Communication networks of wild zebra finches (*Taeniopygia castanotis*)

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Abstract

Communication networks are widespread across species, permitting information flow and facilitating social connections across space and time. In birds, communication networks are well studied in territorial species with long-range songs connecting individuals across space, where unintended listeners extract information from others' signalling interactions. Yet acoustic signals also play important social roles at short range, forming communication networks that connect individuals within larger social units. Wild zebra finches (*Taeniopygia castanotis*) provide a unique model system to examine such communication networks in a non-territorial species with multiple males singing at shared locations in close temporal proximity. Zebra finches breed in loose colonies in the Australian arid zone, typically stay near their partner, move around in pairs or small groups, and gather at social hotspots, thus forming dynamic, potentially multi-level, societies. Here, we used the individually distinctive male song, recorded over 1,835 song bouts at two breeding sub-colonies and three social hotspots to quantify singing activity. We identified 163 males based on spectrographic similarities, verified by a deep learning model (BirdNET), and constructed communication networks based on temporal singing proximity at shared locations, social hotspots and the breeding colony. We reveal higher singing activity at social hotspots, with no dawn song and singing peaking at different times of day between breeding sites and social hotspots. Communication networks, with distinct males singing in close temporal proximity, were apparent in both contexts, with larger networks at hotspots. These networks were not strongly nested, yet many individuals met repeatedly at either the hotspot or breeding sites and some even maintained associations across breeding colonies and hotspots, providing building blocks for a multi-level society. These networks may facilitate synchronized foraging and breeding as adaptations to a harsh and unpredictable environment. Additionally, our approach offers a novel road map for widening the understanding of communication networks.

Keywords: Communication networks, birdsong, multi-level society, social network, zebra finch, BirdNET, fission-fusion societies, vocal communication, environmental unpredictability

Introduction

Animals vary in communication and sociality, ranging from simple to complex signalling interactions and from solitary living to highly complex social groupings and networks (Ward & Webster, 2016). Sociality and communication are tightly linked, yet while social networks typically refer to spatial proximity of individuals (Croft et al., 2008), communication networks have been mainly considered for long-range signalling interactions where individuals do not associate closely (McGregor, 2005). In many cases, these signals peak at specific times of day, such as in the dawn song of territorial songbirds (Staicer et al., 1996; Kunc et al., 2005), and the singing and singing interactions can influence which individuals perceive the signal and how they respond (McGregor & Dabelsteen, 1996; Naguib et al., 1999; Todt & Naguib, 2000; McGregor, 2005; Foote et al., 2010; Logue, 2021). Such long-range signals may enable information transfer across large distances and can thus be crucial to determine movements, social decisions, such as mate choice, breeding decisions, responses to predators and other aspects of social synchronisation (Catchpole & Slater, 2008; Snijders & Naguib, 2017).

Studies on these long-distance networks have shown that information is not only gathered from a singer and its song but also by eavesdropping on the dynamics of vocal interactions among others, information that is not available when attending to singers separately, leading to the initial definition of communication networks (McGregor & Dabelsteen, 1996). Such relative differences can be important for decision making, such as reproductive decisions (Otter et al., 1999; Schmidt et al., 2006) and priorities in territory defence (Peake et al., 2001; Mennill & Ratcliffe, 2004; Naguib et al., 2004; Peake et al., 2005; Fitzsimmons et al., 2008; Amy et al., 2010; Foote et al., 2010). Eavesdropping on vocal interactions among others has been at the core of communication network approaches to birdsong (Peake, 2005; Naguib et al., 2011). Yet, biologically, a communication network, defined as

patterns of potential information flow, would be much larger, also including information extracted from individual songs and from direct interactions. Such wider approaches can be useful to better understand the link between communication networks and spatial networks, as well as to obtain a better understanding of information flow across large and complex social organizations in animal societies (Snijders & Naguib, 2017)

Because information from signals affects social decision making, including the initiation, maintenance and dissolution of social bonds, they can be expected to play a key role in the social organisation of non-territorial animal societies. For instance, in dynamic and more complex animal organisations such as multi-level fission-fusion societies, in which not only individuals but also social units at higher levels of organisation fission and fuse (Papageorgiou et al., 2019; Papageorgiou & Farine, 2021), signals carrying individually specific information might be key facilitators allowing individuals to maintain one-to-one or pair-to-pair connections within larger social units. However, the quantitative use of individually-distinct signals by animals in dynamic, potentially multi-level, societies has received little attention.

The zebra finch (*Taeniopygia castanotis*) in its natural habitat, the Australian arid zone, offers a highly suitable study system to address these knowledge gaps. Zebra finches provide a unique model organism for many lab-based studies (Griffith & Buchanan, 2010), and their dynamic social organisation offers scope to broaden the traditional concept of communication networks in order to better understand the role of signals in social organisation. Zebra finches live throughout the Australian arid zone and move around together with their mate (Tyson et al., 2024) and are encountered mostly as a pair and not in a group (McCowan et al., 2015). These pairs gather at social hotspots also during non-breeding times (Loning et al., 2023a) and additionally during breeding will associate with others in their loose breeding colonies (Brandl et al., 2021). When resources are highly clumped, birds can form temporarily large groups, such as near water (Zann, 1996; McCowan et al., 2015). These fission-fusion dynamics suggest that they might live in multi-level societies (e.g. pairs within loose groups, loose

groups within larger aggregations). Since male zebra finches each sing a single unique song motif with minor variation (Sossinka & Böhner, 1980; Sturdy et al., 1999) and both sexes have individually distinct calls (Elie & Theunissen, 2018), their dynamic social organisation is most likely facilitated by these distinctive vocal signals, allowing receivers to potentially identify others in different social settings and in different locations. Zebra finch vocalisations are very short-distance signals, with an average range of nine meters for their song, and the loudest calls in their repertoire have an average range of only 14 meters (Loning et al., 2021). These individually distinct close-range vocalisations therefore likely function to establish and maintain social connections through information exchange at gathering points, such as at the breeding area (Brandl et al., 2019c), at foraging sites (Brandl et al., 2019a; Brandl et al., 2021) or at the social hotspots (Loning et al., 2023a).

We took advantage of the wild zebra finch social system, in which birds vocalise and encounter conspecifics at different locations, to integrate communication networks and spatial networks (Snijders & Naguib, 2017; Loning et al., 2024) and so examine the network structure of a highly dynamic wild bird society. We quantified male singing activity throughout the day in a wild population of zebra finches in the Australian Outback, recording singing both at breeding sites and social hotspots (Loning et al., 2023a) using automated audio recorders. Using the individually distinctive male song (Sossinka & Böhner, 1980; Sturdy et al., 1999), we used singing as a proxy for presence at nests and hotspots and determined if different males would repeatedly sing at the same time at these locations. From these songs, we created communication networks and expected larger networks at the hotspots, with more individuals heard singing and associating there than in the breeding colonies. We also expected a hierarchical social structure with individuals at the hotspots interacting with conspecifics they associated with in the breeding colony, as well as others. Although only males sing, leading here to male-focussed networks, pairs stay almost constantly together (Tyson et al., 2024), suggesting that male song networks reflect a network among pairs.

