The social network of wild zebra finches (*Taeniopygia castanotis*) at the nest and at social hotspots

Abstract

Multilevel societies (MLSs), where stable social units are nested within higher grouping levels, are thought to be one of the most complex social structures. While predominantly studied in large-brained mammals, there is increasing evidence for the presence of MLSs in birds. One bird species that shows elements of a multilevel society is the gregarious zebra finch (*Taeniopygia castanotis*). Zebra finches form life-long pair bonds, breed in loose colonies and gather at temporally stable social trees or 'hotspots'. What is not yet known is how individuals use these social hotspots and if this is related to their social network in the breeding colony. We studied a population of wild zebra finches breeding in nestboxes. I identified individuals from recordings at nestboxes and at social hotspots through their song characteristics and constructed social networks. I show that zebra finches associated with more and different conspecifics at social hotspots than at nestboxes. Strengths of associations were low, providing little evidence of stable preferred associations. This study provides tentative support for the presence of a multilevel society in zebra finches, with a social network in the breeding colony and a larger, different social network at hotspots. Zebra finches are a widely-used model species in laboratories, and these results can help inform captive housing decisions and interpret laboratory findings. This study adds to a growing body of research showing multilevel societies are more widespread than previously thought.

Keywords: Field study, multilevel society, social network, zebra finch.

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Introduction

Animals vary in sociality: from for example solitary living insects, to highly complex social groupings as seen in chimpanzees (Ward & Webster, 2016). The degree of sociality is determined by trade-offs. On the one hand, sociality can increase cooperation, predator protection, opportunities for mating and acquisition of socially transmitted information (C. R. Brown et al., 2003; Griesser, 2008; Ward & Webster, 2016). On the other, it can lead to increased competition, conspicuousness to predators and risk of pathogen and parasite transmission (Altizer et al., 2003; Ward & Webster, 2016). Different ecological and social pressures can result in different social groupings (Clutton-Brock, 2016; Farine & Sheldon, 2019). One form of social grouping is a multilevel society (MLS). In MLSs animals are organised in two or more hierarchical levels, each of which is stable and in general socially cohesive (Grueter et al., 2020). The lowest level is often called the core unit, and is usually a breeding pair or small polygynous group (Camerlenghi et al., 2022; Grueter et al., 2020). Individuals are most loyal to this level, and most social interactions occur here. These core units move through the landscape and specific groups interact with each other, forming the upper level (Grueter et al., 2020). This level can number hundreds of animals (Grueter et al., 2012, 2020; Schreier & Swedell, 2009). Additional lower and higher levels are possible as well, respectively called intermediate and apex levels (Grueter et al., 2020). In order to maintain such complex social networks, individuals need to be able to recognize each other and maintain different types of relationships at several levels (Grueter et al., 2017). This multilevel social structure is one of the most complex social groupings and interesting for the study of animal sociality and its evolution (Grueter et al., 2012, 2020).

MLSs are thought to increase flexibility in response to changing environmental conditions, since group size can increase or decrease without losing the cohesion of the social (sub)groups (Camerlenghi et al., 2022; Grueter et al., 2020). Individuals can benefit from the functions that different group sizes provide, such as decreased harassment by conspecifics in the core units and increased predator protection at the higher levels (Camerlenghi & Papageorgiou, 2025; Grueter et al., 2012, 2017; Krützen et al., 2003). They were first described in hamadryas baboons (*Papio hamadryas*) (Abegglen, 1984; Kummer, 1984; Schreier & Swedell, 2009) and are still predominantly studied in primates and large-brained mammals such as elephants (*Loxodonta africana*) and cetaceans (R. A. Hill et al., 2008; Krützen et al., 2003; Stead & Teichroeb, 2019; Whitehead et al., 2012; Wittemyer et al., 2005). Increasingly, there is evidence for MLSs in birds (Farine & Sheldon, 2019; Papageorgiou & Farine, 2021), such as the small-brained vulturine guineafowl (*Acryllium vulturinum*) (Papageorgiou et al., 2019) and cooperatively breeding birds like the superb fairy-wren (*Malurus cyaneus*) (Camerlenghi et al., 2022). The highly gregarious zebra finch (*Taeniopygia castanotis*) also shows characteristics of an MLS (McCowan et al., 2015; Papageorgiou & Farine, 2021). The zebra finch is a preferred model species in behavioural studies in laboratories worldwide (Griffith & Buchanan, 2010). However, in laboratories, they are often kept in same-sex groups or breeding pairs, which might not be representative of their social organisation in the wild (McCowan et al., 2015). Knowing how these birds organize themselves in the wild can help to interpret findings in the lab, inform captive housing decisions and potentially increase the welfare of captive zebra finches.

Zebra finches are the most ubiquitous estrildid finches in Australia and live primarily in arid areas (Zann, 1996). They are socially and genetically monogamous, with very low extra pair paternity

rates (1-2%) (Griffith et al., 2010; Zann, 1996). They live in dynamic fission-fusion societies, where the life-long, stable breeding pairs form the core units (Tyson et al., 2024). Pairs and individuals can form small mixed-sex groups of 3-10 birds which often come together in trees near a food or water source. These groups move around together, forage and likely share information (McCowan et al., 2015). When breeding conditions are right, pairs form loose breeding colonies, choosing to nest close to conspecifics at early nesting stages to optimize breeding synchrony (Brandl et al., 2019). They can retain social bonds with their synchronous breeding neighbours across non-breeding seasons (Brandl et al., 2021), suggesting a complex multilevel social network. This sociality is probably selected for by the unpredictable environment, with scarce and patchily distributed resources (Rafacz & Templeton, 2003a; Rubenstein & Lovette, 2007). Strong social bonds can offer many benefits here, such as information transfer about resources like food (Aplin et al., 2012; Benskin et al., 2002; Mariette & Griffith, 2013) or breeding synchrony and success (Brandl et al., 2021; Mariette et al., 2012a, 2012b).

To maintain these complex relationships, zebra finches need to be able to recognize individuals. The song of the males is individually distinctive (Elie & Theunissen, 2018; Geberzahn & Derégnaucourt, 2020; Sturdy et al., 1999; Zann, 1996) and zebra finches have a high auditory sensitivity (Dooling & Lohr, 2006; Prior et al., 2018), which could facilitate communication. However, zebra finch song is a very short-distance signal, with an average range of nine meters, and the loudest calls in their repertoire have an average range of only fourteen meters (Loning et al., 2021). Thus, vocalisations are not efficient in locating and attracting conspecifics in the open, arid habitat zebra finches live in. Instead, they frequent semi-permanent 'social hotspots' in specific trees and bushes, where they can interact socially with other conspecifics (Loning, Fragueira,et al., 2023). The birds primarily arrive at these social trees in breeding pairs or small groups. In a study during a drought, group sizes at the social trees could reach several dozen individuals, but were commonly smaller at around 5 individuals (Loning, Fragueira, et al., 2023). The social trees could serve as spaces where individuals can benefit from being in a larger group: sharing information on resources (Aplin et al., 2012), relative safety from predators (Silk et al., 2014) or relocating a partner after becoming separated (Loning, Fragueira, et al., 2023).

Little is known about the social network at the trees and who individuals interact with while there. A previous study found that individuals met multiple times with the same conspecifics at social hotspots, indicating that zebra finches have preferred social relations at the trees (ter Avest, 2024). Moreover, synchronously breeding neighbours can retain social bonds outside of the colony context, as they were found to forage together more (Brandl et al., 2021). In colonies, individuals will also inspect other nests to check on breeding status and even sing there (Brandl et al., 2018; Loning, Verkade, et al., 2023; Mariette et al., 2012a). This indicates that zebra finches preferentially associate with specific individuals both in the breeding colony and at the hotspots. Maintaining stable social bonds over time and across different contexts could be beneficial to individuals by increasing breeding synchrony and vigilance or reducing aggression (e,g, Beck et al., 2020; Griffiths et al., 2004; Kurvers et al., 2013; Rose & Croft, 2017). It is however not known if the social networks at the breeding colony and hotspots are related.

In this thesis I studied if social bonds in the breeding colony differ from those at the social hotspots. The study was carried out on a wild population of zebra finches at Fowlers Gap Arid Zone Research Station, Australia. At the field site, automated acoustic recorders were used to

record vocalizations at the nestboxes in the breeding colonies and at social trees. Zebra finches have an individually recognizable song. The song consists of introductory notes followed by distinct motifs containing different vocalizations such as tets, stacks and distance calls (Elie & Theunissen, 2018; Geberzahn & Derégnaucourt, 2020; Sturdy et al., 1999; Zann, 1996). In the recordings I identified individual birds and scored their associations. I examined the size and strength of the social networks at the nests and at the social trees. Furthermore, I determined if individuals preferentially meet with the same conspecifics at nests and hotspots. I expected that the social network is larger at the hotspots, with more individuals heard singing and associating there than in the breeding colonies. I expected to find a hierarchical social structure with individuals at the hotspots interacting with conspecifics they associated with at the nestbox as well as others. On the one hand I expected birds at the hotspots to strengthen existing relationships because of the advantages of stable social bonds. On the other hand, I expected hotspots to increase sociality and link individuals from different breeding colonies, to maximize social information uptake on e.g. breeding success (Mariette et al., 2012a) and resources (Aplin et al., 2012). I therefore predicted individuals to have stronger but less associations at the nestboxes while expanding their network at the hotspots resulting in more but less strong interactions, corresponding to an MLS.

