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## Research article

### Hanging out in the outback: the use of social hotspots by wild zebra finches

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The social and spatial organisation of avian societies is often complex and dynamic with individuals socialising with others in a local population. Although social interactions can readily be described in colonial breeders through the location of nests, social interactions regularly take place in other contexts that are often not considered. Social behaviour in the colonially breeding zebra finch, *Taeniopygia guttata*, has been the focus of much work in the laboratory, but very little is known about their social organisation in free-living populations, especially outside the breeding context. Here we characterise semi-permanent gathering locations, or ‘social hotspots’ in the zebra finch in the wild. We determined the use of such social hotspots and the resulting group dynamics by quantifying movements to and from these locations through direct observation and by quantifying the vocal activity at these locations using acoustic recorders. We show that, throughout the day, zebra finches regularly visit these hotspots, and the hotspots are occupied for a substantial proportion of the day. Individuals typically arrived and left in pairs, or small groups, indicating that these social hotspots do not function just for flock formation. Instead, the high levels of vocal activity at these hotspots indicate that they may potentially function as local hubs for socialisation and information exchange, whilst also perhaps providing safety-in-numbers benefits to individuals during periods of resting. These findings characterise an important component of the natural social life of one of the most widely studied birds in captivity. The characterisation of these social hotspots highlights the use of landmarks by birds to facilitate social contacts, cohesion, and behaviour, in a social bird. Similar hangouts and social hotspots may be a feature of social behaviour in other multi-level aggregative species in which the fission and fusion of groups is an important component of daily life.

Keywords: acoustic behaviour, birdsong, fission–fusion society, social behaviour, social dynamics, *Taeniopygia guttata*



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## Introduction

Many birds live in complex multi-level or fission–fusion societies where social structure changes over time when exploring the environment (Silk et al. 2014, Loretto et al. 2017, Aplin et al. 2021, Papageorgiou and Farine 2021). In these avian societies, individuals maintain close relationships with a partner or a few others but at the same time regularly gather in larger groups during periods that are distinct from social foraging or other group-related activities such as colonial breeding or roosting (Papageorgiou and Farine 2021). Many songbirds are territorial for part of the year and some form social flocks outside the breeding season. During these periods, social networks have been described, for example in great tits, *Parus major*. During breeding, great tits are territorial and they form social networks with their neighbours (Snijders et al. 2014), but during the winter they form different, two-level social networks at foraging sites (Aplin et al. 2015, Papageorgiou and Farine 2021). Thus, on a daily basis, and aside from commonly studied contexts in which social behaviour is characterised (i.e. at foraging or roost sites), there are other important contexts underlying social interactions in birds that are widely overlooked. For example, the spatial and social mechanisms allowing multi-level organisation in the absence of territories, fixed foraging sites, or outside the context of roosting or breeding sites remain poorly understood (Papageorgiou and Farine 2021). Given that individuals are unlikely to spend their whole day engaged in essential activity like foraging, one possibility is that they could aggregate and socialise during periods of downtime, where individuals will hang out with other conspecifics.

Zebra finches live in multi-level societies (McCowan et al. 2015) and are non-territorial songbirds that have only short-range vocalisations (Loning et al. 2022). Zebra finches are distributed throughout most of Australia, but are mostly found in arid habitats (Zann 1996). They are a gregarious species that can breed colonially while primarily moving around in pairs or small mixed-sex groups (Zann 1996, McCowan et al. 2015, Brandl et al. 2021). Yet, as a key avian model organism they are usually studied in caged pairs or kept in stable, often single-sex, groups in aviaries (Shahbazi et al. 2014, Griffith et al. 2017a, Kalnins et al. 2022), thus strongly deviating from the social organisation under which their behavioural processes have evolved (McCowan et al. 2015). Social ties between different pairs in the wild appear to remain intact across multiple years, while playing a role in breeding synchronisation, suggesting that there is some degree of social cohesion and structure within a local population (Brandl et al. 2021). However, whilst there is a low but certain degree of spatial coordination between many individuals within a population (Brandl et al. 2021), their vocalisations have recently been shown to be very short-range signals: song is barely audible by conspecifics at distances beyond nine meters, for distance calls, the loudest vocalisation in the repertoire, this detection range is 14 m (Loning et al. 2022). These quiet acoustic signals are therefore not suited to detect and locate conspecifics over larger distances. Therefore, semi-permanent

gathering sites would provide a useful mechanism through which individuals can locate and socialise with others, if they are frequented predictably and regularly.

Here, in the zebra finch, we characterise ‘hangouts’ as events where individuals engage in a period of socialising, passing the time with, or waiting for, conspecifics. These hangouts can be defined by social gatherings that do not necessarily need to have a fixed location. However, they may be more likely to occur in a particular location – a ‘social hotspot’. Having such a social hotspot in which to hang out facilitates joining or re-joining with other conspecifics in a reliable way and will facilitate the benefits of socialising with others (Silk et al. 2014, Loretto et al. 2017, Papageorgiou and Farine 2021). We characterised the repeated use of social hotspots by wild zebra finches by quantifying the presence of zebra finches on trees and bushes at multiple sites by direct observation sessions and audio recordings. We quantified the social dynamics of social hotspots by noting the timestamps and group sizes of arriving and departing birds and by measuring the duration of hangouts and the group sizes on the focal tree or bush. We specifically tested the prediction that some trees (or bushes) in the environment serve as persistent social hotspots, having significantly greater social activity than other trees. We predicted that if social hotspots are sites used repeatedly for local gatherings rather than just transient assemblages for subsequent group movements, that birds will arrive and leave in smaller group sizes, relative to the number of individuals typically found socialising in the location. This characterisation of social hotspots in wild zebra finches will help us to understand natural social behaviour in this species, which continues to provide a core model system in behavioural studies (Griffith et al. 2021, Hauber et al. 2021). The characterisation of both hangouts and social hotspots in this species may in turn lead to the identification of similar features of the social landscape in other gregarious species, improving our understanding of social behaviour in birds more generally.