Methods

The study was conducted from September to October 2024 in the Gap Hills area of the Fowlers Gap Arid Zone Research Station, New South Wales, Australia. This area consists of open shrubland with low bushes such as bluebush (*Maireana* sp.) and saltbush (*Rhagodia* sp.) as well as higher vegetation along natural creeks, mostly shrub-like trees such as prickly wattle (*Acacia victoriae*) and dead finish (*Acacia tetragonophylla*). There is an artificial water reservoir in the area (Fig. 1), and zebra finches at this site use nestboxes to breed, which are placed on poles near trees for shelter (Griffith et al., 2008). Nestboxes are placed in the area in six sub-colonies of about 30 boxes each.

Audio data collection

We recorded vocal activity at nestboxes and nearby social hotspots using time-programmable audio recorders (AudioMoth; Hill et al., 2019). AudioMoths were set to record from 90 minutes before sunrise to 90 minutes after sunset (settings: 32 kHz sample rate; medium gain; energy saver mode on). We monitored breeding activity by checking all nestboxes in the area every three days and attached AudioMoths to nestbox poles of active nests. We identified social hotspot locations by walking repeated transects, registering recurring observations of zebra finches and checking for the presence of faecal droppings. We combined this information with hotspot locations obtained in the same way in previous years, as they are generally temporally stable (Loning et al., 2023b). We then observed these potential hotspots three times for one hour between 0800 and 1230 hours on different days to confirm that they were actively used by zebra finches. We then placed AudioMoths at three identified social hotspots (all three were also in use in the previous year). Two social hotspots were located at the edges of a breeding sub-colony (colony D), and one was located between another sub-colony (colony E) and the central water reservoir (Fig. 1).

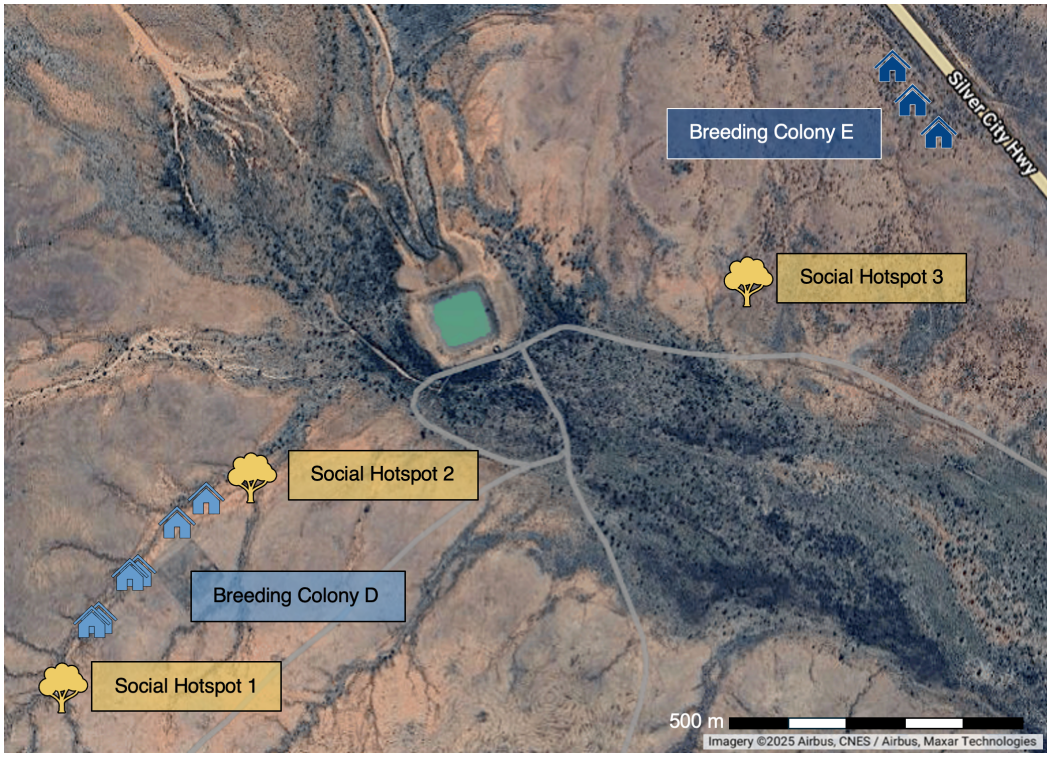

Figure 1. Map showing the field site at Gap Hills with positions of analysed nestboxes and social hotspots. Tree icons denote social hotspots, house icons denote nestboxes selected for audio analysis, with six located in breeding colony D and three in breeding colony E. The central dam, creek lines and highway are visible. Satellite image retrieved from Google Maps.

Audio analysis

For each of nine nestboxes (Fig. 1), we selected one day of audio recordings for analysis, assuming that one day is sufficient to record the locally breeding birds. We selected the day with the most favourable weather condition (i.e. no rain, little wind) during the egg-laying phase as males sing most during this phase of breeding (Loning et al., 2023b). The selected nests all produced fledglings but were active at different times during the study period. For the three hotspots, we selected audio from seven different days, two days for hotspots 1 and 2 and three days for hotspot 3 (Fig. 1). Where possible, we analysed hotspots on the same day as a nearby nestbox (at most five days difference), to minimise environmental variation such as wind affecting movement and sociality. In total, we analysed 248

hours of audio recordings, consisting of 140 hours of recordings at nine nestboxes (one day per nestbox) and 108 hours at three social hotspots (two to three days per hotspot).

Within these audio recordings, we first assigned zebra finch songs to individual males by listening to the song recordings and visually inspecting their sound spectrograms (window type: Hamming, window size: 1024) in Audacity® (version 3.7.1; Audacity Team, 2024), and later verified this using deep learning logarithms (see below). Zebra finch song has a distinct structure, with each male repeatedly singing an individually distinct motif (series of syllables), which is readily recognizable on spectrograms (Fig. 2) although some intraindividual variation exists (Sossinka & Böhner, 1980; Sturdy et al., 1999). A gap of more than five seconds between song motifs separated song bouts. We assigned a recording quality score to each song bout on a scale of one to 10. Only songs of high quality, typically with a score of six or higher, were assigned to an individual bird, while songs of lower quality were not included here. We established a database containing clear spectrograms of individual birds and compared newly encountered songs to this database. If song element frequencies, shapes and sequence within motifs, as well as the motif organisation of a new song, matched that of an already encountered individual, we assigned it to the same individual. Ambiguous cases were checked by a second observer. If there was no consensus on the classification, that song was not assigned to a specific individual. Out of the total 2,552 song bouts present in our recordings (248 hours), we assigned 1,835 song bouts (71% of song bouts) to 163 individuals (mean ± SD: 11.3 ± 15.9 song bouts per individual, range 1-113).

Based on the occurrence of individual songs, we determined the number of different locations visited by each individual. We quantified song activity over the day by summing the number of seconds containing song within each half-hour block, allowing us to compare singing activity at nestboxes and social hotspots.

