Social information use in an unpredictable environment – a case study on wild zebra finches

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SUMMARY

The use of social information in habitat choice has often been studied in species breeding in temperate environments which underlie a relatively stable periodicity. In these highly seasonal habitats, it is a common strategy for birds, but also many species from other taxa, to prospect for high quality breeding sites, before commencing a reproductive attempt. That means that individuals visit many nests of conspecifics, or sometimes even nests of heterospecifics, and use their reproductive success as a predictor for the quality of this habitat in the future, which can enhance their fitness. This, however, requires that the quality of the habitat remains stable until the next reproductive period, which in breeders of the Northern hemisphere means the following year. If environmental conditions change meanwhile, as it can be expected in a highly fluctuating and unpredictable habitat, the predictions regarding the habitat quality might not hold true, and the social information can thus be regarded as unreliable.

Zebra finches are an iconic model species for laboratory studies, but naturally occur in the highly unpredictable arid zone of Australia. They are granivorous and highly monogamous passerines which aggregate in colonies for breeding. Their reproduction follows an opportunistic strategy, meaning that breeding can occur any time of the year when conditions allow for it, and reproductive bouts can last over extended periods. Thus, multiple successive broods might be possible in the same breeding period, depending on environmental conditions. This creates the possibility that social information can be acquired by nest prospecting at different times, because the reproduction across the population is asynchronous, which will reduce the trade-off between information acquisition and reproduction. Further, the information could be used for a breeding attempt in the near future, which could make social information advantageous, even in this highly fluctuating habitat.

The aim of my thesis was to investigate whether and how social information use can be a successful and adaptive strategy in an unpredictable habitat. I performed a series of field experiment and correlational studies on a wild population of zebra finches in the Australian outback and used an electronic monitoring system (based on RFID technology) at nest boxes to monitor the prospecting activity in two consecutive years.

I described the general patterns of nest prospecting and demonstrated that prospecting activity can be very high in certain ecological conditions, but that there is also a lot of condition-dependent variation. This suggests that prospecting behaviour might be a more dynamic and flexible process, than we know from birds in the Northern hemisphere. I further showed, that nests are not visited at random times, but peaks occur shortly before fledging and in the first days of a newly established nest. Additionally, my results suggested that particularly successful nests with large broods are targeted. The mechanism underpinning this selective nest prospecting constituted the research question of another experiment in which I presented different visual and acoustic cues to prospectors, to test which cues lead to increased prospecting activity. My findings revealed that prospectors were attracted by the begging calls of nestlings of large broods.

To investigate the ultimate cause of prospecting at nests at late stages and, particularly those with successful broods, I tested a hypothesis which has received a lot of support from

studies on species breeding in the Northern hemisphere, i.e. whether nest prospecting is used for the assessment of the quality of a patch. To put this hypothesis to a test, I conducted a brood manipulation experiment, creating patches of perceived low and high reproductive success. However, my results indicated that social information garnered from nest prospecting was not used for nest site choice and clutch size determination, as it is known from many bird species in temperate habitats. It is possible that zebra finches rely more strongly on a personal assessment of the environment for these reproductive decisions.

Another new discovery I made when examining the timing of prospecting visits was that nests at early stages, i.e. during nest building and egg laying, were visited frequently. This non-random behaviour indicates that the nests at this stage might be of high informational value. I hypothesized that information garnered from nests at this stage could be involved in reproductive timing. To investigate this hypothesis, I conducted an experiment examining mechanisms of reproductive synchronization. My results revealed that breeding pairs preferentially bred close to other pairs at the same breeding stage. To breed synchronously with other individuals in the vicinity can bring great fitness advantages by reducing predation risk and providing opportunities for group foraging. Breeding synchrony should require a high level of social coordination, which could be facilitated by transferring social information via nest prospecting. Thus, I further explored the role of sociality between synchronous breeding pairs, by conducting a social network analysis. My results demonstrated that synchronous breeders also had strong social ties in another context, i.e. they also foraged together significantly more often than expected by chance. These social ties were maintained over a long period without breeding activity, and into the next season. We currently know little about the role of stable social ties in colonial breeders, but my results, together with the findings of other recent studies, suggest that social ties might be involved in various behavioural contexts, supposedly also in social information transfer, and might be strongly interconnected across contexts.

Overall, the results of my field studies on wild zebra finches provide various new insights into the role of social information use in unpredictable habitats. I have demonstrated for the first time that high levels of prospecting activity can occur, even in fluctuating conditions and that similarities, but also differences exist to social information use in highly seasonal habitats. The role of social information in unpredictable environments might be even more complex and dynamic than previously assumed and could involve several potentially fitness enhancing mechanisms. Zebra finches are highly adapted to the harsh environment of the arid zone, and only well adapted behavioural mechanisms can explain their success and widespread occurrence across the Australian continent. The results in this thesis will hopefully facilitate and encourage more research on information use in this important model species, but also comparative studies are needed to explore the evolutionary background of information use in unpredictable habitats.

ZUSAMMENFASSUNG

Die Umwelt verändert sich ständig. Alle Lebewesen müssen daher laufend Informationen sammeln um ihr Verhalten optimal an die derzeitigen Umweltbedingungen anzupassen. Wir können allgemein zwischen zwei Typen von Informationen unterscheiden: persönliche Information, die von jedem Individuum selbst durch direkte Interaktion mit der Umwelt gesammelt wird; und soziale Information, also das Kopieren und Lernen von anderen, die ähnliche Bedürfnisse haben. Bei sozialen Informationen kann es sich um Signale, Verhaltensweisen oder auch den Erfolg von anderen handeln. Während das Sammeln persönlicher Information oft aufwendiger und kostspieliger ist, kann sich soziale Information in Populationen teils sehr einfach und schnell verbreiten – hier besteht aber die Gefahr, dass die Information nicht verlässlich ist.