## Material and methods

We conducted the study at Fowlers Gap Arid Zone Research Station across five populations of zebra finches separated by at least 4 km (Fig. 1) from October to December 2019. Each study site is an open *Acacia* shrubland with a relatively low density of acacia trees being separated by patches of open ground (examples from two sites in Fig. 2). Low bushes such as bluebush *Maireana* sp. and saltbush *Rhagodia* sp. (syn. *Chenopodium* sp.) occur in variable densities in these open patches (examples in Fig. 2d). In most years, the local population of zebra finches breed during this time of the year with an average of 174 clutches laid each year during this period, in an earlier study of breeding in the nest boxes in the same areas (total clutches for four of the five areas in the present study from the years 2005–2007, Griffith et al. 2008). However, due to a period of low rainfall through 2018 and 2019 zebra finches had not bred in this area in significant numbers since

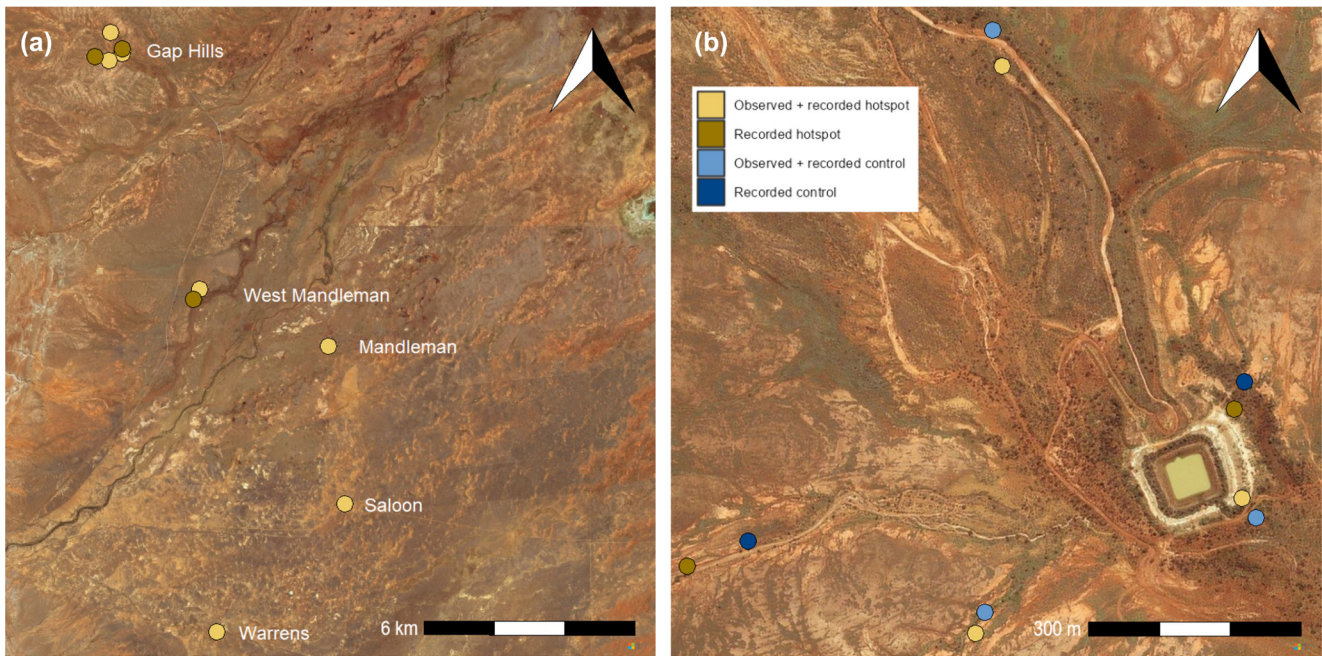


Figure 1. Satellite picture of the position (a) of the hotspots (which were all paired with a control tree, not drawn to maintain legibility) on each site ( $n=5$  at Gap Hills,  $n=2$  at West Mandleman and  $n=1$  at Mandleman, Saloon, Warrens) at Fowlers Gap Arid Zone Research Station. (b) Satellite picture of the five tree pairs in Gap Hills (there was no water in the dam during the study period). Microsoft product screen shots reprinted with permission from Microsoft Corporation.

November 2017 (Loning et al. 2023a). Ecological conditions were such that breeding activity by this opportunistically-breeding species was very constrained with only nine clutches laid during the study period (Loning et al. 2023a), and probably, the population sizes at the five areas were lower at about 150–300 birds per population. As such, although conducted during the Austral spring, we considered the study to represent a non-breeding period. Almost all the many hundreds of individuals whose behaviour we have characterised were not actively breeding and therefore were not engaged in either parental care or general breeding activity.

### Identification of social hotspots

The trees or bushes (simplified to ‘trees’ from here on, but about half of them were bushes) that were putatively assigned as social hotspots were visually identified by considering the occurrence of groups of birds at these trees repeatedly during opportunistic walks through the area as part of other work (Loning et al. 2022, 2023a). Some of the included trees were already putatively identified as hotspots of zebra finch activity as early as 2017 (as part of earlier work, Brandl et al. 2019), whereas for other trees we only regularly noticed large groups of zebra finches around the start of this study in 2019. For each putative social hotspot (simply ‘social hotspots’ from here onward, in principle all social hotspots were putative until confirmed by the data presented in here) we assigned a comparable tree nearby, on average  $50 \pm 20$  m apart ( $\pm$  SD, range 31–94 m), as a control tree. These control trees were matched for size, structure, surrounding

vegetation, and species as much as possible. Only in one location, Mandleman, a particularly open site, was there just one other tree in the vicinity that we had to pick as the control tree, although it was smaller and less dense in structure than the social hotspot. At all other sites, we usually had two to five similar trees to pick from for a control, within a radius of about 60 m. When we had to choose between several equally suitable control trees, we decided on a particular candidate control tree due to its suitability for observing both the social hotspot and the control tree at the same time from a location nearby. Figure 2 provides two visual examples of representative contexts in which the social trees were identified.

To confirm the selection of social hotspots and control trees, we counted the number of droppings underneath the trees in a  $10 \times 10$  cm square. These dropping counts were done in three different spots under the tree to account for variation. We repeated these three dropping counts, so that we usually had several days of counts per site (two days:  $n=1$ , three days:  $n=5$ , four days:  $n=3$ , five days:  $n=1$ ). Under the social hotspots, the count of droppings in a  $10 \times 10$  cm square was  $19 \pm 3.4$ , whereas it was only  $0.7 \pm 0.4$  under the control trees (mean  $\pm$  SD). Visual inspection of the droppings per site over time indicated that this difference between social hotspots and control trees was consistent and that measurements at the respective trees were highly repeatable across time. The accumulation of droppings under the social trees was indicative of a period of consistent use by zebra finches in the period prior to the selection of social trees. We attributed all small droppings to zebra finches, as there were no other small granivorous birds present at our study site during