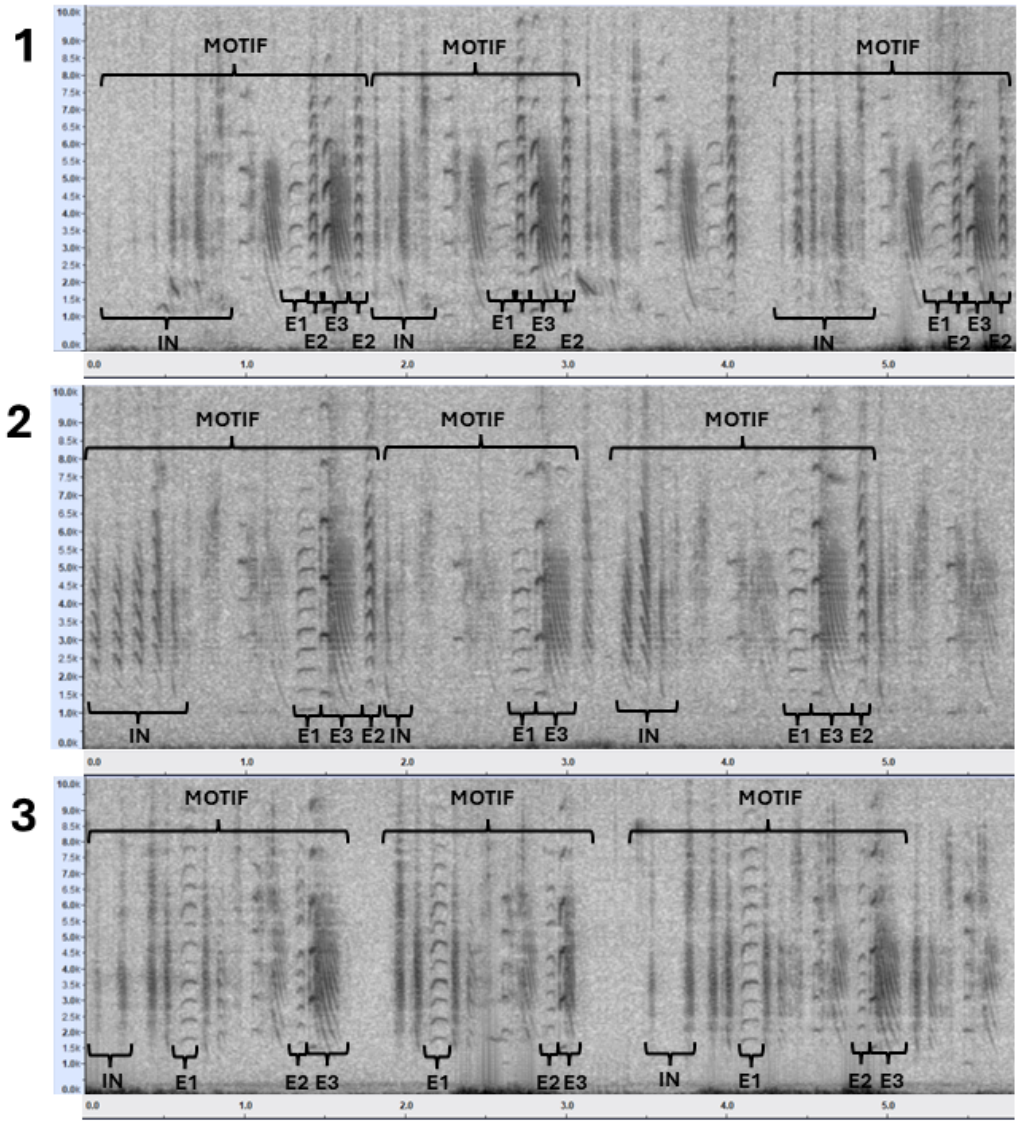

Figure 2. Example spectrograms of song bouts from three different individuals. The y-axis shows the frequency in kHz and the x-axis time in seconds. Darker shades correspond to a higher sound energy. Different elements of the motifs are annotated. IN denotes introductory notes, E1, E2 and E3 denote different song element types. The individuals (one per row) differ in element sequence, frequencies, and shapes. Intraindividual differences such as variation in motif duration and content are visible, e.g. individual 2 does not have element E2 in the second motif. Spectrograms were made using Audacity.

BirdNET validation of audio analysis

To validate whether or not the songs we had manually assigned to an individual based on visual inspections of sound spectrograms were indeed more similar to each other than to songs that we assigned to other individuals while accounting for potential bias and unavoidable variation in recording conditions, we used BirdNET (model version 2.4; (Kahl et al., 2021) as an impartial observer. BirdNET is a deep-learning model trained to recognise the vocalisations of over 6,000 bird species to the species level (including zebra finches), but it has not been trained to distinguish between zebra finch individuals. BirdNET was used as a pre-trained model without additional training or fine-tuning on our dataset, as this would have required using our individual labels, which we intended to validate independently. BirdNET's deep neural network processes each sound fragment and extracts a set of 1,024 numerical features. These so-called embeddings are a compact representation that captures the patterns relevant for distinguishing bird species (McGinn et al., 2023). While originally designed to support species classification, the embeddings can also be treated as a 1,024-dimensional feature vector that characterises the acoustic properties of individual bird sound recordings.

We extracted BirdNET embeddings representing zebra finch songs for subsequent intra- and inter-individual comparison. Since BirdNET internally uses three-second segments for classification, we trimmed song bouts to the first three seconds and also kept the last 3 seconds for bouts over 6 seconds long. Song bouts shorter than three seconds were left unaltered (BirdNET pads segments shorter than three seconds). This resulted in 2,617 song segments (belonging to 163 individuals) for which we extracted the corresponding embeddings using BirdNET-Analyzer (GUI version 2.1.1; settings: overlap 0 seconds, batch size 1, no speed modification, bandpass frequency 0-15 kHz). We then calculated cosine distances (i.e. 1 - cosine similarity, which measures the angle between vectors irrespective of their magnitude) between the embeddings for all combinations of segments using SciPy's *spatial.distance.pdist* (with metric="cosine") function in Python (version 3.13.5). This resulted in a combined 3.4 million intra- and interindividual comparisons. We further divided comparisons into

three categories based on where the two compared segments originated: comparisons made between segments from (1) the same one-hour audio recording, (2) the same date, and (3) different dates. These categories reflect a potential increase in recording condition differences and a decrease in certainty of songs actually having been sung by the same individual.

Video recordings at social hotspots and analysis

To quantify zebra finch visit durations for constructing communication networks, we filmed the three social hotspot trees using tripod-mounted action cameras (GoPro Hero5 Black, resolution of 1280x720, 25 FPS, narrow field of view) for a total of six days (one to three days per social hotspot) from a height of about 150 cm at a distance that allowed the whole tree to be in frame in order to approximate visit durations by scoring arrivals and departures. To estimate a conservative (i.e. minimum) average time zebra finches spend at a social hotspot, we analysed 64 hours of video footage of the three social hotspots. Each departure from and arrival at the hotspot was scored using BORIS (Behavioural Observation Research Interactive Software; version 9.2.1). For each arrival, we matched the next available departure to calculate the minimum duration each bird spent on the tree by keeping a queue of arrival times, matching each arrival to the earliest unmatched departure. To compute visit durations, we excluded visits lacking matching pairs attributable to missed arrivals or departures on video and birds staying for extended periods. To limit the influence of extreme outliers and focus on typical visit durations, bird visits lasting longer than one hour were excluded from the main analysis. This cutoff was based on preliminary data exploration, which showed that durations exceeding one hour were rare and probably represented atypical or faulty events. Applying this filter improved the robustness of summary statistics while retaining the majority of observations. In total, we recorded 686 bird visits with a mean duration of 1,263 seconds (± 21 minutes; median 1,364s ± 722s; IQR 634 – 1,750s).

