Ever so softly

The role of song in the social life of wild zebra finches

Hugo Loning

Propositions

1. There is no point in studying a taxon without first studying its natural history.
   (this thesis)

2. Considering the sensory capabilities of signal receivers is required when studying communication systems.
   (this thesis)

3. Convenience is the only factor driving the selection of model systems.

4. The avoidance of high-risk projects is harmful to science.

5. Capitalism leads to a problematic undervaluation of priceless matters.

6. Absence of boredom results in absence of creativity.

Propositions belonging to the thesis, entitled

Ever so softly: the role of song in the social life of wild zebra finches

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Chapter 1 | General introduction

Many animals do not spend their entire life alone. Indeed, to survive and reproduce, animals from many species depend on conspecifics at some point in their life. For example, sexually reproducing animals (some hermaphrodites excepted) need to mate with a conspecific of the other sex (Crow, 1994). Long-distance migratory animals might migrate more safely or efficiently in a group (Boinski & Garber, 2000; Krause & Ruxton, 2002), and animals that feed on widely distributed food patches might join others that have already located such a feeding site (Adrian et al., 2022; Thiebault et al., 2016). Some of these roles could be fulfilled by simply paying attention to unintentional cues produced by other animals, e.g. a seabird might find a school of fish by looking for flocks of other seabirds (Haney et al., 1992). However, in many cases animals will need to actively interact with each other, e.g. once that seabird has found the feeding patch and joined the flock, it will pay off to call continuously while flying so that their flock mates are aware of them and can avoid collision (Thiebault et al., 2016). This active interaction involving specially evolved signals between animals of the same or different species (Wheatcroft & Price, 2013, 2015) is called animal communication (Bradbury & Vehrenkamp, 2011). The ability to communicate with others likely carries strong evolutionary benefits, as it appears to be omnipresent in animals (that have nervous systems).

Communication systems

What, technically speaking, is animal communication? Communication between animals happens when an animal produces a signal that traverses the environment and is detected and perceived by another animal which, as a consequence of perceiving the signal, alters its physiology or behaviour (Endler, 1993; Owren et al., 2010; Wiley, 2006; Wiley & Richards, 1978). Therefore, communication allows an individual to influence its biotic environment (Owren et al., 2010). For effective communication, all three components of the communication system (producer, environment, receiver) need to match. Given the enormous diversity in animal taxa, environments, and signal functions (Endler, 1992), animal signals encompass many sensory modalities (e.g. visual, auditory, olfactory, touch, seismic, electric), and signals are often multimodal – spanning several sensory modalities simultaneously (Halfwerk & Slabbekoorn, 2015; Partan & Marler, 2005). Which signals animals use to communicate with each other depends on the signal production capabilities of the sender, the environment through which the signal needs to travel, and the sensory capabilities of the receiver, their Umwelt (Caves et al., 2019). A few examples: roosting bats use acoustic signals to find their pups when nursing (Thomson et al., 1985); birds-of-paradise produce tantalising audio-visual displays to court their mates (Ligon et al., 2018); moths, which have an acute sense of smell, use chemical bouquets to attract their partners at night (Roelofs, 1995); rattlesnakes, which are deaf themselves, rattle their tails to alert the ears and eyes of heterospecific predators to deter them (Allf et al., 2016); and honeybees communicate the location of nectar patches with their closely related hive members through specific dances in combination with odours (Dornhaus & Chittka, 2004; von Frisch, 1974).

Adaptiveness

The benefits of communication are clear from these examples. Effectively communicating individuals are more likely to propagate their genes than individuals that fail to communicate or fail to do so effectively. In other words, we expect that communication is adaptive – it enhances an individual's Darwinian fitness, a measure of evolutionary success defined as the expected number of surviving offspring an individual (more precisely, a genotype or phenotype) produces over its lifetime (Maynard Smith, 1978). This is a key assumption in this study domain, but in practice, quantifying fitness in natural contexts is difficult, and fitness proxies are used, such as the number of offspring (regardless of whether they manage to survive to reproductive age) or the number of matings (Alif et al., 2022). An important reason why we expect animal communication to be adaptive is because, like all things in biology, there are trade-offs in animal communication. Producing signals itself or producing inaccurate signals can be costly (Lachmann et al., 2001). For example, by signalling, an animal might lower their guard or increase their conspicuousness towards unintended eavesdroppers such as competitors, parasites and predators that overlap in sensory domains (Klump et al., 1986). For example, tungara frogs *Physalaemus pustulosus* call to attract mates. By calling more elaborately, they have higher mating success, but at the same time, these more elaborate calls are also easier to pick up by frog-eating fringe-lipped bats *Trachops cirrhosus*, and elaborately calling frogs experience a higher predation risk (Halfwerk et al., 2014; Ryan et al., 1982). In this case, signalling behaviour is undergoing opposite selection pressures, with natural selection by bats selecting for reduced conspicuousness, and sexual selection by females selecting for increased conspicuousness.

Signals of quality

Several of the examples mentioned above concern the attraction or selection of mates based on the signals these potential mates produced. One important assumption in these sexual selection contexts (although this also applies to other contexts) is that the signals are reliable indicators of an individual's quality (Dawkins & Guilford, 1991; Maynard Smith, 1991; Zahavi, 1975). They should allow the choosy individual (Bateman, 1948; Kokko et al., 2003) to assess the implied genetic and/or energetic contribution by the potential mate to the offspring. For example, in blackbirds *Turdus merula*, both sexes feed the young (Préault et al., 2005). It is likely that a healthy partner contributes more to the feeding of young than a sick partner and is thus preferred by females. A male blackbird's beak is orange, but the intensity of this colour depends on whether it is immunologically challenged as the carotenoids that give the beak its orange colour also play a role in the immune system – therefore, orange-beaked birds are healthier than yellow-beaked birds (Biard et al., 2010; Simons et al., 2012). In line with this reasoning, it was found that the orangeness of the bill correlates positively with provided paternal care (Préault et al., 2005). This is a system where it is difficult to cheat, as investing in an orange beak despite being sick is a strategy that should shorten the remaining lifespan of an individual. If these signals were not honest and individuals could easily cheat the system, i.e. if blackbirds could produce bright orange beaks with no effects on immune function, such a cheating strategy should run rampant within a few generations and individuals should stop paying attention to these particular signals – those strategies would not be evolutionary stable. So overall, an important assumption when studying animal communication is that what we observe in nature is probably evolutionary stable (Maynard Smith, 1979), as long as environments do not change substantially. We assume that selection pressures maintain the reliability or 'honesty' of signals (Gil & Gahr, 2002).

Birdsong

One aspect of animal communication which has been the focus of much work, is birdsong (Catchpole & Slater, 2008; Naguib & Riebel, 2014). Birdsong is the collective name for complex species-specific learned vocalisations produced by songbirds (Rose et al., 2022; Slabbekoorn & Smith, 2002), which comprise about 50% of all known bird species to date (Gill et al., 2023). There are many reasons why birdsong became an important model in the study of animal communication. Firstly, birdsong signals overlap with our sensory capabilities (practically all birdsong is audible to humans, Mindlin & Laje, 2006) and it is conspicuous, with a seasonal (Catchpole, 1973) cacophony of sound during the morning known as the dawn chorus (Henwood & Fabrick, 1979). Secondly, birdsong is accessible because many songbirds live in our city gardens and university campuses (Cox et al., 2016; Proppe et al., 2013). Thirdly, not to be understated in the selection of model systems, many would argue subjectively that birdsong is charismatic and beautiful (Blackburn et al., 2014). Moreover, birdsong is readily quantifiable since many temporal and spectral parameters can be measured from recordings using spectrograms, especially since the advent of digital signal processing (Kahl et al., 2021; Lohr & Dooling, 1999; Tchernichovski et al., 2001; Zollinger et al., 2012). Furthermore, since many bird species are territorial (Tobias et al., 2016), their song behaviour can be easily linked to their reproductive success (Brunton et al., 2016; Reid et al., 2005), as territorial birds will often sing at the same song posts across days and in relative vicinity to their nest (Mathevon et al., 1996; Sprau et al., 2012). Finally, experimental playback studies can be conducted in field conditions since bird vocalisations are easily played back from loudspeakers. Due to these many boons of studying birdsong, there is now a wealth of literature focusing on why birds sing. The dominant view, cemented by the book by Clive Catchpole and Peter Slater (2008), is that birdsong is a sexually selected signal that has two main functions: mate attraction and territory defence.

For the first function, mate attraction, a well-known example comes from nightingales *Luscinia megarhynchos*, where the production is tightly linked to the search for a mate. Male nightingales drastically reduce nocturnal song output after finding a partner, whereas unpaired males keep singing (Amrhein et al., 2002). In the same study, individuals that were deserted by their partner also increased their song output again. Similarly in other species, experimental removal of a paired male's partner prompts a male to increase its song output (Dunn & Zann, 1996b; Tobias et al., 2011). Birds from those species that do not drastically lower their song output after pair formation might keep singing to gain extra-pair matings (Hasselquist et al., 1996). Indeed, that song is sexually selected is suggested by the observation that females prefer the song of some males over other males in song preference studies (Holveck & Riebel, 2010; Riebel, 2009; Searcy, 1992). Additional evidence comes from song playback experiments. In some species, e.g. flycatchers *Ficedula*, playback experiments in the natural environment may attract females (Eriksson & Wallin, 1986), although patterns are not always that clear as both sexes may be attracted, e.g. in starlings *Sturnus vulgaris* (Mountjoy & Lemon, 1991).

The second function of birdsong, territory defence, is illustrated well by the great reed warbler *Acrocephalus arundinaceus.* Like nightingales, great reed warbler males drastically lower the output of a particular song type (long songs) after pairing. However, this species also sings a different song type (short songs), which is unaffected by its relationship status (Catchpole, 1983). Great reed warblers use this song type to negotiate territory boundaries with conspecific neighbouring males. Experimental evidence for this territorial function comes from the work on several other species using speaker replacement experiments. During these experiments, a singing male is removed from its territory and replaced by a speaker broadcasting its song (experimental treatment) or silence (control). After removal, silent territories are invaded earlier than those with song (Falls, 1988; Krebs et al., 1978; Searcy et al., 1998), suggesting that the song itself deters competitors. Moreover, territory-holding birds typically respond aggressively to speakers broadcasting conspecific song on their territories (Dabelsteen & Pedersen, 1990; Schmidt et al., 2008), and this aggressive response can be reduced when the territory decreases in value (Hyman, 2005), further indicating that song functions in territory defence.

Much of the birdsong literature referred to above concerns species from temperate regions of the Northern Hemisphere (i.e. Europe and North America), and historically there has been a bias towards studying species from this region, such as tits, starlings, flycatchers and song sparrows (Bircher et al., 2020; Catchpole & Slater, 2008; Krebs et al., 1978; Mountjoy & Lemon, 1991; Templeton et al., 2012). This has created general ideas on birdsong which are not necessarily representative for the wide variety of species across the globe. For example, all species mentioned above sing loudly, and acoustic communication in general is framed as a classic form of long-range communication (E. S. Morton, 1975; Naguib & Wiley, 2001; but see Lemon et al., 1981). Indeed, many studies have addressed the idea that vocalisations evolved to transmit optimally, known as the acoustic adaptation hypothesis (Erdtmann & Lima, 2013; Ey & Fischer, 2009; Weir et al., 2012; Wiley & Richards, 1982), or sensory drive hypothesis (Endler, 1992; Tobias et al., 2010). Only more recently, less conspicuous soft vocalisations have received more attention (Dabelsteen et al., 1998; Naguib et al., 2008; Rek & Osiejuk, 2011; Zollinger & Brumm, 2015). In a similar way, in the historically well-studied species, males are typically (assumed to be, see Sierro et al. 2022) the singing sex, yet it was recently discovered that female song, i.e. where both sexes sing, is the ancestral state in songbirds, with about 70% of songbird species having song in both sexes (Odom et al., 2014; Riebel et al., 2005). This changed the perspective from asking why males sing to why females in certain species stopped singing. Furthermore, it implies that birdsong is not necessarily a sexually selected, but also a socially selected (competition for non-sexual resources) signal (Hall, 2009; Hall & Langmore, 2017; Price, 2019). As this emancipation of the birdsong literature progresses and biases are getting increasingly addressed, it is likely that we will also encounter additional functions of song (Rose et al., 2022).

Birdsong is not only suitable for answering questions of a functional nature. It also lends itself well to investigating developmental aspects of song production and perception (Nottebohm et al., 1990). This is because birdsong is a learned behaviour, its development being analogous to how humans learn speech (Tchernichovski et al., 2001). First, several weeks after hatching, birds enter a sensitive phase in which they need to be exposed to song of their conspecifics. Second, a few weeks to months later, they start practicing with singing. Finally, after several weeks to months of practice, depending on the species, they will have mastered their conspecific song and the learning process is completed in so-called close-ended learners, or they will have mastered a part of their repertoire and will expand this repertoire throughout their life, so-called open-ended learners (Brenowitz & Beecher, 2005). Studies on songbirds, where the early life is easily experimentally altered by brood manipulation (Burness et al., 2000), are therefore well suited to address questions on mechanistic effects of early life on the development of song (Nowicki et al., 1998) and song preference (Riebel, 2009; Riebel & Slater, 1998), and for making comparisons in these aspects with human speech, where we find it unethical to manipulate the early life. Another advantage of birdsong being a learned behaviour, is that one can study cultural transmission, dialects (Parker et al., 2010; Riebel et al., 2015; Wheatcroft et al., 2022) and consequently, the loss of culture (Crates et al., 2021). A species that has been instrumental regarding our understanding of the mechanistic aspects of song learning and cultural transmission is the Australian zebra finch *Taeniopygia guttata castanotis* (Hauber et al., 2021; Tchernichovski et al., 2001, 2021), the most studied songbird under captive conditions (Griffith & Buchanan, 2010).

Zebra finches became such a well-studied model species, not because they necessarily represent songbirds well (Griffith et al., 2021), but because they are a popular pet species that has simple dietary requirements, is easy to breed and rear, and has short generation times (Hauber et al., 2021; Morris, 1954). Zebra finches have these traits because they are adapted to the harsh, unpredictable, and dry Australian outback they inhabit (Griffith et al., 2021). However, despite the large body of literature addressing proximate aspects of their song, we have a poor ultimate understanding of their song, i.e. why zebra finches sing, with only a few studies on the song of zebra finches in the wild (Dunn & Zann, 1996b, 1996a; Woodgate et al., 2012), and most other knowledge consisting of anecdotal evidence (Immelmann, 1968; Zann, 1996). As shown above, most of our ultimate understanding of birdsong, i.e. why birds sing, comes from studies on wild songbirds inhabiting the Northern Hemisphere temperate zone. These evolved under conditions that differ substantially from those of the zebra finch (Griffith et al., 2021). Currently, due to potentially large and unknown differences in ecological context, it is difficult to extrapolate mechanistic findings in captive zebra finches to ecologically relevant contexts and vice-versa. This thesis attempts to bridge these two bodies of birdsong literature by gaining a better understanding of wild zebra finch song ecology, closing (or at least shrinking) this knowledge gap.

Study species

Zebra finches are the most abundant and widespread estrildid on the Australian mainland, occurring on grasslands of the hot arid and semi-arid zone, as well as grasslands and farms of the more temperate coastal regions (Zann, 1996). They are strict vegetarians, feeding exclusively on grass seeds (S. R. Morton & Davies, 1983). The availability of these grass seeds depends on rainfall and is therefore variable across time and space across much of their range. Zebra finches seem to match their timing of breeding with an abundance of unripe grass seeds to feed their offspring (Zann et al., 1995). This means that zebra finches breed seasonally in the more temperate regions of their range, while breeding can be less seasonal and more erratic across much of the arid zone (Zann, 1996). When conditions are favourable, birds will keep breeding regardless of the season and, as zebra finches mature rapidly, birds that hatch in the beginning of a breeding period may themselves reproduce later in that same period (Zann, 1996). In natural conditions, zebra finches require water for drinking (MacMillen, 1990), and they will move on when surface water runs out (Zann, 1996). Consequently, like many other bird species that inhabit the Australian interior, zebra finches are nomadic, but the extent of their nomadism is variable (Gibson et al., 2022) and how far individual birds may migrate is not known due to the vastness of Australia (a problem for mark-recapture studies) and the small body size of zebra finches (they are too light to equip with a GPS tag). Because it is ambiguous whether disappearing birds have died or emigrated, we also have a limited understanding of their average lifespan under natural conditions, although their maximum lifespan is probably not more than five years (Zann, 1996).

Zebra finches mate for life, early in life (Zann, 1994), and they are socially and sexually monogamous, with extra pair paternity rates of only about 2% in wild populations (Birkhead et al., 1990; Griffith et al., 2010). In the wild, the main unit in which they are observed is the pair, which is inseparable with exception of the incubation period (Zann, 1994). Zebra finch pairs live in fission-fusion societies, with flocks of aggregated pairs (and unmated individuals) foraging together, and large aggregations of zebra finches can assemble in the arid zone at scarce water resources during dry periods (McCowan et al., 2015). Zebra finches are not territorial (they only defend their nest and its immediate vicinity, Zann, 1996), they breed in loose colonies (Zann, 1996), and this breeding seems to be synchronised locally. However, unlike those birds breeding in temperate conditions, zebra finches cannot rely on photoperiod as indicator of favourable breeding conditions across much of zebra finches' distribution range (Englert Duursma et al., 2017). Early observational work by Immelmann (1968) suggested that rain itself elicits song and breeding, but as conditions are not immediately favourable after a rain event (grass needs to grow and flower before unripe seeds are present), it is more likely that they use other environmental cues, such as the availability of ripening grass seeds (Zann et al., 1995). Additionally, zebra finches use social cues to coincide their breeding effort with others. Zebra finches inspect conspecific nests and preferentially start building their own nest near conspecific nests in an early stage of breeding (Brandl, Griffith, & Schuett, 2019). They also seem to pay attention to acoustic cues from nestlings when judging the suitability of breeding habitat (Brandl, Griffith, Laaksonen, et al., 2019). Acoustic cues themselves also influence the breeding phenology of zebra finches. In a study on captive zebra finches, birds that received additional recorded sound from their own colony bred more synchronously than a colony that did not receive sound supplements (Waas et al., 2005). However, due to the setup of this study it is not possible if specific calls or their song caused this effect.

In zebra finches, only males sing (Morris, 1954). However, similarly to how males learn to sing (Slater et al., 1988), females also develop a song preference early in life (Riebel, 2003). Individual males can be recognised based on their song signature, as each male sings a more-or-less stereotypic motif (Sossinka & Böhner, 1980) consisting of various classifiable element types (Sturdy et al., 1999). The song is part of the courtship display that serves to establish the pair bond and song in this context is referred to as directed song. After pair formation, zebra finch males keep singing, but all songs produced outside courtship contexts are so-called undirected songs (Morris, 1954; Riebel, 2009). These song types are almost identical acoustically, with undirected song having fewer introductory notes and being sung marginally slower than directed songs (Sossinka & Böhner, 1980), and there are also differences in the underlying neurobiology (Jarvis et al., 1998). As song is produced in the courtship context, and males will readily display and sing when exposed to a female after being housed in single-sex groups, their song has received much attention in the context of sexual selection studies, with many studies investigating which aspects of their song are preferred by females (reviewed in Riebel, 2009).

Although captive zebra finches have been actively studied, much about the song of wild zebra finches is still unknown. The one mechanistic study, focusing on song learning, found that song tutors in the wild often include the father, with 17 out of 23 zebra finches having learnt parts of their song from their father, but that only two out of 23 sons fully copied their father’s song (Zann, 1990). There are three studies that focused on the functional aspect of zebra finch song in the natural context, all of them focusing on the sexual selection aspect. In one study, males regularly sang at provided feeder locations, and when their partner was experimentally removed, these males increased their song rate, and consequently found a new partner within days of their partner being removed (Dunn & Zann, 1996b). In another study, the song of their partner, perched besides the nest, also stimulated the female to stay in the nest, with the amount of song varying with the breeding stages, peaking during egg-laying (Dunn & Zann, 1996a). The occurrence of song outside of the breeding context was interpreted as solicitation for extra-pair matings, while singing at the nest was interpreted as a mate-guarding against extra-pair fertilisations (Dunn & Zann, 1996a, 1996b), even though an earlier study in the same population found an extra-pair paternity rate as low as 2.4% (Birkhead et al., 1990). A cross-fostering study in another population found that song appeared to be a signal of genetic quality, not parental ability, with higher genetic offspring survival correlating with song structure (a principle component capturing mostly variation in syllable number and motif length, which were correlated), independently of in which nest the chick was raised (Woodgate et al., 2012). Overall, these few studies on the song of wild zebra finches have mostly interpreted zebra finch song as a sexually competitive signal that advertises a male's quality to attract (extra-pair) matings.

Thesis outline

The song of the zebra finch has been the focus of many physiological and behavioural studies in laboratories around the world (Griffith & Buchanan, 2010). Yet, we know little about the functional aspect of zebra finch song, with only three studies addressing this aspect (Dunn & Zann, 1996a, 1996b; Woodgate et al., 2012), and the rest of our knowledge being anecdotal (Immelmann, 1968; Zann, 1996). These few studies have exclusively focused on the mate attraction function of their song. However, zebra finches can mate very early in life (Zann, 1994), so that most of their song is produced after pair formation. Furthermore, extra-pair paternity in the wild is low (Griffith et al., 2010) and territoriality practically absent. What is the function of their song? Is it only used for mate attraction; is it another social cue that drives breeding synchrony; or are there other general, unconsidered, functions of their song? These questions cannot be answered without extensive knowledge on the elements of circumstance (Sloan, 2010) surrounding zebra finch song: who is singing; who are the receivers of song; what distance can song be detected; what are the social contexts in which song is produced; where is song produced; when do individuals sing; and how does this relate to breeding? This fundamental information on the contexts in which song is produced under natural conditions is still largely missing. In this thesis I target this knowledge gap by investigating the communication system of wild zebra finch song in detail; by quantifying several ecologically relevant contexts of song in wild zebra finches; and by describing a key component of their social and spatial organisation that ties into their communication system, their use of social hotspots (Figure 1). I conducted all my fieldwork for this thesis in Fowlers Gap Arid Zone Research Station, about 110 km North of Broken Hill, in the West of New South Wales, Australia. During the first years of my work on this thesis, this part of Australia was hit by a severe drought, which only broke at the start of the Covid-19 pandemic in 2020. During this drought, breeding activity was practically absent.