Methods

Study site

The study was conducted at Fowlers Gap Arid Zone Research Station, New South Wales, Australia, from September to October 2024. The area consists of relatively open shrubland with some trees and low bushes, including prickly wattle (*Acacia victoriae*), dead finish (*Acacia tetragonophylla*), bluebush (*Maireana* sp.) and saltbush (*Rhagodia* sp.) (Loning et al., 2021; Loning, Verkade, et al., 2023). Rainfall does not follow seasonal patterns (Griffith et al., 2008). There are natural creeks and an artificial dam in the area (Fig. 1; Brandl et al., 2019).

Study species

Zebra finches are small passerine birds that eat mostly grass seeds, which are relatively abundant and stable in the (semi-)arid zones. They have a broad environmental tolerance and live mostly in open areas with grasses for food and low bushes and trees for nesting. They are reliant on rainfall for grass growth. Zebra finches breed opportunistically when environmental conditions allow, but breeding is most prevalent in the spring months (Zann, 1996). The zebra finches at this site use nestboxes to breed. Nestboxes are placed in the area in groups and located near trees for shelter. This study focussed on the area Gap Hills, where there are currently around 180 nestboxes, grouped into 6 breeding colonies.

Data collection

We recorded audio at nestboxes and social trees using 70 small acoustic recorders (AudioMoths: Hill et al., 2019). Sampling rate was 32 kHz and recording files were 59:55 minutes with 5 second pauses to allow ample time for the AudioMoth to save data. The devices were programmed to run from 90 minutes before sunrise to 90 minutes after sunset. Due to logistic issues on two days recordings started 60 minutes before sunrise (on the 14th and 17th of September 2024). Batteries and SD-cards were exchanged regularly to allow for continuous recording throughout the breeding season (Eneloop rechargeable batteries; 64GB SanDisk Extreme UHS Speed Class 3 microSDXC cards, made in China). A table of all settings used is available in Appendix A.

To mitigate wind disturbance, AudioMoths were placed with the microphone facing north to north-west as much as possible. At the study site, most wind is southerly to south-easterly, with this percentage increasing over spring (WillyWeather, 2024).

Nestboxes

We attached AudioMoths to the poles directly underneath nestboxes with breeding activity. To monitor breeding activity we inspected the contents of all nestboxes every three days. Chicks were weighted regularly, ringed, and we noted the number of surviving and fledged chicks to monitor breeding success.

I selected nine nestboxes with surviving fledged chicks for analysis (Fig. 1). These nests were active at different times during the breeding season, ranging from the beginning of September to the end of October. Six of the nests were located in breeding colony D, three in breeding colony E. I analysed one full day of audio recordings during the egg-laying phase for each nestbox, since

males sing most during this phase of breeding (Loning, Verkade, et al., 2023). Days were chosen based on data availability and most suitable weather conditions (e.g. no rain, little wind).

Social hotspots

We identified social hotspots through transects and observations. We planned seven transects of 900 meters long, spread out over the study area. These were walked on multiple days between 08:00 and 14:00. For a tree to qualify as a social hotspot, it must frequently contain groups of zebra finches and be resource-independent (Loning, Fragueira, et al., 2023). Therefore, observers looked for trees with groups of three or more zebra finches. We observed these trees for several minutes and inspected the number of zebra finch droppings under the tree. A large amount of droppings could indicate frequent occupation by zebra finches. If there were signs of ongoing breeding activity in a tree, this tree was excluded.

For trees that met these criteria, we took a GPS point. These potential social hotspots were checked on a different day to see if they contained multiple zebra finches again. Next, we observed the potential hotspots three times for one hour between 08:00 and 12:30 to see if they were actively used by zebra finches. We noted the number of birds leaving or arriving along with the time. Furthermore, every ten minutes we estimated the approximate group size in the tree. In this way, I informally verified if the trees were used in a similar manner as reported in a previous study and could thus be classified as social hotspots (Loning, Fragueira, et al., 2023). Based on this information, AudioMoths were placed in trees that seemed like stable social hotspots.

I selected three social hotspots for analysis based on activity and proximity to breeding colonies. Two hotspots are located at the edges of breeding colony D (SH1 and SH2) and one is located between breeding colony E and the dam (SH3; Fig. 1). In total, I analysed audio from seven different days (n=2 for SH1 and SH2, n=3 for SH3). Where possible, I analysed hotspots on the same day as a nestbox close by (n=5), to minimize external variation in among others weather conditions. However, due to time and data constraints this was not always possible. For these four nestboxes, I analysed a nearby social hotspot on a different day.

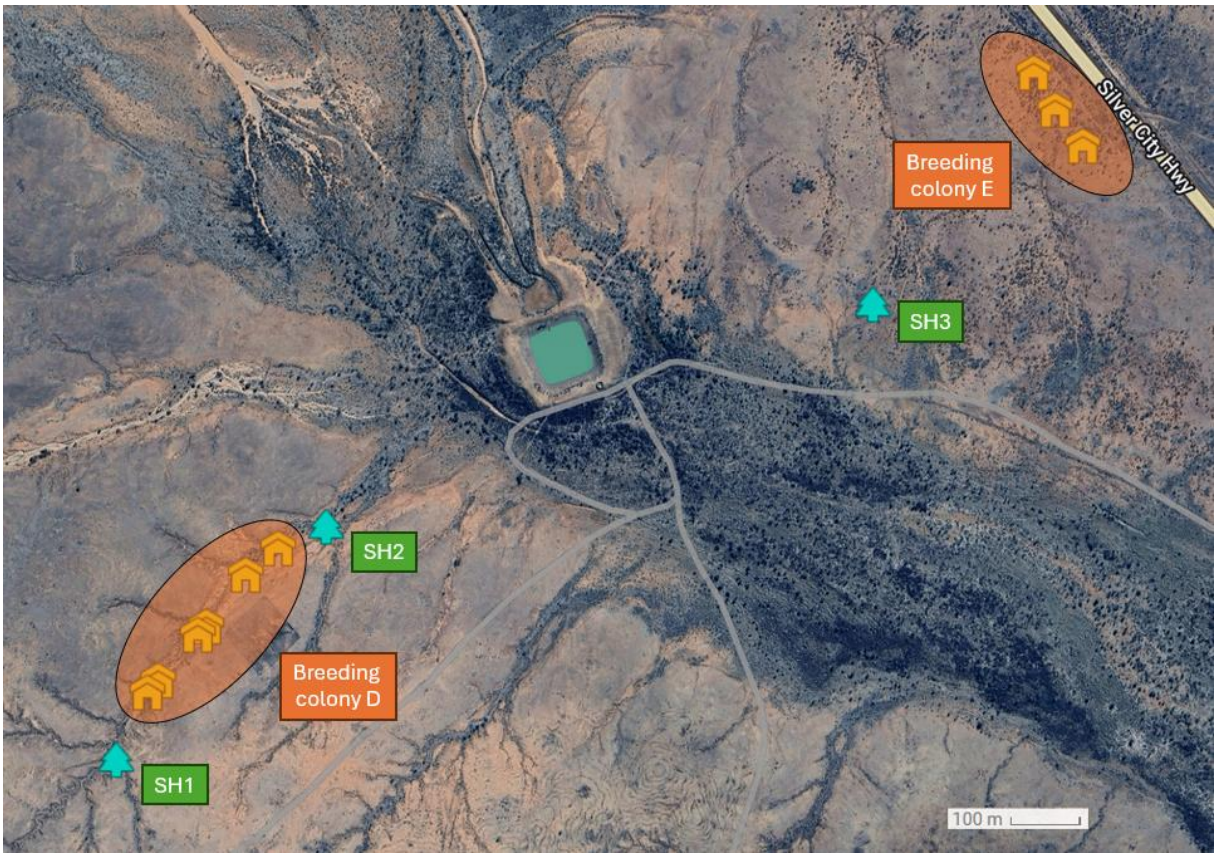

Figure 1: Map showing the field site and positions of analysed nestboxes and social hotspots. *Tree icons denote social hotspots (SH). House icons denote nestboxes, with six located in breeding colony D and three in breeding colony E. The central dam, creek lines and highway are visible. Image made using Google Maps.*

Audio analysis

All audio recordings were analysed using Audacity® (version 3.7.1; Audacity Team, 2024). I identified songs in the audio through auditory and visual inspection, using spectrogram mode (sample rate: 44.1 kHz, window type: Hamming, window size: 1024). Zebra finch song has a distinct structure and is easily recognizable in the audio files. Example songs of three different individuals are shown in Figure 2. If there was a gap of more than 5 seconds between song motifs, I scored these as separate song bouts.