Die Wahl eines geeigneten Brutgebietes ist von essentieller Bedeutung mit weitreichenden Konsequenzen für die evolutionäre Fitness der Organismen. Ein Weg um soziale Information über die Qualität eines potentiellen Brutgebietes zu erlangen, ist es mögliche Brutplätze vorab zu „prospektieren". Prospektieren bedeutet Nester von Artgenossen zu besuchen, um ihren Bruterfolg abzuschätzen und davon Rückschlüsse auf die Qualität des potentiellen Brutgebietes zu ziehen. So kann diese Strategie dabei helfen einen qualitativ hochwertigen Standort zu identifizieren und die eigene Fitness zu steigern. Diese Strategie ist vor allem in den stark saisonalen Habitaten der nördlichen Hemisphäre gut erforscht, wurde aber in anderen Ökosystemen kaum überprüft. Theoretische Modelle sagen allerdings vorher, dass derartige Strategien nicht erfolgreich sein sollten, wenn die Umweltbedingungen starken, unregelmäßigen Schwankungen unterliegen.

Zebrafinken (*Taenopygia guttata*) leben in den ariden Zonen des australischen Kontinents, die durch stark schwankende und vor allem unvorhersagbare Bedingungen geprägt sind. Als Anpassung an diese Bedingungen verfolgen Zebrafinken die Strategie des opportunistischen Brütens. Das heißt, dass ihre Reproduktion nicht saisonal gebunden ist, sondern zu jeder Zeit stattfinden kann, sobald günstige Umweltbedingungen dies ermöglichen. Zebrafinken sind monogame und soziale Singvögel und leben in Kolonien, in denen man sie oft dabei beobachten kann wie sie Nester ihrer Artgenossen inspizieren, vermutlich um dort nach sozialen Informationen zu prospektieren. Dieses Verhalten in einer Art zu beobachten deren Lebensraum von derart starken Schwankungen geprägt ist, scheint unerwartet, da soziale Information schnell nicht mehr aktuell ist, wenn die Umweltbedingungen stark schwanken.

Ziel meiner Feldstudien war es daher, zu erforschen wie soziale Information auch in sehr unberechenbaren Umweltbedingungen eine erfolgreiche Strategie darstellen kann. Ich habe dazu eine Population von Zebrafinken im australischen Outback über zwei Jahre beobachtet und mit einem elektronischen Überwachungssystem (RFID) die Besuche von Zebrafinken an den Nestern ihrer Artgenossen automatisch aufgezeichnet. In meiner Arbeit habe ich die zeitlichen Muster beschrieben, wann Zebrafinken Besuche an den Nestern anderer Individuen vermehrt durchführen. Daraus konnte ich Rückschlüsse ziehen und Hypothesen aufstellen, welchen adaptiven Nutzen die Information, die sie durch die Nestbesuche gewinnen können, für sie haben könnte. Ich konnte zeigen, dass Nester nicht zufällig, sondern besonders in frühen und späten

Stadien besucht werden und auch, dass Nester mit großem Reproduktionserfolg eher prospektierende Individuen anlocken als solche mit kleinen Bruten.

Auf diesen Erkenntnissen basierend, führte ich ein Experiment durch, dass einen möglichen zugrundeliegenden Mechanismus dieser selektiven Nestbesuche testete; also welche Hinweise prospektierende Individuen nutzen, um bestimmten Nester gezielt zu besuchen. Meine Ergebnisse zeigten, dass die Bettelrufe von Nestlingen großer Bruten prospektierende Individuen anlocken. Große Bruten sprechen für einen hohen Reproduktionserfolg und könnten daher eine besonders relevante Informationsquelle darstellen, wenn nach einem hochwertigen Brutplatz gesucht wird. Diese Hypothese, ob auch Zebrafinken in ihrem stark schwankenden Habitat, das Prospektieren an Nestern dazu nutzen, um zu entscheiden welche Gebiete qualitativ hochwertig und für die eigene Brut zu bevorzugen sind, habe ich in einem Brutmanipulationsversuch überprüft. Hierzu habe ich die Bruten aller Nester in einigen Gebieten reduziert und in den anderen vergrößert um die wahrgenommene Qualität der Gebiete zu verändern. Mein Ergebnis zeigte, dass Zebrafinken die soziale Information offenbar nicht für ihre Reproduktion genützt haben. Vermutlich verlassen sie sich bei Entscheidungen über das Brutgebiet stärker auf ihre persönliche Evaluation des Habitats, die hier verlässlicher sein könnte.

Eine weitere Beobachtung während meiner Studien war, dass auch Nester im Anfangsstadium oft prospektiert werden, was der sozialen Brutsynchronisation dienen könnte. Mit einem Versuch konnte ich zeigen, dass Zebrafinken bevorzugt nahe an einem Nest von Artgenossen brüten, welches sich im gleichen Stadium befindet. Vermutlich dient dieses Verhalten dazu die Fortpflanzung zu synchronisieren, was viele Fitnessvorteile bringen könnte, wie zum Beispiel bessere Feinvermeidung und gemeinsame Futtersuche. Es ist denkbar, dass das Nestprospektieren mit dieser gezielten Synchronisation zusammenhängt, sie so also Individuen in einem ähnlichen Brutstadium ausfindig machen können. Um der Rolle von Sozialität im Zusammenhang des synchronisierten Brütens weiter nachzugehen, führte ich eine soziale Netzwerkanalyse durch. Dadurch konnte ich zeigen, dass synchron brütende Paare auch in anderem Kontext häufiger zusammen anzutreffen sind. Genauer gesagt waren Paare, die miteinander synchronisiert brüten, auch signifikant häufiger gemeinsam an Futterstellen, als durch Zufall zu erwarten wäre. Das war nicht nur der Fall während einer aktiven Brutsaison, sondern auch noch mehr als acht Monate später, nach einer langen Phase ohne Reproduktion. Diese stabilen sozialen Verbindungen zeigen, dass komplexe Mechanismen in die Brutsynchronisation, und vermutlich allgemein, in den Informationstransfer, involviert sind.

Zusammenfassend konnte ich zeigen, dass soziale Information mit gewissen Anpassungen auch in Gebieten mit unvorhersehbar schwankenden Umweltbedingungen als erfolgreiche Strategie sehr wahrscheinlich ist. Für Zebrafinken könnte das Prospektieren in mehreren Aspekten adaptive Vorteile bringen. Die hier vorgestellte Arbeit zeigt völlig neue Aspekte über den Nutzen sozialer Information in Gebieten, die keiner starren Saisonalität folgen, auf, stellt neue Hypothesen vor, und bereitet den Weg für gezielte, weiterführende Forschung in diesem Bereich. Speziell für Zebrafinken als häufige Labortiere sind solche Erkenntnisse in ihrem ökologischen Kontexts hoch relevant, aber auch vergleichende Studien mit anderen Tieren in fluktuierenden Lebensräumen wären wichtig um den evolutionären Hintergrund der Verhaltensanpassungen besser zu verstehen.

