gradient, with pink lines representing individuals with a less similar preference to the population one and blue lines representing individuals with a more similar preference to the population one. B: Rate of the time each bird spent on each feeder, ordered from 1 (more peripheral) to 6 (more central). Each line represents an individual and they are coloured according to a gradient, with pink lines representing individuals with more peripheral preferences and blue lines representing individuals with more central preferences. C: Rate of the time each individual spent on the feeders, ordered from 1 (least used) to 12 (most used) for each specific individual. Each line represents an individual and they are coloured according to a gradient, with pink lines representing individuals with weak spatial preferences and blue lines representing individuals with strong spatial preferences.

3.3. Phenotypic predictors of individual differences in spatial preferences

When testing for associations between individuals' phenotypes and strength of their spatial preference (SPI), I found that more central social network positions were associated with weaker spatial preferences (social network centrality: $\beta = -4.555$, SE = 1.696, $P = 0.008$; Figure 7A; Table 2) and that social dominance predicted stronger spatial preferences (social dominance: $\beta = 0.001$, SE = 7.003e-04, $P = 0.036$; all other effects: $\beta < 0.049$, SE < 0.204, $P > 0.348$; Figure 7B; Table 2). None of the phenotypes studied predicted individual differences in their similarity to the population-wide spatial preference (IGI; Table 2), nor in their peripheral-central spatial preferences (CI; Table 2).

Table 2. Results from three GLMM performed with the predictors 'Social Dominance', 'Social Network Centrality' and 'Mirror Test', and as controls the 'Time spent in Feeders' and 'Sex', and as response variable the indexes SPI, IGI or CI, showing the coefficients (β), standard errors (SE), P values (P).

	SPI	IGI	CI
	$\beta \pm SE (P)$	$\beta \pm SE (P)$	$\beta \pm SE (P)$
SOCIAL DOMINANCE	0.001 \pm 0.0007 (0.036)*	-0.0006 \pm 0.0006 (0.344)	0.0006 \pm 0.0008 (0.469)
SOCIAL NETWORK CENTRALITY	-4.555 \pm 1.696 (0.008)*	-2.478 \pm 1.503 (0.101)	1.877 \pm 1.811 (0.302)
TIME SPENT IN FEEDERS	0.020 \pm 0.113 (0.860)	0.103 \pm 0.101 (0.308)	-0.131 \pm 0.087 (0.206)
SEX	-0.194 \pm 0.204 (0.348)	-0.212 \pm 0.196 (0.283)	-0.363 \pm 0.240 (0.135)
MIRROR TEST	0.049 \pm 0.071 (0.500)	0.060 \pm 0.069 (0.384)	0.032 \pm 0.083 (0.702)