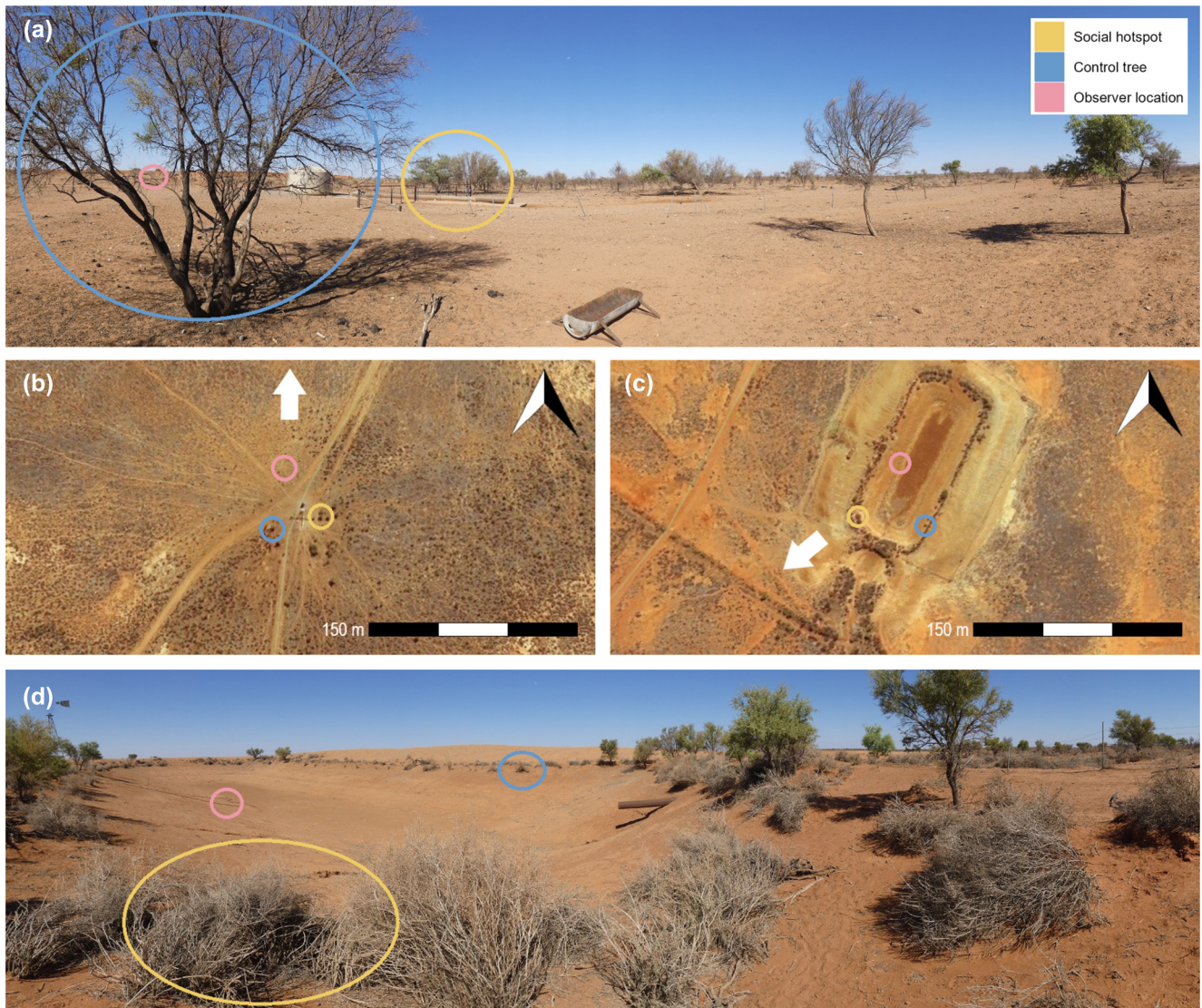


Figure 2. Social hotspots, control trees and observer locations indicated for two sites. (a) Warrens seen from a panorama photo taken near the control tree. Here, the social hotspot and control tree were in a prickly wattle *Acacia victoriae* and many trees of this species can be seen nearby. (b) A satellite image of site Warrens. (c) A satellite image of site Saloon. Here, the social hotspot and control tree were low spiny saltbushes *Rhagodia spinescens*. (d) A panorama photo of site Saloon. For (b) and (c): Microsoft product screen shots reprinted with permission from Microsoft Corporation.

our study period (e.g. no other estrildids or budgerigars *Melopsittacus undulatus*), and due to the drought, densities of insectivorous passerines was much lower than that of the zebra finch, so we can be confident that most if not all of the small droppings that we counted are indeed zebra finch droppings.

The structure of the tree probably plays an important role for them becoming adopted as a social hotspot. Social hotspots were often shrub-like trees of 1–4 m height from the wattle genus *Acacia* most notably prickly wattle, *A. victoriae*, which has spines (this is the most common ‘tree’ on the study site, all trees in Fig. 2a are prickly wattles), or dead finish, *A. tetragonophylla*, which has spiny leaves. In other sites, the social hotspots were in the 0.5–1.0 m high bushes

of either the bluebush genus *Maireana* or saltbush genus *Rhagodia*. Vegetation that was identified as a social hotspot included both live and dead plants, sometimes these were fallen over, and bushes were often either structurally dense or spiny (or both). Although we did not test this specifically, all vegetation identified as hotspots provided shade as well as allowing for good protection against aerial attacks (aerial predators of zebra finches present on our field site include black kite *Milvus migrans*, brown goshawk, *Accipiter fasciatus*, collared sparrowhawk, *Accipiter cirrhocephalus*, Australian hobby, *Falco longipennis*, brown falcon, *Falco berigora*, and pied butcherbird, *Cracticus nigrogularis*; Zann 1996).

Our search for social hotspots suggested that in several cases the location of social hotspots might be linked to water

resources, e.g., being near drinking sites or being on a flyway from local breeding/roosting sites to the drinking sites. In two cases (the sites Mandleman and Warrens), the selected social hotspot was the tree closest to a local drinking site, in one case (Saloon) it was the bush closest to where water had been in previous years although because of the drought this location had been dry for over a year prior, and during the study the birds were drinking from a livestock trough over 300 m away. We are unable to exclude the possibility that some of the selected social hotspots or control trees were near food resources at some point, as the grass seeds zebra finches eat are ephemeral and scattered in distribution (Zann et al. 1995, Funghi et al. 2020). However, closeness to food resources was likely not a main factor during our study as due to the drought, we had not seen grass set seed for over a year prior. It is also unlikely that high concentrations of seed would still be present in the immediate vicinity of these well-frequented social hotspots (if they ever were). At one site (West Mandleman) on one day, during the direct observation periods we saw some birds feeding on the ground in the area within 50 m of the focal tree, we did not observe this at any of the other sites, and only in the morning at the one site. Even though most of our selected hotspots were apparently not close to resources, it is likely that they were situated on flyways (Adrian et al. 2022) between different resources or between resources and roosting sites.