GENERAL INTRODUCTION

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Information use in unpredictable environments

The environment is characterized by constant change and uncertainty. Unless we are putting animals in rigorously controlled laboratory conditions, the parameters of their environment are always underlying fluctuations. This means that gathering information to reduce uncertainty is a continuous effort. Gaining access to information on the variables defining the environment is the only way to reduce uncertainty. Further, being well-informed about environmental parameters is the basis for developing and adjusting behavioural strategies. Thus, information use is a key element in the study of adaptive behaviour (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). The available information, including the knowledge of alternatives, will considerably affect decision making and ultimately the fitness of animals (Dall et al., 2005; Danchin, Giraldeau, Valone, & Wagner, 2004).

Often, a variety of sources and strategies are available to acquire information, each entailing their own set of costs and consequences. We can broadly distinguish between two main strategies. One option is to directly interact with the environment, i.e. gathering personal information by trial-and-error (Valone, 1989). This approach requires the individual to invest time and energy and will consequently reduce the time available for other activities. An alternative strategy is to use social information, that is, information acquired from other individuals with similar requirements, by exploiting cues, signals or the performance of these individuals (Danchin, Giraldeau, & Cézilly, 2008; Danchin et al., 2004).

The term 'public information' is sometimes used to specifically describe the copying of the performance of conspecifics (e.g. reproductive success), thus referring only to inadvertently produced social information (Danchin et al., 2004). However, different researchers have provided varying definitions of this term (Wagner & Danchin, 2010). Consequently, throughout this thesis, I mostly avoid this ambiguous term and instead use the term social information, as defined above, comprising all forms and including public information.

No matter which pathway is used to acquire information, it is always a trade-off between costs and benefits. Personal information might provide a highly reliable reflection of environmental parameters, such as food availability in a patch, but collecting it individually might result in exposure to predators or a missed mating opportunity (Kendal, Coolen, van Bergen, & Laland, 2005). Social information can spread fast in populations and can often be easy to obtain, by, for example, simply following a group to a rewarding food source. However, only some individuals will hold reliable information themselves, and copying blindly from others can lead to informational cascades (Bikhchandani, Hirshleifer, & Welch, 1992), in the worst case, an erroneous cascade with negative consequences for the population (Beauchamp, Belisle, & Giraldeau, 1997; Dall et al., 2005).

Whether social information is used or not will depend on multiple factors, including the species (Coolen, Bergen, Day, & Laland, 2003), the availability of social information (Coolen, Ward, & Laland, 2005), the cost of obtaining it (Boyd & Richerson, 1988; Webster & Laland, 2008), and the stability of the environment (Doligez, Cadet, Danchin, & Boulinier, 2003;

Feldman, Aoki, & Kumm, 1996; Rafacz & Templeton, 2003). If an environment fluctuates unpredictably, copying other individuals might be unreliable, as the information can rapidly become outdated (e.g. Erwin, Nichols, Eyler, Stotts, & Truitt, 1998; Feldman et al., 1996).

It is a common strategy, particularly in a high number of bird species (Reed, Boulinier, Danchin, & Oring, 1999), to use the reproductive success of conspecifics as social information on the quality of a breeding site. This form of social information can be easily garnered from the nests of conspecifics by visiting and inspecting them, known as nest prospecting. Nest prospecting for habitat choice has been well explored and experimentally tested in a large number of species breeding in relatively predictable temperate environments, following a stark periodicity, leading to well defined breeding seasons (e.g. Danchin, Boulinier, & Massot, 1998; Doligez, Danchin, & Clobert, 2002; Parejo, White, Clobert, Dreiss, & Danchin, 2007).

It is, however, postulated that nest prospecting can only be a successful strategy for predicting habitat quality, if this remains stable across time (Boulinier, Danchin, Monnat, Doutrelant, & Cadiou, 1996; Doligez et al., 2003), which is unlikely in unpredictable habitats. If one individual applies a strategy, such as breeding in a certain area with high reproductive investment, it might result in high reproductive output, because the food availability was high and predation was low at that time. Another individual observing this successful reproductive attempt through nest prospecting, might now be inclined to copy this behaviour by also investing in a large brood in the same location. However, if the conditions have meanwhile changed for the worse, the latter individual, which has relied on the social information, might now not be able to feed the large number of offspring it had invested in, with considerable negative fitness consequences. However, social information use in unpredictable habitats has rarely been experimentally investigated in the wild. The low numbers of studies examining information use in unstable environments are mostly theoretical (e.g. Boyd & Richerson, 1988; Feldman et al., 1996) and thus, this represents a considerable gap in the study of information use.

While all predictions argue against social information use and, in particular, nest prospecting as successful strategies in unpredictable habitats, it is highly unlikely that social information is simply not used in such environments. Many gregarious species inhabit the arid zone of Australia and not garnering social information from each other would seem like a wasted opportunity for potentially adaptive behaviour. Instead, strategies of social information use might simply be different to the strategies known from highly seasonal habitats and adapted to the unpredictably fluctuating conditions, by, for example, using social cues on a shorter time-scale, where conditions are less likely to have changed in between.

Study species

Zebra finches are small, colonially breeding passerines, which have been coined "the ultimate Australian supermodel" (Griffith & Buchanan, 2010), due to their tremendous importance as a model species for most zoological disciplines, including physiology, neurology and ethology. A combination of interesting traits, such as their social behaviour and their simple and stereotyped song (Mello, 2014), and the ease of with which they can be bred in captivity has led to the

majority of zebra finch research being conducted in the laboratory. The fact that researching them in the Australian outback is challenging, and the unpredictable conditions affect birds and researchers alike, has additionally contributed to the lower number of field studies in this species. Nevertheless, to fully understand the ecology of this small, opportunistic passerine, and its adaptions to surviving in this harsh habitat, researching it in the field is inevitable.