Subsequently, I assigned all songs a score using a ranking system from 1 to 10 (Appendix B). Songs with a score above 6 were considered clear enough to assign to an individual bird, songs below 6 were only occasionally recognizable enough to be assigned to a specific individual. For identification purposes, I created a database containing clear spectrograms of individual birds. I compared newly encountered songs to this database. If the sequence of calls, motifs and frequencies (in particular the frequency of a distance call element (Zann, 1984)) of a new song were similar to that of an already encountered individual, I labelled the new song as belonging to that individual. If not, I created a new individual label. In case of ambiguity, spectrograms were presented in random order to an experienced observer (Hugo Loning). If there was no consensus on the classification, that song was not assigned to a specific individual. Figure 2 shows example songs of different individuals, highlighting different elements and structures.

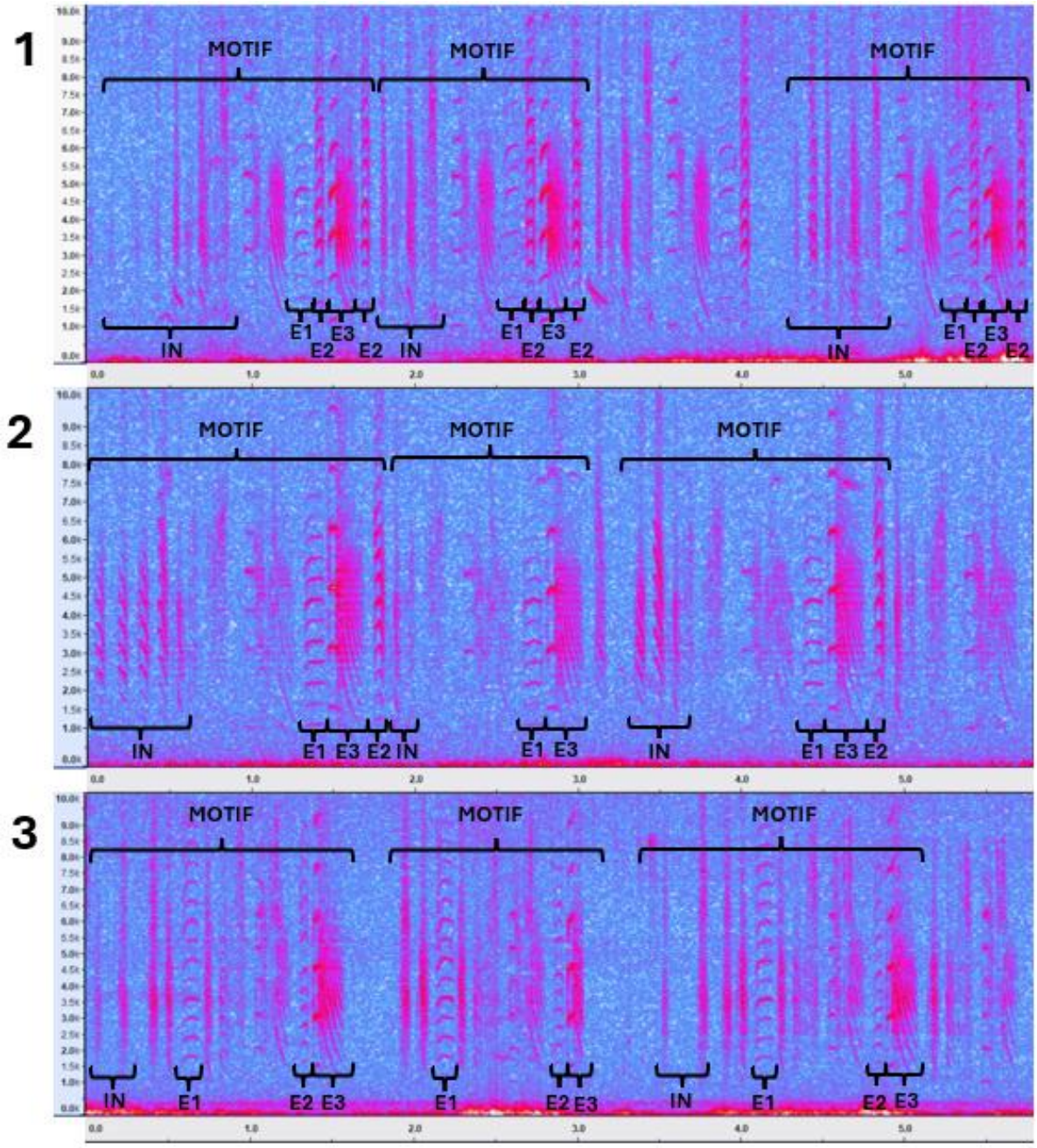

Figure 2: Spectrograms of song motifs from three different individuals. *Each row (1-3) shows the spectrogram of a different individual's song. The y-axis shows the frequency in kHz, the x-axis time in seconds. The colour of the spectrogram corresponds to the energy of the sound, with red being higher in energy than blue. Different elements of the motifs are depicted. IN stands for introductory notes, E1, E2 and E3 denote different song elements. The different individuals show a different order of these elements and elements have different frequencies. Interindividual differences are also visible, such as incomplete motifs or different numbers of introductory notes. For example, individual 2 does not have element E2 in the second motif. Spectrograms were made using Audacity software.*

Statistical analysis

All statistical analyses were performed using R (version 4.3.3) in R Studio (Posit team, 2024; R Core Team, 2024). Network metrics and graphs were created using the *igraph* and *sna* packages (Butts, 2024; Csárdi & Nepusz, 2006). To test for differences between nestboxes and social hotspots, I used (generalised) linear mixed effect models (*lmer* and *glmer* from package *lme4* (Bates et al., 2015)). I used the linear mixed effect model *lmer* for the continuous variable song

duration. The other variables were discrete, thus I used a generalized linear mixed effect model (*glmer*) with a Poisson distribution. No under- or overdispersion was detected. The type of location (nestbox or social hotspot) was input as fixed effect. Random effects included the individual identifier, the location (the specific hotspot or nestbox) and the date, and are specified for each model below. To test for significance, I compared the models to null models with a likelihood-ratio test, using the function *anova* from the package *stats*. For the *lmer* model, I used ML estimations to this end (Bolker et al., 2009).

Social acoustic environment of breeding colonies and social hotspots

I started by looking at general characteristics of the acoustic environments at the nests and hotspots. First, I calculated the number of different locations visited by individuals. Secondly, I determined the presence of song over the day at each type of location to compare general use of the nestboxes and social hotspots. For each second of the day, I scored presence of song in a binary way. Since many songbirds show a dawn and dusk chorus (T. J. Brown & Handford, 2003; Schlicht et al., 2023), I wanted to relate the song over the day to sunrise and sunset. In order to do this, I calculated the average day length during the study period, which was 12.5 hours. I then scaled each day to 12.5 hours so that I could compare song around sunrise and sunset over multiple days. For every location, I then divided each day in half hour blocks and for each block scored how many seconds contained song. I then divided this by the total number of seconds of song of that day. In this way, I obtained the proportion of all song during the day that occurred per half hour block. I then averaged these proportions for all the nestboxes and all social hotspots to compare the different types of locations.

Next, I calculated and compared the duration of zebra finch song each day at nestboxes or social hotspots using a linear mixed-effect model. I selected location and date as random effects. Lastly, I compared the number of identified individuals heard per day at a nestbox or social hotspot using a generalized linear mixed-effect model. To account for the different number of observation days for the different locations (n=1 for all nestboxes, n=2 for SH1 and SH2 and n=3 for SH3), I included the date nested in the location as a random effect. I also tested this for a subset of the data containing only the days on which I had analysed both a nestbox and social hotspot (n=5). Here, I included location and date as separate non-nested random effects.

Social network characteristics

Next, I determined interactions between individuals. If individuals sang within three minutes of each other, I assumed that they could hear each other and scored this as an interaction. I chose this time window of three minutes because it aligned with previous thesis research into social networks in this area (ter Avest, 2024). Results were qualitatively robust when changing the time window to 1 or 5 minutes. Using these interactions I created edge lists, containing the edges (interactions) between two individuals. I created graphs for the whole network and after filtering for dyads that had at least two interactions.

For the nestboxes and social hotspots I calculated and compared the number of nodes and edges of the network per day using generalised linear mixed models. Again, to account for the different number of observation days per location I included the date nested in the location as a random effect. To model the number of edges in the network, I increased the maximum number of iterations to 100.000 because the original model failed to converge. I also modelled the data after

filtering for dyads that had at least two interactions. Here, for the number of nodes I included only the location as a random effect to deal with singularity.

To look at the average strength of interactions at both types of location, I calculated the frequency of each dyadic interaction. I used a generalized linear model (*glm* from package *stats* with Poisson distribution) to compare the frequencies per type of location. No under- or overdispersion was detected.

Social network at the individual level

Finally, I looked at specific individuals that were heard both at a nestbox and a social hotspot, to compare how they interacted socially at these different types of locations. For these individuals (n=24), I calculated the degree (number of interactions) and the number of unique interactions they had at nestboxes and social hotspots. If the bird was heard at multiple nestboxes or multiple social hotspots, I took the total degree or number of unique interactions. I also calculated how long each individual had sung at each type of location. To account for the different scales the degree, number of unique interactions and song duration were normalized. In the models, I looked at the effects of the type of location and song duration and their interaction. I included the individual identifier as a random effect to account for the paired nature of the data. For the number of unique interactions the original model failed to converge so I tested for different optimizers, used the optimizer *nlminbwrap* and increased the maximum number of iterations to 100.000. Furthermore, I checked if there was overlap in the individuals that a bird interacted with at the nestbox and social hotspot.