### Focal observations

To determine the use and group dynamics of specific trees as social hangouts we conducted 174 h of focal observations at seven social hotspot and control tree pairs between 12 November and 8 December 2019 (three pairs at Gap Hills, one pair at Saloon Tank, one pair at Mandleman, one pair at West Mandleman and one pair at Warrens (Fig. 1), details on the location of these areas given in Griffith et al. (2008). For each selected site, we conducted two full-day observations (12.5 h per day of observations to account for the whole day, from 6:30 until 19:00, occasionally starting earlier, with one occasion of starting later than 6:30 on one site due to practical problems) with one person observing both the hotspot and control tree simultaneously. For each arrival and departure event, i.e. when any bird landed in or respectively flew off the social hotspot or control tree, we noted the time, type of movement (arrival or departure), the tree involved (hotspot or control), the number of arriving/departing birds (counted), and the group size of birds in each tree (social hotspot and control) before the event (counted and calculated). This allowed us to keep track of the total number of birds present in both trees throughout the day. Even during higher movement activity, this process allowed us to calculate a posteriori the group size in each tree (shown for two example sites in Fig. 3, and for all sites in the Supporting information). Additionally, we also scanned the social hotspot and control tree every ten minutes regardless of whether we had observed activity, to ensure we had not missed any arrivals or departures.

Although we had long observation times, this method was reliable for this species and in this environment due to their vocal behaviour and the open nature of the environment, respectively. Flying zebra finches have a high call activity, and birds present at trees typically also vocalise when there are fly-overs close-by or at take-off (pers. obs., Zann 1996). This enabled the monitoring of arrivals and departures at both trees simultaneously. Additionally, vegetation in this open environment is low (the *Acacia*, the main 'trees' in this environment do not grow higher than 3–4 m) and sparse, with clear space between them, at the ground and canopy level (Fig. 2). Similarly, there were no large rock formations or other structures hindering vision at our selected locations, or that would have deterred birds from being able to fly equally easily into either the social hotspot, or control tree. This made it relatively easy to score arriving and departing zebra finches. Nevertheless, we replicated observations for each site, while rotating observers, so that for each site, the data were gathered by a different observer on the second observation day. We had three different observers that all had more than 10 h of experience in scoring zebra finches in this way at the start of the study. For each site, we selected an observation distance that allowed for minimal disturbance of the birds and simultaneous observation of the hotspot and control tree without much head-turning, which resulted in a mean distance of 37 m (observer-tree distance ranging from 16 to 51 m, measured using GPS). Observers were equipped with binoculars to help with scanning the trees, and occasionally, counting the group size of arriving and departing birds (usually the naked eye was sufficient for this).

To characterise the social dynamics on the social hotspots, we quantified several parameters related to the hangouts. For each tree (social hotspot and control) we calculated the duration of hangouts, i.e. periods in which any zebra finch was present (an example of a hangout is indicated in Fig. 3a), and the periods during observation time when there were no birds present, this included the time in-between hangouts as well as the period from the observation start (usually 6:30) until the first arrival, and the time between the last departure and the end of observation time (always 19:00). Additionally, we calculated per tree per day the total duration that any zebra finch was present (sum of hangouts), and the proportion of time that any zebra finch was present (total duration divided by total observation time, usually the 12.5 h from 6:30 to 19:00). To further determine the dynamics of birds on the social hotspots, we also calculated a posteriori the group size of zebra finches on the social hotspot (and control tree) for the whole observation day, which we plotted to gain a better understanding of the dynamics throughout the day on these social hotspots. Additionally, using this dataset, we calculated the distributions of group sizes on all social hotspots (and control trees) overall, averaged for time, which we compared with the overall distribution of group sizes of arriving and departing birds. Using these analyses of the dynamics and group sizes of arriving/departing birds as well as the birds on the focal trees over time, we could make conclusions on