The Australian arid zone, the natural habitat of zebra finches (*Taeniopygia guttata*), is characterized by highly unpredictable rainfalls, that vary in scale and timing, and in consequence, lead to unpredictable primary productivity (Fig. 1a; Morton et al., 2011). Unpredictable conditions favour species with an opportunistic life-history, which can be seen as adaptive strategy to cope with the uncertainty of the environment (Hau, Wikelski, Gwinner, & Gwinner, 2004; Morton et al., 2011; Sergio et al., 2011). Breeding opportunistically means to reproduce whenever conditions are favourable, which can occur at any month of the year and last over extended periods (Duursma, Gallagher, & Griffith, 2017). Opportunistic breeding is a great example of an adaptive strategy to unpredictable conditions and it can be assumed that other behavioural adaptions are used by the organisms surviving and thriving in the harsh conditions of the arid zone. In the wild, zebra finches are socially and genetically monogamous (Griffith, Holleley, Mariette, Pryke, & Svedin, 2010) and have a strong pair bond.

Phylogenetically, zebra finches belong to the family of Estrildidae, which consists of approximately 141 species, distributed across Asia, Africa, and Australia (Payne & Bonan, 2018). Within the Australian grassfinches, the zebra finch represents the species with the largest distribution range in Australia, covering 75% of mainland Australia, omitting only more humid regions (Zann, 1996). Often, zebra finches are further split into two subspecies: *Taeniopygia guttata castanotis* (Gould, 1837), inhabiting continental Australia, and *Taeniopygia guttata guttata* (Vieillot, 1817), which is also referred to as the Timor zebra finch (Payne, 2018) or the Lesser Sundas zebra finch (Zann, 1996), referencing its main area of distribution. Throughout the thesis, I am solely referring to the former variant, *Taeniopygia guttata castanotis*, hereafter only referred to as *Taeniopygia guttata*, or zebra finch.

Zebra finches are often referred to as being nomadic, suggesting that they are in a constant state of movement and travel great distances across the Australian continent. However, since the available technology, to date, does not allow tracking such a small bird over long distances, we currently have no evidence supporting this hypothesis. The longest ever verified travel of a zebra finch was over a distance of 168 km, revealed through a band recovery in Western Australia, while the mean recovery distance is only 2 km (Forshaw & Shephard, 2012). Also movements between colonies of just few kilometres apart are rarely observed, and based on our current knowledge, zebra finches should rather be described as predominantly sedentary, with occasional excursions to other areas, and perhaps the potential to move away in longer periods of drought (Forshaw & Shephard, 2012; Zann, 1996). On the other hand, we also have to acknowledge that the chances of a successful recapture or band recovery in the vast and thinly populated area of inland Australia are presumably slim. Overall, there are still many aspects in the ecology of zebra finches which deserve a more thorough investigation.

Figure 1. The Australian arid zone is characterized by erratic rain falls which control the primary productivity and shape the landscape which represents the natural habitat of zebra finches (a). Zebra finches are gregarious and breed, forage and drink in often large groups; (b) shows a large flock of zebra finches aggregating on a tree close to a water source. A female (left) and male (right) zebra finch are visiting a nest box (c).

Study aims

Zebra finches are highly social and gregarious birds (Fig. 1b), living in a highly unpredictable environment. They can be frequently observed prospecting on the nests of conspecifics (Fig. 1c), presumably to acquire social information (Brandl, Griffith, & Schuett, 2018; Mariette & Griffith, 2012a). Nevertheless, the adaptive value of nest prospecting in unpredictable habitats is unclear and widely unexplored. Thus, zebra finches make a highly suited and interesting study species to explore the pattern and purpose of social information use in the context of the unpredictable environment they inhabit.

In this thesis, I present a series of experiments and correlational studies, investigating social information use in a population of zebra finches in the wild. I particularly focus on nest prospecting behaviour as a potential vector of social information, which can be well monitored with RFID (radio-frequency identification) decoders. The work I present here aims to bridge some of the vast gaps in the understanding of information use in unpredictable environments.

In Chapter 1 of this thesis, I characterize the temporal and spatial patterns of nest prospecting in wild zebra finches. In order to gain insight on the informational value of the visits made to nests of conspecifics, we need to understand when and where they occur. I use an electronic monitoring system to record prospecting visits of RFID-tagged zebra finches. I test the effect of nest stage and brood size on prospecting behaviour and compare data from two consecutive years, which were ecologically very different, to explore the range of behavioural flexibility.

Building on the insights from Chapter 1, where I describe that prospecting peaks occur at very early and late nest stages, I experimentally investigate the proximate mechanism, which can lead to the observed behavioural patterns in Chapter 2. I use an acoustic playback and visual signals to represent nests at different stages and with different reproductive output, to explore which cues might lead prospecting zebra finches to the respective nests.

To gain insight into the adaptive value of nest prospecting in an unpredictable habitat, I explore two hypotheses, outlined in the Chapters 3 and 4. The first hypothesis I explore, in Chapter 3, states that nest prospecting is used to assess the habitat quality and aids in the choice of a nest site, which is the common theory to explain prospecting in species breeding in temperate, seasonal habitats. I use an experimental design, to test if zebra finches use social information garnered from conspecifics' nests in the same manner as the temperate breeders, regarding the quality of the information. I manipulate clutch and brood sizes in a wild breeding population of zebra finches thus, creating patches of seemingly varying quality. If the birds use social information from the conspecific reproductive success to assess the patch quality, I expect them to adjust the nest site and the reproductive investment in the subsequent brood.

Another hypothesis postulates that social information can be involved in the timing of reproduction. Thus, in Chapter 4, I explore the mechanism of reproductive synchronisation in zebra finch colonies. I conduct a field experiment to test if breeding pairs preferentially initiate nests adjacent to neighbours at a similar stage. If this is the case, it suggests that the synchronised breeding might give them a fitness advantage. Further, the synchronisation of reproduction

between colony members requires a high level of social coordination. It is thus likely that social information is involved in this process, possibly acquired by nest prospecting. This hypothesis is further strengthened by the finding that prospectors frequently visit newly initiated nests, during the first days (Chapter 1).

Based on the insights into reproductive synchronisation (Chapter 4), and the hypothesis that social information could be strongly involved in the underlying mechanism, I investigate social ties between synchronised breeding pairs in Chapter 5. I apply social network analysis to test if dyads of breeding pairs within a colony, have stronger social co-foraging ties if they are breeding synchronously, than it could be expected by chance. I further explore if the social ties between individuals which are not paired with each other persist over two breeding periods, separated by a long period of reproductive inactivity. If synchronously breeding pairs have strong social ties across behavioural contexts, and maintain the social ties across years, it implies that, even in a highly opportunistic species, these relationships are of high importance and might provide multiple advantages. Further, it could suggest, that the social structure of a breeding population might be strongly linked to reproductive synchronisation and the transfer of social information.