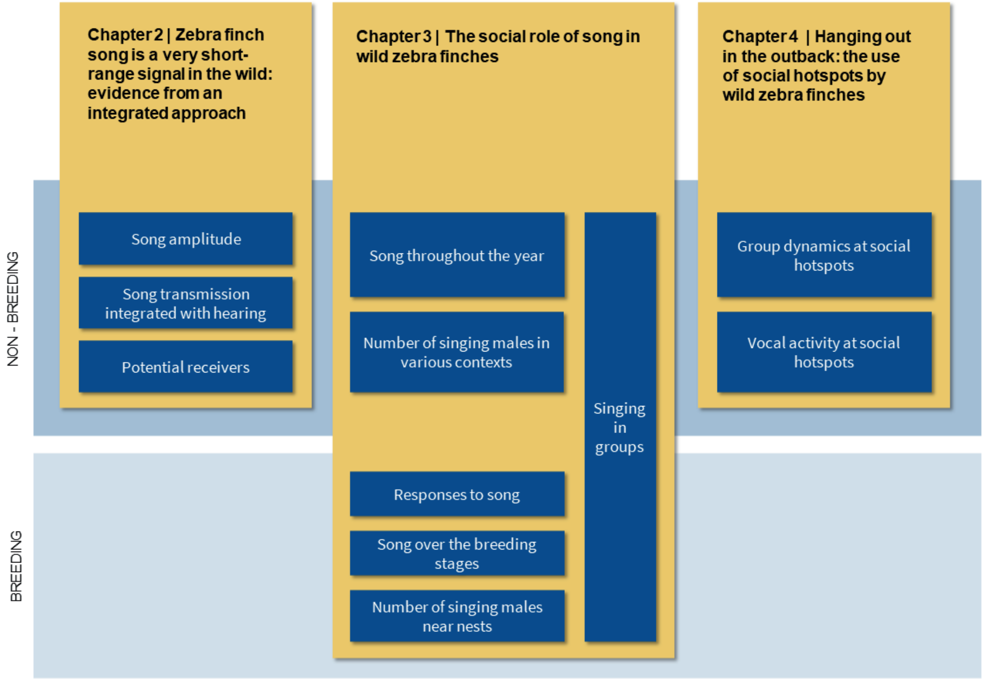

Figure 1. Chapter overview of the aspects of zebra finch song and social organisation that were studied under natural conditions, with indication of the breeding status of the local population.

In **chapter 2** I studied the communication system: signal production, transmission through the environment, and receiver detection. First, I quantified the amplitude of wild zebra finch song. Although amplitude represents signal conspicuousness and is therefore one of the most important parts of an acoustic signal, it is often overlooked or standardised in studies as it is difficult to quantify it. Secondly, after quantifying song amplitude, I broadcasted songs at natural amplitude and re-recorded these at set distances. This transmission experiment allowed me to quantify signal attenuation in the natural environment. Finally, I integrated the findings of this transmission experiment with hearing literature to calculate the detection distance or maximum communication distance of wild zebra finch song in the natural environment. Additionally, I conducted observational transects to check who the potential receivers of this song are, and whether natural singing behaviour reflects this calculated value, by measuring the distance between individuals when there was song.

In **chapter 3** I explored and quantified the broader ecological context of zebra finch song, asking whether their song plays a role in general social affiliative interactions or perhaps in the synchronisation of breeding attempts across pairs. This study integrated data from five consecutive field seasons (mostly the Austral spring, including two seasons before the start of my

PhD). These field seasons encompassed periods when zebra finches were actively breeding, and a severe drought during which breeding was severely restricted or absent. The study combines natural history and experimental approaches by integrating observational transects, passive recordings at active nests, year-round recordings at zebra finch hotspots, hand recordings, and an experimental playback. By integrating the data from these methods, this chapter provides a thorough quantification of several key questions surrounding zebra finch song ecology. Who is around when there is song? Where do zebra finches sing? When do they sing? And is song linked to breeding (stages)?

In **chapter 4** I quantified an important component of social and spatial organisation in wild zebra finches: their use of social hotspots, fixed locations where zebra finches spend substantial parts of the day (hanging out) in aggregations. Although this behaviour is anecdotally described by Richard Zann (1996) and was also observed by my supervisor Simon Griffith (pers. comm.), this aspect which underlies their fission-fusion society had not been formally described and quantified. This hangout behaviour is especially relevant in the context of my work on the communication system in **chapter 2**, where I found that their vocalisations are short-range, and **chapter 3**, where I found that zebra finches regularly sing in groups, and these social hotspots provide one of the main platforms to do that.

In **chapter 5** I synthesised these three data chapters and discuss the implications my work has for interpreting lab-based findings in zebra finches, and the study of functional aspects of birdsong in general.

Chapter 2 | Zebra finch song is a very short-range signal in the wild: evidence from an integrated approach

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Abstract

Birdsong is typically seen as a long-range signal functioning in mate attraction and territory defence. Among birds, the zebra finch is the prime model organism in bioacoustics, yet almost exclusively studied in the lab. In the wild, however, zebra finch song differs strikingly from songbirds commonly studied in the wild as zebra finch males sing most after mating and in the absence of territoriality. Using data from the wild, we here provide an ecological context for a wealth of laboratory studies. By integrating calibrated sound recordings, sound transmission experiments and social ecology of zebra finches in the wild with insights from hearing physiology we show that wild zebra finch song is a very short-range signal with an audible range of about nine meters and that even the louder distance calls do not carry much farther (up to about fourteen meters). These integrated findings provide an ecological context for the interpretation of laboratory studies of this species and indicate that the vocal communication distance of the main laboratory species for avian acoustics contrasts strikingly with songbirds that use their song as a long-range advertisement signal.

Introduction

Animal communication plays an integral role in life history events, such as finding a partner, defending a territory, or warning for predators (Bradbury & Vehrenkamp, 2011; Searcy & Nowicki, 2005). As a consequence, animals produce a striking diversity in signals, from very subtle short-range signals to conspicuous far-ranging displays like many acoustic and visual advertisement signals, adapted to function in the environment in which they have evolved (Brumm & Naguib, 2009). A key factor for a signal to function is that its coded information reaches the intended receiver. Indeed, the active space of a signal (Brenowitz, 1982), the distance over which a signal can function, is key in unravelling the function of a signal, as the signal structure and its information at the distance at which a receiver responds pose a primary selection pressure (Gerhardt, 1994). Some animals maximize their conspicuousness by using elevated display posts, as used for long distance vocalisations (Sprau et al., 2012), or by seeking display sites that maximize contrast and visibility (Endler & Théry, 1996; Uy & Endler, 2004). Yet while the active space of a signal is often determined by its amplitude or conspicuousness and the transmission constraints of the physical environment, eventually the sensory and perceptual ability and acuity of the receiver (Gall et al., 2012; Lohr et al., 2003; Naguib & Wiley, 2001; Wiley & Richards, 1978) need to be considered. This is indeed crucial when assessing which parts of the information emitted by a signaller can be picked up from attenuated and degraded signals after transmission through the environment.

Among animal signals, vocalisations and specifically birdsong and calls are among the best-studied communication systems, and insights from birdsong have fundamentally shaped the broader view on the evolution of animal communication (Searcy & Nowicki, 2005). The most studied functions of birdsong are mate attraction and territory advertisement, yet song can also have more subtle functions affecting daily behavioural routines and decisions among pair members, the wider neighbourhood, and socially relevant individuals in groups (Snijders & Naguib, 2017). One of the main model bird species is the Australian zebra finch (*Taeniopygia guttata castanotis*), providing the primary avian model organism in laboratory studies world-wide (Griffith et al., 2021; Griffith & Buchanan, 2010). Zebra finches have been key in studies on mate choice (Kniel et al., 2015; Riebel, 2009; Slater et al., 1988), long term effects of early developmental stress (Honarmand et al., 2015; Monaghan et al., 2012; Spencer et al., 2005) and specifically are a textbook model for the physiology, neurobiology and genetics of the song system (Gil et al., 2006; Haesler et al., 2004; Ma et al., 2020; Warren et al., 2010) including song development and learning (Hauber et al., 2021; Kriengwatana et al., 2016; Slater et al., 1988; Tchernichovski et al., 2021). Yet, very few studies have addressed zebra finch song in the wild (Dunn & Zann, 1996a, 1996b; Woodgate et al., 2012), so that the ecological context and perspective on the findings from laboratory studies is largely lacking and often based on anecdotal observations (Immelmann, 1968; Zann, 1996). Zebra finches are social, non-territorial birds that live in fission-fusion societies in the arid zone of Australia (Brandl et al., 2021; McCowan et al., 2015), and thus are exposed to different selection-pressures, both socially, and environmentally compared to the well-studied temperate forest birds that dominate the literature on bird song (Catchpole & Slater, 2008).

Advantages of using zebra finch song under laboratory conditions as a model for animal communication and the neural basis of song learning, are that males sing all year round, individuals sing a unique single motif (song) produced with only small variation across repetitions (Sturdy et al., 1999), and males sing reliably when exposed to females (Riebel, 2009). Whilst the latter characteristic has made the zebra finch song a major focus of work on mate choice, wild males continue to sing outside breeding events (Griffith, 2019; Zann, 1996), and indeed most males are paired for life from an early age (Zann, 1996). As such, most of a male's song is produced after the initial formation of the pair bond. Additionally, extra-pair paternity rates in the wild are low (2.4% in Birkhead et al., 1990; 1.7% in Griffith et al., 2010). These observations question the general assumption that the primary function of song in this species is mate attraction (Griffith, 2019). Yet, while in the laboratory birds are usually kept in stable, single sex groups, or pairs, in the wild they live in loose associations, where individuals stay with their partner for life, but with pairs joining and leaving broader social groups on a regular basis (Brandl et al., 2021; McCowan et al., 2015). To understand the function of vocalisations within social groups and their potential role in social facilitation, a key step is to understand the communication range, as it provides the context in which the signal can function within the natural setting and in which it is selected by receiver responses.

Communication range in birds is often studied by combining estimates of sound amplitude of vocalising individuals with either a modelling approach (Derryberry et al., 2016, 2020; Lohr et al., 2003; Nemeth & Brumm, 2010) or sound transmission experiments, in which the sound is broadcast and re-recorded across a range of distances for subsequent acoustic analyses (Brenowitz, 1982; Gall et al., 2012; Naguib et al., 2008). Such transmission experiments have been key in discussions on the communication distance, how sounds regulate the spacing of individuals (Bradbury & Vehrenkamp, 2011; Waser & Wiley, 1979; Wiley & Richards, 1978) and on information transfer in social networks among individuals without close spatial associations (Snijders & Naguib, 2017). Yet, animals often do not respond to very distant signals, as they appear to be less salient (Naguib & Wiley, 2001). Thus, a complementary approach to assess communication distance, next to playback experiments, is to integrate signal broadcast amplitude, with sound transmission experiments and the actual hearing abilities of the receivers. Hearing curves, the sensitivity to different frequencies of a sound, are commonly determined under standardized conditions with psycho-acoustic experiments in the laboratory (Dooling et al., 2000; Henry et al., 2016). Studies in invertebrates in contrast have been able to use the neurobiological responses to sound in the field as a 'biological microphone' (Rheinlaender & Römer, 1986; Römer, 1993, 2021), revealing auditory responses to long distance signals directly under field conditions. Field studies integrating such hearing thresholds in birds have focused mainly on signal detection in noise, an important approach specifically with respect to communication at high environmental or anthropogenic noise levels (Derryberry et al., 2016, 2020; Gall et al., 2012; Lohr et al., 2003; Nemeth & Brumm, 2010). Among birds, zebra finches are among the few species in which hearing thresholds as well as masked thresholds, the precise signal-to-noise ratio within relevant frequency bands that still allows for detection, have been determined (Okanoya & Dooling, 1987; Prior et al., 2018). Zebra finches thus provide an excellent opportunity to integrate data from hearing thresholds with acoustic signals in the wild, allowing us to fill a major gap in understanding on communication ranges in animals, and in this important model species in particular.

To determine the communication distance of song and distance calls of wild zebra finches we (1) made calibrated recordings to determine natural signalling amplitudes of wild zebra finches, (2) conducted sound transmission experiments of songs and distance calls at their natural amplitude in the native environment in the Australian arid zone and (3) integrated the results with laboratory data on zebra finch hearing physiology. Additionally, we conducted field transects to characterize perch height and the distance between individuals when singing. These integrated approaches provide an important ecological base for understanding the function and evolution of song in the primary laboratory-based avian model organism.

Methods

We conducted all fieldwork at Fowlers Gap Arid Zone Research Station, New South Wales, Australia, using a population of nest-box breeding zebra finches (Brandl, Griffith, & Schuett, 2019; Griffith et al., 2008). The areas inhabited by zebra finches typically consist of several creek lines vegetated by widely spaced low bushes such as bluebush (*Maireana* sp.) and low trees and shrubs, such as prickly wattle (*Acacia victoriae*), dead finish (*Acacia tetragonophylla*), boobialla (*Myoporum montanum*) and native apricot (*Pittosporum angustifolium*). There was an ongoing drought during this study and most natural sources of surface water in the surrounding were dry. Water was thus available almost exclusively through livestock troughs.

Calibrated recordings and amplitude measurements

We recorded wild zebra finch songs and distance calls between 26 September and 31 October 2018 on days with low wind between 08:00 and 15:00 hours. Recordings were made opportunistically throughout the study site when the singing individual was in sight, so that we could determine its orientation and distance from the microphone, determined afterwards using a measuring tape. All recordings were made under very low wind conditions and under the extremely low noise levels of the Australian arid zone. For each recorded vocalisation we scored the orientation of the bird in relation to the microphone and whether it originated from the focal individual, since recordings were made in social contexts. Zebra finches are mostly seen with their partner or in small groups (McCowan et al., 2015) and their song is not used as individual territorial advertisement but given in social contexts. All of the opportunistically recorded males were singing with at least one conspecific nearby and we could always clearly identify the singing male due to the short range at which we recorded them. We used directional microphones (Sennheiser MKH60 in MZS 20-1 + MZH + MZW 70-1 basket windscreen and Sennheiser ME66/K6 with foam windscreen) and recorded at 44.1 kHz 16 bit on digital recorders (Tascam DR100-MKIII) with standardized gain (55 dB for both microphones). For each day we recorded a 1kHz tone (created in Audacity 2.2.2) at 1 m with both microphones (gain also at 55 dB) for sound file calibration. The tone was played at 65 dB (1 m, Voltcraft SL-300 sound pressure level (SPL) meter, A-weighted, slow response, precision ± 1.4 dB at 1kHz) from an Olympus DM-670 recorder through a UE Megaboom loudspeaker, mounted on a tripod at 1.6 m.

In total we recorded 193 distance calls from 40 males and 345 song motifs (Sossinka & Böhner, 1980; Sturdy et al., 1999) from 45 males, of which 16 individuals were recorded in a pair context and 33 were recorded in a social context (i.e. more than two other individuals present), with five individuals having been recorded in both contexts and one individual in an undocumented context. To maintain a high degree of accuracy for the amplitude measurements, we used vocalisations only of focal individuals facing the microphone and recorded within eight meters. This resulted in high quality recordings of a total of 26 individuals, of which 10 individuals were recorded in a pair context and 17 in a social context, with one individual having been recorded in both contexts. We measured 5.3 ± 4.0 (mean ± SD, range 1 - 18, N = 26) song motifs per individual, recorded at 3.8 ± 1.2 m (mean ± SD, range 1.8 - 6.5 m).

All recordings were high-pass filtered (settings: 400 Hz, 48 dB roll-off/octave) in Audacity. Since the relative amplitude of specific elements appears consistent within males (Brumm, 2009 and personal observation), we measured the root mean square (RMS) of the loudest 125 milliseconds of a song motif/distance call using the 'contrasts' function in Audacity (Brumm, 2009 also measured 125 ms). This often corresponded with the duration of the single song element and spanned most of the duration of the distance calls. Per individual male we always selected the same part of the same song element/distance call. The measured values were in decibels relative to full-scale (dBFS), which we then subsequently translated to SPL (all SPL reported are re 20 µPa) using the calibration tones. Other than the high-pass filter, we did not additionally correct for noise, as noise levels at our field sites in the absence of wind were extremely low (see the spectrum-level background noise of our transmission experiment in Results).

Similarly, we A-weight-filtered each calibration tone ('equalization' function in Audacity) and measured the RMS over 125 ms, omitting environmental noise. Because there was variation per day (SD of 2.2 and 1.5 dB for the MKH60 and ME66, respectively) and not all calibration tones were recorded on the same day as the recording days for practical reasons, we averaged these per microphone. This resulted in an overall average calibration value used for all recordings of a specific microphone, the microphone dependent calibration value c_{mic}: 65 dB SPL corresponded with -7.6 ± 0.8 dBFS (mean ± SE, N = 7) for the MKH60 and with -5.6 ± 0.7 dBFS (mean ± SE, N = 5) for the ME66/K6. We obtained the calibrated RMS of the vocalisations in SPL by subtracting this calibration value of the used microphone and adding the sound pressure level of the calibration tone, SPL_{tone}, 65 in our case. Then, for each calibrated vocalisation RMS value, we calculated the dB level at one meter using spherical spread, $20 * \log_{10}(d)$, where d is the recording distance ($RMS_{calibrated} = RMS_{measured} - c_{mic} + SPL_{tone} + 20 * \log_{10}(d)$).

Transmission experiment and analysis

We conducted transmission experiments on low-wind days between 18 and 30 November 2018, playing seven high-quality recordings of song, male distance calls and female distance calls each (21 vocalisations in total). Using the RMS in dBFS of the loudest 125 ms (like our amplitude measurements) we normalized all songs to the same amplitude and set both male and female distance calls to be 7.4 dBFS (the amplitude difference between song and distance calls, see Results) louder than the songs. We added a 1 kHz calibration tone that was 14.5 dBFS louder than the songs for calibration purposes.

We broadcast this master file at six locations (with a tripod-mounted UE Megaboom and an Olympus DM-670 recorder, with the speaker center at 1.6 m height, the average perch height of singing individuals in our area, see Results), re-recording it (Sennheiser microphone MKH40 in the basket windscreen; same height as loudspeaker; Tascam DR100-MKIII recorder) at the distance of 1, 2, 4, 8, 16, 32, 64, 128 and 256 meters for each transect. These transects varied in the amount of vegetation to span the range of microhabitats present in the natural environment of this zebra finch population. We broadcast the zebra finch vocalisations at the pre-determined average natural amplitude (see results) by ensuring a sound pressure level of 65 dB (A-weighted, slow-response) for the 1 kHz calibration tone with our SPL meter. We used a fixed microphone sensitivity (53 dB gain) for all recordings in all transects. Although wind speeds were low during recording days, we still recorded the broadcast master file multiple times at each distance (usually three to four times) to have sufficient repeats for analysis in case of occasional gusts masking a signal.

We manually checked every recorded repetition's spectrogram to exclude ones with wind or insect noise and cut out each repeat at the same starting point, resulting in aligned sound files with each specific vocalisation at a fixed timestamp. Then, we fed these selections through a custom-made Matlab script (version 2020b) which applied for every vocalisation a series of band-pass filters over the 500 - 8,000 Hz range (in 100 Hz steps), calculating the root-mean-square value (RMS) of the loudest 125 ms for every band. 125 ms corresponds with the 'fast' setting of a SPL meter and is a time that falls within the perceptual time integration of zebra finches (Okanoya & Dooling, 1990). The band-pass filter was a minimal-order chebyshev1 filter with a passband frequency that corresponded with the critical bandwidth, a stopband frequency of 0.05 times the passband frequency (e.g. from 290 to 300 Hz and from 500 to 510 Hz for a 200 Hz passband), a 0.01 dB passband ripple and a 30 dB stopband attenuation. The critical bandwidth was calculated as $10^{(CR/10)}$ (Kittel et al., 2002), where CR is the critical ratio in dB calculated as 9.92 * $\log_{10}$(frequency) - 4.8 (Okanoya & Dooling, 1987). For every band-pass filtered vocalisation we also measured 0.4 seconds of band-passed background noise in the silence after the specific vocalisation. Such noise measured over the critical bandwidth functions as the masking threshold (GM Klump, personal communication). This process resulted in a total of N = 214,396 spectrum-level amplitude measurements for both vocalisations and background noise (song: N = 64,372, male distance calls: N = 73,948 and female distance calls: N = 76,076).

We calibrated all values to SPL using the 65 dB (A-weighted) reference tone that we recorded. For each transect, we measured the RMS in dBFS of one of these recorded A-weight filtered 1 kHz reference tones at 1 m in Audacity (using the contrasts function and equalization, see above). The resulting calibration value that we added to each amplitude measurement of that transect was therefore: the absolute value of this measured dBFS value of the reference tone + 65 (its dB in SPL) – 3.01 (the RMS in dBFS of the loudest tone possible).