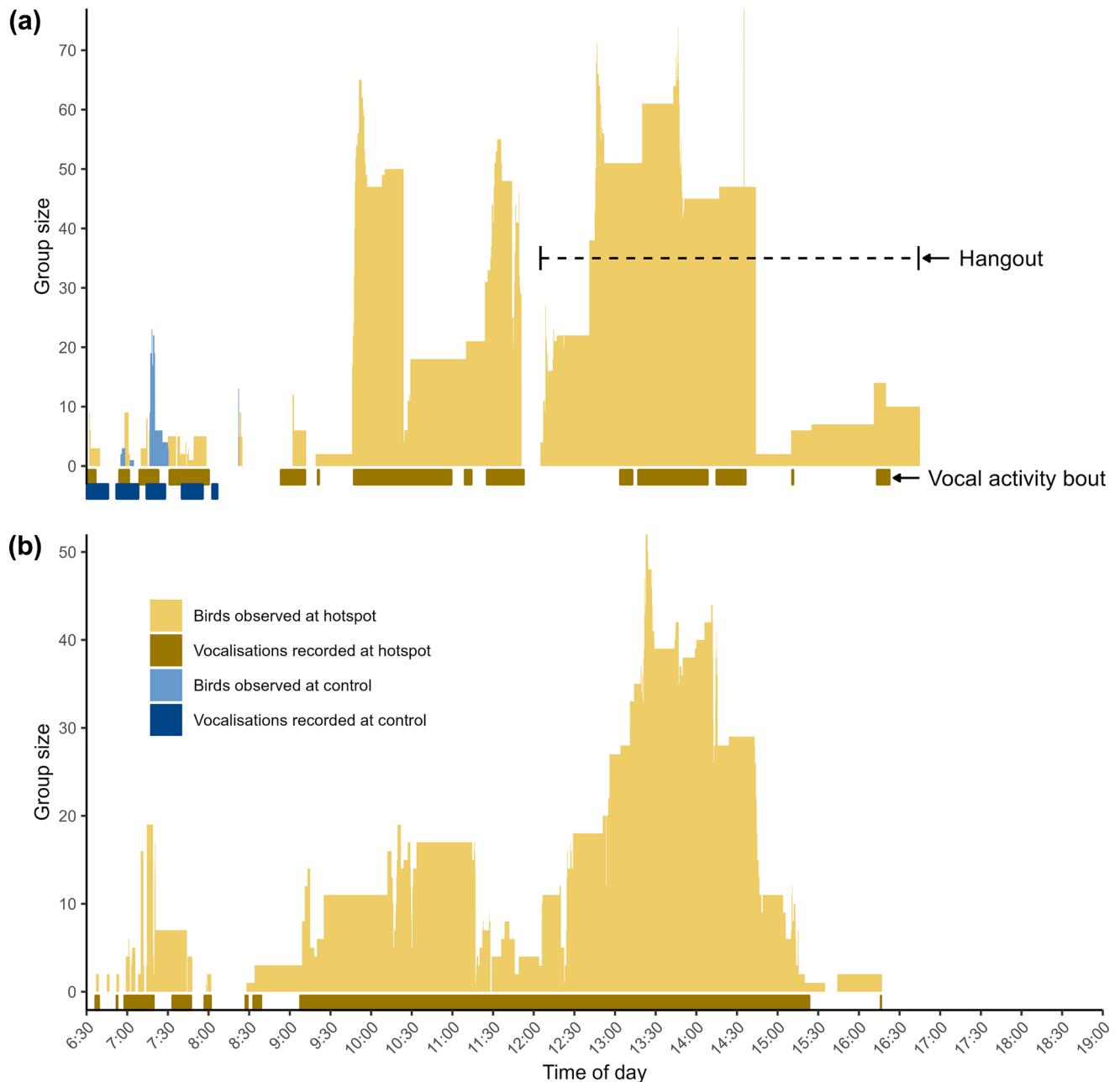


Figure 3. Group size dynamics, as well as vocalisations on social hotspots and control trees of two sites on 11 November 2019. (a) Warrens, where we had overall highest activity on the control tree out of all days on all sites. A hangout, i.e. a period during which any bird was present on the tree, and a vocal activity bout, i.e. a period during which vocalisations could be heard, are indicated as example. (b) Saloon, where we recorded no vocal activity and observed no bird at the control tree. These figures illustrate well how big the difference between control trees and social hotspots was, the social hotspots shown here represent the upper range of activity that we observed at social hotspots in our study. Figures illustrating all data can be found in the Supporting information.

whether or not these hotspots play a role in the formation of flocks.

### Audio recordings

To determine all vocal activity by zebra finches at these social hotspots, we placed time-programmable audio recorders at each social hotspot and control tree at ten sites across

Fowlers Gap (the same sites as for the focal observations and three additional sites – two additional pairs at Gap Hills and one additional pair at West Mandleman; Fig. 1) between 28 October and 8 December 2019. Each recorder was programmed to record for 12 h (the maximum length for the internal memory when using wav files, using the ‘high’ microphone sensitivity setting), from 6:30 until 18:30. We recorded both trees on each site on two to five days and

selected the recording of the day in which wind was lowest (as zebra finch vocalisations are soft, Loning et al. 2022), or in which wind was acceptable and we had observations for the same day. Nevertheless, recording days were not always the same due to equipment failure and because many recording days happened opportunistically when we visited sites as part of other work (Loning et al. 2023a). For four out of seven sites, a low wind recording day and an observation day overlapped (two are pictured in Fig. 3). We analysed each audio recording using Audacity 2.2.2 (Audacity Team 2018), applying a 1 kHz high-pass filter and a background noise reduction of 10 dB.

We noted the time during the day and duration of each bout of vocal activity across the entire recording time, starting when a first vocalisation could be heard until no vocalisations could be heard (an example of a bout is indicated in Fig. 3a). We here assumed that no zebra finches were present at the tree when no vocalisations could be detected for five minutes of recording (an earlier analysis where we assumed one minute instead of five minutes gave the same qualitative result), or all vocal activity halted after the recorded birds all flew away, which has a distinct acoustic signature due to wing beats and calling behaviour. Bouts of vocal activity shorter than ten seconds were not considered, as we assume that these came from birds flying by (this was often clearly audible). We assessed the duration of these vocalisation bouts and the duration of silent periods, which were the periods during the recording time when there was no vocalisation bout, this included the time in-between vocalisation bouts as well as the period from the start of recording (6:30) until the first vocalisation bout, and the time between the last end of a bout and the end of recording time (18:30). We did not quantify song behaviour extensively, but we noted for each recording site for each tree whether we encountered song motifs or not.

## Statistical analyses

We conducted all statistical analyses in R ver. 4.1.1 ([www.r-project.org](http://www.r-project.org)). We tested for differences between the social hotspots and control trees using generalised linear mixed models (glmmTMB package, Brooks et al. 2017). All of our measured variables were discrete in nature, e.g. the group sizes of birds, durations of vocalisation bouts (in seconds) or the number of arrivals and departures. They also showed high variation (so a Poisson distribution would have been overdispersed) and especially for the control tree, there were sometimes zeros present. Therefore we used the negative binomial distribution with a quadratic term for the dispersion parameter (i.e. the glmmTMB family was 'nbinom2') to model these variables, which were: group sizes of birds of arrival events, on the tree (time-averaged, meaning that there was an entry for every minute a particular group size was on the tree) and of departure events; the sum of the number of arrivals and departures per site; the total duration of observed hangouts; the duration of observed hangouts; the duration of periods without observed birds; the total duration of vocalisation bouts; the duration of vocalisation bouts and the duration of

silent periods. We selected site as a random factor to account for the variability among sites. Thus, for each model we had type of tree (hotspot or control) as independent variable and date nested within site (for focal observations, where we had two days of observations per site) or just site (for audio recordings, where we had one day of recordings per site) as random factor. For testing whether the group sizes of arrivals, departures and on the trees for both the social hotspots and control trees were different, we followed up with a pairwise comparison test after the model fit using function *emmeans* (from the 'emmeans' package), which penalises for multiple testing.

All results are presented as the summary statistics (mean  $\pm$  SD or median) of the raw data with supporting statistics between brackets. As we had two observation days for the focal observations, for these data we first calculated the means per tree (social hotspot and control tree) per site. Then we calculated the overall mean among the sites, where  $n=7$  sites for the focal observations and  $n=10$  sites for the audio recordings. In a few cases, the sample sizes for the control trees are lower due to a lack of visiting zebra finches. Although we present summary statistics in the text, all statistical models used the raw data, apart from the tests on summary statistics which were: the sum of arrivals and departures (per day, so  $n=14$ ); the total duration of hangouts (per day, so  $n=14$ ) and the total duration of vocalisation bouts (per site, there was only one day,  $n=10$ ).

## Results

For all measures that we considered, there was much more activity at the social hotspots than at the control trees, both in terms of observed zebra finches, as well as recorded vocalisations.