Results

Social acoustic environment of breeding colonies and social hotspots

In total, 163 individuals were acoustically identified. Of these, most individuals were only heard at one location, with fewer individuals heard at more locations (Fig. 3). In total, 24 individuals (14.7%) were heard at both a social hotspot and a nestbox.

In general, birds started singing around the same time of the day at both nestboxes and social hotspots (Fig. 4). At the nestboxes, most song occurred early in the day, a little after sunrise until solar noon. At the social hotspots, most song occurred during the second half of the day. Furthermore, song continued at the social hotspots for longer, with a higher prevalence of song after sunset than at the nestboxes.

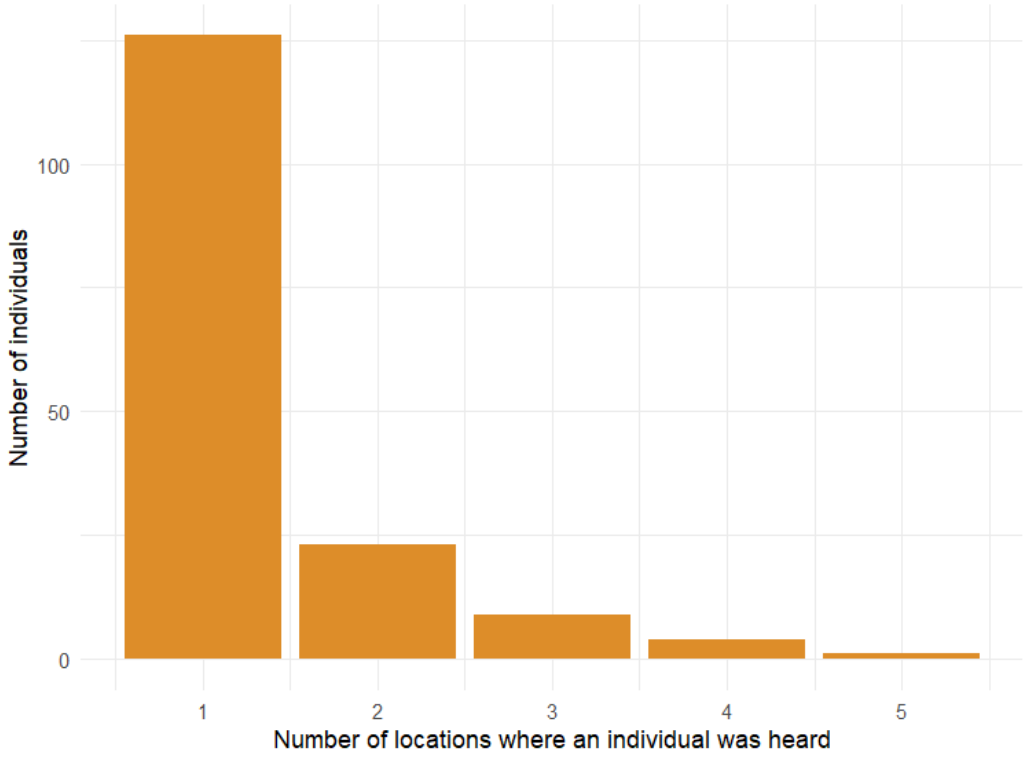

Figure 3: The number of individuals that were heard at different locations. *The x-axis shows the number of locations that a specific individual has been heard singing. The y-axis shows the number of individuals. Most individuals were only heard at one location (n=126), with fewer individuals heard at more different locations (two locations: n=23, three locations: n=9, four locations: n=4, five locations: n=1).*

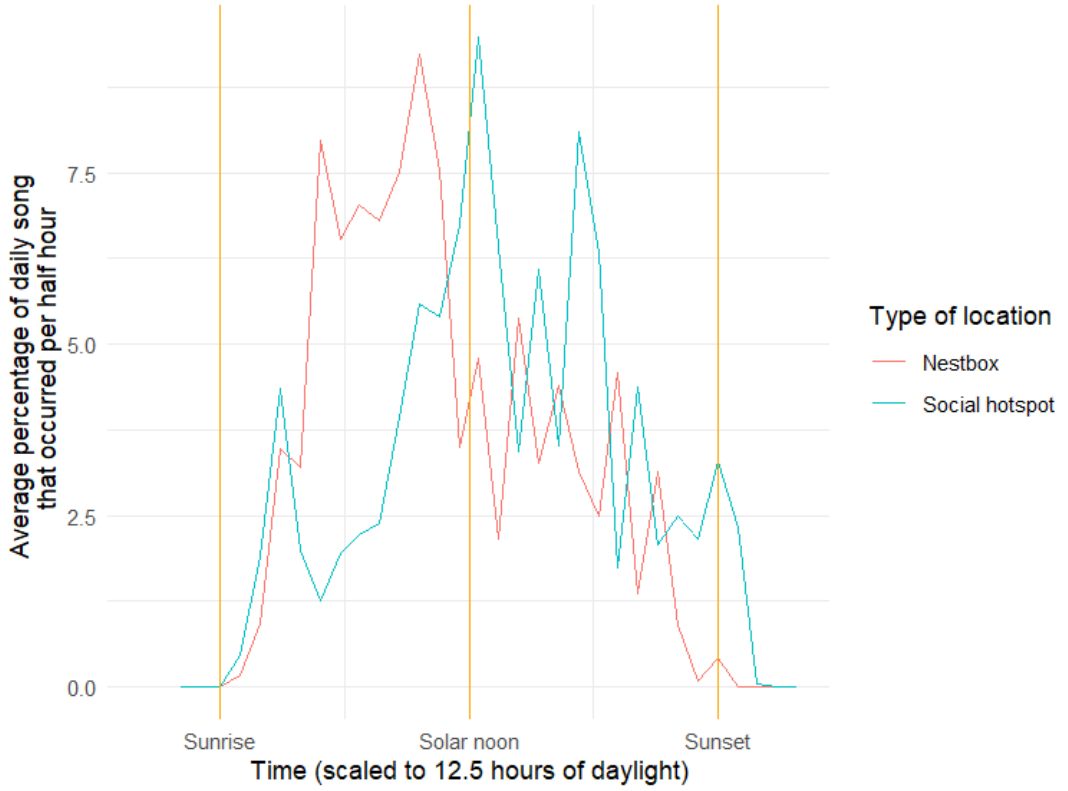

Figure 4: The average distribution of song over the day for nestboxes and social hotspots. *The time is scaled to an average day of 12.5 hours. Sunrise, solar noon and sunset are denoted by the orange vertical lines. The y-axis shows the proportion of total daily song that occurred per half hour. The red line corresponds to the average proportion for the nestboxes, the blue to the social hotspots.*

The duration of birdsong during the day was longer at social hotspots than at nestboxes (Fig. 5, likelihood-ratio test : $\chi^2(1)=8.863$, $p=0.003$). On average, there was 6.7 ± 3.3 minutes of song per day at a nestbox, whereas there was 17.2 ± 5.0 minutes of song per day at a social hotspot. Furthermore, significantly more individuals were heard during the day at social hotspots than at nestboxes (Fig. 6, likelihood-ratio test: $\chi^2(1)=6.36$, $p=0.01$). On average, 8.8 ± 1.2 individuals were heard per day at a nestbox, whereas 20.3 ± 1.3 individuals were heard at a social hotspot. When comparing nestboxes and social hotspots only on days that there was information for both (n=5), the relationship remained (nestbox: 7.0 ± 1.3 individuals, social hotspot: 20.5 ± 1.4 individuals; likelihood-ratio test: $\chi^2(1)=7.40$, $p=0.007$).