Transects

We walked transects in six sites on a weekly basis between 7:30 and 17:00 from 12 October – 4 December in 2018 and 29 August – 6 December in 2019. All transects consisted of an observer walking from a local water point used by zebra finches (e.g., a trough, or a water basin) towards a vegetated area with nest boxes, and then continuing in the nest box area (which often followed creek lines) until the total distance walked was 1 km. Transects followed the same route every time.

When zebra finches were detected, we scored group size and whether there was singing. For singing zebra finches we estimated perch height (2018) or distance to group members (2019). If there were other groups around in other bushes and detected, this was sometimes noted, but not systematically. During 77 of a total 116 transects, we observed zebra finches a total of 265 times, of which 94 observations included singing birds. Of 49 singing birds we scored the perch height of the singing individual to validate our transmission experiment broadcast height. Of 43 singing birds we scored the maximum distance to group members, in other words, the distance between the two birds in a group farthest from each other. This allowed us to estimate zebra finches' receiver distance in the wild. In seven of these we also estimated the distance of the next nearest group that was detected at the same time. We received approval by the Macquarie University Animal Ethics Committee (Animal Research Authority 2018/027) for all work in this study.

Statistical analysis

All statistical analyses were conducted in R (version 4.0.2). For calculating the mean vocalisation amplitude, we averaged all amplitude values per individual (because of the large variation in number of songs per individual) and then averaged all individuals. To determine inter-individual differences in amplitude we used an ANOVA (function aov) on a dataset which included all vocalisations of the type investigated. To additionally explore whether the two different social contexts (pair or social group) in which we recorded male song, had an effect on song amplitude, we conducted a linear mixed model (function lmer of lme4 package) with song amplitude as a response variable and context (i.e. pair or social) as an explanatory variable and individual as a random effect. To determine the significance of this model, it was compared with the null model (using function anova).

For the transmission experiment, we conducted linear mixed models with the band-passed vocalisation amplitude (N = 214,396) as response variable and vocalisation-type, doubling of distance, frequency, and background noise amplitude as explanatory variables, with two-way interactions between doubling of distance, frequency and background noise amplitude, respectively, as well as a three-way interaction between these three factors. Although vocalisation-type was our main focus here, we included these other physics-based factors because we can reasonably attribute a large part of the variation in measured amplitude to them, e.g. (doubling of) distance because sound attenuates over distance; frequency because our broadcasted vocalisations contained relative amplitude differences over the range of frequencies; and background noise because it, even at low amplitudes, should still affect amplitude measurements since sound amplitude is additive (Embleton, 1996). The interactions are warranted because frequency-dependent attenuation is expected (frequency * distance), background noise is not flat but biased towards lower frequencies (frequency * noise), and the relative impact of background noise should increase with distance (distance * noise) and this will, too, be frequency-dependent due to the noise bias towards the low end of the spectrum (frequency * distance * noise) (Brumm & Slabbekoorn, 2005). We included transect ID (N = 6) as random intercept. This model was the full model, so no stepwise reduction of model parameters was performed (parameter reduction resulted in poorer fits). Subsequently, using the significant model coefficients (± standard errors) of the full model, we modelled the communication distance of the different vocalisations at average natural amplitude with average natural levels of background noise (at -0.93 dB) to calculate at which distance all frequencies of a vocalisation were under the absolute hearing threshold of zebra finches (Okanoya & Dooling, 1987). We conducted post-hoc tests to test for differences in communication distance between the vocalisation types (function emmeans of emmeans package).

Results

Calibrated recordings

Amplitude at 1m was 50.5 ± 0.8 dB SPL (mean ± SE, range 44 - 58.6 dB, N = 26, Figure 1a) for songs and 57.9 ± 0.8 dB SPL (mean ± SE, range 52.1 – 64.6 dB, N = 14, Figure 1a) for male distance calls. Individual males varied significantly in their song amplitude (Anova, $F_{25, 112} = 66.8$, $P < 0.001$, Figure 1a) and distance call amplitude (Anova, $F_{13, 24} = 4.5$, $P < 0.001$, Figure 1a). The social context also had a small but significant effect on the song amplitude with males in a pair context having sung about 1.9 ± 0.8 dB SPL (mean ± SE) louder than males in a social context (linear mixed model, $\chi^2 = 5.3$, $P = 0.02$, pair context N = 10, social context N = 17, Figure 1b).

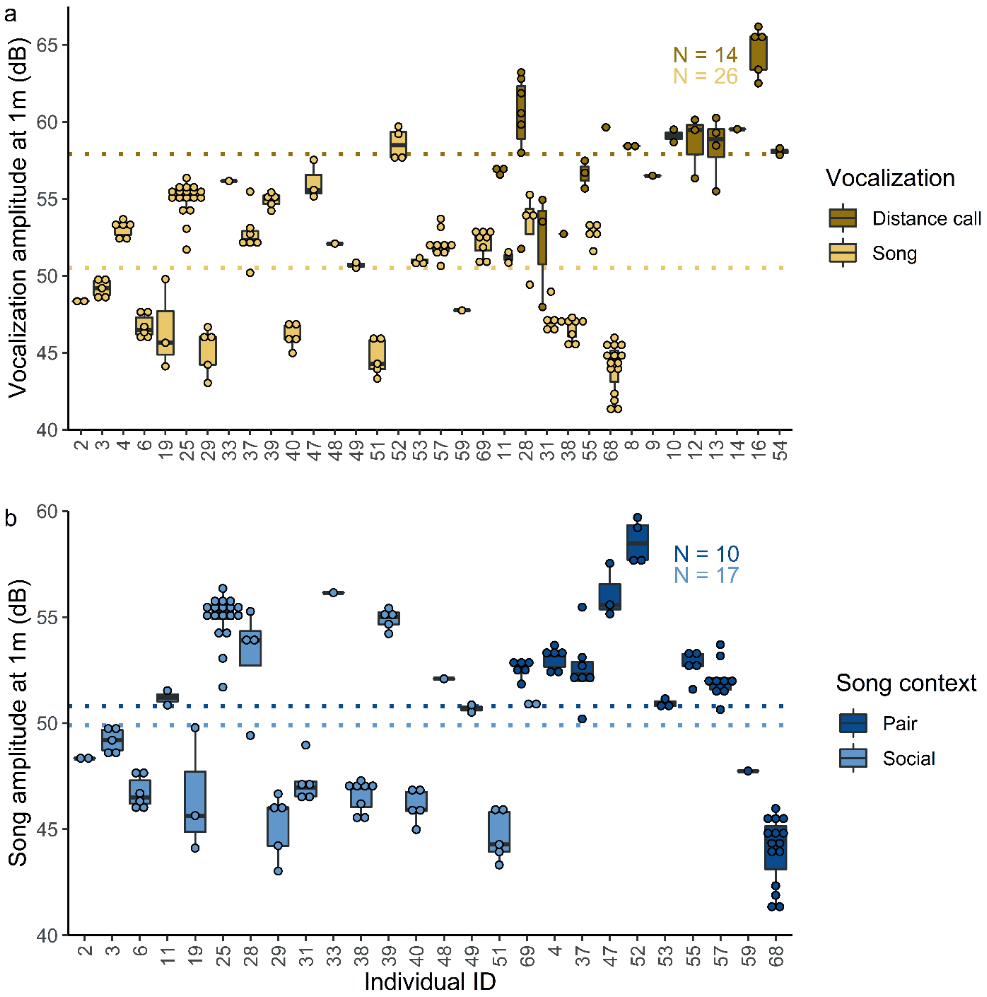

Figure 1. (a) Song and male distance call amplitude (dB re 20 µPa of the loudest 125 ms segment) of calibrated recordings in wild zebra finches. Individuals of which we acquired only song or distance calls are on the left and right side, respectively, with the six individuals of which we acquired both song and distance calls in the middle. (b) Song amplitude (dB re 20 µPa of the loudest 125 ms segment) of the same calibrated recordings in their respective context, that is, pair or social (>2 birds present). For one individual (# 69), we acquired song in both contexts. Points represent songs or distance calls, boxes encompass the first to third quartiles, thick lines are medians and whiskers extend until 1.5 times the inter-quartile range. Dotted lines indicate sample means.

Transmission experiment

Transmitted zebra finch song, which also was broadcast at lower amplitudes, was significantly softer than male distance calls (Tukey post-hoc test, z-ratio = 87.635, N = 214,396, P < 0.001) and male distance calls were softer than female distance calls even though the latter two were broadcast at the same amplitude (Tukey post-hoc test, z-ratio = 2.881, N = 214,396, P = 0.011). Considering absolute hearing thresholds of zebra finches (Okanoya & Dooling, 1987) and using the significant linear model coefficients (Table 1), all wild zebra finch song produced at average natural amplitude in the natural environment with average spectrum-levels of background noise (-0.93 dB SPL for N = 214,396 noise measurements) would not be audible for conspecifics after 8.9 ± 0.7 meter (mean ± SE, raw data plotted in Figure 2a). Average male and female distance calls in the same conditions would not be audible after 13.7 ± 1.0 and 13.9 ± 0.9 meter, respectively (Figure 2b and 2c, respectively). The low levels of background noise in the Australian arid zone did not impose limits on zebra finch communication distance (dotted lines in Figure 2).

Table 1. Model parameters from the linear mixed model on measured amplitude of the transmitted zebra finch vocalisations in the natural environment, with Transect ID as a random effect (N = 214 396).

Variable	Coefficient	SE	t	P value
Intercept (of female distance call)	47.707	0.460	103.65	< 0.001
Doubling of distance (i.e. $\log_2$(m))	-6.371	0.018	-347.12	< 0.001
Frequency (in kHz)	-1.246	0.015	-84.79	< 0.001
Background noise	-1.715	0.010	-164.12	< 0.001
Male distance call	-0.121	0.042	-2.88	< 0.001
Song	-3.952	0.043	-90.86	< 0.001
Doubling of distance * frequency	0.103	0.004	25.38	< 0.001
Doubling of distance * noise	0.147	0.004	40.98	< 0.001
Frequency * background noise	0.384	0.003	124.22	< 0.001
Doubling of distance * frequency * noise	-0.032	0.001	-31.43	< 0.001

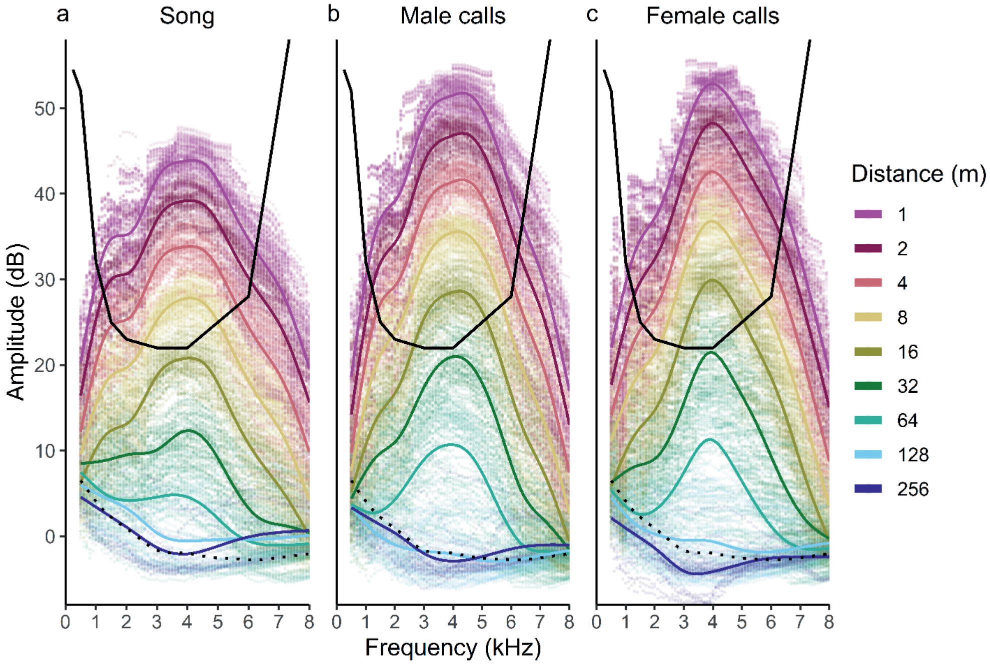

Figure 2. Amplitude (dB re 20 µPa of the loudest 125 ms segment) of wild zebra finch vocalizations (a: song, b: male distance calls, c: female distance calls) transmitted over a 1–256 m distance at average natural amplitude in the natural environment, integrated over critical ratio-based hearing bandwidth. Raw data points (N = 214 396) on which the lines are based are shown in corresponding colors. The black line is the audibility curve of (domesticated) zebra finches based on pure tones from Figure 3 in Okanoya and Dooling (1987). The part of the transmitted sound that is above the curve is an approximation for the sound that is audible at that distance by zebra finches. The dotted lines resemble the environmental noise integrated over the respective auditory bandwiths, which is the masking threshold, indicating that masking by environmental noise is not relevant in this environment.

Transects

At our study site, which is mostly dominated by low shrubs and trees, the mean perch height of singing birds was 1.6 ± 0.1 m (mean ± SE, range was 0.3 - 3 m, N = 49, Figure 3a). The maximum distance between group members when there was singing (a measure of receiver distance of song) was 1.5 ± 0.2 m (mean ± SE, range was 0.2 - 6 m, N = 43, Figure 3b). The distance of groups with singing zebra finches to closest neighbouring groups was 24 ± 3 m (mean ± SE, range was 15 – 35 m, N = 7, Figure 3c). Of 94 song observations, 12 observations (13%) were of males apparently singing alone, 25 observations (27%) were of paired birds and 57 observations (61%) were of groups (range 3 to 43 individuals, mean ± SD: 12.4 ± 9.0 individuals).

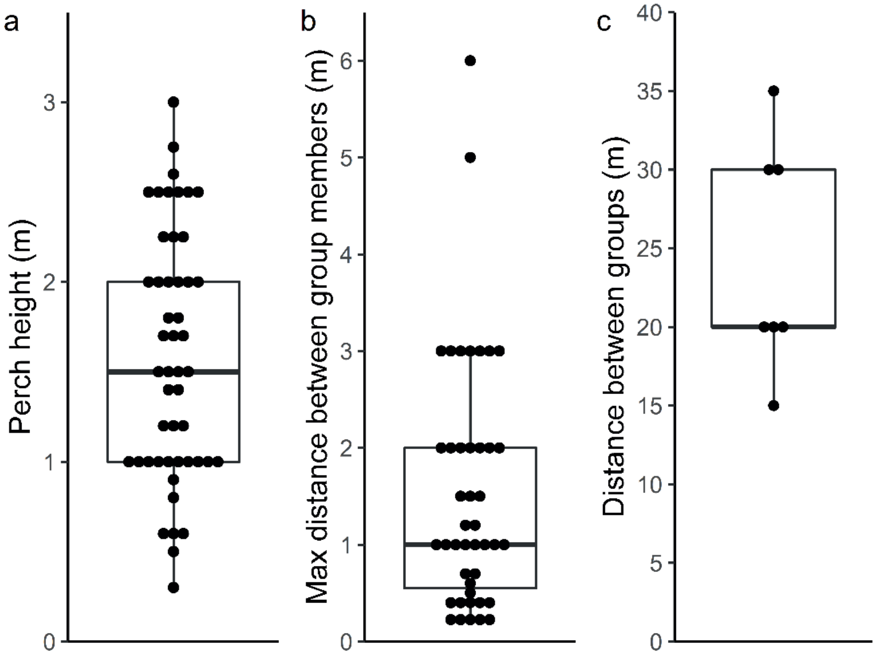

Figure 3. (a) Perch height of observed singing zebra finch males during observational transects. (b) Maximum distance between group members in zebra finch groups that had one or more singing individuals, a measure of communication distance of wild zebra finch song. (c) Distance between zebra finch groups when singing individuals were present, not always scored due to practical constraints. Points represent observations of singing males, boxes encompass the first to third quartiles, thick lines are medians and whiskers extend until 1.5 times the inter-quartile range.

Discussion

By integrating calibrated sound recordings, sound transmission experiments and social ecology with insights from hearing physiology we show that wild zebra finch song is a very short-range signal with an estimated audible range of merely 9 m and that even the louder distance calls do not carry much farther (up to about 14 m). These findings are in line with the results of our transects showing that singing individuals are in more than 85% of the observations in very close proximity to conspecifics and they demonstrate that vocalisations would not be heard by birds gathering in the wider vicinity. Together these results shed new light on the communication distance and thus the potential function of vocalisations in one of the main study species for avian acoustics around the world (Griffith & Buchanan, 2010; Hauber et al., 2021). By relating our findings with well-established studies on hearing physiology of this prime model organism on avian acoustics in the lab, we are able in an unprecedented way to make much more accurate estimates on vocal communication distance in animals, and specifically with this integration obtain a better understanding of the ecology of avian acoustics.

These integrated findings caution general interpretations about animal communication range as the perceptual system is often not fully integrated in studies on communication distance or assumed to be similar to the human perceptual system, as discussed by Caves et al. (2019). Studies that did consider the hearing mainly focused on the effects of noise on signal detection (Derryberry et al., 2016, 2020; Gall et al., 2012; Nemeth & Brumm, 2010). Our findings that singing zebra finches can be heard by other conspecifics over merely a few meters at extremely low noise levels show that the song of this model species is very different in communication range, and thus potential function compared to the widely studied territorial song of temperate zone songbirds. Classically, birdsong is seen as long-distance advertisement signal (Brumm & Naguib, 2009), and sound transmission experiments have been used to determine the space across which the signal can function (Dabelsteen et al., 1993; Richards, 1981), leading to transmission ranges of 100 and more meters (Naguib et al., 2008). Even in our own sound transmission experiment shown here, we reveal that the rather soft song and the slightly louder distance calls can be re-recorded over a substantial range (64+ m), albeit in a low-noise environment (dotted line Figure 2). Yet, combining these physical measurements with the relevant hearing curve and critical ratio function (the signal-to-noise ratio at masking threshold within a particular frequency band), derived from a controlled laboratory experiment (Okanoya & Dooling, 1987), shows that sound transmission experiments alone can be very misleading by overestimating the communication range. This overestimation of communication distance is striking when comparing our calculated ± 14 m distance call detection threshold with the previous experiment by Mouterde et al. (2014), where zebra finch calls could still be discriminated at 256 m distance by applying sophisticated software (or 64 m when corrected for the 12 dB higher broadcast amplitude in their study), but zebra finch auditory capabilities were not considered.

Despite having a very high temporal hearing resolution (Dooling & Lohr, 2006; Lohr et al., 2006; Prior et al., 2018), zebra finches, like many other birds, have a higher overall hearing threshold and narrower audible frequency range compared to humans (Dooling, 1982, 1992; Dooling & Saunders, 1975), thus are less sensitive in detecting sound than humans are. This knowledge on hearing thresholds is not new (Dooling, 1982), yet has rarely been integrated in ecological field acoustics (but see Klump et al., 1986; Henry & Lucas 2008; Gall et al. 2012; Derryberry et al. 2016; Henry et al. 2016). By integrating hearing thresholds our data shed a different light on conclusions drawn from previous sound transmission experiments which determined very long communication ranges in animal vocalisations (Mouterde et al., 2014; Naguib et al., 2008). Since, in our study the hearing curve was taken from laboratory experiments with a different population and sounds, we need to consider that some birds hear better than others and that hearing curves of animals in the wild might vary more (Henry et al., 2016). However, due to the very low vocalisation amplitudes of wild individuals we found, hearing thresholds would need to be drastically lower to qualify as long-range communication in their spacious native environment. Even if hearing thresholds would be a 10 dB lower in wild bird than in domesticated birds, the audible range for song would still be very short at 28 m (calculated from model parameters in table 1). To further specify the communication range, ideally also the hearing curve of wild zebra finches should be measured. Moreover, testing the distance at which receivers respond to playback experiments in the field would be very interesting for future studies. Yet, since zebra finches are not territorial, typical strong responses to playback are not expected. A lack of response, however, then cannot simply be attributed to the communication range as an individual that detected the playback, may decide not to respond due to the perceived distance (Naguib & Wiley, 2001). Therefore, such playback experiments would require either sophisticated sensors, such as heart-rate monitors, or very specific contexts, such as during mate separation, when females may be specifically responsive when searching their partner.

Our field observations are in line with the calculated very short communication range as zebra finches mostly sang when in pairs or groups, usually within 1.5 m of each other, much closer than the 9 m we calculated. Indeed, our hearing range estimate is conservative since we measured the loudest sections of the song, reflecting primarily the detection range. Zebra finch song is dynamic, with low-amplitude elements being much softer than their loudest elements (Brumm, 2009; Ritschard & Brumm, 2011). Individual recognition and extraction of subtle information coded in repertoire size or element structures (Woodgate et al., 2012) would require a receiver to be much closer (Lohr et al., 2003; Wiley, 2006), and with this knowledge it may be not so surprising that, despite being unpaired, most males would not sing for females at distances of 3 m in the study by Brumm & Slater (2006). Such variation in transmission range of different signal components has been shown previously in nightingales (*Luscinia megarhynchos*) in which the bandwidth of broadband trills does not even transmit to the nearest neighbour, while whistle-like structures transmit across multiple territories (Naguib et al., 2008). Furthermore, given that hearing thresholds for higher frequencies generally are higher, the difference in audible range of high frequency components and medium-frequency sounds which mainly fall in the typical range of highest avian hearing sensitivity of 2 to 4 kHz (Dooling et al., 2000), would even be larger. Since information about condition and arousal can be coded in such subtle features (Perez et al., 2012), such specifics about an individual's state are likely unavailable at the, often larger, communication distances in widely spaced animals.