238 **Communication network characteristics**

239 To determine the connections between individuals, we considered individuals that sang within 1,263
240 seconds of each other (the mean visit duration at social hotspots, see above) as being present at the
241 same time (associating) and as being socially interacting. Using these associations, we determined
242 social network edges, representing connections between two individuals. We constructed networks
243 (1) based on all associations and (2) based only on repeated associations. For individuals that were
244 heard both at a nestbox and a social hotspot (N = 24), we calculated the number of associations and
245 the number of unique associations (i.e. the number of unique individuals associated with) they had at
246 nestboxes and social hotspots. If the bird was heard at multiple nestboxes or multiple social hotspots,
247 we used the total number of associations or the number of unique associations and calculated how
248 long each individual sang (summed duration of all the song bouts) at each type of location.

249

250 **Statistical analysis**

251 All statistical analyses were performed using R (version 4.5.1; R Core Team, 2025). Linear mixed-effect
252 models (LMMs) and generalised linear mixed-effect models (GLMMs) were constructed using the *lmer*
253 and *glmer* functions from the 'lme4' package, respectively (Bates et al., 2015). Model assumptions
254 were checked using the *simulateResiduals* and *testDispersion* functions (for Poisson GLMMs) from the
255 'DHARMa' package (Hartig, 2024). We tested for statistical significance of variables with two categories
256 using estimated marginal means (EMM) with the *emmeans* function from the 'emmeans' package
257 (Lenth, 2025). We also used this function to obtain the reported mean ± SE and contrasts for all mixed
258 model data. To test interaction effects and variables with more than two categories, we compared an
259 interaction model to a model without the interaction term with a likelihood-ratio test, using the
260 function *anova* from the 'stats' package.

261 To test for differences in singing at the nestboxes and social hotspots, we compared the total duration
262 of song and the number of individuals heard per day between social hotspots and nestboxes using a

LMM and a GLMM with a Poisson distribution, respectively. For both models, we accounted for the different number of observation days for the different locations (N = 1 for all nestboxes, N = 2 for hotspot 1 and 2, N = 3 for hotspot 3) by adding the date and the location as non-nested random intercepts.

For each comparison between BirdNET embeddings, we calculated the cosine distance. We then used a LMM to test the effect of comparison type (intra- or interindividual) as well as song origin (from the same one-hour audio recording, the same date, or different dates) and their interaction on cosine distance. We included the assigned individuals of both compared songs (the individual for song 1 and for song 2 was the same in the case of an intraindividual comparison) as crossed random intercepts.

To quantify the communication/social networks, we obtained network metrics and graphs using the *igraph* package (Csárdi & Nepusz, 2006). For the nestboxes and social hotspots, we calculated and compared the number of nodes (order) and edges (size) of the repeated association network (defined as dyads with two or more interactions between them) per day using Poisson GLMMs with the same random effect structure (see above). For these order and size models, we set the maximum number of iterations to 100,000 and changed the optimizer to 'bobyqa' to solve convergence issues. We then compared the total number of associations per individual and the number of unique associations between breeding sites and social hotspots using Poisson GLMMs with individual ID as a random intercept. For these models, we included song duration in minutes as a covariate.

Ethical note

We collected all audio and video data using non-invasive methods. Audio and video equipment was placed while minimising disturbance. Approval was granted by the Macquarie University Animal Ethics Committee, and the study was conducted under a New South Wales DPIE Scientific Licence SL100378, Ethics ARA 2018/02.

287 **Results**

288 **Singing activity at breeding sites and social hotspots**

289 In 246 hours of recordings, comprising nine nestboxes (breeding sites) at two breeding sub-colonies
290 and three hotspots, a total of 163 males were identified individually by their song. Most individuals
291 were heard at only one location (N = 126), with fewer individuals heard at more than one location (two
292 locations: N = 23, three locations: N = 9, four locations: N = 4, five locations: N = 1). In total, 24
293 individuals (14.7%) were heard at both a social hotspot and the breeding sites. Zebra finch males did
294 not sing at dawn, i.e. the hour before sunrise, at either location. Birds started singing around the same
295 time of the day at both locations, breeding sites and social hotspots (Fig. 3a). Yet, at the breeding sites,
296 most song occurred earlier in the day between sunrise and noon. At the social hotspots, most song
297 occurred during the second half of the day. Furthermore, song continued at the social hotspots for
298 longer, with a higher prevalence of song after sunset than at the breeding sites. The average duration
299 of song in minutes per day at social hotspots (mean ± SE: 23.9 ± 4.4, N = 7) was significantly higher than
300 at breeding sites (6.8 ± 3.5, N = 9; EMM: $t(6.4) = 3.2$, $P = 0.02$; Fig. 3b). Furthermore, significantly more
301 individuals were heard during the day at social hotspots (21.2 ± 4.9, N = 7) than at the breeding sites
302 (8.7 ± 1.6, N = 9; EMM: $z = 3.3$, $P = 0.001$; Fig. 3c).

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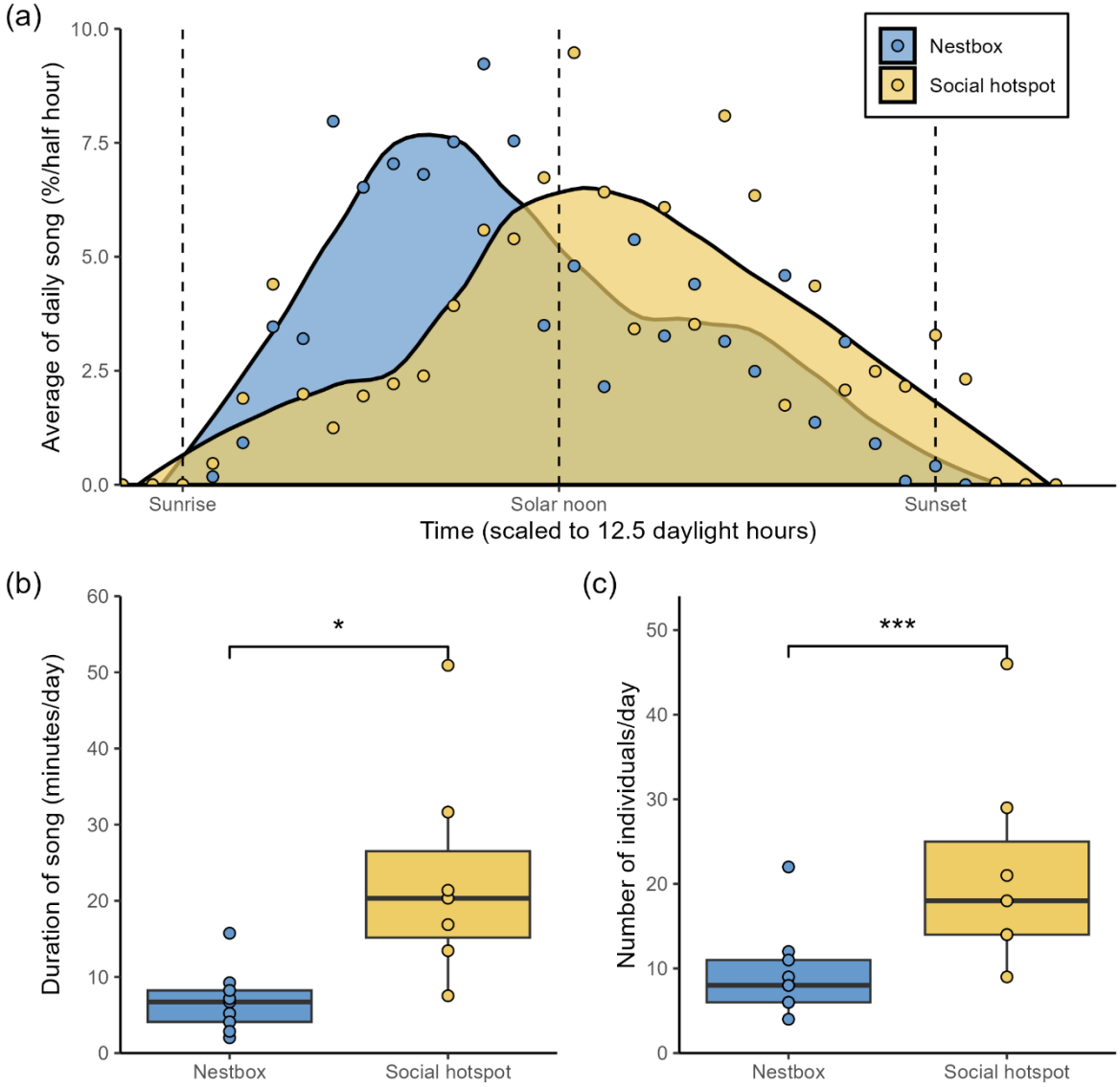