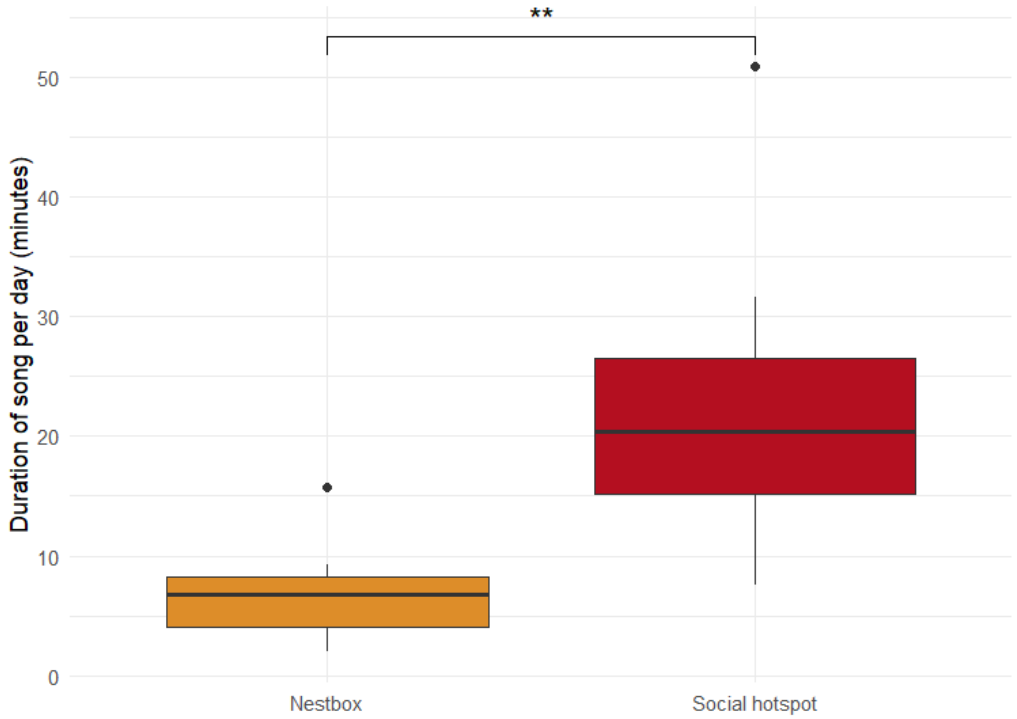

Figure 5: The duration of song per day. *The song duration is given in minutes for both nestboxes and social hotspots (n=9 and n=7 resp.). On average, there was 6.7 ± 3.3 minutes of song per day at a nestbox and 17.2 ± 5.0 minutes of song per day at a social hotspot (likelihood-ratio test: $\chi^2(1)=8.863$, p=0.003).*

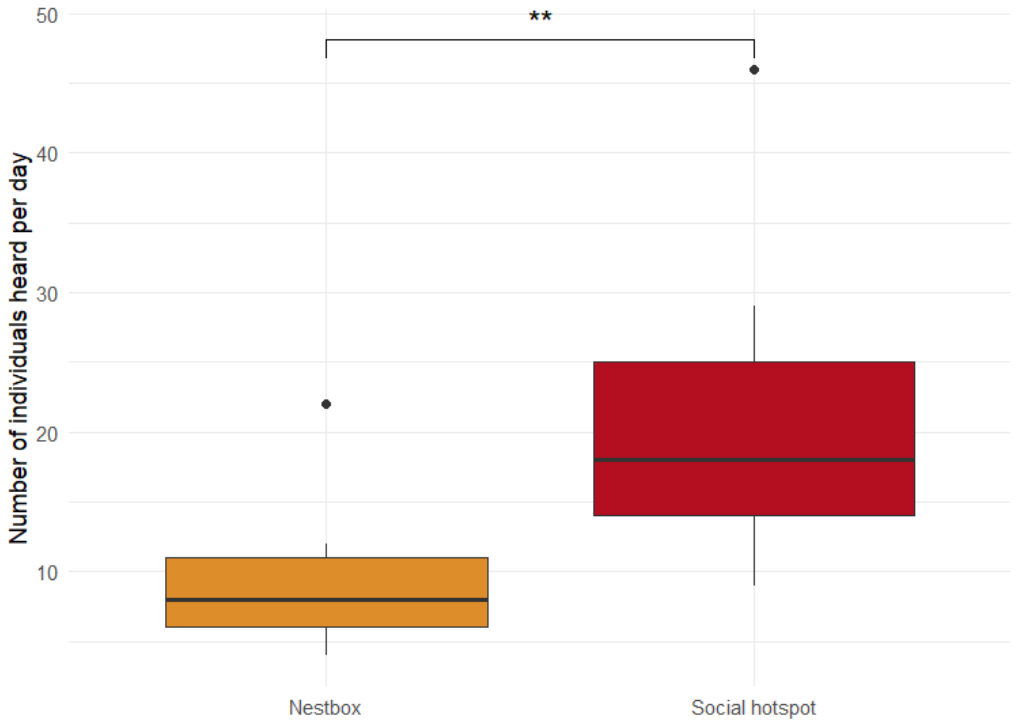

Figure 6: The number of individuals heard per day. *The number of individuals heard per day at a social hotspot (20.3 ± 1.3, n=7) was higher than at a nestbox (8.8 ± 1.2, n=9; likelihood-ratio test: $\chi^2(1)=6.36$, p=0.01).*

Social network characteristics

Figure 7 shows the social network without the isolated individuals. Many dyads are connected through one interaction (85.2% of dyads), and just 3.1% of dyads interacted three or more times, indicating that the network is not very strong. One of the social hotspots (SH3) is relatively isolated from the other locations, with only one individual that interacted there heard in an interaction at another location in E. Furthermore, there is only one dyad linking the breeding colonies in D and E. At one nestbox in E (E122) no interactions took place.

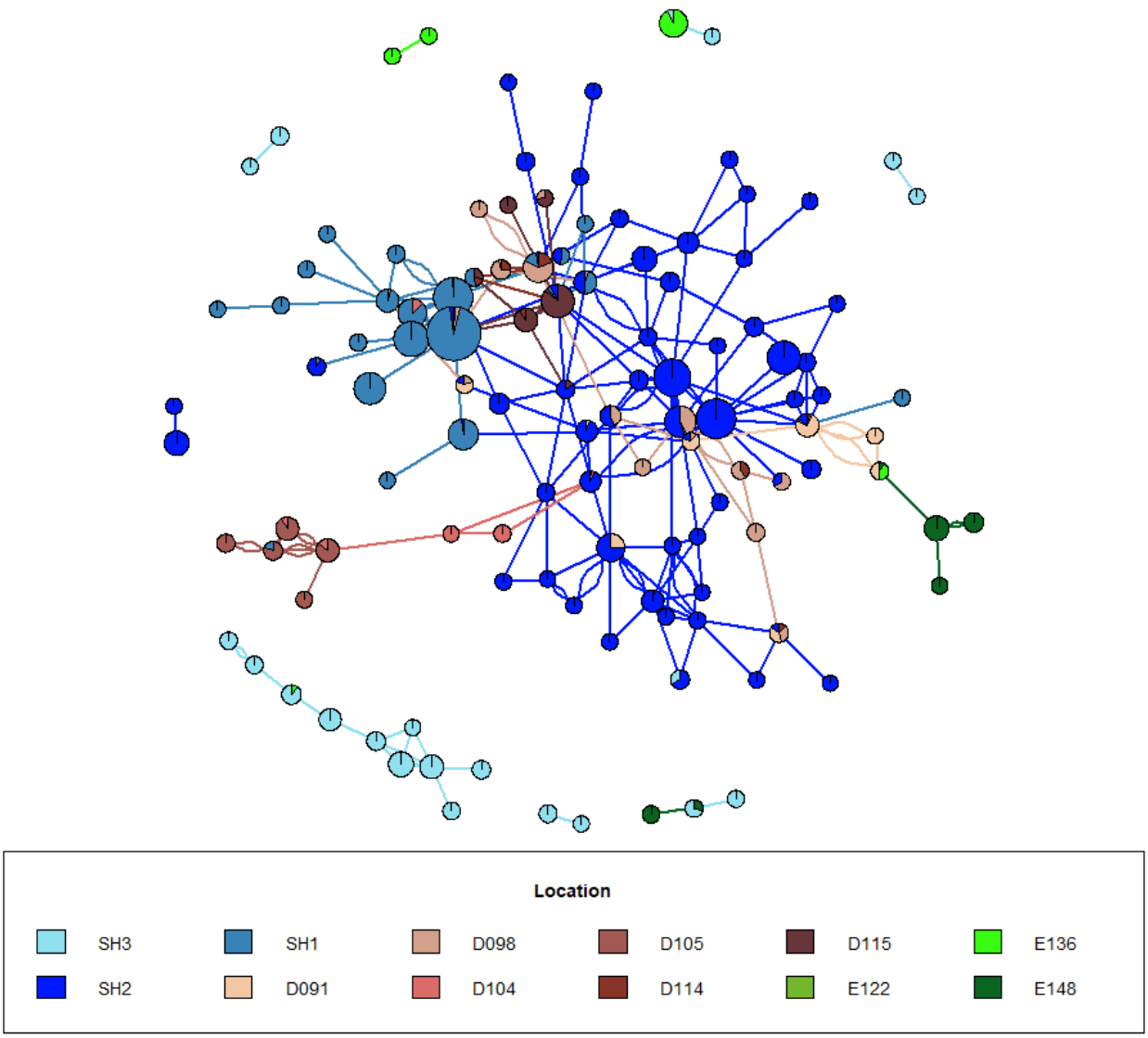

Figure 7: The social network filtered for individuals that had at least one interaction. *The pie shapes represent individuals (nodes), with coloured slices representing the relative amount of time they spent singing in different locations. The size of the node scales by the total amount of time that node was heard singing. The lines represent the interactions (edges). The colours of the edges correspond to the location where that interaction took place, with blues for social hotspots, browns for breeding colony D and greens for breeding colony E.*

This can also be seen in Figure 8, where the network is filtered for dyads that had at least two interactions. Little of the structure of the larger social network remains. Primarily dyads remained with two interactions, separate from other individuals. Two larger clusters of three and four connected individuals are seen at the nestboxes in D. One of these networks is more clustered, with three individuals interacting with each other multiple times. At SH1 a cluster of six individuals was identified. At SH2 four individuals are connected linearly. The largest cluster of seven individuals is mostly made up of interactions taking place at SH2, however one dyad is connected through interactions in D. This network graph indicates that there is little mixing between the individuals that interact at the nestboxes and social hotspots. Individuals tend to have stronger social ties either in the breeding colony or at the nestbox, but generally do not interact strongly with others at both.