With an average difference of 14.5 dB between our calibrated recordings and those of domesticated zebra finches by Brumm (2009), our field recordings revealed much lower amplitudes of the loudest song elements (at 50.5 dB) compared to his recordings in the lab (Brumm 2009: Figure 5, with an average of 71 dB, where amplitude was measured at 50 cm, thus would be 6 dB lower at 1 m). Likewise, the 50.5 dB song amplitude we measured is much lower than the 74 – 100 dB range of 17 previously reported territorial songbird species (Brackenbury, 1979). Although song amplitude itself seems to be affected by vocal learning, but is not particularly heritable in zebra finches (Ritschard & Brumm, 2011), there could be several reasons for the strikingly lower amplitudes measured in the wild compared to the lab. First of all, domesticated birds typically are heavier and larger than wild-type birds (Forstmeier et al., 2007; Sossinka, 1982). Although Brumm (2009) did not detect a relation between body size and song amplitude within domesticated zebra finches, differences between wild and domesticated zebra finches might be more pronounced despite the large individual variation in song amplitude present in both captive (Brumm, 2009; Brumm & Slater, 2006) and wild birds (Figure 1a). Such potential song amplitude differences between wild and domesticated birds remain to be tested. Secondly, the singing males in the study by Brumm (2009) were unpaired and housed in single-sex groups prior to being exposed to a female for song recording. Thus they likely were extremely motivated to sing for mate attraction, while most singing adult birds in the wild are likely to be paired, as that is the normal state for a wild adult zebra finch (McCowan et al., 2015). Moreover, next to potential differences in wild and domesticated birds, we cannot discount that the wild birds in our study potentially were in poorer condition, and due to the long-term drought were not breeding during the period of data collection, when they would in better years. Therefore, we cannot rule out that the wild birds might have sung at lower amplitudes than wild birds in better conditions would, although condition alone cannot explain the 14.5 dB difference between our study and (Brumm, 2009), since Ritschard and Brumm (2012) observed an amplitude difference of about 4 dB between diet-restricted and control birds. Similarly to Brumm and Slater (2006) and Brumm (2009), we found high variation in song amplitude across individuals, which we expect to be an important driver of variation in communication distance in this species, potentially signalling condition (Ritschard et al., 2010), although this remains to be tested in the wild. Yet, combined with the hearing curves, louder than average singing zebra finches would still not be heard substantially farther, presumably only on few occasions reaching individuals outside their current social group. Specially so in the wide open Australian arid zone with widely spaced vegetation where zebra finches are usually very close to each other or very far apart and outside of hearing range as our transect observations show.

Finally, singing at low amplitude can be considered as an adaptation to the short communication distance when receivers are nearby, as it is the case for the highly social zebra finch. Low amplitude song also occurs in other bird species, where it is usually termed soft song (Reichard & Anderson, 2015). Such soft song is a context-dependent low amplitude signal that has been seen as an adaptation to prevent eavesdropping from distant individuals when the signal is intended only for a receiver nearby (Ali & Anderson, 2018; Dabelsteen et al., 1998; Rice et al., 2013; Zollinger & Brumm, 2015). Such soft song is indeed common in territorial bird species with otherwise loud territorial advertisement song (Anderson et al., 2008; Reichard & Anderson, 2015). Blackbirds (*Turdus merula*) for instance produce soft song during times of high arousal during territorial intrusions, referred to as strangled song, possibly to actively limit the signalling range (Dabelsteen & Pedersen, 1990). Likewise dark eyed juncos *(Junco hyemalis*) respond more strongly to soft song than to louder song (Reichard et al., 2011). Yet, as in blackbirds, the soft song in dark-eyed juncos also differs in structure from the louder song so is more than just a soft version of an otherwise louder song. Indeed, Reichard et al. (2011) showed in dark-eyed juncos that the differential response is more linked to the structure of the soft song than to its amplitude. Finally, in these, and other species in which soft song has been observed, the soft song is easily overlooked and typically not the most frequent song that would be opportunistically encountered (Reichard & Anderson, 2015). These examples of soft song in other species therefore represent something quite different from the low amplitude singing we have characterized in zebra finches. Zebra finches, despite the variation in singing amplitude within and between individuals, do not produce structurally different songs in different contexts (despite adding extra initial elements on some occasions; Sossinka & Böhner 1980; Sturdy et al. 1999). We did find that males sang slightly louder in pairs than when in social groups, suggesting some degree of context-dependent adjustment of signalling amplitude as shown in domesticated zebra finches (Brumm & Slater, 2006; Cynx & Gell, 2004). However, our average 1.9 dB context-related difference contrasts with typical differences between quiet and broadcast song. For instance, in song sparrows (*Melospiza melodia*), soft song ranged from 55 - 77 dB while “regular” song ranged from 78 - 85 dB (Anderson et al. 2008). The low amplitude of zebra finch song in both contexts thus appears functionally distinct from the context-dependent soft song of territorial bird species. Of course, we cannot completely rule out that zebra finches in some contexts could potentially utter much louder songs or calls, but there is currently no evidence for this in either our data or, as far as we know, in the extensive song literature. This is relevant when using the findings from zebra finch song from lab studies to generalize to other songbirds, as the overall communication range along with the social and functional context in which the song system has evolved, is different from most other species used for avian song research in the wild.

Taken together, the integrated findings imply that song is a within-group signal and information transmitted by singing males can be used only after birds have gathered at close range, and thus cannot drive spatial movements at a larger scale as shown for the loud territorial song of other songbirds (Bircher et al., 2020; Snijders & Naguib, 2017). Early in life when pairs form (Zann, 1996), a singing male will only reach a female which is already present in the same group, not attract a mate from the distance, as in other songbirds (Catchpole & Slater, 2008). Therefore, the song is best considered as part of a sexual display to the multiple individuals that are already in close proximity, and many of which will also be singing, making the mate choice context much more complex than in species in which the signal is used to attract potential mates to a unique location from the distance. While such vocalisations and the complex multimodal displays in groups have been evident in animals, and specifically so in aviary kept zebra finches for a long time (Immelmann, 1968), the ecological implications highlighted here are quite fundamental. In the open landscape of the Australian arid zone, zebra finches split up and reunite frequently (McCowan et al., 2015). While acoustic signals can be key to guide the spatial movements of animals (Waser & Wiley, 1979; Whitehead, 1987; Wilczynski & Brenowitz, 1988), this is apparently limited to a small spatial scale in zebra finches. Even their relatively soft distance calls are not suited to attract others over long distances. Since vocal signals are of limited use for finding a lost partner or other group members in their vast habitat and home range, they must have evolved other mechanisms underlying their dynamic social organization. The use of stable water sources, specific habitat features or regular flight routes along creeks as well as joint breeding are such potential adaptations that can facilitate joining others to form temporary groups for roosting or foraging.

In summary, integrating knowledge on the perceptual and processing mechanisms in a broader sense will substantially enhance our understanding about the ecological conditions in which signals have evolved. Likewise, understanding the ecological conditions in which signals function, provides a relevant framework for interpreting mechanistic studies conducted under controlled laboratory conditions.

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Chapter 3 | The social role of song in wild zebra finches

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Summary

Male songbirds sing to establish territories and to attract mates (Catchpole & Slater, 2008; Gil & Gahr, 2002). However, increasing reports of singing in non-reproductive contexts (Rose et al., 2022) and by females (Odom et al., 2014; Riebel et al., 2019) show that song use is more diverse than previously considered. Therefore, alternative functions of song, such as social cohesion (Rose et al., 2022) and synchronisation of breeding, by and large were overlooked even in such well-studied species as the zebra finch (*Taeniopygia guttata*). In these social songbirds only the males sing and pairs breed synchronously in loose colonies (Brandl et al., 2021; Brandl, Griffith, & Schuett, 2019) following aseasonal rain events in their arid habitat (S. R. Morton et al., 2011; Zann et al., 1995). As males are not territorial, and pairs form long-term monogamous bonds early in life, conventional theory predicts that zebra finches should not sing much at all; yet they do and their song is the focus of hundreds of lab-based studies (Boogert et al., 2008; Fishbein et al., 2020; Forstmeier et al., 2009; Gil et al., 2006; Hauber et al., 2021; Honarmand et al., 2015; Kriengwatana et al., 2014; Kubikova et al., 2010; Pfenning et al., 2014; Riebel, 2009; Slater et al., 1988; Tchernichovski et al., 2021; Williams & Lachlan, 2022). We hypothesise that zebra finch song functions to maintain social cohesion and to synchronise breeding. Here we test this idea using data from five years of field studies, including observational transects, focal and year-round audio recordings, and a large-scale playback experiment. We show that zebra finches frequently sing while in groups, that breeding status influences song output at the nest and at aggregations, that they sing year-round, and that they predominantly sing when with their partner, suggesting that song remains important after pair formation. Our playback reveals that song actively features in social aggregations as it attracts conspecifics. Together, these results demonstrate that birdsong has important functions beyond territoriality and mate choice, illustrating its importance in coordination and cohesion of social units within larger societies.

Results

Zebra finches form monogamous pair bonds early in life, do not hold territories, and in the wild mate almost exclusively with their social partners (Buchanan et al., 2010). Therefore, their singing behaviour is insufficiently explained by conventional theory that song functions in territory defence and mate attraction. To uncover the likely other functions of their song, we studied zebra finches in their natural environment. Currently, their song has been studied intensely in captivity, but insights from natural singing contexts have been only anecdotal (Immelmann, 1968; Zann, 1996), or based on a few studies from a sexual selection perspective (Dunn & Zann, 1996b, 1996a; Woodgate et al., 2012). Yet, since social cohesion is important in their loose colonies, their singing may rather function mostly in facilitating social cohesion (Immelmann, 1968) and in synchronising their opportunistic breeding.

We thus tested the social context of singing and its implications using multiple quantitative complementary approaches (Figure 1) at our study site in the Australian arid zone. First, by sampling birds along transects in non-breeding and breeding years we determined in which social contexts song is produced. Next, by making focal audio recordings of birds that were either not breeding and at active nests during breeding we quantified the number of singing individuals in these contexts. Then, using time-programmed audio recorders at selected locations for year-round recordings we quantified whether zebra finches sing throughout the year. Finally, using a playback experiment we tested if song attracts inspecting conspecifics. We predicted that if song functions in social cohesion, males would sing in social contexts throughout the year as determined in the transects, focal audio recordings and year-round audio recordings. If song plays a role in synchronising breeding, we expected singing at the population level to fluctuate with breeding events, as determined by year-round audio recordings and transects. At the pair level, we expected singing to also fluctuate with breeding stage at the nest as determined by the nest recordings. Additionally, if song plays a role in synchronising breeding, it should also attract inspecting conspecifics as inferred from the playback experiment.

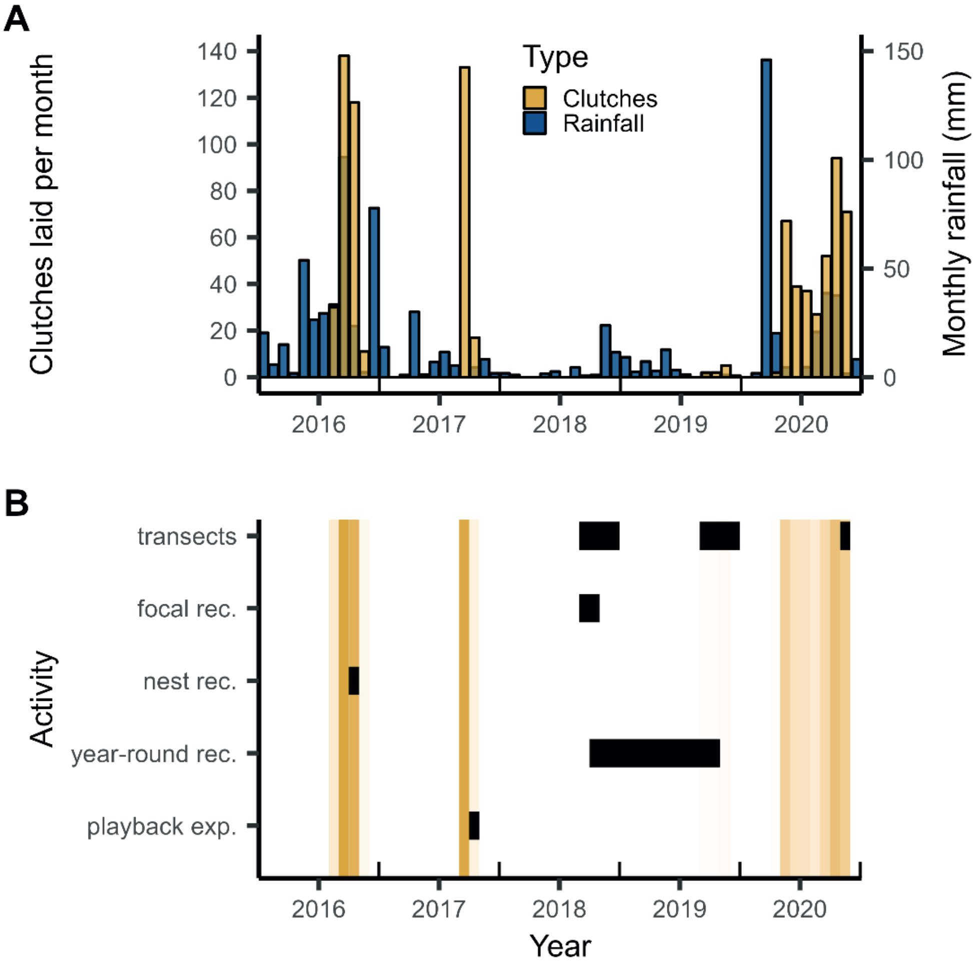

Figure 1. Breeding followed rain events and study setup. (A) Occurrence of zebra finch clutches, based on nest-box checks, and rainfall based on data from the local Bureau of Meteorology weather station. There was a drought in 2018–2019 resulting in the absence of breeding. After drought-breaking rains in March 2020, zebra finches bred throughout winter, which is uncommon in this population. (B) Gantt chart of the methods used, indicated by black bars, with breeding context based on clutches laid in yellow shading. Our study encompasses breeding and non-breeding contexts.

Zebra finches sing when with their partner and in groups, with more group-singing during breeding than non-breeding periods

We determined the social contexts of singing by walking standardised transects throughout our field site in breeding and non-breeding periods (Figure 1B). For every zebra finch observation, we scored the group size and presence or absence of song. Zebra finches in their natural habitat regularly sang at social aggregations in years with breeding and non-breeding (Figure 2A). The group size of these aggregations did not differ between the years sampled (Generalised Poisson GLM, 2018 – 2019: $z_{351} = 0.33$, $P = 0.74$; 2018 – 2020: $z_{351} = 1.09$, $P = 0.28$; 2019 – 2020: $z_{351} = 0.73$, $P = 0.47$). If birds sang randomly, the relationship between singing and group size should have been the same in all years. However, in 2020, when birds in the population were breeding, the occurrence of song at these aggregations increased with group size (Binomial GLM, $z_{349} = 3.46$, $P < 0.001$), such that we always encountered singing individuals in large groups, whereas in the non-breeding years, the occurrence of song was not affected by group size (Binomial GLM, year * group size, 2018 – 2019: $z_{349} = 1.59$, $P = 0.11$; 2018 – 2020: $z_{349} = 3.23$, $P = 0.001$; 2019 – 2020: $z_{349} = 2.02$, $P = 0.04$; Figure 2A).

Focal audio recordings made in non-breeding contexts (Figure 1) likewise revealed that wild zebra finches sung predominantly when others were nearby. Indeed, all singing males that we encountered were in a paired (n = 14) or a social (n = 30) context, that is, with more than two birds present in the same focal bush or tree. Additionally, as zebra finch song has an individual signature (Miller, 1979b; Zann, 1990), we established that 14 out of 44 focal recordings (32%) featured more than one singing individual at the same location in the short time window of these recordings (on average 197 ± 253 seconds, mean ± sd). We thus show that, in non-breeding contexts, zebra finches sing when with their partner and that both males and females of a pair are exposed to other singing males in close proximity.

Multiple males sing at a given nest and song of breeding males reflects breeding stage

To determine the acoustic environment at active nests, we analysed sound spectrograms of 14 consecutive hours of recordings made at each of 44 nests. On average 5.7 ± 3.5 and a maximum of 15 different individuals were detected singing at a given nest (Figure 2B). Since sound degrades over distance (Naguib & Wiley, 2001) and zebra finch song is very soft (**chapter 2**), we used spectrogram quality as proximity measure. When considering only high-quality spectrograms from songs detected near a nest, on average 3.0 ± 1.8 and a maximum of seven individuals were identified (Figure 2B). Thus, breeding birds at their nest could hear songs from others nearby. When considering the songs of breeding males at their own nest, a nest owner's breeding stage predicted his singing activity (ANOVA, $F_{3,40} = 6.08$, $P = 0.001$; Figure 2C). Singing activity during egg laying was significantly higher than during the incubation and nestling stages (Tukey HSD post-hoc, egg laying – incubation: $P = 0.011$; egg laying – nestlings: $P = 0.003$; all other combinations: $P > 0.14$; Figure 2C).

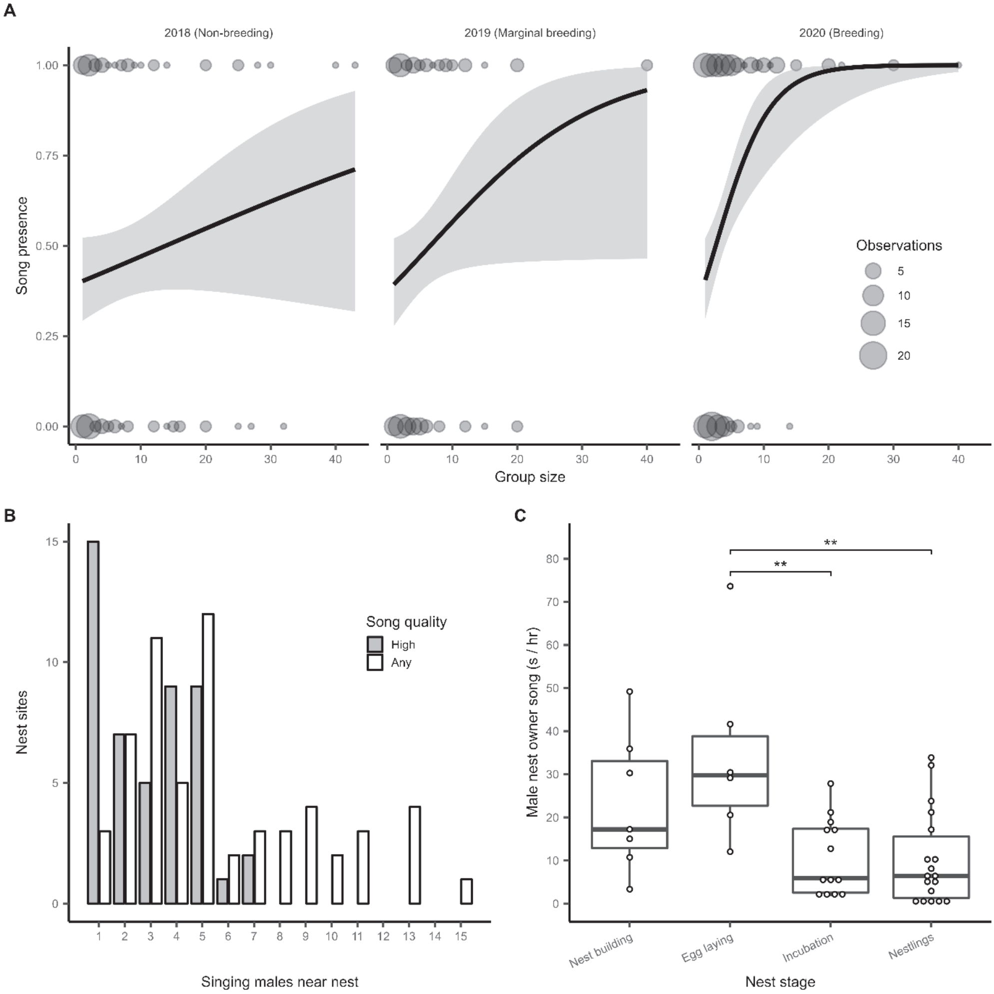

Figure 2. Zebra finches sing in group contexts and breeding status influences song at the nest and at these aggregations. (A) Song (present/absent) increased significantly with group size when birds were breeding, but not when there was no or marginal breeding. Shaded areas denote standard errors of the logistic model. (B) Multiple singing males could be heard at the nest. Song quality is a measure of proximity, where high-quality song is uttered by birds near the nest, and ‘‘any’’ quality represents all identifiable song. (C) Nest stage predicted song output of the male nest owners, peaking at egg laying. The dots represent the males. Boxes encompass the first to third quartiles, thick lines are medians and whiskers extend until 1.5 times the inter-quartile range.

Zebra finches sing throughout the year

To quantify singing activity throughout the year, we placed time-programmable audio recorders at local hotspots of activity. For one day per month for 13 months, for four recorders, we scored the presence of song (Figure 3A) and general vocal activity including calling by both sexes (Figure 3B) as a baseline measure of bird presence at the recording site. This activity score was a 0 – 4 Likert-scale reflecting the amount of vocal activity, comprising both calling and singing. Males sang in almost all months of the year at these social sites (Figure 3A). However, the daily percentage of hours with song clearly fluctuated over the year. Song detections peaked in October, when birds would normally breed but did not in the year of our data sampling (Figure 1), and were at their lowest in May, late autumn (Figure 3A). Nevertheless, birds may also have been singing in the quieter months as the activity score showed the same pattern as the singing pattern. That is, in quieter months individuals were present less often, with the least amount of vocal activity, when we detected the fewest songs (chi-square test, activity score: $\chi^2_4 = 387.3$, P < 0.001; Figure 3B).