Figure 3. (a) The average distribution of song over the day for breeding sites (nestboxes) and social hotspots. The time is scaled to an average day of 12.5 hours. Sunrise, solar noon, and sunset are denoted by the dashed vertical lines. The y-axis shows the proportion of total daily song that occurred per half hour. The average duration of song in minutes per day (b) and the number of individuals heard per day (c) was higher at social hotspots than at breeding sites. * denotes $P < 0.05$, *** denotes $P = 0.001$.

312 **BirdNet validation of song classification**

313 Songs that we assigned by visual inspection of sound spectrograms as produced by the same individual
314 were more similar using BirdNet analyses, as cosine distance for intra-individual song comparisons
315 (0.304 ± 0.004) was significantly lower than for inter-individual comparisons (0.362 ± 0.004; EMM: z =
316 156.3, $P < 0.001$; Fig. 4). There was also a significant interaction between song comparison type (same
317 individual and different individual) and sound origin (same bout, same day, different day) (likelihood-
318 ratio test: $\chi^2(2) = 578.5$, $P < 0.0001$). The difference between intra-individual and inter-individual song
319 comparisons was largest for compared songs from the same one-hour recording (0.070 ± 0.001),
320 smaller for the same date (0.053 ± 0.001), and smallest for different dates (0.050 ± 0.001; all $P < 0.0001$;
321 Fig. 4). However, the BirdNET embeddings probably did not exclusively reflect zebra finch song, but
322 also reflected recording conditions, as sound origin differences also affected the cosine distance (Fig.
323 4). Overall, songs originating from the same one-hour recording had lower cosine distances (0.305 ±
324 0.004) than those recorded at the same date (0.340 ± 0.004), and these in turn were lower than those
325 comparisons with songs recorded on different dates (0.354 ± 0.004; likelihood-ratio test: $\chi^2(2) = 19{,}346$,
326 $P < 0.0001$). These differences likely cannot be attributed exclusively to potential errors in individual
327 assignment as not only the intra-individual, but also the inter-individual comparisons originating from
328 the same one-hour recording had lower cosine distances (intra: 0.270 ± 0.004 ; inter: 0.340 ± 0.004)
329 than those made between recordings of the same date (intra: 0.313 ± 0.004 ; inter: 0.366 ± 0.004) and
330 those of different dates (intra: 0.329 ± 0.004 ; inter: 0.380 ± 0.004; EMM: all pairwise $z > 16.7$ and $P <$
331 0.0001; Fig. 4).

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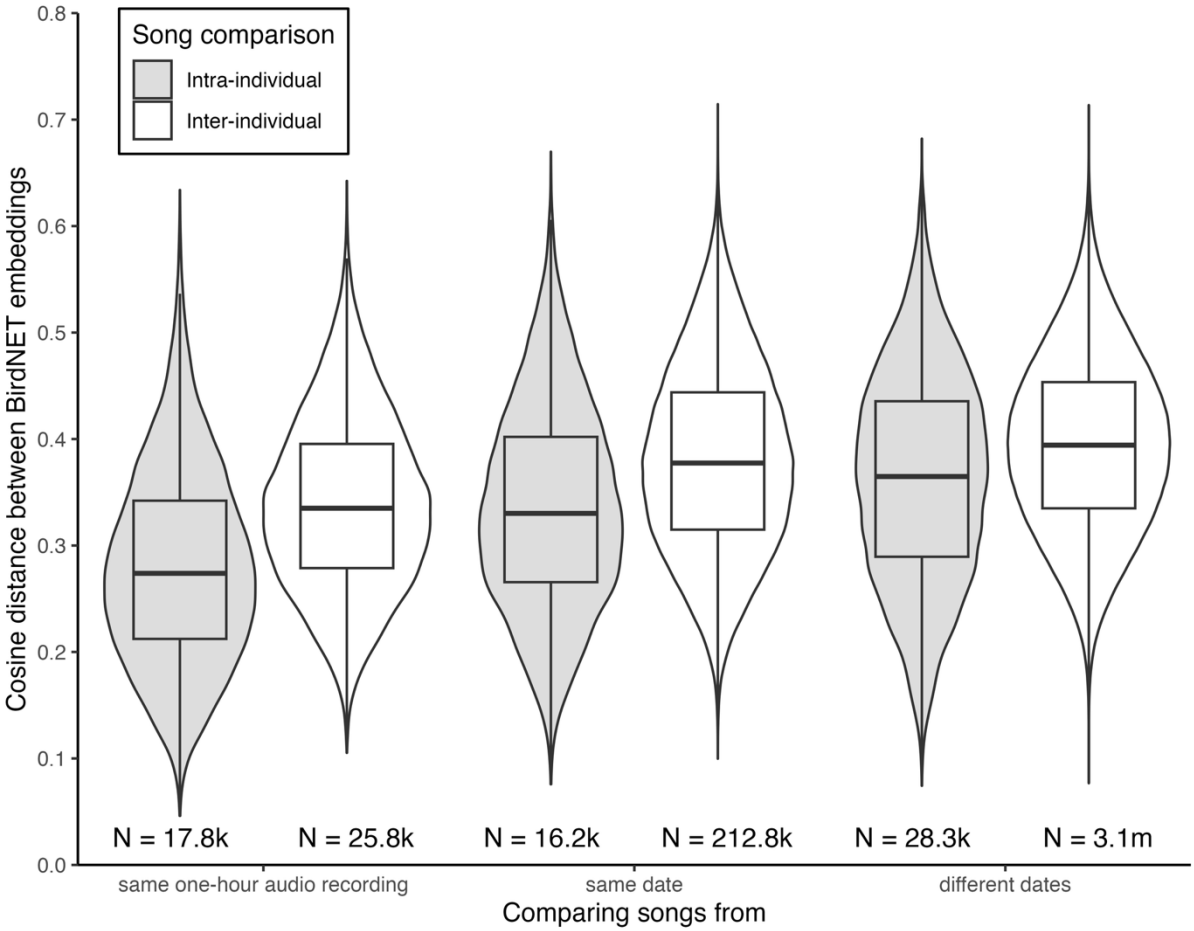

Figure 4. Comparisons of extracted BirdNET embeddings as validation of individual identification. We calculated cosine distances between embeddings of 2,617 songs, resulting in 3.4 million comparisons. The cosine distance or dissimilarity ranges from zero (vectors have the same direction) to two (vectors have the opposite direction). Across song origins, cosine distance was lower for intraindividual song comparisons (i.e. between songs of the same individual as assigned based on spectrographic similarities) compared to interindividual comparisons. This difference was biggest when recording conditions were similar (i.e. with both songs originating from the same one-hour audio recording), whereas it was smallest when conditions were potentially most different (songs recorded on different days). Each song comparison type-origin combination differed from the other five (EMM: all pairwise $z > 16.7$ and $P < 0.0001$).