CHAPTER 1

Nest prospecting in an opportunistic breeder – acquiring social information on reproduction in an unpredictable habitat

ABSTRACT

Prospecting at the nests of conspecifics to predict the habitat quality of a potential breeding site in the following year is well established in species breeding in seasonal temperate climates. By contrast, there has been little work in this area in more unpredictable and aseasonal environments. Zebra finches (*Taeniopygia guttata*) are opportunistic breeders adapted for life in the Australian arid zone where rainfall, and therefore primary productivity, is highly unpredictable and the autocorrelation in habitat quality over time is likely to be significantly lower. However, conditions will frequently permit extended periods of breeding where individuals will have multiple consecutive broods and the level of reproductive activity across a population is relatively asynchronous. Information can therefore be gleaned from conspecifics breeding locally, and the time between information acquisition and application can be much shorter, than in the across season information use known from seasonal breeders in the northern hemisphere. We used an automated PIT-tag detection system in the field to characterise prospecting visits of over 200 wild zebra finches at their conspecifics' nests over two months in each of two consecutive years. During 200 breeding attempts we recorded more than 10,000 visits by adult prospectors. Patterns of prospecting varied considerably between the two study years, when considered from a focal nest perspective. Predictions based on the behaviour of European breeding birds were only supported in the first study year: large broods were preferentially visited, and especially in the late stage of chick rearing, which presumably provides the most reliable information. Overall, information use in unpredictable habitats is likely to be more complex than that previously observed in other ecological contexts, such as the seasonal breeders of the northern hemisphere, and indeed, could be even more prevalent and important as a source of reliable information to guide reproductive investment.

INTRODUCTION

The quality of a foraging (e.g. Brambilla et al., 2017; Franco & Sutherland, 2004) and breeding site (e.g. Boulinier & Lemel, 1996; Chalfoun & Schmidt, 2012; Tremblay, Thomas, Blondel, Perret, & Lambrechts, 2005) has important consequences to an animal's fitness. Particularly in animals that have a high level of mobility, such as birds, individuals often explore a range of opportunities before settling in a good location for breeding (e.g. Reed et al., 1999). Once they have settled in an area, individuals also face decisions in optimising the timing and level of investment in breeding in relation to the resources locally available.

Nest prospecting behaviour, whereby individuals inspect the breeding sites and reproductive attempts of conspecifics, has been described in many taxa (and isopods: Baker & Steven, 2004; meerkats: Doolan & Macdonald, 1996; e.g. in lizards: Stamps, 1987) and especially in numerous bird species (e.g. Parejo, Pérez-Contreras, Navarro, Soler, & Avilés, 2008; Schuett, Laaksonen, & Laaksonen, 2012; Ward, 2005). Many studies have provided evidence that social information is acquired through visits at conspecifics' (or even heterospecifics'; e.g. Forsman & Thomson, 2008; Jaakkonen, Kivelä, Meier, & Forsman, 2014) nest sites, and that these social cues can be used in subsequent settlement and reproductive decisions (e.g. Boulinier, McCoy, Yoccoz, Gasparini, & Tveraa, 2008; Pärt, Arlt, Doligez, Low, & Qvarnström, 2011).

Prospecting is a form of social information gathering (often referred to as public information, as it is specifically based on the performance of others; Danchin et al., 2004; Valone, 1989) and as such can provide fast and reliable information (e.g. Valone, 2007; Valone & Templeton, 2002). The original hypothesis states that, if a temporal autocorrelation in patch quality exists, prospecting can help individuals to make predictions about the quality of a breeding site in the future. Theoretical models predict that in this scenario individuals selecting nest sites based on public information should have an increased lifetime reproductive success (Boulinier & Danchin, 1997). In support of this theory, there is evidence from experimental studies in several species breeding in Europe showing that social information acquired by prospectors is used in the subsequent breeding site selection. In collared flycatchers (*Ficedulla albicollis*), the number of fledglings a patch produces in a year predicts the recruitment of new breeders in the following year, and the level of emigration out of an area (Doligez et al., 2002); blue tits (*Cyanistes caeruleus*) use offspring quality or quantity of conspecifics when deciding on a new breeding site in a subsequent year (Parejo et al., 2007); and finally in the colonial breeding lesser kestrel (*Falco naumanni*) fledgling quantity of successful nests predicted adult immigration into patches for the following year (Aparicio, Bonal, & Muñoz, 2007). In regards to the timing of prospecting it was discovered that nests are prospected with higher frequency during the late stages of the chick rearing period as most reliable information on reproductive success can be gleaned at this time point (e.g. Boulinier et al., 1996; Parejo et al., 2008), and active nests may be easier to locate because of the nestling begging calls. Further, a positive

association between brood size and prospecting level has been described in several species (Schuett, Järvistö, Calhim, Velmala, & Laaksonen, 2017; Zicus & Hennes, 1989); presumably because individuals looking for patches of high reproductive output invest more into prospecting visits at nests with large broods.

Only a few studies have investigated prospecting and habitat selection in species breeding in unpredictable and fluctuating environments. The mostly theoretical work on information use in unpredictable habitats is usually focused on the lack of temporal autocorrelation in patch quality and, under this premise, views social information as unreliable (Doligez et al., 2003; Erwin et al., 1998) and suggests random settling as a superior strategy (Boulinier & Danchin, 1997). As a result of this theoretical work we would therefore not anticipate high levels of nest prospecting in unpredictable habitats. The existing framework on information use in fluctuating habitats, however, usually fails to take into account the specific adaptions of animals living in such habitats, which can involve a generally more dynamic life-history strategy (Shine & Brown, 2008) and a range of adaptions to reproduction, such as opportunistic breeding, which can result in extended bouts of reproduction that permit multiple sequential reproductive attempts in a location (Duursma et al., 2017; Perfito, Zann, Bentley, & Hau, 2007; Sossinka, 1980). In species with such a flexible breeding ecology it can be expected that there is a poor correlation between the conditions at any given time and the conditions a year later. However, bouts of continuous reproduction within a population can last for more than twice as long as those in more phenologically constrained

locations, such as the temperate region of northern Europe (Duursma et al., 2017). Therefore, information that can be garnered from nest prospecting may be informative about the current state of a patch of suitable habitat and applied to more immediate reproductive decisions than those typically observed in temperate climates (e.g. Doligez, Pärt, & Danchin, 2004; Ward, 2005).