### Group sizes of arrivals, departures, and at social hotspots

In total we observed seven separate social hotspot – control tree pairs for a total of 174 h across the five different populations of zebra finch. With an average of  $63.6 \pm 40.3$  total arrivals+departures on social hotspots per day there was substantially more activity at the social hotspots than at the control trees where on average only  $2.1 \pm 3.3$  total combined arrivals and departures happened per day (GLMM;  $z_{23} = 8.3$ ,  $p < 0.0001$ ; Fig. 4a). Birds primarily arrived and left the social hotspot in pairs, with a median group size of two arriving birds and two departing birds (Fig. 4b). Thus, group sizes of arrivals and departures did not differ (GLMM pairwise comparison;  $t_{4643} = 0.5$ ,  $p = 1$ ; Fig. 4b). For the control trees the number of birds were similar across contexts (GLMM pairwise comparison; all  $t_{4643} < 0.6$ , all  $p = 1$ ; Fig. 4b) with median group sizes of two (arrivals and on the tree) to three (departing birds). However, with a median of five birds, significantly larger groups of zebra finches could be observed on the social hotspots than control trees (GLMM pairwise

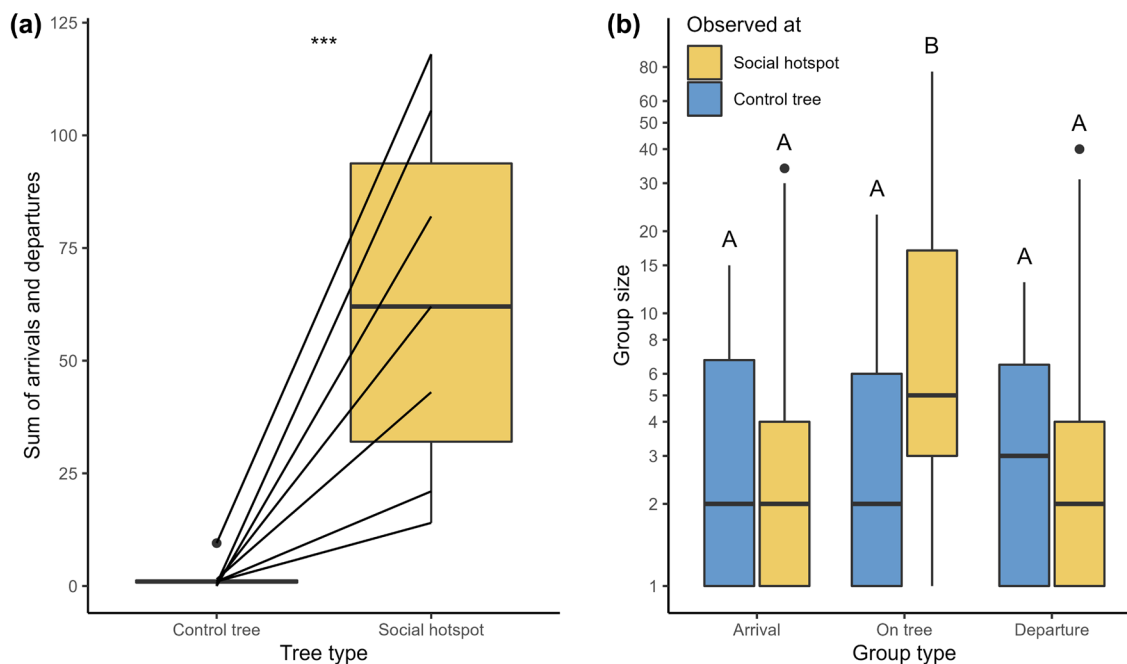


Figure 4. (a) The sum of arrivals and departures, with each line connecting the daily averages (of two days) for each of the seven observation sites. There was substantially more activity on the social hotspots than on the control trees. Statistical significance of \*\*\* corresponds with  $p < 0.001$ . (b) Group sizes of arrival and departure events, as well as the per-time-averaged group sizes on tree for both the social hotspot and control tree. The different capital letters indicate which groups were statistically different from each other. Groups were typically small, with a median group size of two, indicating that many birds arrived and departed in pairs. Large gatherings of zebra finches differing from this organisation in pair units were only seen on the social hotspots, not on the control trees. Boxes encompass the first to third quartiles, thick lines are medians and whiskers extend until 1.5 times the inter-quartile range.

comparison;  $t_{4643} = 9.2$ ,  $p < 0.0001$ ; Fig. 4b). Substantially higher numbers of zebra finches were common at these hotspots (Fig. 4b), with a mean maximum per tree of  $32.3 \pm 23.5$ , and a maximum of 77 birds at a particular hotspot (Fig. 3a).

### Hangout durations at observed social hotspots

Zebra finches were observed in the social hotspots across the day, i.e. hanging out for  $262 \pm 152$  min representing  $36 \pm 21\%$  of the entire observational time at the social hotspots; significantly greater than the  $3 \pm 7$  min representing  $0.4 \pm 0.9\%$  of the entire observational time on the control trees ( $z_{23} = 5.7$ ,  $p < 0.0001$ ). In social hotspots, each hangout lasted on average  $48 \pm 75$  min which was significantly longer than the  $2 \pm 4$  min in control trees (GLMM;  $z_{176} = 3.6$ ,  $p < 0.001$ ; Fig. 5a). When considering an observation time of about 12.5 h per day, the time that the social hotspots were unattended by birds during the day was relatively short, with an average length of periods without birds of  $99 \pm 141$  min. For control trees, this was significantly longer with  $539 \pm 132$  min (GLMM;  $z_{204} = 8.3$ ,  $p < 0.0001$ ; Fig. 5b).

### Vocal activity at social hotspots

We analysed all vocal activity at the social hotspot and control tree for a total of ten tree pairs across five sites on

five different days and over 12 h per site per day (240 total recording hours). Overall, the vocalisations that we recorded showed the same patterns that we observed in the duration of hangouts and nonactive periods (see above and compare Fig. 5a–c and Fig. 5b–d). We detected zebra finch vocalisations for  $187 \pm 137$  min representing  $26 \pm 19\%$  of the entire recording time at the social hotspots, this was much lower at control trees with  $31 \pm 31$  min, representing  $4 \pm 4\%$  of the entire recording time (GLMM;  $z_{16} = 3.5$ ,  $p < 0.001$ ). Although we did not quantify this extensively, from these vocalisations, we could also detect zebra finch song motifs at nine of the ten social hotspots; on control trees this was at six trees across the ten sites. Each bout of vocal activity lasted, on average, for  $13 \pm 13$  min at the social hotspots, longer than the  $4 \pm 4$  min on the control trees (GLMM;  $z_{231} = 4.9$ ,  $p < 0.0001$ ; Fig. 5c). The periods of silence identified throughout the whole recording period were on average  $42 \pm 37$  min on the social hotspots, much shorter than the  $164 \pm 217$  min on the control trees (GLMM;  $z_{250} = -6.5$ ,  $p < 0.001$ ; Fig. 5d).