346 **Communication network characteristics**

347 Zebra finches showed non-uniform network structures at both breeding sites and social hotspots. 151
348 out of 163 identified individuals had an association. However, most of the 473 observed dyads
349 consisted of only one association (86% of dyads), while only a small fraction of dyads associated three
350 or more times (3.2%; Fig. 5a). When we filtered the network to represent repeated associations
351 (defined as dyads with two or more interactions between them), 59 individuals and 66 dyads remained
352 (Fig. 5b). Of these 66 dyads, five dyads showed associations at both location types, indicating that most
353 individuals, within the analysed time frame, have social ties either in a breeding colony or at social
354 hotspots, but not both.

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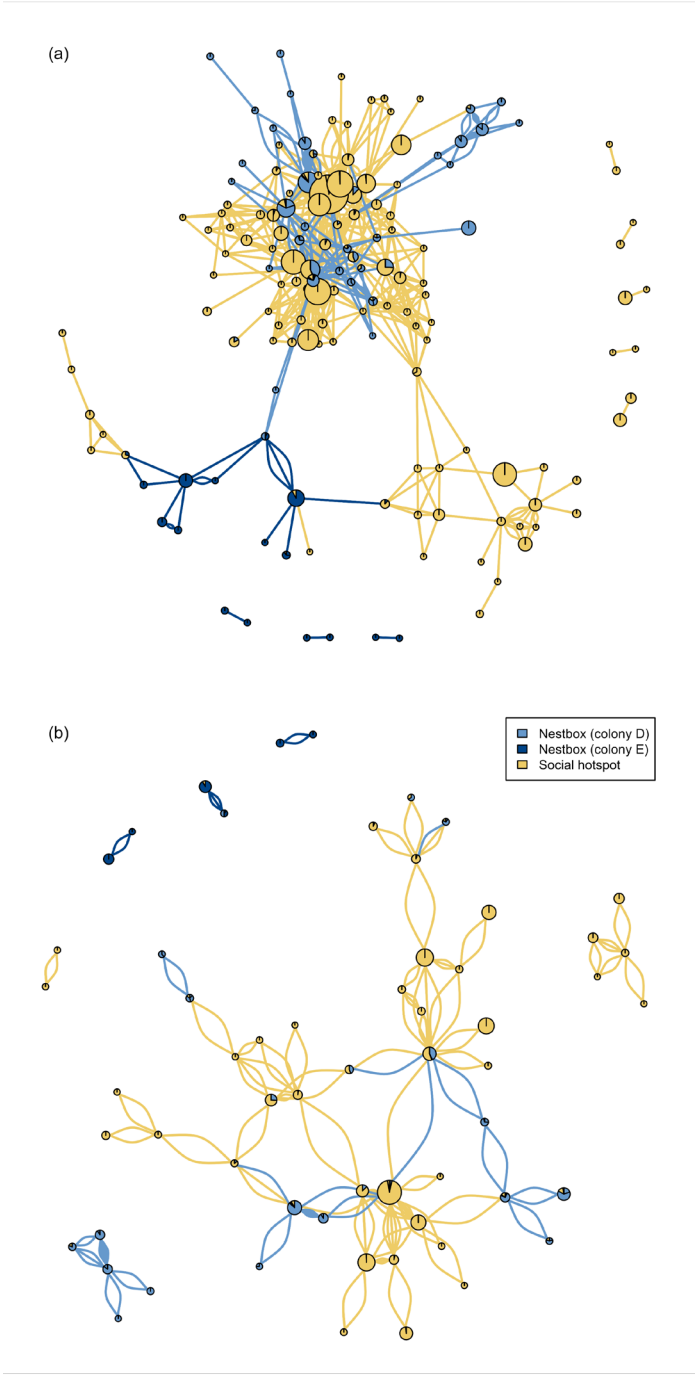

Figure 5. The social network for (a) all associations and (b) all repeated associations, i.e. dyads that were identified together at least two times. The pie shapes represent individuals (nodes), with coloured slices representing the relative amount of time they spent singing in different locations. The size of the node scales by the total amount of time that node was heard singing. The lines represent the song-based associations (edges). The colours of the edges correspond to the location where that singing took place.

When taking all associations into account, the network on a given day was larger at social hotspots than at the breeding sites. At social hotspots, networks had more nodes (58.6 ± 24.8; EMM: $z = 3.3$, $P < 0.001$) and more edges (48.1 ± 20.0; EMM: $z = 3.3$, $P = 0.001$) than at the breeding sites (13.1 ± 4.0 and 11.4 ± 3.5, respectively). Results were qualitatively similar for the repeated association network (containing only those dyads with two or more associations) on a given day. Also, at social hotspots, networks had more nodes (9.2 ± 3.5; EMM: $z = 2.7$, $P = 0.01$) and more edges (9.5 ± 4.2; EMM: $z = 2.1$, $P = 0.04$) than at breeding sites (3.6 ± 1.3 and 3.9 ± 1.5, respectively).

Network at the individual level

In total, 24 individuals were recorded singing at both a social hotspot and a breeding site. Birds that sang longer had more associations, and this relation was stronger at social hotspots than at breeding sites (likelihood-ratio test: $\chi^2(1) = 4.0$, $P = 0.05$; Fig. 6a). Furthermore, these individuals had more associations at social hotspots than at breeding sites (social hotspot = 8.6 ± 1.2, breeding site = 3.9 ± 0.6; EMM: $z = 6.6$, $P < 0.0001$; Fig. 6b). Individuals also had more unique associations (i.e. associated with more individuals) at social hotspots than at breeding sites (social hotspot = 7.0 ± 1.0, breeding site = 3.4 ± 0.5; EMM: $z = 5.9$, $P < 0.0001$; Fig. 6c).