Perhaps the most classically studied and opportunistically breeding species is the zebra finch (*Taeniopygia guttata*), which lives in the unpredictable arid zone of Australia, where primary productivity is largely driven by temporally and spatially erratic rainfall (Morton et al., 2011; Zann, 1996). We therefore aimed to investigate the patterns of prospecting behaviour in this species to characterise nest prospecting for the first time in an opportunistic and highly flexible breeder in an environment that is markedly less predictable, temporally, than the northern temperate habitat in which most work on nest prospecting has been conducted. We used an automated Passive Integrated Transponder (PIT)-tag detection system to monitor prospecting behaviour and breeding activity of a wild zebra finch population across two consecutive years, and for two months in each year. We took a nest-centric perspective and investigated (i) the temporal aspect of prospecting (i.e. at what stages are nests of conspecifics prospected on) and (ii) whether the level of prospecting activity at a nest is related to its reproductive success.

METHODS

Study site and study species

Zebra finches are granivorous passerines living in the arid and semi-arid zones of Australia. They are socially (Zann, 1996) and genetically (Griffith, Holleley, Mariette, Pryke, & Svedin, 2010) monogamous, with bi-parental brood care (Mariette & Griffith, 2012b). Zebra finches are opportunistic breeders; i.e. their reproduction is largely aseasonal with multiple successive broods if conditions are favourable (Zann, 1996). Furthermore, the reproductive investment in each breeding opportunity should be optimised with respect to local conditions that vary considerably within and across seasons, and clutch size varies between two and eight eggs (Griffith, Pryke, & Mariette, 2008). Zebra finches can move over large distances in search of favourable conditions and the distribution of food and water in the landscape determines their nest site choices on a larger scale (max. observed nest distance from water 25 km; Zann, 1996). Zebra finches often breed in loose colonies which are formed by conspecific attraction (Mariette & Griffith, 2012a).

Our study was conducted at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05'13.1"S 141°42'17.4"E), New South Wales, Australia, over two consecutive years (2015 and 2016), between August and December. The study site (about 1.5 x 2 km in area) has a dam in the centre which provided permanent drinking water throughout the duration of this study. In the surrounding area, wooden nest boxes attached to metal stakes were provided; in this study we focused on the colonial nest boxes arranged in six clusters of ca. 30 nest boxes each: 180 boxes in 2015; 174 boxes in 2016.

Nest box and bird monitoring

All reproductive activity in the area was monitored between August 1st and December 20th in both years. Nest boxes were routinely inspected every four days to monitor nest building and egg laying and then daily around the calculated approximate hatch date to determine the actual hatch date. Zebra finches lay one egg per day (Zann, 1996) and clutches were considered complete when no new egg was added within a 24-hour period. Upon hatching we counted the number of chicks on day 3, day 7 and day 11 (day 0 as hatch date). We did not check nest boxes after day 11 to avoid the risk of premature fledging and assumed that they had fledged if the nest box was empty on day 20.

In 2015, clutch and brood size manipulations were conducted between August 28th and November 15th. All the clutches laid in the nest boxes in this period were adjusted to either three eggs (in three of the nest box clusters) or to seven eggs (in the remaining three clusters); for details on the manipulation see Brandl et al. (2018). In 2015 we also provided supplementary food (dry seed mix) in feeding stations as part of other work (for further details on feeders see: Brandl et al., 2018; Mariette et al., 2011a).

Capturing and tagging of birds

Between nestling day 6 and 11, adults were caught in the nest boxes using nest box traps. Only one parent was caught at each nest box

per day to minimize stress and the risk of nest abandonment. In 2015 we successfully trapped 399 adults (190 females, 209 males), in 2016 we trapped 230 unmarked adults (116 females, 114 males) at nest boxes (in addition to many previously marked and tagged birds that were recaptured). All captured adults were banded with a uniquely numbered metal band (Australian Bird and Bat Banding Scheme) and subcutaneously injected (Ratnayake et al. 2014) with PIT-tags (Minichip; Micro Products Australia, Perth, Australia). Breeders were identified by catching them in their respective nest boxes and additionally parenthood was confirmed through high regular visitation rate at nest boxes in the decoder data obtained at nest boxes (see below: Automated monitoring of prospecting activity). Previously tagged parents on a subsequent breeding attempt were often identified in this manner without having to recapture them. In addition to the capture of adults in nest boxes, 142 adults (98 males, 44 females) were caught and PIT-tagged at feeder cages with walk-in-traps in 2015, as part of other experiments (Hardenbicker et al., unpublished).

Automated monitoring of prospecting activity

In 2015 and 2016 the nest boxes of two nest box clusters (i.e. two groups of 30 boxes in 2015, two groups of 27 boxes in 2016) were equipped with RFID decoders (RFIDRW-E-232; Priority 1 Design, Melbourne, Australia). In 2015 the decoders were put up in the areas 'A' and 'F', in 2016 areas 'A' and 'E' were used, because birds were not breeding in area 'F' in that year. In 2015, the RFID decoders were gradually added to nest

boxes as they became active starting on September 20th. All nest boxes in the respective areas (2015: 60 boxes; 2016: 54 boxes) had decoders installed for 56 days in 2015 (between October 10th and December 5th; 22,768 hours of decoder runtime). In 2016, decoders were installed at the boxes over the course of two days and were active for 46 days in 2016 (between October 13th and November 28th; 36,412 hours of decoder runtime). Decoders were connected to antenna coils superglued behind the entrance from the inside of the nest boxes, which could detect birds with PIT-tags when in proximity of about 4 cm. The decoders registered a PIT-tag only once when in the range of the antenna and again once it left and re-entered the range. Batteries of the RFID decoders were changed every four days. At these instances, functionality of the decoders was also tested, and data were downloaded.