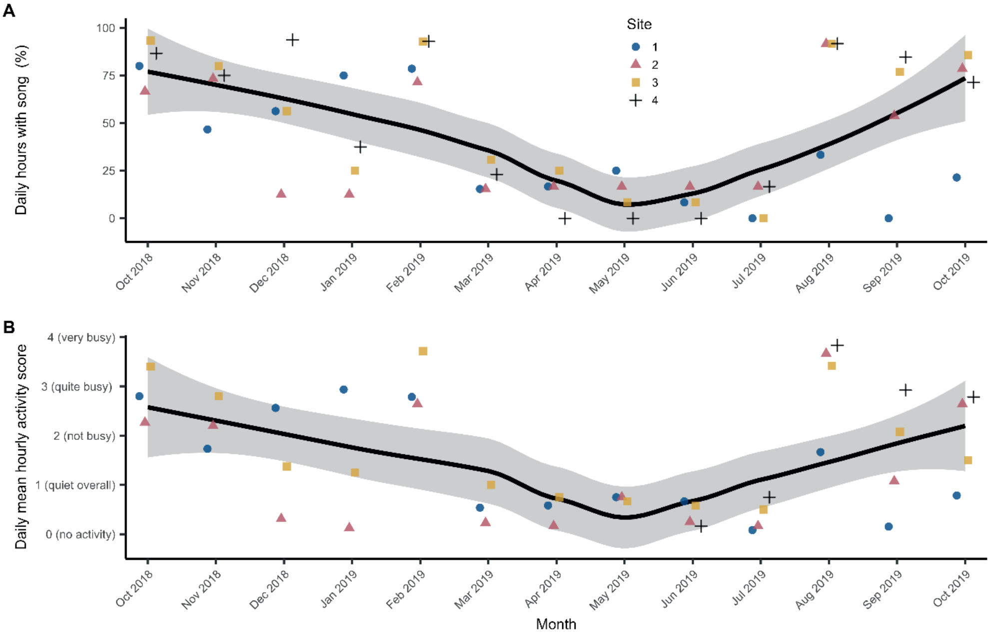

Figure 3. Zebra finch song was present throughout the year, but fluctuated with activity levels at the recording site. (A) Song was present throughout all months of the year, but the percentage of hours with song and (B) the mean activity score per day fluctuated. As these were correlated, we conclude that when no song was detected, it was because birds were absent, not because they were present but not singing. Colored shapes distinguish the four recording sites, and the shaded area is the standard error of the local polynomial smoother.

Zebra finch song playback attracted individuals, pairs and flocks

To experimentally test the response of conspecifics to song, we conducted a large-scale playback experiment. This experiment comprised automated simultaneous playbacks with three treatments: zebra finch song, nightingale *Luscinia megarhynchos* song (heterospecific control) and silence (additional control). Sound files contained two minutes of either zebra finch or nightingale song followed by 13 minutes of silence, played as a loop for ca. eight hours. Experimental setups consisted of a nest box, containing a nest with 3D printed eggs next to a bush with the loudspeaker. Playbacks were organized in multiple triplets with the three treatments in one triplet in the same area, respectively. Experiments were filmed continuously, and we scored these videos for zebra finch visits to the bush or nest box. For each visit, we noted the group type (single male/female, pair, flock) and arrival and departure timestamps. Then, using these timestamps, we calculated the latency since playback end for each arrival, omitting visits that happened when there were already birds present, as these might have attracted others regardless of the playback treatment. We also noted if visiting males sang.

Zebra finches visited nests of all treatments but visited the zebra finch song treatment with significantly lower latency, i.e., when the playback was on or had just stopped, when compared to their responses to nightingale song playback, which showed no such pattern and which did not differ from the silence treatment (Tweedie GLMM, zebra finch – nightingale: $z_{151} = 4.39$, $P < 0.001$; zebra finch – silence: $z_{151} = 6.32$, $P < 0.001$; nightingale – silence: $z_{151} = 1.61$, $P = 0.11$; Figure 4A). Zebra finches visited 19 out of 23 triplets and visited most treatments of most triplets (Figure 4B). The nightingale treatment was visited less than the silent control (Generalised Poisson GLMM, zebra finch – nightingale: $z_{52} = 1.43$, $P = 0.15$; zebra finch – silence: $z_{52} = 0.32$, $P = 0.75$; nightingale – silence: $z_{52} = 1.99$, $P = 0.047$; Figure 4B). Of a total 157 visits, 59 visits were by pairs, 48 were by individual males, eight by individual females and 29 by flocks of more than two birds (for 13 visits the sex or number was unclear from the video). In line with our acoustic observations based on the nest recordings (see above), visiting males sang during at least 74 visits. Visiting zebra finches showed no aroused behaviour, e.g. hopping around or flying over the loudspeaker, as territorial songbirds do in response to song playback (Gil & Gahr, 2002). Taken together the experiment shows that the playback of zebra finch song directly attracted other zebra finches.

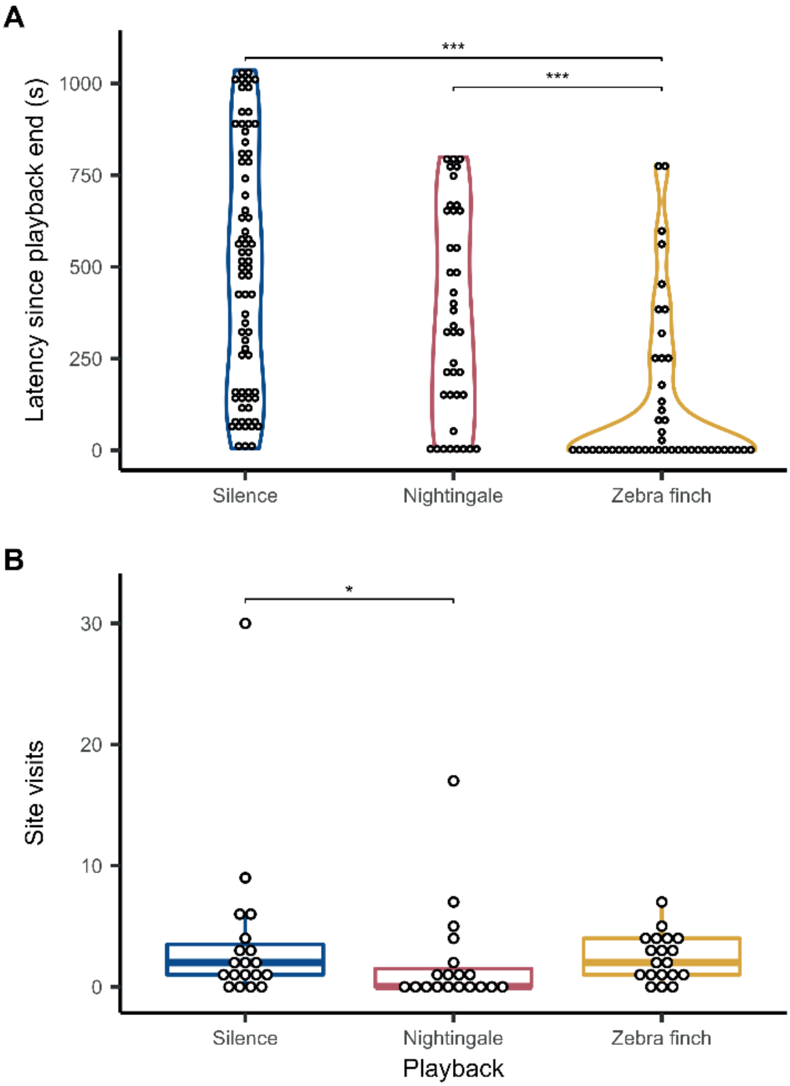

Figure 4. Zebra finch song attracted conspecifics. (A) Zebra finches arrived predominantly at our experimental nest boxes when the conspecific song playback was on or had just turned off (low latencies). Conversely, arrivals to the nest-box at the nightingale control showed no pattern of arriving during or outside of playback cf. the silent control. Dots represent arrivals. (B) Zebra finches visited most treatments of most sites, nightingale playback received fewest visits. Dots represent experimental trials.

Discussion

Our results show that across several natural contexts, zebra finch song has a clear social component and that unlike in many other species it is not used primarily to compete for space or to attract mates. Given that males sang throughout the year, we here provide multiple lines of field-based evidence suggesting an important role of song in coordinating these birds' social lives in their unpredictable environment, further broadening (Price, 2019; Riebel et al., 2019; Rose et al., 2022) the dominant view on the function of birdsong.

Our nest audio recordings further showed that song is likely to play a key role in the coordination of breeding. Breeding males sang at their nest most around egg laying, an observation also reported earlier for zebra finches (Dunn & Zann, 1996a) and other species (Gil et al., 1999; Kunc et al., 2005; Møller, 1991). This could evolve if song stimulates the females' reproductive organs (Bentley et al., 2000; Kroodsma, 1976; Slater et al., 1988) or investment in eggs (Gil, 2008; Gil et al., 2004; Leitner et al., 2006) and could be a signal of the male's commitment (Bolund et al., 2012) or readiness to breed. Indeed, in an experiment with captive zebra finches, females increased their reproductive investment with the song output of their partner (Bolund et al., 2012), and vocal activity of the colony facilitated breeding and breeding synchronization (Waas et al., 2005). Therefore, as with their calling behaviour at the nest (Boucaud et al., 2016, 2017; Elie et al., 2010), singing could facilitate the coordination of the pair's breeding effort. Nonetheless, whilst we clearly demonstrate that singing is linked to reproduction, a striking finding from our focal and year-round audio recordings is that males sang substantially with their partner alone and in groups throughout the year, including through prolonged drought conditions and autumn and winter, periods when there was no breeding at all. Thus, despite a peak of singing during egg laying, most of the singing by a male zebra finch is outside the breeding context. This makes them highly distinct from the well-studied song of territorial songbirds of the temperate zones that show a short burst of singing around breeding and then commonly do not sing outside the breeding periods (Catchpole & Slater, 2008; Gil & Gahr, 2002), and from continued singing in year-round territorial species (Hall, 2009; Kriner & Schwabl, 1991; Templeton et al., 2011; Wiley & Wiley, 1977).

Indeed, the social organisation and natural environment of zebra finches are very different from those of territorial songbirds, particularly those from temperate zones, as zebra finches live in multi-level societies in an unpredictable environment, where the phenology of breeding is less dependent on seasonal cues than in temperate species (Englert Duursma et al., 2017). In the zebra finch, reproductive physiology is not stimulated by changes in the photoperiod and they maintain a readiness to breed throughout the year (Perfito et al., 2007). As a result, they rely more on other environmental cues to stimulate breeding (Zann et al., 1995) as well as conspecific cues like the breeding stage of visited nests (Brandl, Griffith, & Schuett, 2019) and acoustic cues such as nestling begging calls (Brandl, Griffith, Laaksonen, et al., 2019) to reproduce synchronously. Such synchronous breeding at a local level will likely dilute the effects of predation on breeding adults and their offspring, and also result in the presence of peers for their offspring that contribute to their social development (Honarmand et al., 2015; Ruploh et al., 2013, 2014). In line with these mechanisms for attaining synchronous breeding in the wild, captive zebra finches that received additional colony sounds bred more synchronously than those that did not (Waas et al., 2005). Furthermore, males and females were equally motivated to hear song in an operant conditioning setup (Riebel et al., 2002), and in another study, a male adjusted its song to the singing of a male companion (Hyland Bruno & Tchernichovski, 2019), suggesting that attending to song is important for both sexes. Indeed, our transect data show that when there was breeding in the population, the singing in groups increased, and our nest recordings show that breeding stage influenced song output of breeding males at their nest. Furthermore, our playback experiment in a breeding context attracted inspecting conspecifics of both sexes. These field data fit with the idea that social stimulation helps birds to attain breeding synchrony, suggesting that social (Rose et al., 2022; Tobias et al., 2012), not sexual, selection might be the most important driver of song evolution in zebra finches.

Other features of zebra finch song identified in prior studies also suggest that it has cooperative functions. For example, inconspicuous signals are more likely to evolve in cooperative contexts (Dawkins, 1993; Johnstone, 1998) and song of wild zebra finches is strikingly soft, being audible to conspecifics within only a few meters (**chapter 2**). Similarly, the clear individual signature in male zebra finch song (Miller, 1979b; Sturdy et al., 1999; Woodgate et al., 2012) allows for instant vocal individual recognition and a simple individual head count, assessment of local breeding commitment, status, or condition (Brumm, 2009; Cynx et al., 2005; Honarmand et al., 2015; Ritschard & Brumm, 2012), and thus possibly foraging efficiency. Continuous singing throughout the year and non-breeding periods might then also be favoured by selection as birds may need to maintain some continuous readiness for breeding in this unpredictable environment. Maintaining singing, including mechanistic factors such as keeping the syringeal muscles active and trained (Adam & Elemans, 2019; Nelson et al., 2005; Nowicki & Marler, 1988), can be part of this process. Indeed, arguably the two characteristics that make zebra finches such a good model species for understanding the neural processing of song (Forstmeier et al., 2009; George et al., 2020; Hauber et al., 2021; Kubikova et al., 2010; Pfenning et al., 2014) – individually distinct song, and continuous singing throughout the year – have probably evolved as a result of the social functions of song.

Our findings on the extensive singing by paired males are inconsistent with the idea of inter-sexual selection such as mate attraction being the primary function of song. Clearly, singing in zebra finches has been shown to play a key role in mate preferences in laboratory-based studies (Riebel, 2009), and in the wild when individuals need to find a new partner (Dunn & Zann, 1996b). Yet, this ‘directed’ song in mate choice is far less common than the so-called ‘undirected’ song produced outside the mating context (Morris, 1954; Riebel, 2009). Acoustically, directed and ‘undirected’ songs are almost identical in structure, carrying the same individual signature, but with directed song having more introductory notes and being sung marginally faster than ‘undirected’ song (Sossinka & Böhner, 1980). The main difference is that directed song is combined with visual displays directed at a female, whereas ‘undirected’ song lacks the visual display (Sossinka & Böhner, 1980). However, both song types function in mate choice (Riebel, 2009), weakening the often implied functional difference between directed and ‘undirected’ song. Previously, ‘undirected’ song has been attributed to function in motor-practice (Jarvis et al., 1998), as well as being socially inhibited (Caryl, 1981), but our data do not support these ideas as our transect and nest recordings showed that song changed with context and our song playback attracted conspecifics. Indeed, our transect and focal audio recording data on group singing suggest an important social role for song, in line with a more recent laboratory experiment where ‘undirected’ song was facilitated by companionship of either sex (Jesse & Riebel, 2012). We also show here that zebra finches sang predominantly after pair formation and outside breeding contexts, as determined by our focal and year-round audio recordings, revealing that by far most of the song a female hears is after pair formation and during periods outside reproduction. Indeed, zebra finches sang year-round, and typically near their partner throughout a serious drought, in which birds hardly bred for an extensive period of 28 months. As such, song appeared to be an integral part of the within-pair communication, possibly to coordinate the pair’s foraging or dispersal movements. Overall, our findings fit better with Immelmann’s (1968) and Zann’s (1996) anecdotal observations that song functions within a social coordination, not mate attraction, framework, possibly as an adaptation to the less predictable environmental conditions compared to songbirds breeding in the well-studied northern hemisphere temperate zone (Englert Duursma et al., 2017).

Likewise, also with respect to intra-sexual selection, we show that zebra finch song differs substantially in its function and context from song produced by territorial species, in which typically only resident birds sing, and song by intruders is met with aggression (Geberzahn et al., 2010; Helfer & Osiejuk, 2015; Hof & Podos, 2013; McGregor, 1992; Naguib & Mennill, 2010). Zebra finch males instead sang in multiple social contexts, at the nest during breeding as determined by our nest-recordings, and at gatherings during non-breeding contexts with multiple males singing at the same location, as determined by our transects and focal audio recordings. Additionally, playback of zebra finch song attracted pairs and sometimes flocks of zebra finches to our experimental nest boxes, without any sign of arousal or aggression. Evidence that males may be attracted to conspecific song is rare but also has been shown for starlings *Sturnus vulgaris* (Mountjoy & Lemon, 1991) at their defended nest sites and otherwise may play a role in locating suitable habitat (Alatalo et al., 1982; Mountjoy & Lemon, 1991) or to synchronise breeding at the colony level. Given that zebra finches base breeding decisions on visits to conspecific nests (Brandl, Griffith, & Schuett, 2019; Brandl, Griffith, Laaksonen, et al., 2019), the latter explanation fits well for zebra finches. Since song in the wild is very soft, being audible to conspecifics within only a few meters (**chapter 2**), birds would need to gather and sing with conspecifics nearby and this is indeed what we observed.

In summary, we show that zebra finch song, the prime model for understanding mechanisms underlying song in the laboratory, in the wild has a primarily social component and thus deviates from conventional assumptions of how birdsong functions. Our findings thus raise questions about how applicable findings from lab-based studies in this species are across songbirds, and additionally, how widespread social birdsong functions are, and if they are linked to the ecological conditions of low seasonality in unpredictable environments. Our understanding of birdsong remains strongly biased towards male territoriality (Riebel et al., 2005), probably because male territorial birds are striking in their sudden appearance, are convenient to study, and historically there is a strong bias towards birdsong studies in the northern hemisphere temperate zone (Stutchbury & Morton, 2001). Similarly only recently was a bias identified with respect to female birdsong, which is an ancestral trait that appears to be lost or overlooked (Sierro et al., 2022) in most species of the northern hemisphere temperate zone (Odom et al., 2014; Price, 2019). Specifically in many tropical birds both sexes sing year-round (Hall, 2009; Templeton et al., 2011; Wiley & Wiley, 1977) where song often appears to have a year-round territorial function but seems less linked to reproduction, with also different hormonal regulation underlying song production (York et al., 2016). Our findings, along with such other studies on female song and song from tropical species (Austin et al., 2021; Riebel et al., 2019; Tobias et al., 2016), thus raise the question if in other species with clear evidence for sexually selected song functions, social factors also play a stronger role than previously thought (Griffith, 2019; Roughgarden, 2012; Tobias et al., 2012). Future studies should take a broader view and consider a wider range of singing species across social organisations and environmental conditions, to better understand the selection pressures and functions of birdsong, one of the best studied communication systems in animals.

STAR methods

Experimental model and subject details

We studied a population of free-living zebra finches in Fowlers Gap Arid Zone Research Station in western New South Wales, Australia, from October 2016 till November 2020. This zebra finch population has been well-studied since the introduction of nest boxes in 2005 (Griffith et al., 2008). From banding work in the area during previous years, we know that recapture rates of individuals between years are very low (about 5%, unpubl. data), suggesting that zebra finches at our field site are nomadic. We did not capture individuals for this study, but during the years of this study we routinely checked nest boxes, usually from August till December (in 2020 already from June onwards due to drought-breaking rain), when most breeding activity in this population is observed (Figure 1A). We received approval by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017 and 2018/027) for all work in this study.

Method details

Observational transects

To determine the social context of singing in breeding contexts and non-breeding contexts, we walked 1 km transects to standardise encounters with zebra finches at our field site. We walked transects in six locations on a weekly basis between 07:30 and 17:00 hours from 12 October to 4 December in 2018 and 29 August to 6 December in 2019, when there was no breeding (as the result of an extended drought, Figure 1A). In 2020, when there was much breeding activity (Figure 1A), we walked transects from 18 to 23 November. Transects always covered a local water site, habitat in which breeding occurs (when conditions are suitable), and an open foraging area to represent the various activities zebra finches might be engaged in, e.g., drinking, resting, breeding, and foraging. During these transects, for every zebra finch observation we scored the group size and presence of song.

Focal audio recordings

We used handheld directional microphones (Sennheiser MKH60 in MZS 20-1 + MZH + MZW 70-1 basket windscreen and Sennheiser ME66/K6 with foam windscreen) to record wild zebra finch songs between 26 September and 31 October 2018 on days with low wind. Recordings were made opportunistically throughout the study site when the singing individual was in sight. For each recorded song we scored which individual produced it, since recordings were made in social contexts. Recordings were made as 44.1 kHz 16-bit WAV files on digital audio recorders (Tascam DR100-MKIII). Using spectrograms generated in Audacity (version 2.2.2), we scored per recording how many males were singing on a particular recording and in which context. This was possible because we mentioned the different individuals during the recording and zebra finch song has an individual signature (Miller, 1979b), allowing for individual recognition by comparing spectrograms.

Audio recordings at active nests

During breeding in 2016, we installed time-programmable audio recorders (Olympus DM650 and DM670) within two meters of 63 active nest boxes, in various stages of breeding, by mounting them on poles or trees. These recorded 64 kbps MP3 files for 14 hours a day (between 06:30 and 20:30 hours) from 25 to 28 October 2016. We used MP3 files to maximise battery life and storage efficiency. From each nest we used the recording of one day, the 26th of October 2016, for analysis, because nests were undisturbed on that day and it had low wind conditions, resulting in good sound.

Using spectrograms in Audacity (version 2.4.1), we scored for each singing bout the start and end times and the recording quality as high, medium, or low as an indication of how close the bird was to the recorder. Song bouts were considered separate if there was a silence of at least ten seconds. Zebra finch songs start with repeated introductory notes (Sossinka & Böhner, 1980), which are variable in number and can be hard to tell apart from the calls uttered before. To have a consistent cut-off point, we imposed a limit of a maximum of three seconds of introductory notes at the start of a singing bout. Since zebra finch song has an individual signature (Miller, 1979b), we could discern multiple singing individuals on most recordings.