### Comparison of the focal observations and the audio recordings

Out of four observation days across four sites that also had audio recordings (two of which are shown in Fig. 3),  $79.4 \pm 18.6\%$  of minutes with vocal activity also had birds observed in that hotspot. On those same days,  $58.2 \pm 21.0\%$  of minutes



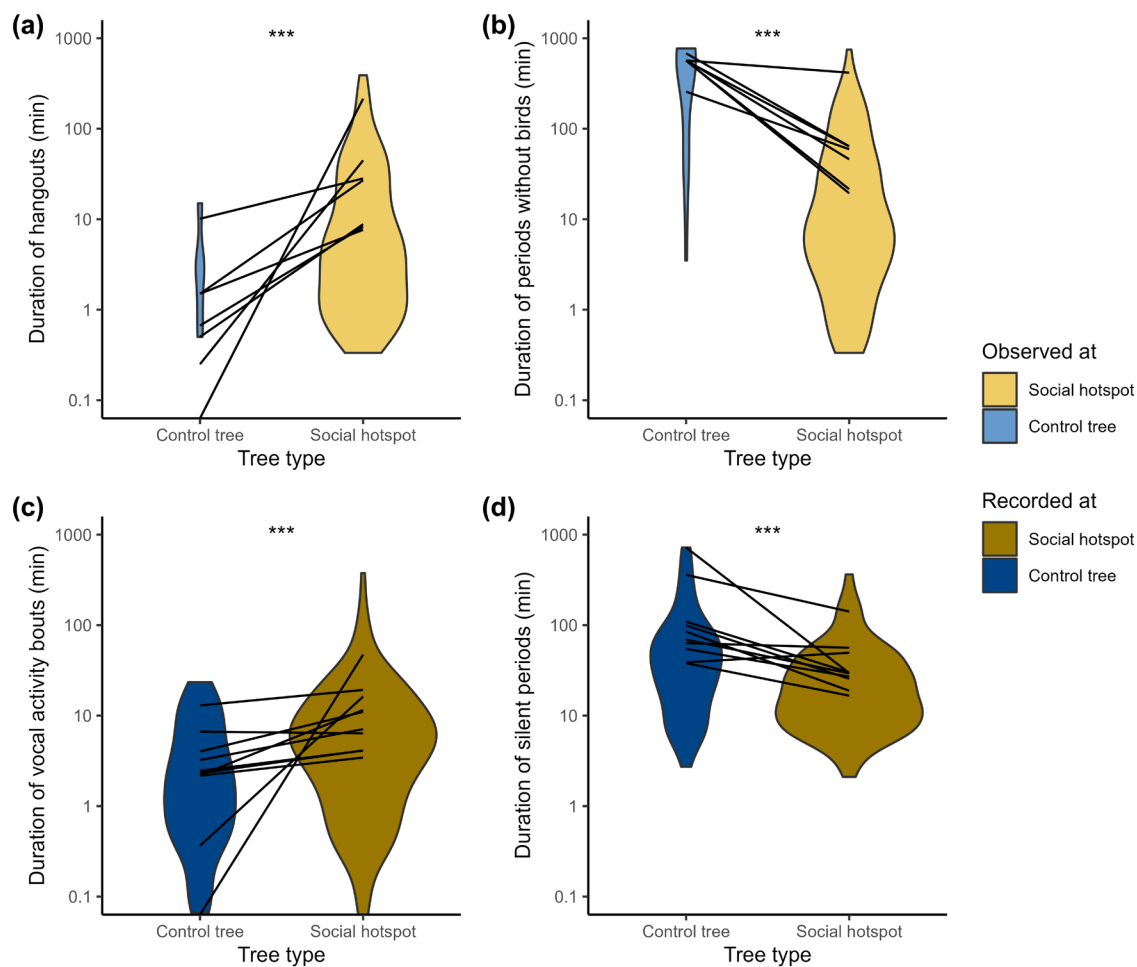


Figure 5. Duration parameters associated with observations (a, b) and recordings (c, d). Violins represent the raw data and their size is indicative of the relative amount of data. Lines indicate the site means ( $n = 7$  for observations,  $n = 10$  for recordings). For the observations, this was averaged for two days. For recordings, only one day was scored. (a) Duration of observed hangouts. There are two lines that do not seem to fall in the raw data for the control tree, in one case this is caused by averaging where one day did not get visits. The other one is a case where no birds visited the control tree on both days. (b) Duration of periods without birds, taking into account the whole observation period of each respective day ( $\pm 12.5$  h). (c) Duration of recorded vocal activity bouts. (d) Duration of silent periods, taking into account the whole recording period of 12 h. Statistical significance of \*\*\* corresponds with  $p < 0.001$ .

that we observed birds on the hotspot were accompanied by vocal activity. So, vocal activity is a stronger predictor of bird presence than bird presence is a predictor of vocal activity. Regardless, zebra finches spent considerable time vocalising during their hangouts at these social hotspots.

## Discussion

Here we show that zebra finches spent substantial time hanging out with conspecifics throughout the day at specific gathering sites in their natural environment. Even though these social hotspots were not always immediately adjacent to either food or water resources, we regularly observed and recorded large groups of birds hanging out at these social hotspot locations, compared to similar trees in the vicinity. Birds arrived and departed primarily in pairs or small groups, indicating

that the function of these social hangouts was not primarily the formation of flocks. That is, it was not the case that individuals aggregated at a social hotspot and then collectively left in a larger group. That sometimes happened, but more typically a small group, most commonly a pair, would arrive, spend a period of time in the social hotspot and then leave on their own. On several occasions, during large hangouts, pairs also departed in short succession after each other. The hangouts, which occur at quite specific social hotspots will have provided individuals with the opportunity to socialise with many other individuals, and provide the potential for information exchange, and safety in numbers benefits. Indeed, our audio analyses revealed that birds were often vocally active throughout most of the time in a hangout. Whilst it was not possible to determine the arrival and departure of specific individuals, it is clear from the data collected during the direct observations that individuals, and groups, could spend

considerable time in the social hotspot, hanging out with a number of others.

However, the social dynamics at these hotspots show that hangouts can be quite variable in the duration, level of acoustic activity, size of group, and how they build up and break down as individuals come and go. Again, whilst it is currently unclear which individuals are hanging out in any particular social hotspot at any time, our data certainly suggest that when, for example, thirty zebra finches are encountered together in a social hotspot, that is not because they are all moving around together as a coherent social unit. Thus, although it is well described that zebra finches are often being observed in flocks (Zann 1996), such flocks are not fixed entities and occur particularly at resource locations such as water. The flocks that we observed at the social hotspots at any given point in time were comprised of a set of individuals or pairs that have arrived at that location largely separately. Although it was not feasible here to determine the sex of each arriving and departing bird, non-systematic sampling suggested that practically all observed pairs of birds were mixed sex. This is consistent with the earlier finding by McCowan et al. (2015), that zebra finches primarily move around in partnerships, even in a non-breeding period, but that these pairs readily and frequently aggregate with others in larger social flocks. Furthermore, given the scale of movements in and out of a social hotspot throughout the day, and the size of the local population of birds, it seems more likely that an individual that frequents the social hotspot either throughout the day, or across different periods of the day, will encounter many more individuals than the number that are there at any one time. Our findings therefore highlight a key component of the dynamic and variable social life of zebra finch multi-level societies in the wild. Understanding the natural social organisation is specifically relevant for zebra finches as important model system in the study of avian behaviour in laboratories worldwide, where birds are commonly held in stable groups or as pairs (Zann 1996, Griffith and Buchanan 2010).