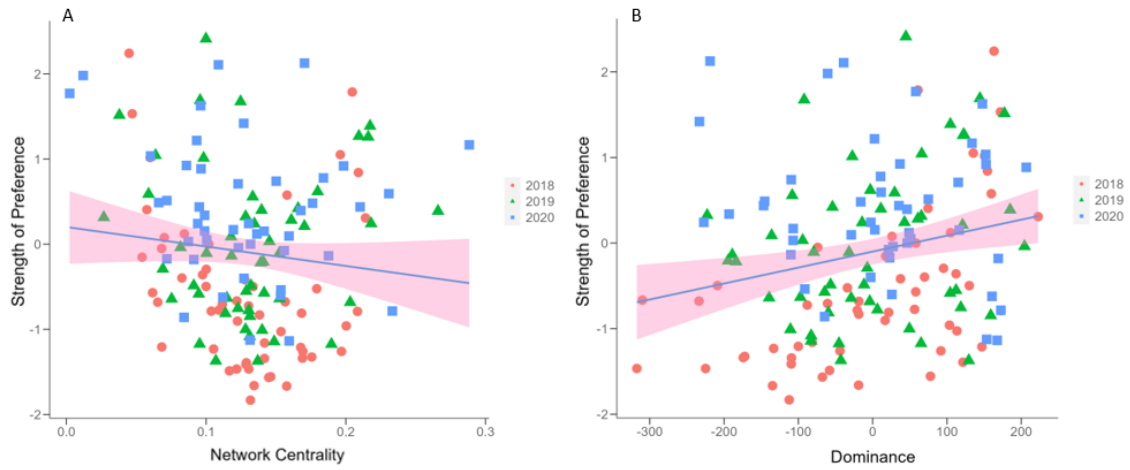


Figure 7. **A:** Relationship between the individuals' strength of preference and their social network centrality in each interval of study. The red dots represent the interval of 11-04-2018 to 31-01-2019, the green triangles represent the interval of 01-02-2019 to 31-01-2020 and the blue squares represent the interval of 01-02-2020 to 09-11-2020. The blue line represents the trend line and the pink shade the confidence interval. **B:** Relationship between the individuals' strength of preference and their dominance rank in each interval of study. The red dots represent the interval of 11-04-2018 to 31-01-2019, the green triangles represent the interval of 01-02-2019 to 31-01-2020 and the blue squares represent the interval of 01-02-2020 to 09-11-2020. The blue line represents the trend line and the pink shade the confidence interval.

4. Discussion

Some feeders were preferred over others, as indicated by the time the birds spent in them. Most differed little in the amount of usage by the population, but some were noticeably more used, especially two near the centre of the feeding area. Aggression rates differed between feeders and were on average higher in the feeders most preferred by the population. Individual waxbills differed from each other in their left-to-right spatial preferences and in the strength of those preferences. The strength of preferences was higher in individuals with a higher dominance rank, as well as individuals with less central positions in the social network. These results are discussed in turn.

The two most used feeders by the population were located near the centre of the feeding patch, one in the very centre and the other slightly to the right side. Since in this study system all feeders have *ad libitum* food, there are no advantages of peripheral individuals finding food first. Therefore, a more central position could be the best option, since the occasional appearance of predators in the surrounding area of the mesocosm could trigger their natural anti-predator behaviour, giving the centre feeders a feeling of “more protection” than the periphery feeders. Some empirical studies propose that only the most peripheral individuals in a group are attacked by predators (Milinski, 1977; Romey et al., 2008), suggesting that intermediate positions are as safe as central positions. One aspect of the mesocosm that might have some influence on the preferred feeders being slightly to the right side, rather than exactly in the middle of the patch, is a small window to a dormitory located on the right side of the feeding patch, and also an asymmetrical distribution of perches near the feeders.

Not all central feeders were heavily visited by the population, and some peripheral feeders had higher usage than some of the central feeders. This could be due to a higher rate of aggressive displacements in the preferred feeders. By calculating the rate of aggressive displacements in each feeder and later performing a comparison between this and the time of usage by the population, it was possible to conclude that, overall, feeders preferred by the population were also the ones where aggressive displacements were more likely to occur. Preferred feeders will be more sought out, which will cause more feeding interference and aggressive displacements. Higher feeding interference in the centre of the group has also been seen in other studies of spatial positioning (Janson, 1990b; Krause, 1994; Krause & Ruxton, 2002).

Regarding spatial preferences, there was a clear difference between individuals' left-to-right feeder usage preferences (some prefer the left side of the patch while others prefer