To determine which of the recorded males was the nest owner, we considered the total song duration of each bird, the recording quality and how often the bird returned. Especially for nests in the incubation and nestling stages, when the couple needed to visit the nest regularly, the number of times a bird returned to the nest was an important indicator. For nests in the nest building stage, we paid extra attention to noise of moving branches accompanying the singing bouts. We calculated the average singing activity (seconds of song per hour) for the nest owners.

Nests were checked regularly during the time these recordings were conducted (not on the selected recording day). The observations made of brood development were used to determine the breeding stage of the pair at the time the audio recordings were taken. A pair was in the nest building stage when nest material was present in the nest box and nest construction had continued by the next observation of the nest. The egg laying stage started when the first egg was laid. When the female had laid her last egg the incubation stage started, as zebra finches in the wild start incubating just one or two hours before they lay the last egg of the clutch (Gilby et al., 2013). And finally, when the first nestling emerged the pair was in the nestling stage.

Year-round audio recordings

To determine singing activity throughout the year, we placed time-programmable audio recorders (Song Meters, SM3 and SM4 recorders equipped with SMM-A2 external microphones, Wildlife Acoustics; recording 16 kHz 16-bit mono WAV files) at local hotspots of activity, such as near water sites or near feeders that were occasionally stocked. These recorders were active from sunrise to sunset every four days. For analyses, we selected the four recorders on which we expected the highest chance of obtaining zebra finch activity, which were situated at feeders (3x) and an artificial water site (1x).

For sound analysis, we selected the day of the month with the lowest average wind speeds per month for October 2018 – October 2019, a period in which there was no breeding (Figure 1). To obtain the day with lowest average wind speeds, we used a python (version 3.7.0) script to link the recording timestamps to the half-hourly wind speed data from the Fowlers Gap weather station (station 046128, Australian Bureau of Meteorology) with the half hour closest to the start time of the recording used as indication of wind speed for that recording. Then, we calculated the average wind speed on the recording days and selected the day of the month with the lowest average wind speeds.

Using sound spectrograms in Audacity (version 2.2.2) we scored per hour the presence of song and the vocal activity level, which considers that zebra finches regularly vocalise, which is in line with our field experience. This activity score was a 0 – 4 Likert-scale resembling the amount of vocal activity (0: no activity, 1: quiet overall, < 5 min of vocalisations, 2: not busy, 5 - 15 min, 3: quite busy, 15 - 30 min, 4: very busy, > 30 min). We zoomed in until not more than 30 seconds were visible at one time, to avoid missing short vocalisation bouts. In cases where we were uncertain using visual inspection alone, we listened to the recording as identification aid. Vocalisations which were clearly given by a bird flying over the recorder without perching, such as calls which become louder and then softer again within a small time-window, were scored as fly-overs and these then were not considered as indicating zebra finch presence for the activity score in the bush with the recorder, since zebra finches do not sing while flying. When there was substantial wind present on the recording, we high-pass filtered the recording at 1,000 Hz with 48 dB/octave roll off. In total, we analysed 701 recordings representing about 675 hours of recordings (files were one hour long, but the last file of the day was shorter as recording stopped at sunset), coming from the four sites.

Playback experiments combined with nest boxes

To experimentally determine the response of conspecifics to song, we conducted a large-scale playback experiment from the 5th to 10th October 2017, when there was breeding (Figure 1). This experiment consisted of automated simultaneous playbacks with three treatments: zebra finch song, nightingale song (as a novel non-endemic heterospecific control) and silence (as an additional control). Playback setups consisted of a nest box, containing a nest with four 3D-printed eggs, attached to a steel post next to a bush or tree where a monopod-mounted loudspeaker (UE boom, Ultimate Ears) was placed, resulting in playback at about 1.5 meter height. The nest boxes with eggs were placed the evening before the playback. To control for local variation in zebra finch presence, treatments were organised in triplets (n = 23), with the three simultaneous treatments in the same general location, 22 m (± 7.9 m SD, range 8 - 40 m) apart. On a given day three or four triplet experiments were conducted at the same time in different areas of the study site, resulting in a total of 23 sites, of which 19 received visits by zebra finches.

Sound files were played from Olympus DM670 audio recorders at 58 dB (re 20 µPa of individual files, measured at 1 m with Voltcraft SPL meter; settings: fast, A weighting) and consisted of two minutes of either zebra finch or nightingale song followed by 13 minutes of silence, resulting in a 15-minute loop playback. Song files had natural species-specific pauses, there was only one individual per file, and individuals were not reused for a different triplet to avoid pseudo-replication. Zebra finch song was taken from high-quality examples of the 2016 breeding recordings, nightingale song was recorded earlier at the Petite Camargue Alsacienne in France (Sprau et al., 2010). Playback experiments started between 06:45 and 10:05 in the morning and lasted about 7.5 hours. All treatments were filmed continuously from about 10 m (GoPro 5 cameras connected to power banks, 720p MP4 files) so that the tree and the nest box were clearly visible.

We (M.N., S.v.L.) scored the videos (Quicktime video player) by noting the timestamp for all visits to the bush or nest box. Initial scoring of visits was done without sound so the playback status was not evident to the observer. However, in case of doubt, sound was used as a cue to determine sex or species, and multiple observers (H.L., M.N., S.v.L.) discussed the videos if necessary. We did not consider foraging movements (birds only on the ground) or visits that happened after there were already birds present as these visitors might have been attracted by the birds that were present instead of the playback. We also scored the sex and group size (pair or flock) of arriving birds. Additionally, after visits were noted we turned on the sound and we scored whether arriving males were singing although this was not always possible due to a combination of wind, presence of other birds and the low amplitude of zebra finch song in the wild (**chapter 2**). As a separate step, after all visits were scored in all videos, we (H.L.) calculated for each arrival the visit latency, that is, how many seconds passed since the playback ended (using VLC video player to detect playback end-times), scoring a zero if the visit was during playback.

Quantification and statistical analysis

Observational transects

In 95 of a total 135 transects, we observed zebra finches a total of 355 times, of which 183 observations included singing birds. We tested whether group size (as response) differed between the years (as predictor) with a general linear model with a Generalised Poisson family (which is robust to overdispersion, Gschlößl & Czado, 2008) for the response (using R 4.1.1, function glmmTMB from R package glmmTMB (Brooks et al., 2017). To test whether group size influenced the occurrence of song and whether this was influenced by year (as years varied in their amount of breeding activity in the population), we ran a general linear model (function glmmTMB) with as binomial response variable song presence and as predictors group size, year, and their interaction.

Audio recordings at active nests

Of the 63 recorded nests, 44 were used in the analyses. The nests that were excluded were failed nests, likely abandoned already on the recording day and therefore not a reliable measure of the male's singing activity at that nest stage. On three occasions, we excluded a nest as no owner could be appointed. We summarised the amount of high-quality song and song of any (high, medium, and low combined) quality per nest box to visualise the social context of the soundscape at all nest boxes. Additionally, we tested whether breeding stage influenced a nest owner's singing activity at the nest with an ANOVA (function aov in R) and followed up with a Tukey post-hoc test (function TukeyHSD in R).

Year-round audio recordings

We had 701 recordings from the four sites (three sites with 176 and one site with 173 recordings). To analyse whether the different categories of activity level (0-4) correlated with the chance of obtaining song in a given recording, we used chi-square tests (function chisq.test in R).

Playback experiments combined with nest boxes

Zebra finches visited treatments in 19 out of 23 treatment triplets. For the visited triplets, we tested the relation between visit latency and treatment in a generalized linear mixed model (function glmmTMB in R), where we modelled latency as response variable against the predictor of treatment (zebra finch song, nightingale song or silence), we added the triplet as a random effect. We used the Tweedie family for the response variable because this distribution is especially suitable for a continuous positive distribution that contains zeros (Hasan & Dunn, 2011), such as the latency from playback that we scored, where a zero represents a visit during the playback.

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Chapter 4 | Hanging out in the outback: the use of social hotspots by wild zebra finches

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Resubmission in review

Abstract

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 flocks is an important component of daily life.

Introduction

Many birds live in complex multi-level or fission-fusion societies where social structure changes over time when exploring the environment (Aplin et al., 2021; Loretto et al., 2017; Papageorgiou & Farine, 2021; Silk et al., 2014). 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 & 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*, that form social networks with their neighbours while being territorial (Snijders et al., 2014), but in winter form different, two-level social networks at foraging sites (Aplin et al., 2015; Papageorgiou & 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 over-looked. 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 & 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 (**chapter 2**). 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 (Brandl et al., 2021; McCowan et al., 2015; Zann, 1996). Yet, as a key avian model organism they are usually studied in caged pairs or kept in stable, often single-sex, groups in aviaries (Griffith, Crino, Andrew, et al., 2017; Kalnins et al., 2022; Shahbazi et al., 2014), 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 meters (**chapter 2**). 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 (Loretto et al., 2017; Papageorgiou & Farine, 2021; Silk et al., 2014). 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 (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 November 2017 (**chapter 3**). Ecological conditions were such that breeding activity by this opportunistically-breeding species was very constrained with only nine clutches laid during the study period (**chapter 3**). 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.

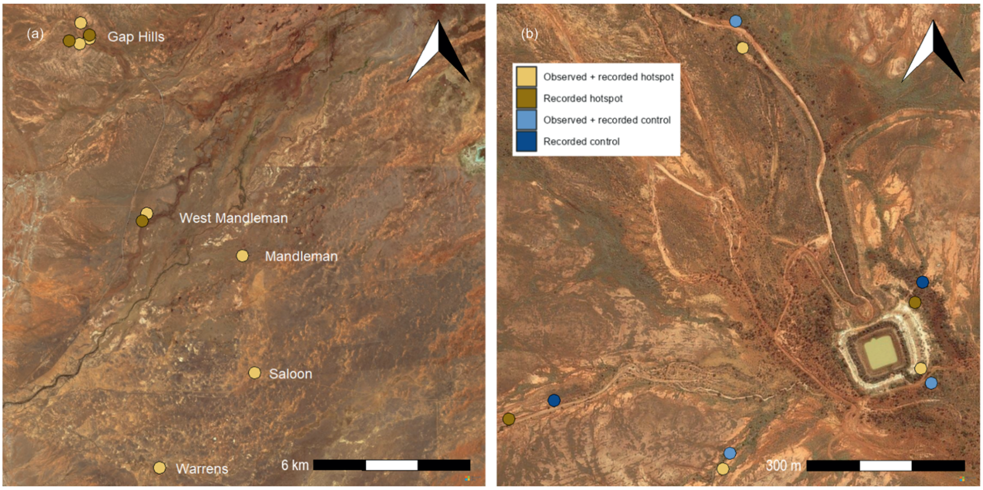

Figure 1. Satellite picture of the position (a) of the hotspots (which were all paired with a control tree, not drawn to maintain legibility) on each site (n = 5 at Gap Hills, n = 2 at West Mandleman and n = 1 at Mandleman, Saloon, Warrens) at Fowlers Gap Arid Zone Research Station. (b) Satellite picture 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.

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 (**chapter 2; chapter 3**). 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 ± 20 m apart (± standard deviation, 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 x 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 x 10 cm square was 19 ± 3.4, whereas it was only 0.7 ± 0.4 under the control trees (mean ± 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.

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 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 (zebra finch predators 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).

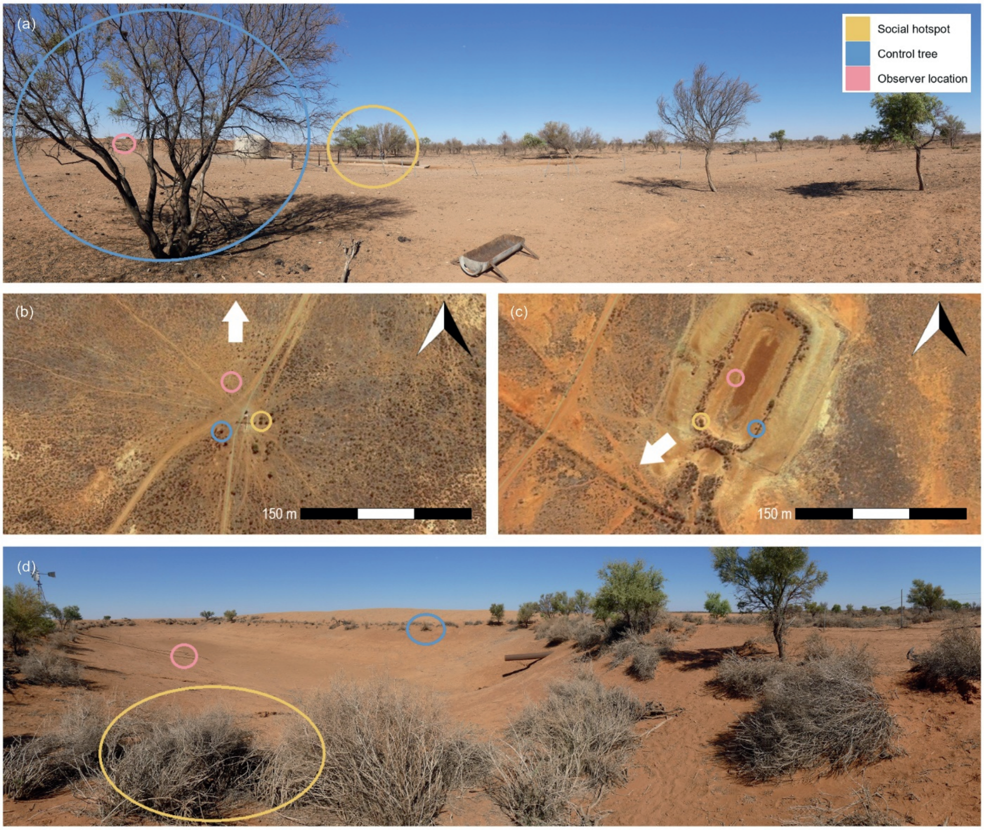

Figure 2. Social hotspots, control trees and observer locations indicated for two sites. (a) Warrens seen from a panorama photo taken near the control tree. Here, the social hotspot and control tree were in a prickly wattle *Acacia victoriae* and many trees of this species can be seen nearby. (b) A satellite 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 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 (Funghi et al., 2020; Zann et al., 1995). 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 hours of focal observations at seven social hotspot and control tree pairs between 12th November and 8th 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 hours 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, and the group size of birds in each tree (social hotspot and control) before the event. 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). 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.

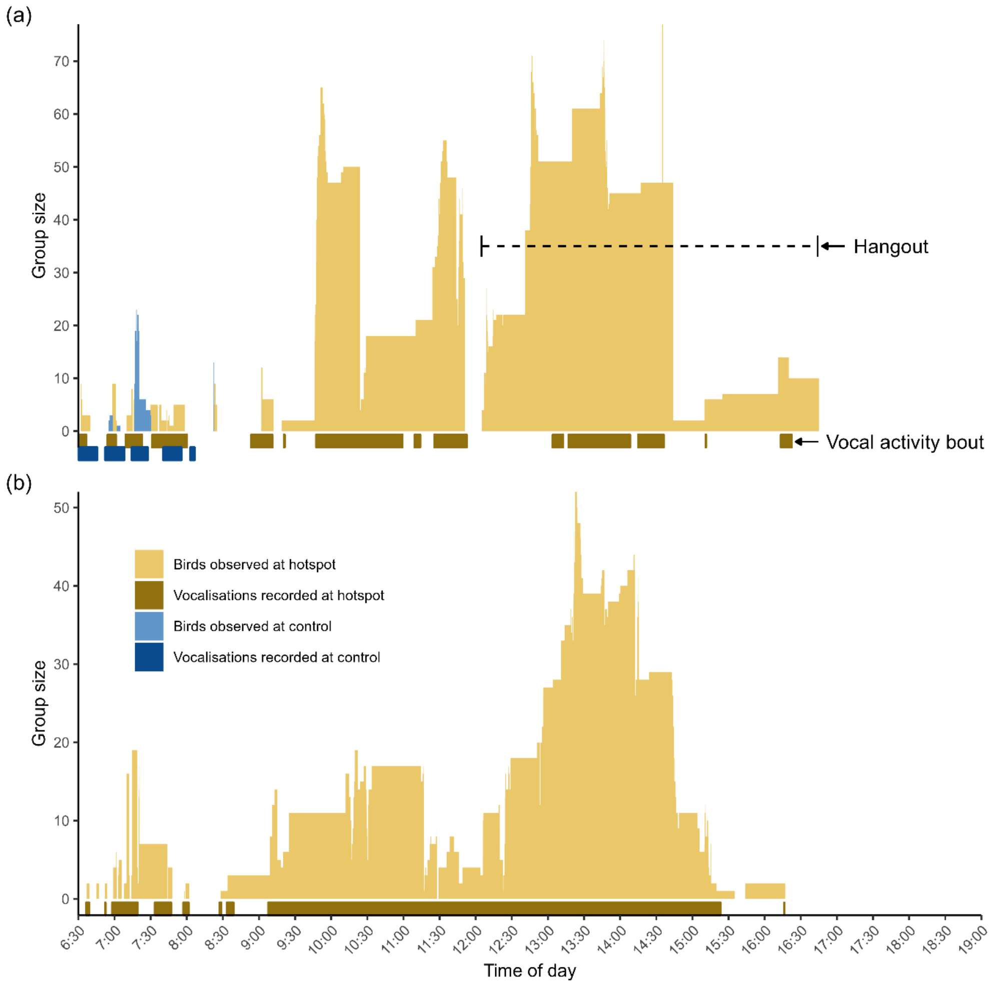

Figure 3. Group size dynamics, as well as vocalisations on social hotspots and control trees of two sites on 11th November 2019. (a) Warrens, where we had overall highest activity on the control tree out of all days on all sites. A hangout and vocal activity bout are indicated as example. (b) Saloon, 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.

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 ten hours 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 m to 51 m).

To identify the persistent use of the selected social hotspots, we calculated the time any zebra finch was present (total duration and proportion of time present) per tree and site per day. Additionally, 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). 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 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 (Olympus, DM670) 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 28th October and 8th December 2019. Each recorder was programmed to record for 12 hours (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, **chapter 2**), 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 (**chapter 3**). 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).

Statistical analyses

We conducted all statistical analyses in R 4.1.1 (R Core Team, 2020). 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 ± 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.

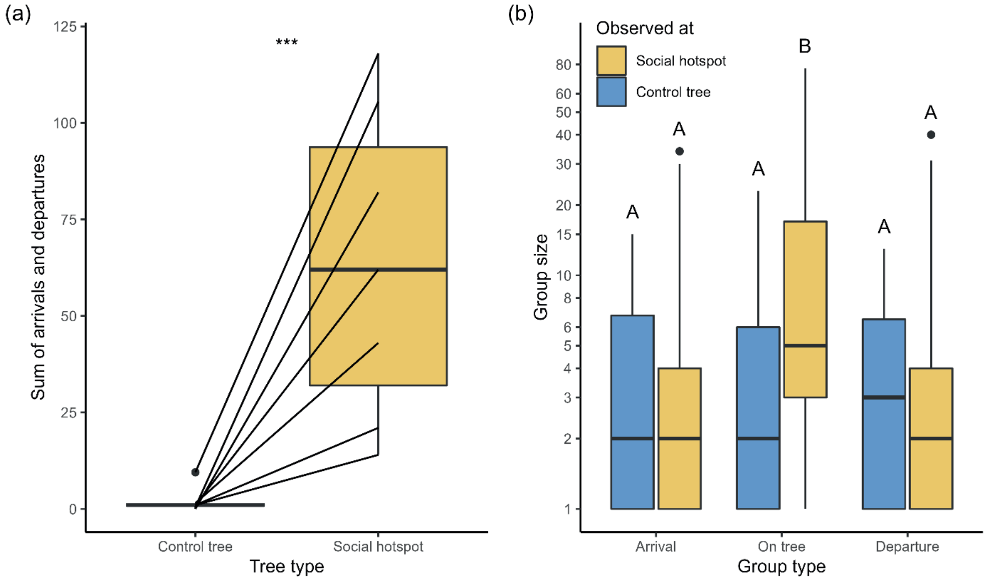

Figure 4. (a) The sum of arrivals and departures, with each line indicating connecting the averages (over two days) for each of the seven observation sites. There was substantially more activity on the social hotspots than on the control trees. Statistical significance of *** corresponds with $p < 0.001$. (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.

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 hours across the five different populations of zebra finch. With an average of 63.6 ± 40.3 total arrivals + departures on social hotspots there was substantially more activity at the social hotspots than at the control trees where on average only 2.1 ± 3.3 total combined arrivals and departures happened (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 comparison; $t_{4643} = 9.2$, $p < 0.0001$; Fig. 4b). As can be seen in Figure 4b, substantially higher numbers of zebra finches were common at these hotspots with a mean maximum per tree of 32.3 ± 23.5, and a maximum of 77 birds at a particular hotspot (Fig. 3a).