Data analysis

Data of the two study years were analysed separately in all analyses throughout, because due to the unpredictability of the environment strong ecological variation can be expected. We could not distinguish between the start and end of a visit at a nest box and therefore applied a filter to avoid a false overrepresentation of birds entering and exiting repeatedly, remaining in close vicinity of the antennas, or birds just looking inside without fully entering: visits of a bird at the same box were only counted if they were minimum 30s apart from the last (Schuett et al., 2017).

The breeding status of nest boxes ('box status') was encoded on a numerical scale,

with zero being the hatch day and subtracting 1 for each day prior to hatching and adding 1 for each day after hatching. Incubation would therefore usually start around day -12, with the days before that being used for egg laying (one egg per day multiplied by the clutch size) and before that nest building. Successfully fledging chicks would be in the nest from day 0 and fledge usually between day 18 and day 21. In some of the analyses, however, we were specifically interested in the difference between the 'stage' of eggs or chicks in the nests, and hence used this broader division, in which case data from the period of nest building and egg laying were not taken into account.

The variable 'brood size' changed throughout the nesting cycle to reflect the actual nest content and, depending on the stage, can hence refer to either number of eggs or number of chicks. For the data of 2015, the number of eggs laid was used from start to day 6 of incubation. At day 6 the clutch manipulation occurred (Brandl et al., 2018), and hence the manipulated clutch size (either 3 or 7 eggs) was used from day 6 of incubation until hatching. For the data of 2016, where no manipulation of clutch size took place, the natural clutch size was used from clutch completion until hatching. From day 0 (hatch day) to day 3 of chick rearing the chick count of day 3 was used, from day 3 to day 7 the chick count of day 7 was used and from day 7 until fledging the chick count of day 11 was used.

To measure the relationship between prospecting visits and breeding activity, we tested for   correlations between the two processes. We performed three separate tests to assess the level of linear dependence of

weekly prospecting rate and the weekly number of nests at one of three different stages: (1) number of nests hatching, (2) number of nests fledging (18 days after hatching), and (3) number of nests being newly initiated (calculated as 22 days before hatching, i.e. 5 days to make an egg, an average of 5 days for egg laying, plus around 12 days of incubation; Blount, Metcalfe, Arnold, Surai, & Monaghan, 2006; Zann, 1996). Thus, we conducted separate Pearson correlation tests between mean number of weekly prospecting visits per nest box and the weekly number of nests per available box at one of three different stages, respectively. This allowed us to compare the relationship between the levels of prospecting with respect to the different informational values of nests at different stages.

We fitted several generalised linear mixed effect models (GLMMs) with binomial error structure to assess the effect of stage and success of nests on prospecting rates at nest boxes, using the data of all non-parental nest visits. Models were run separately for 2015 and 2016, respectively. The binomial variable 'visit' (yes = the box had at least one prospecting visit on the respective day; no = no prospecting visit on the respective day) was used as response variable in both models for each year (see below). The counts of visits were not used, because the data were highly zero inflated. The day of visit and the nest box ID were included as random intercepts in all models; area was additionally included in 2016.

First we fitted a GLMM to test whether clutch and brood size can predict the probability of prospecting visits at nests and if this depends on the nest stage. We hence

used an interaction of brood size and stage (eggs/chicks), as well as their main effects, as fixed effects. This analysis was conducted to test if the 'brood size' (i.e. clutch size and brood size, respectively) of nests can already affect prospecting probability before hatching or, if a potential effect would only be pronounced later, during the phase of chick rearing.

To assess whether prospectors were mainly interested in empty boxes for potential breeding, another GLMM was used to test whether the probability of prospecting was different before or after a nest box became empty. The GLMM used the 'activity state' of the nest box as fixed term; we defined the following states: fledging (i.e. pre-nest vacancy, the last days before fledging), and empty box were used in both years; in 2016, nest failure (i.e. pre-nest vacancy, the last days before a nesting attempt ended without chicks fledging) and new nest (i.e. post-nest vacancy, the first days of a new nest after a box was empty) were used additionally (see below). Fledging and nest failure referred to the same period of a nest (i.e. the last days before becoming empty), but distinguished between the cause of becoming empty. In 2015, too few data points were available of nest that became vacant due to nest failure (two recording days from one nest) and of the period of new nest initiation succeeding periods where the box was empty (eight recording days from three nests); thus, we only used data from the pre-fledging period and from empty nest boxes in that year. For this analysis we only used data from nest boxes where days (at least one) both before and after becoming active or inactive were available to minimize a potential bias of time and location, and only (up to five) days

from these periods (i.e. before, during, and after box vacancy) were used. Hence, if available, we included data of two five day periods, respectively (i.e. the last five days where a box still had an active nest and the five days after that; or the last five days in which a box was still empty and the first five days with the new nest). For some nests less than five days were used, as data were available (mean number of days $\pm$ SE: 2015: fledging: 2.4 ± 0.4, empty box: 4.6 ± 0.3; 2016: fledging: 2.4 ± 0.4, empty box: 3.5 ± 0.2, nest failure: 4.5 ± 0.2, new nest: 4.3 ± 0.3). Tukey's post hoc test was performed for significant results; the p-values reported for the post hoc tests were adjusted using the *single-step* method (Westfall, Young, & Wright, 1993).

If a decoder was found not to be working, we assumed the last prior recorded data point as the final one and excluded the time period thereafter, until the decoder was fixed, from the data. The GLMMs, with box visitation encoded as a binomial variable (see above), were repeated with the data of incomplete days excluded (2015: 107 data points removed; 2016: 87 data points removed) and showed qualitatively the same results in terms of statistical significance and direction of effects (not presented). Data from incomplete recording days were divided by the actual runtime and extrapolated to 14.5 hours (estimated time of daily bird activity) for use in Figures 1.1-1.3. Data from ten nest boxes in 2015 had to be excluded from all analyses, because the decoders failed to record time and date correctly. Also, data from nests were not included where parents (and hence also the prospectors) could not be assigned with high certainty (32 nests in 2015 and 10 nests in 2016).

Full models were always reduced by stepwise removing the least significant term (Crawley, 2007). Terms were only removed if the explanatory power of the simpler model was not significantly reduced, when compared to the more complex model with likelihood ratio tests. Random effects were conservatively not removed. All statistical analyses were conducted in R (R Core Team, 2014); for GLMMs we used the package 'lme4' (Bates, Maechler, Bolker, & Walker, 2014). Results are presented as mean ± SE (standard error of the mean) and median ± IQR (interquartile range).