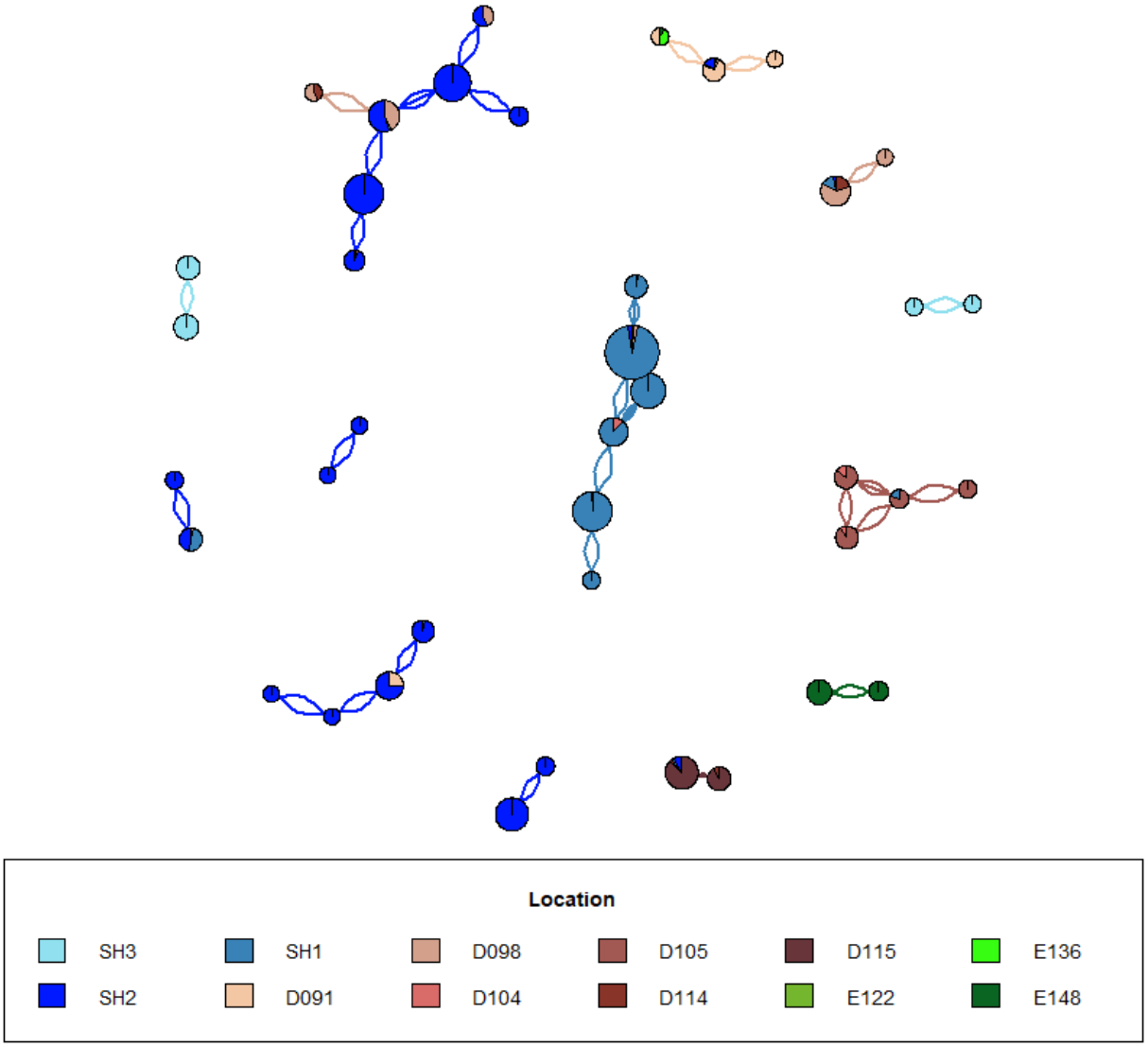

Figure 8: The social network filtered for dyads that had at least two interactions. *The pie shapes represent individuals (nodes), with coloured slices representing the relative amount of time they spent singing in different locations. The size of the node scales by the total amount of time that node was heard singing. The lines represent the interactions (edges). The colours of the edges correspond to the location where that interaction took place, with blues for social hotspots, browns for breeding colony D and greens for breeding colony E.*

When taking all interactions into account, the network on a given day was larger at social hotspots than at nestboxes. At social hotspots, there were more nodes in the network (13.5 ± 1.6; likelihood-ratio test: $\chi^2(1)=5.39,\ p=0.02$) and more edges (17.8 ± 1.9; likelihood-ratio test: $\chi^2(1)=4.04,\ p=0.04$) than at nestboxes (4.3 ± 1.3 and 4.6 ± 1.4, respectively). There was no significant difference in the strength of dyadic interactions between the types of locations (glm: $z=-1.29,\ p=0.2$).

When filtering the network for dyads that had at least two interactions, no significant differences in number of nodes or edges between nestboxes and social trees were found (likelihood-ratio test: $\chi^2(1)=1.74,\ p=0.19$ and $\chi^2(1)=0.787,\ p=0.38$ respectively).

Social network at the individual level

In total, 24 individuals were heard at both a social hotspot and a nestbox. These individuals had more interactions (a higher degree) at social hotspots than at nestboxes (Fig. 9; social hotspot=3.0 ± 1.3, nestbox=1.2 ± 1.3; likelihood-ratio test: $\chi^2(2)=17.9,\ p=0.0001$). Furthermore, they had more interactions if they had sung for a longer time (likelihood-ratio test: $\chi^2(2)=34.6,\ p<0.0001$). An increase in song duration of 1 minute corresponded to an increase in degree of 1.83 ± 1.06. There was no significant effect of an interaction between type of location and singing duration (likelihood-ratio test: $\chi^2(1)=2.69,\ p=0.1$). However, the relatively low p-value and slightly lower AIC score of the interaction model compared to a non-interaction model (AIC=225.5 and 226.2 resp.) could indicate a trend towards singing for longer at nestboxes than at social hotspots.

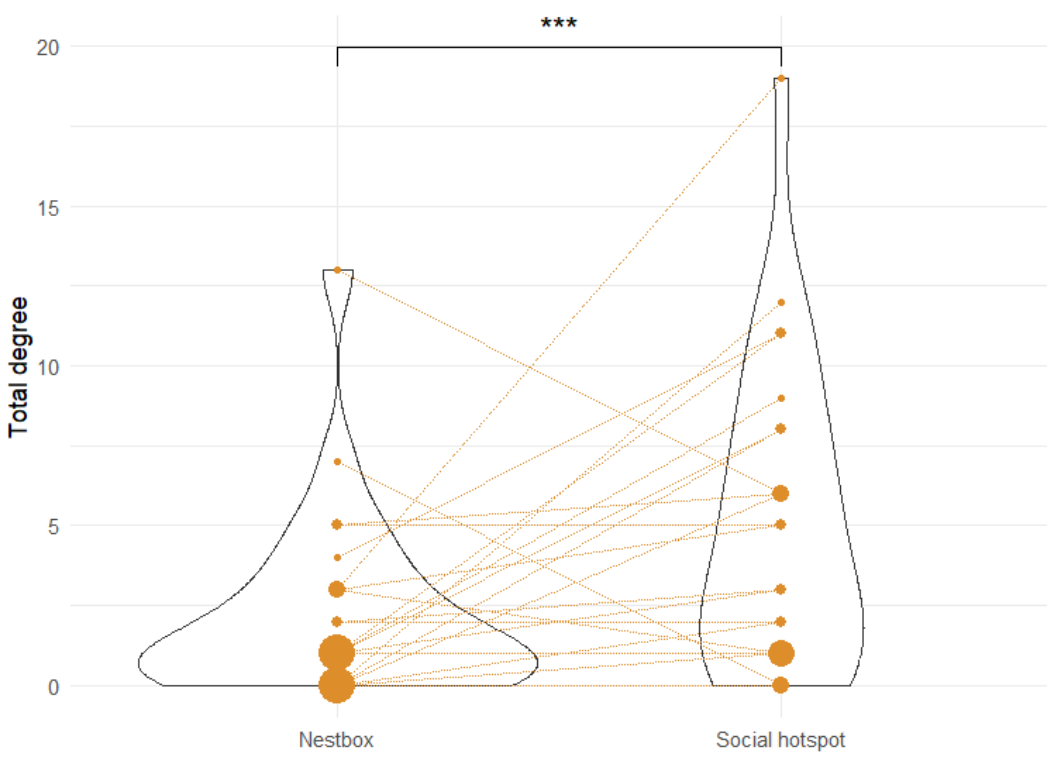

Figure 9: The total degree per individual heard at both types of location. *For all individuals that were heard at both a nestbox and social hotspot, the total number of interactions they had (total degree) is shown. The size of the points corresponds to the number of individuals with the same total degree. Lines link the same individual. Individuals had a higher degree at the social hotspot (3.0 ± 1.3) than at the nestbox (1.2 ± 1.3; likelihood-ratio test: $\chi^2(2)=17.9,\ p=0.0001$).*

Individuals also interacted with more unique individuals at social hotspots than at nestboxes (Fig. 10; social hotspot=2.9 ± 1.3 individuals, nestbox=1.1 ± 1.3 individuals; likelihood-ratio test: $\chi^2(2)=20.5, p<0.0001$). The number of individuals they interacted with increased as song duration increased (likelihood-ratio test: $\chi^2(2)=9.63, p=0.008$). An increase in song duration of 1 minute corresponded to an increase in unique interactions of 0.98 ± 1.14. There was no effect of an interaction between type of location and singing duration (likelihood-ratio test: $\chi^2(1)=0.729, p=0.4$).