Our findings that any zebra finch was present at these special locations for a substantial part of the day suggest that these hotspots play an important role in the social life across the wider population of zebra finches, and could facilitate a number of elements of social coordination that have been recently described in wild populations (McCowan et al. 2015, Griffith 2019, Brandl et al. 2021). Zebra finches form strong social pair bonds during and after breeding that are life-long and last for several years (Dunn and Zann 1996, McCowan et al. 2015). However, although these partnerships are the core social unit, the daily opportunity to hang out and socialise with other pairs and individuals from the wider colony provides an excellent opportunity for individual zebra finches to gather additional social information about the condition of others, resources in the local area (Weimerskirch et al. 2010, Aplin et al. 2013, Mariette and Griffith 2013), and during breeding periods, the synchronisation of reproductive schedules (Mariette and Griffith 2012, McCowan et al. 2015, Brandl et al. 2019, 2021, Camerlenghi et al. 2022). These hotspots also provide a safe place in which individuals can

hang out, and pass the time of day when they are not engaged in active foraging and in a relatively safe place where they gain the benefits of safety in numbers (Krause and Ruxton 2002, Silk et al. 2014) and escape the intense solar radiation, wind, or high ambient temperatures in the extreme climate in which they live (Funghi et al. 2019).

One of the consequences of the persistent use of specific locations, or hotspots, in the environment is that it will provide an important opportunity for lone individuals, or small groups, to reunite regularly with conspecifics. Individuals or small groups may become separated by foraging on widely distributed resources, or perhaps because of disturbance during gusts of wind or when evading perceived predation risks. Our data reveal that a lone bird going to one of these social trees would typically not have to wait long before finding, or being joined by, other conspecifics. If both members of a pair, on becoming separated, followed a rule of thumb of going to the nearest – or one specific – social hotspot, they would quickly find each other to be re-united, which is likely to be important given the high level of coordinated movement between partners (Mariette and Griffith 2012, McCowan et al. 2015). The occurrence of persistent spatially discrete social hotspots (as meeting points) will be particularly useful in a species like the zebra finch, in which acoustic signals are of limited value in locating others. The song of the zebra finch is only audible to other conspecifics within around nine meters, and even the ‘long distance’ contact call is relatively quiet, and quickly lost in the open landscape in which the zebra finch lives (Loning et al. 2022). Thus, vocalisations in the zebra finch cannot function as a long-range signal to regulate spacing (Waser and Wiley 1979, Brumm and Naguib 2009, Snijders and Naguib 2017), or facilitate re-grouping, even though they attract others over short range (Adrian et al. 2022, Loning et al. 2023a), and play a role in close-range spatial coordination when flying in flocks, together with visual cues (Arnold et al. 2022). Of course, it is likely that these visual cues may also play a role in identification of conspecifics beyond the short ranges described here, and probably visual cues are important for the identification of social hotspots by zebra finches traversing their environment.

Our findings in the wild zebra finch have identified an important component of their natural history, in that despite the often-scattered distribution of pairs throughout the landscape (Mariette and Griffith 2013), most individuals living in an area can be socially connected through these social hotspots to many other members of the population, given the regular turnover in birds that we observed. This is of particular relevance to behavioural studies of captive zebra finch populations in which the opportunities for such daily fission–fusion social dynamics are often precluded by the housing situation, where pairs are often caged in isolation, or where birds are kept in single sex flocks or relatively small groups (Beaulieu 2016, Griffith et al. 2017b). The count of arrival and departure events that we observed at social hangouts suggests that even though the median group size present in a social hotspot might be only five, the relatively frequent

rate of individuals arriving and departing will mean that an individual staying there for an extended period of time will have the opportunity to socialise with many more than four individuals, i.e. the size of an individual's social network will be much larger than the number of birds it is observed typically hanging out with at any one time.

The high level of acoustic activity at the social hotspots is interesting in that it points to the potential role of these locations as a place where information can be shared amongst the many individuals often present. Although further work is needed to characterise the acoustic details of vocalisations in these social trees, our recordings picked up substantial contact calling, as well as singing, and when birds were present, they were typically vocalising at a high rate. As such, the social hotspots provide an important, and potentially complex context in which the function of acoustic communication should be understood, particularly in this species in which song is expressed throughout the year and has a social function (Loning et al. 2023a). Our findings, on the complex structure of these social hotspots, have implications for the many studies in the laboratory that are focused on zebra finch song and song learning (Hauber et al. 2021). Indeed, one of the areas in which the captive zebra finch has been widely used is in the neuronal development of acoustic communication, both in song learning and cognition of song structure (Louder et al. 2019, Hauber et al. 2021). Our results provide important ecological context in which vocalisations are expressed and received, and potentially learned by young birds, who will be exposed to many singing males at these social hotspots. This provides developing males and females an acoustically very diverse landscape compared to the standard situation in the laboratory (Gil et al. 2006, Ruploh et al. 2013, 2014, Griffith et al. 2017a). The importance of a diverse social environment on behavioural development has been experimentally identified by studies in birds in captivity (Ruploh et al. 2013, 2014, Honarmand et al. 2015), and the incidence of the social hotspots is entirely consistent with the ideas presented in these studies and suggests that in the wild they are likely to be the key site of this social learning and integration.

Finally, whilst our findings are of particular relevance to our understanding of the natural history of the zebra finch, it is likely that hangouts, in similar social hotspots may exist in many other birds in which collective movement or aggregations are behaviourally important. Using high-resolution tracking technologies (Krause et al. 2013, Snijders and Naguib 2017, Bircher et al. 2020) that allow tracking movements of many individuals within a single population may shed more light on this in the future. For example, our study has identified the existence of social hotspots that are attended during significant periods of the day. At an individual level it will be informative to understand how many different such hotspots a bird attends regularly, how much time they spend, and how many other individuals they interact with socially across the hotspots they are visiting regularly. An investigation of the dynamics at such social hotspots through measuring individual attendance patterns and social repertoires can then lead to

an understanding of the networks of individuals in complex societies such as studied here in wild zebra finches.

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## Author contributions

**Hugo Loning:** Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Software (lead); Validation (equal); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (lead). **Rita Fragueira:** Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Project administration (equal); Validation (equal); Visualization (supporting); Writing – original draft (lead); Writing – review and editing (equal). **Marc Naguib:** Conceptualization (supporting); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Simon C. Griffith:** Conceptualization (lead); Funding acquisition (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (lead).

## Transparent peer review

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## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c866t1gc9> (Loning et al. 2023b).

## Supporting information

The Supporting information associated with this article is available with the online version.

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