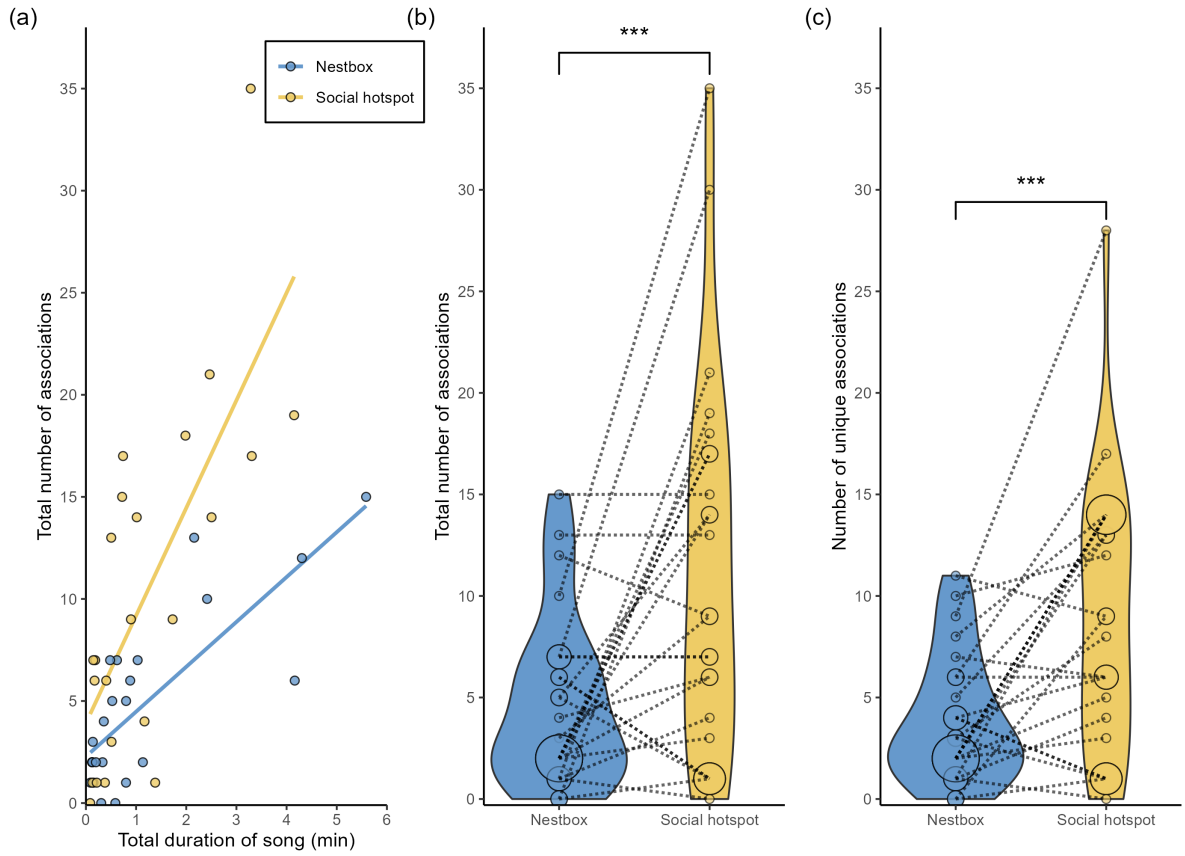

Figure 6. Total number of associations and number of unique associations at the individual level. Only individuals that were heard at both a breeding site and a social hotspot are shown. (a) Birds that sang more had more associations, and this relation was stronger at social hotspots than at breeding sites. (b) Individuals had more associations at the social hotspot than at the breeding site. (c) Individuals met with more unique conspecifics at the social hotspot than at the breeding site. Circle size corresponds to the number of individuals. *** denotes P = 0.001.

Discussion

Here we reveal distinct locations at which wild zebra finches sing in close spatial and temporal proximity, namely their breeding colony and at social hotspots. Song at these locations was never produced at dawn, in contrast to many territorial species, but peaked at different times of day, at the breeding colony in the morning and at the social hotspots in the afternoon. At both locations, multiple

individually identified birds were singing in close temporal proximity in a communication network. The networks at the breeding colony and social hotspots were distinct, with networks at the social hotspots being larger than those in the breeding colony. Most individuals were heard at one location only, and most dyads of males were heard together once, yet we also identified several males that sang together at different times. Most dyads that associated in the breeding colony were not heard together at a social hotspot and vice versa, yet a few dyads (five) were identified at multiple locations. These findings suggest that within this relatively short time frame studied, breeding sites and social hotspots served as distinct sites for social interactions, with a few individuals and dyads forming a bridge between them. These findings also suggest that the males of neighbouring breeding pairs do not move together as a unit to these hotspots, which can be hundreds of meters away from their breeding site, but that the decision to visit social hotspots is likely more a decision taken by an individual or a pair.

The higher singing activity at the social hotspots was predicted, as social hotspots are defined as gathering places (Loning et al., 2023a) and zebra finch males sing all year round at various locations (Loning et al., 2023b). Singing in different social contexts is interesting as it might be triggered mechanistically through different internal and external processes (Waas et al., 2000; Wang et al., 2012), while also having different functions and implications. Singing at the breeding colony may primarily reinforce pair bonds and indicate local breeding activity, thus providing reproductive cues to neighbours (Loning et al., 2023b), which are known to coordinate their breeding with one another (Brandl et al., 2019c). Singing at social hotspots, or in similar contexts in other species where individuals substantially vocalize in groups forming similar types of communication networks (Cure et al., 2009; Major & Jones 2011; Calcari et al., 2021; Devogel et al., 2024) might have a wider social trigger and provides information to larger groups, potentially transferring information about resources, predation risk and reproductive states and allowing individuals to create social bonds, and perhaps coordinate breeding at a broader local scale.

The absence of dawn song at either location highlights an important distinction to the daily singing activity of well-studied territorial songbirds in the Northern hemisphere, where dawn song is strongly associated with territory defence and mate choice (Catchpole & Slater, 2008). These functions appear only marginally relevant in species like zebra finches, as they are not territorial and most of their singing occurs after pair formation. Consequently, song in such species is considered to have its primary function within established pairs and in social groups (Loning et al., 2024). Also, the very clear individual distinctiveness of the single individual zebra finch song motif appears almost unique among songbirds and is likely to facilitate establishing and maintaining social bonds in their dynamic social organisation. Moreover, the difference in peak singing times at breeding colonies and social hotspots suggest behavioural routines which may allow individuals to predict when to meet whom, or how many others, at which location. This pattern might have been specific to the breeding period, as overall birds may visit hotspots more frequently when they are not breeding, and thus do not have to trade off activities for self-maintenance and socialising with reproduction, and are not tied to regular visits to a breeding site. Taken together, the communal singing pattern of zebra finches leading to communication networks, along with the individual distinctiveness of the song and other differences in singing compared to territorial species, widens our view on the function of birdsong, and provides the potential to study how information is shared across communication networks and wider social organisations.

Next to a higher singing activity, social hotspots also included larger song networks, with more distinct individuals and singing associations than in the breeding sub-colonies, further supporting the idea that social hotspots serve as meeting places (Loning et al., 2023a). The larger hotspot network could facilitate enhanced social information exchange across familiar and unfamiliar individuals, which can be increasingly valuable in the relatively harsh and unpredictable environment the zebra finch inhabits (Rafacz & Templeton, 2003; Rubenstein & Lovette, 2007). One benefit could be increased information on the breeding status of other individuals, which could inform breeding synchronization (Mariette & Griffith, 2012b; Brandl et al., 2021) as males also sing more in groups during breeding periods than in

periods without breeding (Loning et al., 2023b). While individuals can obtain breeding information by prospecting others' (Mariette & Griffith, 2012a; Brandl et al., 2019b), social hotspots could provide access to information from a wider area and in a more centralised, readily available location. In zebra finches, reproduction is opportunistic and not only regulated by photoperiod, but instead strongly dependent on rainfall and subsequent food availability (Zann, 1994; Zann et al., 1995). Maintaining social ties with (previously successful) breeding neighbours across contexts and over time could facilitate synchrony across multiple breeding attempts (Brandl et al., 2019a; Brandl et al., 2021). Moreover, in captive zebra finches, colony sounds were found to increase breeding synchronisation (Waas et al., 2000), and the vocalizations at hotspots could have a similar effect. While the existence of social hotspots has been shown earlier (Loning et al., 2023a), our finding that the same individuals repeatedly can be identified to meet, expands on earlier findings, showing that the hotspots are not just anonymous gathering sites, but reveal a social structure with repeated encounters. The combination of encountering known and unknown individuals would allow for different levels of information exchange that can be relevant for various movement, foraging and breeding decisions in such an unpredictable environment (Benskin et al., 2002; Aplin et al., 2012; Mariette & Griffith, 2013).