When comparing each individual's network at the nestboxes and social hotspots, no overlap was found. Individuals did not interact with the same individuals at the nestbox or social hotspot.

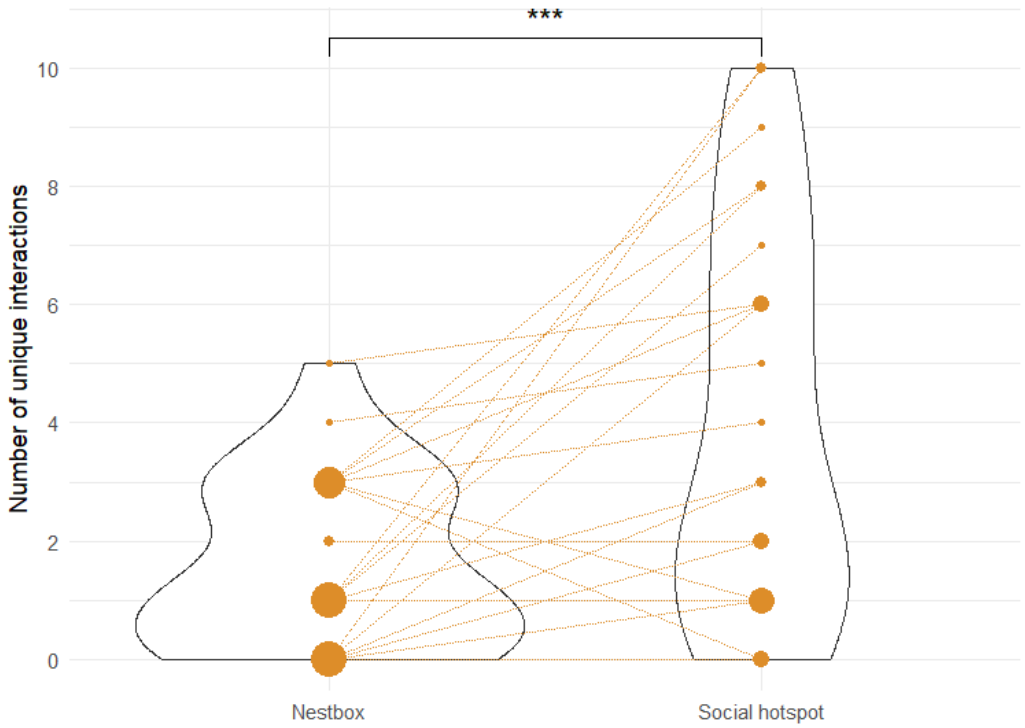

Figure 10: The number of unique conspecifics an individual interacted with at both types of location. *For all individuals that were heard at both a nestbox and social hotspot, the total number of unique conspecifics they interacted with is shown. The size of the points corresponds to the number of individuals with the same number of unique interactions. Lines link the same individual. Individuals met with more unique conspecifics at the social hotspot (2.9 ± 1.3 individuals) than at the nestbox (1.1 ± 1.3 individuals; likelihood-ratio test: $\chi^2(2)=20.5, p<0.0001$).*

Discussion

In this study, I show that the social network of wild zebra finches tends to be larger at social hotspots than in the breeding colony. At social hotspots, more zebra finch song and individuals were heard over the day than at nestboxes. While at a social hotspot, individual zebra finches had more interactions with conspecifics than they did in the breeding colony. However, I have also shown that the social network is not particularly strong or transferrable between different types of locations. Most individuals in this study were only heard at one location, and most dyads were only heard together once. Furthermore, dyads that associated in the breeding colony were never heard together at a social hotspot and vice versa.

As expected, the hotspots under consideration in this study showed higher singing activity during the day than nestboxes, aligning with the characterization of a social hotspot as a gathering place (Loning, Fragueira, et al., 2023). I did not find evidence of a dawn chorus as described for many territorial songbirds (T. J. Brown & Handford, 2003; Schlicht et al., 2023). However, nestboxes and hotspots differed in song distribution. At the nestbox, song production peaked in the morning and declined in the afternoon, corresponding to studies on behaviour and song in captive male zebra finches (Ollason & Slater, 1973; G. Wang et al., 2012). At the social hotspots we see a different trend, with more song during the second half of the day and song continuing even after sunset. This suggests the presence of a dusk chorus. Though not a focus of this thesis, a possible explanation is that males at the nestbox exhibit a similar pattern to captive finches, but that at the hotspots there are more non-breeding males that sing at the end of the day. Wild males in a social context could also exhibit different song patterns from captive single males. Wild males could preferentially go to and sing at hotspots at the end of the day, and this behaviour can simply not be performed during the lab studies. The reasons for a possible dusk chorus are unclear, since most hypotheses were formed for territorial songbirds (T. J. Brown & Handford, 2003; Schlicht et al., 2023) and would likely not apply to zebra finches (Loning et al., 2021; Loning, Verkade, et al., 2023; Tyson et al., 2024). More research looking into the daily singing behaviour of wild focal individuals is needed.

I found a larger social network at hotspots than in the breeding colony, with more individuals and more interactions between individuals. This fits my hypothesis that social hotspots serve as meeting places where zebra finches could benefit from increased sociality compared to the nest. The larger hotspot network could facilitate enhanced social information exchange, which can be increasingly valuable in the relatively harsh and unpredictable environment the zebra finch lives in (Rafacz & Templeton, 2003b; Rubenstein & Lovette, 2007). One benefit could be increased information on breeding status of other individuals, which could inform breeding synchronization (Brandl et al., 2021; Mariette et al., 2012a). Individuals prospect at other nests (Mariette et al., 2012a), but the social hotspots could provide information from a wider area. Hearing other birds at the trees could be informative since song output of zebra finches reflects their breeding stage (Loning, Verkade, et al., 2023) and testosterone levels (Cynx et al., 2005). Moreover, in captive zebra finches colony sounds were found to increase breeding synchronization (Waas et al., 2005), and the vocalizations at hotspots could have a similar effect.

Breeding synchrony is likely to have a positive effect on breeding success (Evans et al., 2016). It can reduce predation risk in multiple ways. For one, wild zebra finch pairs were found to act as

sentinel for each other, warning the partner inside the nest in case of a human disturbance (Mainwaring & Griffith, 2013). If such warnings are coordinated acoustically, e.g. if the male singing to its partner in the nest (Dunn & Zann, 1996) would abruptly stop, it is possible that neighbouring pairs could provide similar warnings as cue. This benefit would be optimized if the neighbours are at a similar breeding stage, with similar nest visitation rates. Secondly, chicks that fledge synchronously could gather in "crèches" where the dilution effect could provide a benefit against predation (Le Bohec et al., 2005; Lehtonen & Jaatinen, 2016; Munro & Bedard, 1977; P. & Balda, 1978). The existence of crèches in zebra finches has not been studied yet but was informally described (Zann, 1996) and during this study groups of recently fledged birds were observed sitting together in bushes and trees.

There are more possible advantages to having a larger social network at hotspots. Firstly, a zebra finch could acquire more information on foraging and resources (Aplin et al., 2012; Benskin et al., 2002; Mariette & Griffith, 2013). Though zebra finches have a stereotypical song, there is intra-individual variation (Hyland Bruno & Tchernichovski, 2017), which could signal information on fitness. Zebra finch song was found to reflect body condition and food availability (Cynx et al., 2005; Honarmand et al., 2015; Ritschard & Brumm, 2012; Zito et al., 2017) and can thus signal foraging success. Individuals with more social connections potentially have a larger benefit since they can receive more information from others (Wey et al., 2008). Birds in larger groups were also found to be more efficient problem-solvers and foragers (Morand-Ferron & Quinn, 2011). Having a larger network could aid social learning, as individuals can learn more effectively from familiar conspecifics (Cadieu & Cadieu, 2004; Swaney et al., 2001). Finally, gathering at hotspots with many conspecifics could decrease the risk of predation through dilution or increased vigilance (Beauchamp, 2008; Lehtonen & Jaatinen, 2016). Social trees are usually thorny and bushy and could therefore provide some safety from (aerial) predators. They can be a relatively safe spot for zebra finches to spend time, more so than the nestbox. All in all, aggregating regularly in these larger groups at temporally stable locations could be beneficial to individual zebra finches.