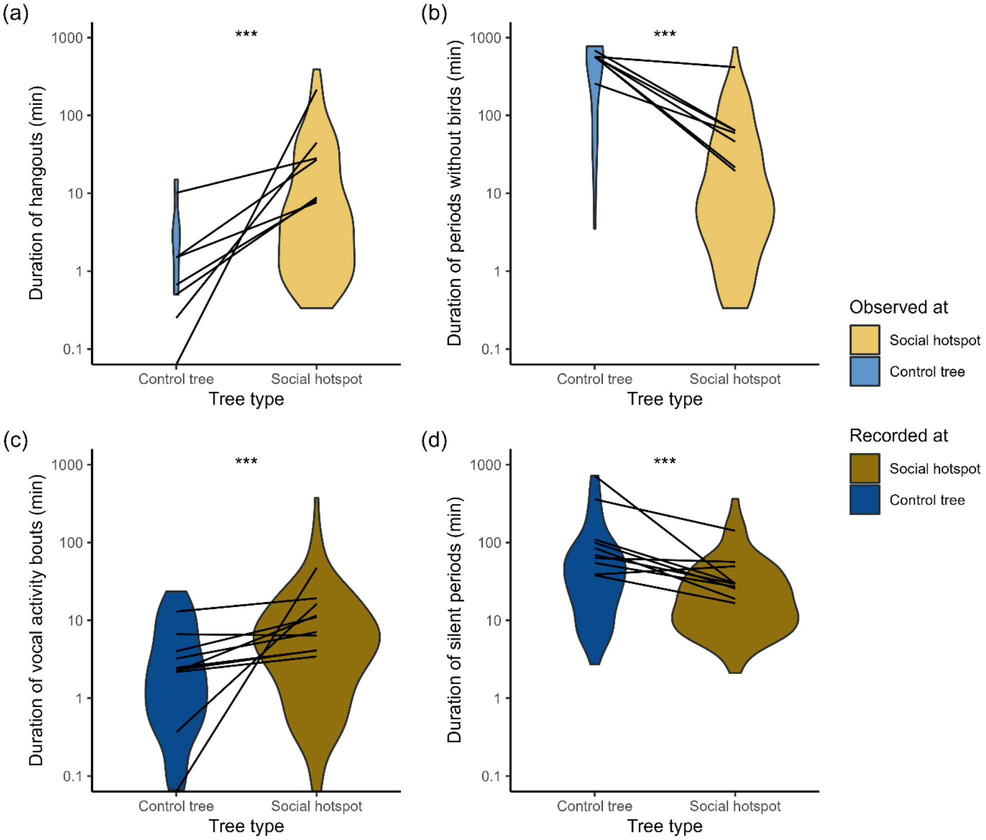

Figure 5. Duration parameters associated with observations (a, b) and recordings (c, d). Violins represent the raw data and their size is indicative of the relative amount of data. Lines indicate the site means (n = 7 for observations, n = 10 for recordings). For the observations, this was averaged for 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 (±12.5 hours). (c) Duration of recorded vocal activity bouts. (d) Duration of silent periods, taking into account the whole recording period of 12 hours. Statistical significance of *** corresponds with p < 0.001.

Hangout durations at observed social hotspots

Zebra finches were observed in the social hotspots across the day, i.e. hanging out for 262 ± 152 min representing 36 ± 21 % of the entire observational time at the social hotspots; significantly greater than the 3 ± 7 min representing 0.4 ± 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 ± 75 min which was significantly longer than the 2 ± 4 min in control trees (GLMM; $z_{176} = 3.6$, $p < 0.001$; Fig. 5a). When considering an observation time of about 12.5 hours 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 ± 141 min. For control trees, this was significantly longer with 539 ± 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 hours 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 5b-d). We detected zebra finch vocalisations for 187 ± 137 min representing 26 ± 19 % of the entire recording time at the social hotspots, this was much lower at control trees with 31 ± 31 min, representing 4 ± 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 ± 13 min at the social hotspots, longer than the 4 ± 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 ± 37 min on the social hotspots, much shorter than the 164 ± 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 ± 18.6 % of minutes with vocal activity also had birds observed in that hotspot. On those same days, 58,2 ± 21.0 % of minutes 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. i.e. it was not the case that individuals aggregated together in a social hotspot before all then leaving as a large 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. 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. (Griffith & Buchanan, 2010; Zann, 1996).

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 (Brandl et al., 2021; Griffith, 2019; McCowan et al., 2015). Zebra finches form strong social pair bonds during and after breeding that are life-long and last for several years (Dunn & Zann, 1996b; 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 such about the condition of others, resources in the local area (Aplin et al., 2013; Mariette & Griffith, 2013; Weimerskirch et al., 2010) and during breeding periods to synchronise reproductive schedules (Brandl et al., 2021; Brandl, Griffith, & Schuett, 2019; Camerlenghi et al., 2022; Mariette & Griffith, 2012; McCowan et al., 2015). 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 & 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 & 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 (**chapter 2**). Thus, vocalisations in the zebra finch cannot function as a long-range signal to regulate spacing (Brumm & Naguib, 2009; Snijders & Naguib, 2017; Waser & Wiley, 1979), or facilitate re-grouping, even though they attract others over short range (Adrian et al., 2022, **chapter 3**), 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 & 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, Crino, & Andrew, 2017). 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 (**chapter 3**). 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 (Hauber et al., 2021; Louder et al., 2019). 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; Griffith, Crino, Andrew, et al., 2017; Ruploh et al., 2013, 2014). The importance of a diverse social environment on behavioural development has been experimentally identified by studies in birds in captivity (Honarmand et al., 2015; Ruploh et al., 2013, 2014), 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 (Bircher et al., 2020; Krause et al., 2013; Snijders & Naguib, 2017) 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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Chapter 5 | General discussion

When studying any behaviour, it is effective to integrate knowledge between proximate (ontogeny, mechanism) and ultimate (phylogeny, function) levels of analysis (MacDougall-Shackleton, 2011; Tinbergen, 1963). Birdsong is one of the most important model systems for the study of animal communication (Naguib & Riebel, 2014). In birdsong literature, the non-territorial zebra finch is the key model species for studying proximate questions under controlled laboratory conditions (Griffith & Buchanan, 2010), whereas field studies on territorial species have predominantly formed our understanding of ultimate (or at least functional) aspects (Catchpole & Slater, 2008). Therefore, an improved integration between these two bodies of literature benefits from a better ultimate understanding of zebra finch song: why do zebra finches sing? To be able to answer this question, we need to understand the ecologically relevant contexts in which zebra finch song is produced. However, although the song of the zebra finch is studied much in captive conditions (Hauber et al., 2021), song studies conducted in the wild are rare (Dunn & Zann, 1996b, 1996a; Woodgate et al., 2012; Zann, 1990) and most of our knowledge is anecdotal (Immelmann, 1968; Zann, 1996). In this thesis, I attempted to fill this knowledge gap by studying zebra finches in the wild using a combination of quantitative observational and experimental methods. I specifically sought to answer the following questions surrounding the ecological context of zebra finch song:

- Who is singing and who are the receivers of this song?
- Where do zebra finches sing?
- When do zebra finches sing? More specifically, is song related to (timing of) breeding?

In this chapter, I will provide a synthesis of my findings on the ecological context of wild zebra finch song. First, I will summarise my findings of **chapters 2-4** by answering the questions on the circumstances mentioned above. Secondly, I will attempt to increase the integration between two bodies of literature: proximate studies on captive zebra finches, and ultimate studies on territorial songbirds. For this, I will compare my results with studies from both these bodies of literature and highlight similarities and discrepancies, going beyond the discussions of **chapters 2-4**, while suggesting future research directions that I think will be important in the context of the questions raised by the synthesis presented here.

The circumstances of zebra finch song under natural conditions

Who is singing and who can hear it?

Knowing which individuals are signalling and who the potential receivers are is important in disentangling the function of a signal. Zebra finch song is usually studied in the context of unpaired males attracting a partner, and it is often recorded by putting males in social isolation to yield high-quality recordings without acoustic interference by non-focal birds (reviewed by Riebel, 2009). Although I do not dispute that zebra finch males sing during courtship or that they can sing in isolation, in the wild most of the song that I observed was produced by paired males in social contexts. Indeed, in **chapter 2**, I show that only about 13% of song observations was from males that appeared to be alone, whereas the other 87% was produced when the partner was around (assuming that a male and female arriving and leaving a site together are actually a pair), with about 61% of total song observations from groups where there were more than two birds. Although we did not formally quantify this, courtship was hardly observed and therefore practically all of this song was produced outside of courtship contexts that are typically interpreted as the main role of their song. Although I calculated in **chapter 2** that their soft song is on average not detectable by zebra finches beyond nine meters, I usually observed that these other birds present, i.e. the partner and regularly also other pairs, were perched much closer, on average within 1.5 m, suggesting that these birds could hear and listen to the song. As I show in **chapter 4** that the pair was the main unit in which zebra finches were observed, it is not surprising that most song was produced when the partner was around. Additionally, in **chapter 4** I found that larger groups of birds could form at local gathering spots, and I also observed song at these social hotspots. In **chapter 3**, I show that this production of song in groups seemed to happen more often when the local population was breeding, but that it also happened when there was no breeding activity. Experimental playback studies are also helpful for elucidating who is interested in a particular signal. During experimental playback of song near a dummy nest (at about the maximum observed natural song amplitude), visiting zebra finches consisted mostly of pairs (n = 59), followed by individual males (n = 48), flocks (n = 29), and only a few females not in a group (n = 8), suggesting that song is not predominantly an intrasexual competition or intersexual attraction signal (**chapter 3**). Overall, I have provided evidence that under natural conditions, most zebra finch song is produced when the partner is around, outside of courtship contexts, and that in many cases, other birds at the same gathering location will also be able to hear the song of males from other pairs, despite it being incredibly soft. Additionally, their song attracts other non-pair individuals, at least in a breeding context.

Where do zebra finches sing?

When studying animal signals, the location where signals are produced is often another important clue towards unravelling a signal's function. As discussed in **chapter 1**, many songbird species hold territories that they announce and defend using their songs (Catchpole & Slater, 2008), which is often performed at fixed locations called song posts (Mathevon et al., 1996; Sprau et al., 2012). Zebra finches, however, are not territorial in that sense (for example, their song does not elicit aggression), although they will behave agonistically in the immediate vicinity of the nest (Zann, 1996; pers. obs.). In **chapter 4** I found that zebra finches aggregated at social hotspots and that they might sing there. This song in the presence of individuals outside the pair was also observed during transect work (**chapters 2 and 3**). For these transect observations, the exact location where I observed song was not the focus of analysis, but anecdotally, song production appeared not to be limited to social hotspots. Additionally, in **chapter 3**, I show that experimental song playback near an artificial nest attracted birds, and I observed during the scoring of the associated video recordings that attracted males would sometimes also sing at these nest locations. In line with these observations, in **chapter 3** I also observed that at active nests, on average there were about 2 (only great signal-to-noise ratio songs) to 4.5 (any identifiable song) other singing individuals at these nests. Given that in **chapter 2** I found that zebra finch song is a soft signal that does not transmit far, these birds must have been singing nearby. In **chapter 3** I also regularly observed zebra finch groups where more than one individual was singing in non-breeding contexts, suggesting that this group singing is the rule rather than the exception. Overall, I could distinguish at least two contexts in which song is produced: at gathering sites, and at the nest. However, I suspect that there are many more locations where zebra finches sing, which I have not formally categorised here. Unlike territorial songbirds, zebra finches do not restrict their song output to a particular location, and I suspect that their song behaviour is probably more influenced by social rather than spatial context.

When do zebra finches sing, and what is the relation to breeding?

The timing of song is in many birds also indicative of its functions. As discussed in **chapter 1**, birds may sing at the start of a breeding season to attract a partner and stop singing afterwards (Amrhein et al., 2002; Catchpole, 1983), whereas other birds keep singing throughout the breeding season to advertise for extra-pair matings or for defending their territory (Hasselquist et al., 1996; Kunc et al., 2005). In **chapter 3**, using automated song recorders that were set up near resources, I observed song at every month of a year during which there was no breeding. Song output at these recording sites fluctuated over that year, peaking during the Austral spring, although I cannot disentangle whether this is actually the case or whether this pattern is simply driven by corresponding fluctuations in bird presence. From transect work conducted during spring in years with and years without breeding (**chapter 3**), it seems that at a population level, zebra finches sang more when they were breeding, as the chance of encountering song increased with group size only when the local population was breeding. This could perhaps partially be explained by the presence of many recently fledged birds that still needed to form pairs. However, this is probably not the only reason, as recordings made at nests at various breeding stages show a clear pattern with most song being produced by the male nest owner during the egg-laying stage (**chapter 3**). So, at an individual level, and in the context of already paired individuals, breeding affects song output. Overall, I can say that zebra finches sang throughout the year, and that at an individual and population level, breeding affects song output.

What are the implications for the study of captive zebra finches?

Zebra finch song is often studied in the context of mate attraction (reviewed by Riebel, 2009). In these studies, individuals are often housed in single-sex groups. When single males are then confronted with a female, they readily produce song and court the female. Of course, with such a study design, it is difficult to interpret song as anything other than a courtship signal. Throughout the fieldwork conducted for my thesis, I did not encounter single-sex groups and the most observed unit of zebra finches in the field is the pair (**chapter 4**), suggesting that there is indeed a substantial drive for zebra finches to form pairs. Given that most song that I observed was by males that were already paired (**chapters 2 and 3**), it seems unlikely that zebra finches only sing to attract a partner. This observation may partly be due to most of my research being conducted during a prolonged drought during which there was no breeding, and that perhaps most individuals that stayed in the area might already have been paired. In line with this, in **chapter 3**, I observed more singing in groups when the population was breeding, and this could perhaps partly be explained by the presence of unpaired young birds that might still need to court others. However, given that zebra finches can pair up very quickly, often within a day of when a partner is removed (Dunn & Zann, 1996b), and my many observations of song throughout a period of non-breeding (**chapters 2 and 3**), it seems likely that this song is important beyond the attraction of the social partner. Dunn and Zann, in their studies of wild zebra finch song, attribute the song behaviour in various contexts by paired males to mate guarding (Dunn & Zann, 1996a) and extra-pair advertisement (Dunn & Zann, 1996b). However, this is an unlikely explanation as zebra finch extra-pair paternity is extremely low in the wild at about 2% (Griffith et al., 2010), which suggests that it is not needed to invest heavily in song to guard one's mate, or that it is worthwhile to invest in song to gain extra-pair fertilisations. Indeed, in a study on captive zebra finches, extra-pair paternity was not related to song output (Bolund et al., 2012).

An alternative explanation for the observation that paired birds may keep singing, which still fits in this mate-attracting framework, is that males may need to stay in shape just in case their partner dies and they need to find a new partner. In a recent study (Adam et al., 2023), it was shown that zebra finches already suffer from reduced vocal performance after two days of no exercise, and that conspecifics can detect this reduction in performance. If there is sufficiently high mortality in wild birds, it might then pay to exercise regularly, regardless of the current breeding context, to remain attractive if your partner dies. Unfortunately, due to the nomadic nature of zebra finches, and the unpredictability of the environment they inhabit, we currently do not have a thorough understanding of population dynamics and differential mortality of free-living zebra finches, although Zann, (1996) mentions that sex ratios seemed to differ per year in his studied population. A long-term tracking study, where individuals can be followed over time (with those not being detected attributed to either mortality or emigration), such as what was set up recently by our group here at Wageningen University, might help to better understand whether this is a plausible explanation for the large amount of non-courtship 'undirected' song that I observed (**chapters 2 and 3**).

Nevertheless, there is a substantial discrepancy between how often zebra finch song is studied as a courtship signal (Riebel, 2009) compared to how relatively rare it is to observe song in this context in the wild compared to non-courtship contexts (**chapters 2 and 3**). Although staying in shape (Adam et al., 2023) might be an explanation for the large amounts of non-courtship song that zebra finches produce, I think a shift in focus towards studying their song in other contexts, with less emphasis on sexual selection, could still be warranted (Griffith, 2019). First of all, the importance of female choice in the courtship context is likely quite nuanced, as male zebra finches also have a preference for certain females (Jones et al., 2001). This implied mutual mate choice is further confirmed by pairs where individuals could select each other as partners being more successful in breeding than pairs that were experimentally constructed (Ihle et al., 2015). Secondly, several underlying assumptions for systems that are strongly sexually selected captured in Bateman's principles, where there is one sex that pays most of the costs of reproduction and is therefore choosier (Tang-Martinez, 2016), perhaps does not apply that well to zebra finches due to their long-term faithful monogamous pair bond where the loss of a partner in the context of an unpredictable environment might be ultimately much more costly than one's contribution to a particular clutch. That partners form strong pair bonds is in line with our observation that pairs and larger groups, not single individuals, were the unit that was most often observed (arriving at and departing from social hotspots in **chapter 4**) and that the majority of song was produced with the partner around (focal recordings data in **chapters 2 and 3**). Thirdly, signals and sexual dimorphisms are often attributed to strong sexual selection, but may also evolve by differential natural selection pressures on the different sexes (Price, 2019). For example, female birds are often more camouflaged than males and this might be because in many species, females spend more time in the nest, not because they sexually select the most attractive male. Finally, our experimental song playback attracted mostly pairs, followed by males and flocks, with only few single females being attracted by the song (**chapter 3**). In line with this field evidence, in operant conditioning setups, males seem to be equally motivated to hear song as females (Riebel et al., 2002) and in an auditory choice test, females prefer the song of the father (Miller, 1979a). As selecting your father or a member of the same sex (Elie et al., 2011) has distinct reproductive disadvantages, these findings are difficult to interpret in a sexual selection context, but even without discounting an important role of song in the attraction of the social partner, it may be worthwhile to extend our scientific inquiry to song in contexts outside of the conflict for sexual resources framework.

Although this work has received relatively little focus compared to the two main studied functions of birdsong – territorial announcement and mate attraction, there is another function of song which might fit well for zebra finches: partner stimulation (Kroodsma, 1976; Kroodsma & Byers, 1991). In some species, e.g. canaries song stimulates the partner to build a nest faster and lay more eggs (Kroodsma, 1976). From song that has this stimulative or coordinative function, one would expect it to be produced mostly after pair formation and when the partner is around, and that on a population scale, song would be produced more often when the local population is breeding, whereas at an individual scale, it should peak somewhere during the early breeding stages (nest building or egg-laying). In **chapter 3**, I observed all these factors. Accordingly, a study in a captive population found that song output correlated with reproductive investment by the female (Bolund et al., 2012). Song in such a scenario might be seen as a measure of male commitment to be gauged by his partner. Song during non-breeding conditions, as I observed in **chapter 2** and quantified over the year in **chapter 3** could then be interpreted as a baseline of low motivation signal to breed, if song output is actually lower during non-breeding. The transect data suggest this is the case, the year-round recording data is ambiguous because the observed lower song presence in some months is attributable to the similarly lower presence of birds (**chapter 3**). If pairs use song to synchronise their breeding effort, it raises the question of whether this signal is only used for within-pair communication, such as what is suggested for their call behaviour at the nest to coordinate parental duties (Boucaud et al., 2016, 2017; Elie et al., 2010), or whether it is also a signal or cue that other zebra finches attend to, for example when they visit social hotspots (**chapter 4**). This would fit well with the other evidence for zebra finch breeding synchronisation, such as inspecting the nests of conspecifics (Brandl, Griffith, & Schuett, 2019), paying attention to begging calls (Brandl, Griffith, Laaksonen, et al., 2019), and that sound supplements lead to synchronised breeding (Waas et al., 2005). There is much scope for further study here, as it remains to be proven whether coordinated and well-synchronised pairs have higher reproductive success and whether song affects this pair coordination. If so, does song exposure stimulate gonadal development? Are there positive feedback loops in male singing behaviour? Does it matter whether song exposure is by a familiar individual (the partner), and does the number of singing individuals increase this stimulation? Additionally, what are the relative roles of the environment and conspecific song signals/cues in the triggering of breeding?

If we interpret (zebra finch) song in this social selection framework (Roughgarden, 2012), focusing on partner coordination and negotiation in the context of common interest (Leigh, 1991, 2010), as opposed to sexual selection, we also need to investigate how song reliability is maintained. It is often assumed that song is a costly, and therefore reliable, signal of some inherent quality of the singer (Gil & Gahr, 2002). However, it is currently not clear whether there are substantial costs associated with singing in zebra finches. Singing with higher amplitudes, at least, appears not to be metabolically costly (Zollinger et al., 2011), although food-deprivation reduces song amplitude in zebra finches (Ritschard & Brumm, 2012). In **chapter 2** I quantified that zebra finches sing very soft songs (at about 50 dB at 1 m) in comparison to several European songbird species (ranging from 74-105 dB at 1 m, Brackenbury, 1979). If there are already no or low metabolic costs associated with increasing the amplitude of song (Zollinger et al., 2011), I suspect that it is especially unlikely that this soft song is energetically costly. This makes me wonder if the observed female preference for high-amplitude song in an operant setup (Ritschard et al., 2010) should be interpreted as a preference for amplitude-coded information on male quality or simply as stronger reactions to more salient signals (Owren et al., 2010). Perhaps, for zebra finches, we should not look at the direct cost of singing in terms of song output (Bolund et al., 2012), song amplitude (Ritschard et al., 2010) or song structure (Woodgate et al., 2012), but rather at the cost of signalling unreliably (Lachmann et al., 2001). Then, even the production of non-costly signals could be maintained if it is costly to produce unreliable signals. In this case, if zebra finch song communicates breeding intent, it would be maladaptive to sing much when conditions are not suitable for breeding or to sing little when conditions are suitable for breeding. Indeed, in **chapter 3**, I observed an increase of singing during egg-laying, and an increase in song observations when the local population was breeding.