the right side), and a non-significant trend for individual preferences differing in their similarity to the population-wise preference. The latter indicates that some birds have preferences that are different to the preference of the population, although most individuals will use the feeders in a similar way to the mean population preference. Individuals' preferences in terms of central-peripheral feeder usage did not differ (individuals' preferences for the centre vs. periphery are similar). The lack of differentiation in central-peripheral preferences between individuals comes as a contrast to findings in many species of mammals and spiders, where it is usually seen a difference in central or peripheral positioning of individuals, either when stationary (Teichroeb et al., 2015) or moving/foraging (Di Bitetti & Janson, 2001; Hall & Fedigan, 1997; Heesen et al., 2015; Hirsch, 2011; Janson, 1990a; Naud et al., 2016; Rayor & Uetz, 1990; Robinson, 1981; Teichroeb et al., 2015). Conversely, Mónus & Barta (2008) state that the within-group position of a bird may change both when a bird itself or its peers move and also according to the feeding tactic they choose to use. Thus, there is a possibility the common waxbills could be switching their within-group positions as an allusion to foraging tactics, since these are associated with central or peripheral positions and are affected by many aspects such as predation. One other hypothesis is that the *ad libitum* access could allow the population to have preferred feeders throughout the whole feeding patch, and the added pressure of aggressive displacements might be driving many individuals towards the less population-preferred feeders. It is also worth considering that the common waxbill feeds in groups (Oren & Smith, 1981), and not all at the same time. This can give most individuals the opportunity to feed on population-preferred feeders, making their feeder usage non limited to the periphery of the feeding patch. In addition to not being a heavily researched topic, most studies of spatial positioning and spatial preferences are done on mammals in the wild, so these results give us a new perspective on this topic, given that the study system used consists of birds constantly monitored in a semi-natural captive environment where many confounding effects are eliminated. When looking at the strength of each individual's preference of feeder usage, there were also significant differences among individuals. In other words, some birds spent most time feeding on their preferred feeders, while others fed in a more homogeneous way across the set of feeders.

There was no association with the individuals' central-peripheral spatial preferences and their phenotypes, contrary to results in some other species. Although the relationship between personality, such as the one based on mirror test scores, and spatial position has not yet been studied, to my knowledge, correlations between dominance rank and spatial position has been observed in many taxa (Hall & Fedigan, 1997; Heesen et al.,

2015; Hirsch, 2011; Rayor & Uetz, 1990; Teichroeb et al., 2015), as well as between sex and spatial position (Heesen et al., 2015; Hirsch, 2011; King et al., 2009; Rayor & Uetz, 1990; Teichroeb et al., 2015). The absence of an association of the individuals' central-peripheral spatial preferences and their phenotypes could be caused by the lack of differences between individuals' peripheral-central spatial preferences. Similarly, phenotypic differences also did not predict the similarity of spatial preferences to the population-wide preference.

In the case of the individuals' strength of spatial preferences, the dominance rank and position in the social network seem to predict differences between individuals, but personality based on mirror test scores, and sex did not. As predicted, more dominant individuals were able to express their preferences more strongly, possibly because they could assert their dominance to displace other birds from their desired feeders, or less dominant individuals may opt for using any other feeder, with no particular preference, to avoid conflicts. In this particular population of common waxbills, associations are on average stronger between individuals similar in social dominance rank (Gomes et al., 2022), possibly as an attempt from lower-ranking individuals to avoid higher-ranking ones, which are more aggressive (Beltrão et al., 2021b). Individuals with less central positions in the social network were also able to express their preferences more strongly. One hypothesis is that birds with less central positions could be part of smaller feeding groups. Low social network centrality, in this study system, seems to imply strong social connections with a sub-group, while the remaining associations are weak (Gomes et al., 2022) suggesting that individuals in more peripheral positions of the social network feed with fewer peers. Feeding in smaller groups may increase the likelihood of accessing preferred feeders due to smaller number of competing peers, and a lower chance of aggressive displacements. Accordingly, Beltrão et al. (2023) found that, during foraging, there were more aggressive displacements in bigger groups of common waxbills.

5. Conclusion

Here I found that spatial preferences can exist even within a static foraging patch where there are no differences in the quantity or quality of food. To my knowledge, this study is the first to analyse the relation between social network centrality and spatial feeding preferences. The results show that individuals occupying more social peripheral positions in the social network have the ability to feed from their preferred feeders, whichever they might be, in a more consistent way. Because of the simplified study system, with homogeneous quantity and quality of food across the foraging patch, fitness consequences of expressing one's spatial preferences strongly may not exist. However, in nature the opposite may be true. The ability to eat from a preferred spot could be advantageous because of differences in the quality and quantity of food patches or protection from predators. If there are such benefits from expressing feeding preferences, my results indicate that more dominant birds could have an advantage, and that occupying less central positions in the social network is an alternative approach to obtaining those benefits.

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