A study at the same site in 2023 found that birds interacted with substantially more individuals than I found (10 vs 3 individuals; ter Avest, 2024). They analysed fifteen days of recordings of hotspots, while I analysed seven days. This difference in sample size could partly explain the higher number of interactions. However, I do not think it explains all variation, as doubling the data would not necessarily lead to triple the number of interacting individuals. Alternatively, the variation could be due to different conditions in the spring of 2023 compared to 2024. In 2023 there was less attempted breeding and a high predation rate of the few initialized nests (Naguib et al., 2024). Possibly individuals spent more time at hotspots and thus had more associations than during a more favourable and successful breeding season. Firstly, non-breeding birds could simply have more time to spend at hotspots, since they are not building a nest, laying and incubating eggs and providing food for their nestlings. Secondly, the mentioned safety benefits of social trees could have been enhanced under increased predator presence. Furthermore, individuals could monitor the presence or absence of acquaintances at the hotspots, informing birds of the predation risk across the area. As theorized by Loning et al. (2024), the individuality of zebra finch song could facilitate this population monitoring. Lastly, visiting hotspots could be a more energetically efficient way to encounter the few breeding pairs and decide if and where to breed than flying over the whole area to check on nests. It is thus possible that the use of social

hotspots is dependent on environmental and ecological conditions, and that the benefits that individuals can obtain from spending time there are variable.

The social network uncovered in this study consisted mainly of single interactions between individuals, indicating that birds were not preferentially associating with specific others. Hearing two individuals together only once could be a chance encounter, whereas hearing them together multiple times (over multiple days) is stronger evidence of preferential association. In this study, only 15% of dyads interacted multiple times, with only 3% interacting three or more times. This indicates a loose, more ephemeral social structure. This contrasts with the study by ter Avest (2024), where a more robust network was found at hotspots and a higher proportion of dyads interacted multiple times. This could again be due to between-year differences. Higher predation risk and loss of familiar individuals was found to lead to stronger social bonds in other species (Firth et al., 2017; Kelley et al., 2011). While nest predation was high in 2023 (Naguib et al., 2024), it is not clear if predation of adults was also higher. If so, it could have strengthened social ties. Furthermore, many bird species mainly associate in pairs during the breeding season and group together during non-breeding seasons (Farine et al., 2015; Griesser et al., 2009; C. Wang & Lu, 2014). Possibly during less successful breeding years the zebra finch relies more on social bonds with others, while it is more focussed on the pair bond during breeding.

Of course, I could have found less repeated associations because of my methodology. It is conceivable that dyads interacted once in my data but interacted more on different days or at different locations. Analysing more data and identifying important hotspots, for example for the individuals from E, would be important for future research looking into the social networks. Moreover, I used the presence of song as a proxy for bird presence, but zebra finches will not sing continuously. Individuals were found to vocalise for just over half of the time that they were actually present at a hotspot (Loning, Fragueira, et al., 2023). Therefore, this approach does not give a complete picture of all birds present in a particular place and associations could be missed. Combining acoustic analysis with observations, or a different methodology using an automated radio tracking system or PIT-tags (Brandl et al., 2021; Tyson et al., 2024) could provide a more complete picture of the networks. Tracking systems would have the added advantage of providing information on females, since these are ignored using the song approach. The social networks of paired male and female zebra finches is expected to be very similar, since they spend most of their time together (Mariette et al., 2012b; McCowan et al., 2015; Tyson et al., 2024), but this has not been studied extensively yet.

I found that individuals did not meet the same conspecifics in the breeding colony as at the social hotspots. This contrasts with previous research where individuals that bred synchronously in the same colony also associated more at feeders (Brandl et al., 2021). Stable preferential associations have been found in numerous bird species and could have multiple benefits (e,g, Beck et al., 2020; Griffiths et al., 2004; Kurvers et al., 2013; Rose & Croft, 2017). In zebra finches, reproduction is opportunistic and not tied to seasonal cues like daylight but instead more dependent on rainfall and subsequent food availability (Zann, 1994; Zann et al., 1995). It is conceivable that maintaining social ties with (previously successful) breeding neighbours across different contexts and over time could help synchronize breeding over multiple breeding seasons (Brandl et al., 2019, 2021). Moreover, captive males sang more and females laid eggs more synchronously when hearing song playbacks of their own rather than a foreign colony (Waas et

al., 2005). This could indicate that being around familiar individuals increases reproductive success, thus promoting stable social ties. Associating with familiar individuals could also reduce energy expenditure on aggressive interactions, saving energy for e.g. predator avoidance (Griffiths et al., 2004).

However, I found that birds associated with different individuals in both contexts. This suggests that broadening the social network and increased information uptake is more important than strengthening familiar bonds. The social networks nevertheless still seem quite local: I found little evidence of mixing between the colonies. Meeting more individuals from the same colony could provide more local information on breeding success, which might be more beneficial than information from a wider area (Boulinier et al., 2008). Furthermore, zebra finches could have a certain measure of site fidelity and therefore, at least in successful breeding seasons, would not prospect or visit other areas a lot. A study at the same site found that most pairs with multiple broods in a season stayed in the same breeding colony instead of switching to another (Brandl et al., 2018). It is also possible that due to methodology I have missed associations linking the different types of locations. For example, Brandl et al. (2021) showed that dyads associated 14% more if they bred synchronously than if they bred 10 days apart, which could be too small of an effect to be perceivable in this study. To validate if the networks are indeed completely separate, more research is needed.

In this study, I found two different grouping levels in wild zebra finches. Combined with previous research showing the constant and stable pair bonds (Griffith et al., 2010; Tyson et al., 2024), this points to a multilevel social structure with pairs as the core unit, a social network at the nest and a larger social network in social trees. However, I did not find evidence of other characteristics of an MLS. There was little evidence of stable individual membership of the grouping levels, with few preferential associations resulting in a loose network. Furthermore, the nestbox network was not nested within the hotspot network and the association strengths did not differ between the two. This does not fit the traditional definition of an MLS as a hierarchical social structure, but points to an interesting social system with grouping levels that are qualitatively and quantitatively different in composition and size. More research is needed to give a clearer picture of the grouping stability over time and nestedness. Meanwhile, my results highlight the complex natural social structure of zebra finches. Since the zebra finch is an important model species in the lab, this could help interpret lab findings and inform housing decisions.

This study tentatively suggests that in wild zebra finch societies there is both an upper level of sociality (the social hotspots) and an intermediate level (the network in the breeding colony) present. This adds to a growing body of research showing that multilevel societies are not restricted to primates or other large-brained mammals, which have been the focus of this topic (Grueter et al., 2020). Finding these complex social structures in this small, nomadic songbird, combined with studies on MLSs in other birds (Camerlenghi et al., 2022; Papageorgiou et al., 2019) gives more insight into the different evolutionary pathways of multilevel societies. Instead of the mammalian focus on brain size, complexity of pair bonds and ecological conditions might be more important to the evolution of complex sociality and cognition in birds (Dunbar, 2009; Emery et al., 2007; Olkowicz et al., 2016). Other bird species with complex pair bonds or cooperative breeding systems would be promising candidates for the continued study of avian MLSs (Camerlenghi et al., 2022; Emery et al., 2007; Papageorgiou & Farine, 2021).

Conclusion

In this study I found different levels of social organization in wild zebra finches. Individuals tended to interact with more and different conspecifics at social hotspots than at the nest. This provides tentative support for the hypothesis that zebra finches live in multi-level societies. Different grouping levels seem to exist, with a smaller social network at the nest and a larger social network at social hotspots. However, the found networks have low strength and there is little support for stable individual membership of the groups. Future research with more data and more precise tracking methods such as automated radio tracking could help elucidate the zebra finch's social structure. Since the zebra finch is an important model species in the lab, understanding their natural social structure could help interpret lab findings and inform housing decisions. Finding evidence of such complex social structures in songbirds provides insight into the evolution of sociality in different taxa.

Acknowledgements & Artificial Intelligence statement

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Appendix A: AudioMoth settings

Table A1: *The settings used to program the AudioMoth recorders.*

Sample rate	32000 Hz
Gain	Medium
Sunrise/sunset rounding	1 minute
Recording duration	3595 seconds
Sleep duration	5 seconds
Energy saver mode	ON

Appendix B: scoring of song quality

Table B1: *Scores used to label songs. Adapted from ter Avest (2024).*

Score	Description
1-2	Can vaguely hear the song, can only see distance calls.
3	Can tell it is a song but cannot determine individual notes.
4	Song is distant, has one motif, or interruption makes song too unclear to identify.
5	Spectrogram is less clear but can still hear song clearly.
6	Song is distant, or increased interruption/noise: spectrogram is less clear.
7	Interruption/noise but spectrogram is still clear enough to determine individual.
8	Interruption/noise but clear spectrogram and can hear song well.
9	No interruption/noise, clear spectrogram but missing some elements of song.
10	Clear spectrogram, no interruption/noise.