Listening to other birds at social hotspots could also be valuable to gain other types of information. Zebra finch song output reflects, for instance, not only breeding stage (Loning et al., 2023b), but also early developmental background (Holveck et al., 2008; Honarmand et al., 2015), condition (Ritschard & Brumm, 2012) and testosterone levels (Cynx et al., 2005) and may therefore signal condition, foraging success, and fitness. Any such more subtly coded information might be more readily accessible from an already familiar song by known individuals. Indeed, our finding that at least some individuals can be identified to meet repeatedly, suggests that the hotspots are not just anonymous gathering sites but locations to encounter specific familiar individuals, facilitating such more subtle information exchange. Such stable preferential associations have been found in numerous bird species and could have multiple additional benefits (Griffiths et al., 2004; Kurvers et al., 2013; Rose & Croft, 2017; Beck et al., 2020). For example, associating with familiar individuals could reduce the frequency

or intensity of aggressive interactions, thereby conserving energy that could be allocated to vigilance or predator avoidance (Griffiths et al., 2004). The combination of encountering familiar and less familiar individuals would also allow for different levels of information exchange that can be relevant for various movement and foraging decisions in such an unpredictable environment (Benskin et al., 2002; Aplin et al., 2012; Mariette & Griffith, 2013). Individuals with more social connections potentially have greater benefits since they have access to more information from others (Wey et al., 2008), leading to higher efficiency in problem-solving and foraging (Morand-Ferron & Quinn, 2011; Aplin et al., 2015; Snijders et al., 2018; Snijders et al., 2021). Having a larger network could also aid social learning, as individuals learn more effectively from familiar conspecifics (Swaney et al., 2001; Cadieu & Cadieu, 2004). Finally, gathering at hotspots with many conspecifics may reduce the risk of predation through dilution or increased vigilance (Beauchamp, 2008; Lehtonen & Jaatinen, 2016). Social network structure indeed can be shaped by predation risk, which is known to strengthen associations in other species (Kelley et al., 2011; Firth et al., 2017; Heathcote et al., 2017). In our study population, predation pressure likely varies between years (Naguib et al. 2024), which likely influences temporal variation in network structures. Further, breeding state may influence social network structure, as many species, including zebra finches, associate mainly in pairs during breeding periods, but form larger groups during non-breeding periods (Griesser et al., 2009; Wang & Lu, 2014; Farine & Whitehead, 2015; Kurvers et al., 2020). This suggests that the loose structure we observed may reflect the breeding season, and networks could be more cohesive outside this period.

The network observed in this study primarily consisted of single encounters between individuals. Only 14% of dyads encountered each other multiple times, with only 3% interacting three or more times, indicating that birds were not preferentially associating with specific others within the short time frame of our analysis. The low rate of repeated dyadic interactions in our data, therefore, points to a loose, more ephemeral social structure. Yet, most likely the dyads recorded as interacting only once actually interacted more frequently, either on different days or at other locations. This is supported by the observation that the relationship between total singing time and the number of detected interactions

did not reach an asymptote, suggesting that additional data collection most likely will reveal a substantially larger and more connected network. In addition, the use of song as a proxy for presence has limitations, as zebra finches do not sing continuously, yet both males and females additionally communicate through frequent calling. Individuals were found to sing for just over half of the time that they were actually present at a hotspot (Loning et al., 2023a), meaning that some associations likely have been missed. Combining acoustic analysis with observations, including the individually specific calls, 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. Such tracking systems would also capture female associations, which are overlooked when relying on song alone, although given their close spatial association (Mariette & Griffith, 2012a; McCowan et al., 2015; Tyson et al., 2024), pair members are expected to form highly similar networks (Brandl et al., 2019a).

The two relatively separate networks at the breeding colony and the social hotspots shown in this study, combined with previous findings of stable pair bonds (Griffith et al., 2010; Tyson et al., 2024), suggest that their social system may share some features of a multi-level social structure, with pairs as the core unit, distinct social associations at the nest and social trees as distinct higher level social units and potentially fusing of these social units later in the season. However, other defining characteristics of a multi-level society were less apparent. Individual membership within grouping levels was flexible, with few repeated associations, resulting in a relatively sparse network. Furthermore, the breeding site network was not clearly nested within the social hotspot network, as we initially predicted, and association strengths did not differ substantially between the breeding colony and social hotspot levels. This does not fit the traditional definition of a multi-level society as a hierarchical social structure (Grueter et al., 2020). Further work is needed to determine whether zebra finch societies show the temporal stability and hierarchical nesting characteristics of a multi-level society or if wild zebra finch social organisation is more consistent with a generally more fluid fission-fusion social structure (Aureli et al., 2008). It is possible that a hierarchical network becomes more evident with longer-term or finer-scale data. Meanwhile, our findings give new insight into the social structure of a widely used model

species. Given this widespread use of zebra finches as a model species in the lab, a clearer understanding of zebra finch natural social dynamics may also improve the interpretation of lab findings and inform best practices in captive housing (Griffith et al., 2017).

Taken together, our findings show that wild zebra finches sing near their breeding site and at social hotspots at different times of day, with a distinct lack of dawn song. This highlights that the context and potential function of their singing differ from those of classically studied territorial songbirds, as previously noted for other song characteristics (Loning et al., 2024). Our establishment of using BirdNET embeddings for the validation of individual classification demonstrates a promising approach to scale up the study of communication networks, opening the door for more advanced future studies. Male song revealed different levels of social organisation, with individuals connecting with more and different conspecifics at social hotspots than at the breeding colony, and a few individuals maintained associations across both sites, linking sub-units and suggesting elements of multi-level societies where information can flow through vocal interactions. However, the overall low strength of the networks suggests that birds mostly move around as pairs, meeting others opportunistically at social hotspots or the breeding area. This reflects a social organization that is at the interface between a multi-level society of stable hierarchical subgroups and a more dynamic fission-fusion society with individualistic network structures. Such a dynamic system might be adaptive in the harsh and unpredictable environment of the Australian Outback, as birds have stable social subunits (the pair) connected to different familiar individuals at different locations, providing relevant information on resource acquisition, predation risk or breeding state. Encountering a variety of other, socially less stable connected individuals will allow both males and females to draw information from a wider network, and may be important to gather population-wide information, for instance, on dispersal and immigration patterns, as well as potential novel food sources, such as when unfamiliar individuals are in better condition.

Acknowledgements & Artificial Intelligence statement

We are grateful to Marie-Anne Bellon and Tis Voortman for their assistance during fieldwork and Vicki and Garry Dowling from Fowlers Gap Arid Zone Research Station for their support. We thank Joan Heikamp and Louis Diekmann for video analysis and Aneesh Chauhan for advice on the deep-learning aspect of the data validation.

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