Another body of literature in which zebra finches feature heavily is the one addressing song learning (Hauber et al., 2021). Zebra finches, like all oscines, learn to sing (males) or to prefer certain songs (females) during their early life (Riebel et al., 2002), usually before they are about 80 days old (Slater et al., 1988). Due to the individual signature of the song (Sossinka & Böhner, 1980; Sturdy et al., 1999), zebra finches are especially suited to study this process of song learning as it is feasible to score the similarity over time between a tutor's and a tutee's song for basically every individual song performance (Tchernichovski et al., 2001). When one is interested in copy accuracy or learning ability, it makes sense to limit a learning bird's exposure to a single song or song tutor. Often, the father is selected for this, although it is likely that this might not be the main or only tutor of zebra finches under natural conditions (Slater et al., 1988), and it is now also recognised that peers also play a role in this learning process (Honarmand et al., 2015). In free-living zebra finches, Zann (1990) found that about 65% of males copy some part of their father song. However, even in those birds that appeared to learn a part of their song from their father, several elements of a son's song were not coming from their father. Intuitively, this makes sense in a system where individuals evolved to have individually recognisable signals (Sturdy et al., 1999). Indeed, it would be counterintuitive if individuals would precisely copy the signature of another individual, and the expectation is that zebra finches in the wild should have opportunities to learn from more than one individual. In **chapter 3** I found that already at the nest, on average three males can be heard singing from nearby (this is before the sensitive period). Furthermore, I show that especially during breeding (**chapter 3**), but also during non-breeding (**chapter 2**) song is produced in social contexts with more individuals than just the partner present and with more than one singing individual at a particular site in 32% of recordings (**chapter 3**). Moreover, in **chapter 4**, I show that zebra finches also gather at social hotspots, where birds were hanging out for substantial amounts of time, during which I also observed song activity. If young birds would spend some time at these hotspots, where birds come and go regularly, they would likely be exposed to several song examples per day. Future work should focus on whether individual song signatures, such as those of zebra finches, are an adaptation to living in fission-fusion societies. Additionally, studies on zebra finch song learning in the wild should in more detail investigate the social environment during adolescence, and whether young birds attend social hotspots (**chapter 4**), for example by tracking individual birds.

To conclude this section on zebra finch song studies, I would like to address one particular term that is much used in the study of zebra finch and other estrildid song: undirected song (Sossinka & Böhner, 1980). This term was coined as an antonym of directed song, the song that a male directs at the female during courtship. Conversely, undirected song was described as the song that is inhibited by the presence of a female (Caryl, 1981). In this thesis, I show that this undirected song is actually predominantly produced when the female is around (**chapters 2 and 3**). Additionally, this song is often also attended by other individuals (**chapters 2 and 3**). The term 'undirected' implies that all these other individuals are not intended receivers of this song, even though I have shown that they are often within audible distance (**chapter 2**). Only if this dominant mode of singing exists to practice to stay in shape (Adam et al., 2023), the term is inoffensive, but in most other scenarios, some of which I have discussed above, this term appears to be a misnomer that potentially hinders the study of this type of song.

What are the implications for the study of birdsong in general?

After studying zebra finches in their natural environment for this thesis, I suspect that if birdsong literature would have started by studying zebra finches, not territorial songbirds in temperate regions, we would have developed a very different view on the functions of birdsong. Based on the evidence that I presented above, it seems that zebra finches are somewhat different in their song behaviour compared to those typically studied songbirds, e.g. tits, flycatchers and song sparrows (Bircher et al., 2020; Catchpole & Slater, 2008; Krebs et al., 1978; Templeton et al., 2012). There are several dominant assumptions (biases) in the current birdsong literature. E.g. the bias towards male song (Riebel et al., 2005) is being increasingly addressed, with establishing that female song is present in many clades (Odom et al., 2014). Subsequently, the birdsong literature is broadening (Brunton et al., 2016; Odom et al., 2015), with also attention for potential other functions of song (Riebel et al., 2019; Rose et al., 2022). In this section, I will compare my findings with a few other dominant assumptions: birdsong is loud, songbirds are territorial, and birdsong predominantly functions in competition for sexual resources. By addressing these assumptions, I will simultaneously investigate the question of how representative zebra finches are as a model for birdsong in general.

Birdsong is loud

Birdsong is typically viewed as a loud and conspicuous signal. Because sound allows for communication even without visual contact, it is especially suitable when communicating in e.g. forests or thick reedbeds. Therefore, it is often assumed that birdsong is predominantly used for long-range communication (E. S. Morton, 1975; Naguib & Wiley, 2001). Indeed, the study of sound transmission, and whether bird sounds evolved to propagate optimally through the habitat in which they are produced, has received much attention, and is formulated in the acoustic adaptation and sensory drive hypotheses (Endler, 1992; Erdtmann & Lima, 2013; Ey & Fischer, 2009; Weir et al., 2012; Wiley & Richards, 1982). It should be noted that this literature and birdsong literature in general has focused mostly on frequency-related and temporal properties of song, not song amplitude (Zollinger & Brumm, 2015). This is because song amplitude is relatively difficult to measure. In addition to the recording of the sound in question, it requires knowing the distance between the focal individual and the microphone, and one needs to control for the relative orientation of the beak. This is why we only have amplitude measurements for about two dozen (sub)oscines, with most measurements on European songbirds (Brackenbury, 1979; Brumm & Todt, 2002); several thrush *Turdus* species, that produce soft song types (Dabelsteen, 1981; Lampe et al., 2010; Vargas-Castro et al., 2017); two very loud suboscines named after the sound they produce, the screaming piha *Lipaugus vociferans* and white bellbird *Procnias albus* (Podos & Cohn-Haft, 2019); rock sparrows *Petronia petronia*

(Zollinger & Brumm, 2015); song sparrows (Akçay et al., 2015; Templeton et al., 2012); red-winged blackbirds *Agelaius phoeniceus* (Patricelli et al., 2008); and zebra finches (Brumm, 2009; **chapter 2**).

Much of this song amplitude literature specifically focuses on surprisingly loud or soft song, and the latter has not received much more attention than the studies listed here. In most species that have been studied, soft song types are produced during moments of high arousal, e.g. in territorial disputes (Akçay et al., 2015; Templeton et al., 2012) or courtship (Dabelsteen et al., 1998). In these critical moments, eavesdropping by competitors is probably avoided by singing softly (Vargas-Castro et al., 2017). Although these soft song types have amplitudes in the same range as natural song amplitude in wild zebra finches (**chapter 2**), these studied species also have louder 'broadcast' song types. That is not the case for zebra finches. The conspecific eavesdropping avoidance interpretation is also not likely for zebra finches, as I regularly saw that multiple individuals were within earshot of singing males (**chapter 2**). However, in the videos from the playback experiment in **chapter 3** there is one occasion of a collared sparrowhawk landing on a nest during playback of zebra finch song, and I have also observed an attack by a collared sparrowhawk during another playback experiment (unpublished data), so perhaps low song amplitude evolved to avoid this eavesdropping by predators. Additionally, the social organisation of wild zebra finches allows for soft song, as local birds hung out at social hotspots (**chapter 4**) and visited and sang at each other's nest (**chapter 3**). It is not distinguishable whether soft singing could evolve due to their social organisation or vice versa. Like for female song (Odom et al., 2014), it would be valuable to conduct comparative analyses to elucidate whether birdsong is ancestrally loud or soft, but for this we should first collect data on vocalisation amplitude in many more species. I suspect that the maximum audible distance for humans (perhaps corrected for age) might already give a usable estimate of vocal amplitude. This would be valuable to test, as this is potentially something that could be implemented in a citizen science project, leveraging the many birdwatchers worldwide.

Songbirds are territorial

Historically, studies on birdsong have almost exclusively studied territorial birds because of their spatial predictability (discussed in **chapter 1**). This has led to the assumption that songbirds are territorial. Indeed, I struggled to find literature that specifically addresses song in non-territorial songbirds, and I think that it is currently impossible to conclude whether this assumption is a bias or a fair representation of songbird ecology. Zebra finches are probably the best-known example of non-territorial songbirds. As the spatial and social organisation is integral to the understanding of song in other songbirds, I specifically investigated this in **chapter 4**. Clearly, zebra finches tolerate in their vicinity, and even seek out, conspecifics by hanging out at social hotspots (**chapter 4**), and song does not elicit aggressive responses (**chapter 3**). Although they defend their nest from conspecifics (Zann, 1996), this is best interpreted as prevention from egg-dumping (Birkhead et al., 1990; Griffith et al., 2010), not a competition for space. Zebra finches probably lack territoriality due to their strict granivorous diet (S. R. Morton & Davies, 1983). The grass seeds they consume are distributed patchily. At these patches, however, seeds are abundant, so that they are unlikely to be dominated by a few individuals. Instead, zebra finches may form feeding flocks, probably to reduce predation risk in the open environment (Zann, 1996).

Future work on non-territorial songbirds beyond close relatives of the zebra finch (Olsson & Alström, 2020) should probably start by identifying and studying species with characteristics similar to zebra finches, e.g. strict vegetarianism, (loose) colonial breeding, the absence of aggressive responses to song, social monogamy, and the presence of group singing or song assemblies. I know only of a few species that seem to satisfy these characteristics. American goldfinches *Spinus tristis* are strict seedeaters (Lynch, 1970), that do not seem to behave aggressively towards conspecifics (Roberts, 1942), and that have been reported to sing in groups (Salzman, 2004). Another fringillid, the European goldfinch *Carduelis cardualis*, is also a strict vegetarian (Glück, 1985), that also forms loose colonies, with birds roosting and singing together (Conder, 1948). All of the literature cited here on these two species is old and half of it is non-peer-reviewed observational work (i.e. theses and ornithological society magazines). I think that field studies on song of these species deserve much more attention. Additionally, common starlings *Sturnus vulgaris*, and house sparrows *Passer domesticus*, are not (strict) vegetarians, but these species can form large flocks and they defend nest sites, not territories (Mountjoy & Lemon, 1991; Summers-Smith, 1958). In starlings, song also attracts males and females (Mountjoy & Lemon, 1991). Careful observational and experimental study of these species mentioned here will help to expand our view on birdsong in the context of (absence of) territoriality. Finally, comparative studies on which factors underlie singing behaviour such as what I observed in wild zebra finches, and how widespread it is across also 'traditional' songbirds are needed. Specifically, especially for migratory songbirds, we often lack a clear picture on what happens on the wintering grounds (Souriau et al., 2019).

Birdsong predominantly functions in competition for sexual resources

The dual function of birdsong (Catchpole & Slater, 2008) represents the view that birdsong evolved as armament and as ornament. Armaments are the behavioural or morphological adaptations individuals use in intra-sexual, usually male-male, competition, whereas ornaments function in intersexual (male-female) contexts such as female choice. Good armaments can also be good ornaments, as males that dominate other males in competitions might be of better quality, which is something females should attend to (Berglund et al., 1996). However, in the birdsong literature, there is also evidence for divergent evolution of these traits, with good ornaments being bad armaments (Leitão & Riebel, 2003). The matter has become more complicated by the further investigation of female song. In many species of (sub)oscines, both sexes sing and pairs may even perform duets (Hall, 2009). Especially in the tropics, this is associated with year-round resource or territory defence (Tobias et al., 2011, 2012). Since these armaments thus also function in competition of non-sexual resources, birdsong can also function in social selection, in this case defined as intraspecific competition for resources in the broad sense, not only sexual (West-Eberhard, 2014).

However, not all species evolve in stable environments where fitness is mainly determined by competition for resources; not all species are K-selected. Some species are more r-selected, typically occupying more unpredictable environments, and their fitness is largely driven by their growth capacity (MacArthur & Wilson, 1967). Among songbirds, zebra finches are towards the r-selected side of the r/K-spectrum (Southwood et al., 1974). It is likely that their fitness mostly depends on a pair's ability to discover ephemeral grass seed patches and provide parental care. It is not difficult to imagine that well-coordinated (D'Amelio et al., 2017), cooperating (Roughgarden, 2012; Roughgarden et al., 2006), and compatible (Ihle et al., 2015) partners will be more successful under these conditions. Throughout my observations, the main unit that I observed was the pair (**chapters 2-4**), suggesting that zebra finches are indeed well coordinated. Also, their calls at the nest seem to play a role in negotiating parental investment within pairs, for example in turn-taking (Boucaud et al., 2016, 2017; Elie et al., 2010). Unfortunately, I am not able to conclusively demonstrate it here, as I was unable to experimentally study their vocal behaviour at the nest during the period of my PhD due to a record drought and a pandemic. Nevertheless, I suspect that their soft song, which is practically always produced when the female is around (**chapters 2 and 3**), likely plays a role in zebra finch pairs becoming such a well-coordinated unit. Perhaps it is almost time to extend the ornament-armament model, and coin the term 'mutuament' in reference to a cooperative adaptation?

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Summary

Birds sing to compete for a partner and territory. The substantial evidence supporting this dual function of birdsong is predominantly based on ecological research conducted in the seasonal northern temperate zone (Catchpole & Slater, 2008). Yet, many environments are not seasonal or temperate, and therefore differ in the selection pressures underlying the evolution of birdsong and communication in general. Zebra finches are not territorial and pairs stay together most of the time, with extra-pair paternity rates being low at 2% (Griffith et al., 2010). While zebra finches are a key model species in the study of mechanistic and development aspects of song (Hauber et al., 2021), our understanding of their song function thus does not fit well within the classic assumptions. To expand our understanding of the function of song in general, and zebra finches in particular, I here studied the singing behaviour and social organisation of zebra finches in a wild population in arid Australia. I integrated multiple observational and experimental methods.

In **chapter 2** I studied the communication system of wild zebra finches. I made calibrated recordings to quantify the song and call amplitude of zebra finches in their natural environment. These showed that zebra finches sing at surprisingly low amplitudes of about 50 dB at 1 m, and that even their loudest call, the distance call, is not much louder at about 58 dB at 1 m. Afterwards, I conducted sound transmission experiments at my field site, broadcasting song and distance calls at the natural amplitude and re-recording it at distances ranging from 1 to 256 m. By integrating knowledge about the auditory system from studies on captive zebra finches (Okanoya & Dooling, 1987), I calculated the maximum detection distance of their song under natural conditions. This measure of communication distance suggested that zebra finches can detect song up to about nine meters away from the singer, and that distance calls reach receivers at distances up to fourteen meters. Observations done during transects confirm that other birds are generally within hearing range of others when I observed song (within 1.5 m). So, zebra finch vocal communication is short-range, and not likely to be used for spatially organising over large distances such as those observed in territorial songbirds.

In **chapter 3** I focused on the ecological contexts of zebra finch song in the broad sense, investigating whether observed patterns fit within a general social affiliative or mediative function (Riebel et al., 2019; Rose et al., 2022). I further explored whether song might play a role specifically in the synchronisation of breeding that is observed in zebra finch populations in the wild (Brandl et al., 2021; Brandl, Griffith, & Schuett, 2019; Brandl, Griffith, Laaksonen, et al., 2019) and captivity (Waas et al., 2005). I integrated findings from five years of field studies that were conducted when the local population was breeding and during a severe drought during which breeding was absent. Used methods included focal calibrated song recordings, transect observations, song recordings throughout different breeding stages at the nest, year-round recordings at social gathering sites, and large-scale playback experiments. I show that zebra finches frequently sing while in groups (focal calibrated recordings, transect observations), that breeding status influences song output at the nest (nest recordings) and at aggregations (transect

observations), that they sing year-round (year-round recordings), and that they predominantly sing when with their partner (focal calibrated recordings, transect observations, nest-recordings), suggesting that song remains important after pair formation. Song playback near dummy nests attracted conspecifics, showing that song may play an active role in the social aggregations that we observed, but also potentially facilitate synchronisation of breeding. Together, these results demonstrate that zebra finch song might play a role in coordination and cohesion of social and breeding units within larger societies. These results expand on the finding that birdsong serves generally in situations such as territory defence, agonistic signalling and partner attraction, and they raise the question of how well the current songbird literature represents the variety seen in natural systems.

In **chapter 4** I investigated the social organisation of zebra finches. In his influential book, Richard Zann (1996), anecdotally describes the use of 'social trees', trees where zebra finches come and go throughout the day, that are consistently used over long periods of time (months to years). However, this had not been formally quantified, even though my co-authors and I suspected that these 'social hotspots' are at the heart of the fission-fusion society that zebra finches form in the wild. Using day-long focal observations and acoustic recordings at these social hotspots, I quantified the group sizes of arriving and departing birds, as well as the number of birds that were at the social hotspots at any particular moment. By combining observation and acoustic data from the same day, I also quantified the vocal activity at these sites. I observed mostly pairs and small groups visiting and departing from these social hotspots, but the numbers of birds on these trees was variable but substantially higher than the visiting and departing groups. This suggests that birds can associate with others at these hotspots, but that they do not play a major role in the formation of e.g. foraging flocks. Zebra finch vocalisations were recorded during about 60% of the time that birds were observed, indicating that these hotspots could serve as hubs for information exchange, and that they might also play a role in potential synchronisation of breeding as suggested in **chapter 3**.

To conclude, I think my data fit best within the social selection framework (Roughgarden, 2012), it is not impossible to interpret my findings on the ecological context of song as a sexually selected signal where males sing to maintain their attractiveness (Adam et al., 2023) in case their partner dies. Consequently, due to their social organisation (**chapter 4**), this means that they happen to sing predominantly when their partner and others are around (**chapters 2 and 3**). That said, my findings on the song as a predominantly within-pair signal, in the context of long-term faithful social monogamy, fit much better within the social selection framework (Roughgarden, 2012), where individuals carefully negotiate about offspring investment in the context of co-operators with common interest (Leigh, 1991). Given that zebra finches also commonly sang in groups and that they did this more often when the local population was breeding (**chapter 3**), there is the exciting possibility that song, as signal or cue, functions in attaining between-pair breeding synchrony. Further mechanistic studies are needed on the role of song in attaining breeding synchrony, as well as whether and how this already observed breeding synchrony benefits fitness. Additionally, given that zebra finches seem to differ substantially in their song and spatial behaviour from the loud, territorial songbirds that have received most study focus (Catchpole & Slater, 2008), I wonder how representative zebra finches are as model songbird. To answer this question, I suggest further comparative ecological studies specifically on other estrildids and non-territorial songbirds, and generally on songbirds inhabiting regions other than the northern hemisphere temperate regions.

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About the author

I was born and raised in Hoogeveen in 1993, where I developed an interest for nature early in life. My parents often took me and my sister Stella for walks in the forest, and when I was still very young, catching aquatic invertebrates in the freshwater lake near our house was my favourite pastime. After observing a bearded vulture in the Pyrenees in 2005, I became especially interested in birds. Birdwatching has been my hobby since. In 2008, on the first biology lesson of the year, my biology teacher mr. Hartog showed us the movie 'Spreeuwenwerk' starring Joost Tinbergen which is on ethological fieldwork of starlings. I had found my dream career.

In 2011, I went to Leiden and started my Bachelor Biology at Universiteit Leiden. I completed my Bachelor in 2014 with a thesis on anthropogenic noise effects on blackbird song, which I did together with Rafael Martig, under supervision of Hans Slabbekoorn and Katharina Riebel. Becoming more and more interested in animal ecology and bioacoustics, I continued my studies with a Master at Wageningen University. Here, I conducted research on artificial light colour effects on bat roosting ecology at the Netherlands Institute of Ecology (NIOO-KNAW) under supervision of Kamiel Spoelstra. I also conducted a comparative study on acoustic adaptation in neotropical frog species in Panama in collaboration with the Vrije Universiteit Amsterdam and the Smithsonian Tropical Research Institute under supervision of Wouter Halfwerk.

After obtaining my Master degree in Biology in 2018, I continued with this PhD at the Behavioural Ecology Group in Wageningen. Here, I studied the ecological context of vocal communication by wild zebra finches. This was done under supervision of Marc Naguib (Wageningen University) and in collaboration with Simon Griffith (Macquarie University, Sydney). I will be able to continue with this work as a postdoctoral researcher for another half year here at Wageningen University.

WIAS training and education statement

Description	Year
The Basic Package (1.8 ECTS)	
WIAS introduction day	2019
Scientific integrity & ethics in animal sciences	2019
Disciplinary Competences (12.5 ECTS)	
Literature survey	2018
Tidy data transformation and visualization with R	2021
An introduction to LaTeX	2021
Introduction to zero inflated GLMs and GLMMs with R	2021
Life history theory (RUG)	2021
Bayesian data analysis	2022
Professional Competences (6.5 ECTS)	
Project and time management	2019
Efficient Writing Strategies	2019
Supervising BSc & MSc thesis students	2020
Career orientation	2021
Managing your scientific network	2021
The final touch: writing the general introduction and discussion	2022
Societal Relevance	
“Evolutie van vogelzang”	2019
Oude School Leiden, 12 July 2019, oral presentation for layman audience	
“Evolutie van vogelzang”	2020
Café de Keyzer Leiden, 25 January 2020, oral presentation for layman audience	
“Zebravink houdt van de woestijn”	2021
NPO Radio 2 Vroege Vogels, 21 November 2021, interview for layman audience	
Presentation Skills (4 ECTS)	
“Song amplitude of wild zebra finches”	2019
Animal Behaviour Group Leiden colloquia, IBL, 13 June 2019, oral presentation	
“Zebra finch song is a very short range signal in the wild”	2020
NVG annual meeting, online, 25 November 2020, poster	
“The communication distance and singing ecology of the wild zebra finch”	2021
WIAS Annual Conference, online, 28 April 2021, oral presentation	

"The short range of wild zebra finch song and its ecological implications" NVG annual meeting, Egmond aan Zee, 26 November 2021, oral presentation	2021
"The social context of zebra finch song in the wild" WIAS Annual Conference, Lunteren, 11 February 2022, oral presentation	2022
"The role of soft and social singing by zebra finches in the wild" European Conference on Behavioural Biology 2022, Groningen, 22 July 2022, oral presentation	2022
"Singing by zebra finches in the wild: soft, social and non-competitive" International Society for Behavioural Ecology conference 2022, Stockholm, 30 July 2022, oral presentation	2022

Teaching competences (6.0 ECTS)

Supervising Animal Behaviour course practicals and supervising Behavioural Ecology course student groups	2018-2022
Reviewing three Research Master Cluster proposals	2019,2022
Supervision of 4 MSc students	2018-2022
Supervision of 5 BSc students	2019-2021

Education and Training Total: 30.8 ECTS[1]

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[1] *One ECTS credit equals a studyload of approximately 28 hours*

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