RESULTS

Spatial and temporal patterns of nest prospecting

In 2015, we recorded 49,734 visits by parents to their own nest box and 5,191 visits by prospecting zebra finches (with prospecting visits defined as visits by adults to nest boxes that they were not currently breeding in; n = 50 nest boxes with decoders monitoring visits). A total of 140 different individuals (54 females, 82 males and 4 unknown, of 541 PIT-tagged birds) prospected at the nests of conspecifics. In the same year, a total of 60 nesting attempts were made in the 50 nest boxes monitored with decoders (up to three breeding attempts in one box). Of these breeding attempts, 54 nests hatched chicks, and 49 of these nests produced fledglings. Taking into account all six areas of the study site, the peak of nest initiation in the monitoring period occurred in calendar week 47 (December 16th – 22nd), with 47 nests being initiated across the 180 nest boxes of the study site (Fig. 1.1a); the hatching peak occurred three weeks later.

The maximum number of prospecting visits within one day was 312 visits on December 3rd in 2015 (calendar week 49; across all 50 boxes). The average number of prospecting visits per box did not correlate with the weekly number of either newly initiated nests (Pearson correlation: r = 0.22, p = 0.64; Fig. 1.1a), hatched (r = -0.65, p = 0.08) or fledged nests (r = 0.48, p = 0.23). Only five of the 50 nest boxes with decoders received no prospecting visits in 2015 (Fig. 1.2a-b).

In 2016 we recorded 30,412 visits of parents to their own nest and 1,581 visits of prospectors (n = 54 decoder-monitored nest boxes). Visits were made by 148 different tagged zebra finches (including 12 birds which had already been PIT-tagged in 2015). Of these individuals, 69 birds (24 females, 45 males) were recorded making prospecting visits. In 2016, a total of 68 nests were found in the 54 nest boxes fitted with decoders; again, up to three consecutive nesting attempts were made per nest box. Out of these nesting attempts, 54 hatched chicks, and 37 of these also fledged chicks. The highest number of nests were initiated in calendar week 36 (September 5th – 11th), with 25 new nests starting across the 174 nest boxes of the study area (Fig. 1.1b). There was no significant correlation between the weekly number of prospecting visits per box and the weekly number of nests hatching (r = -0.13, p = 0.79) or the weekly number of nests fledging (r = -0.18, p = 0.86); and a marginally non-significant positive association between the weekly number of prospecting visits per nest box and the weekly number of nests being newly initiated (r = 0.72, p = 0.07). Only three of the 54 decoder-monitored nest boxes in 2016 received no prospecting visits (Fig. 1.2c-d).
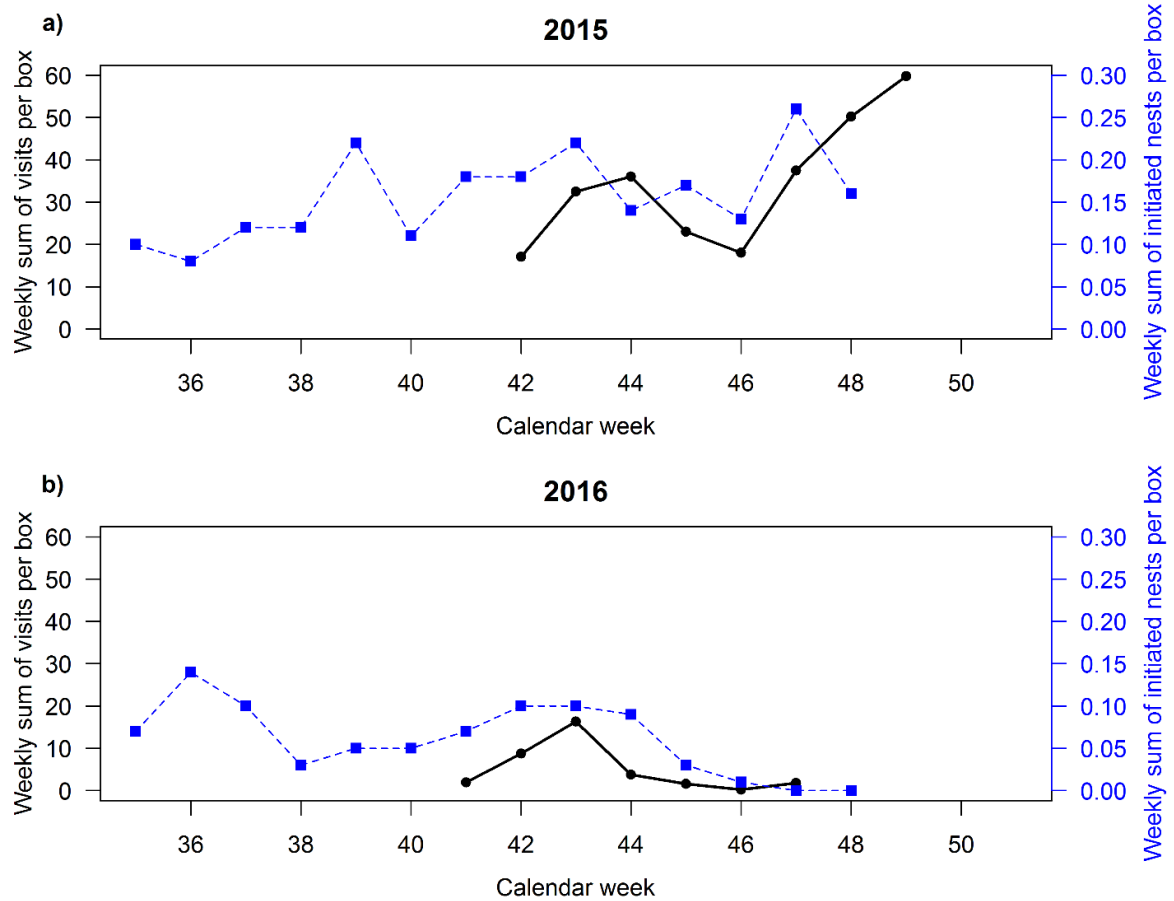
Figure 1.1. The total number of weekly prospecting visits (left axis; solid black line with filled circles) and the number of newly initiated nests (right axis; dashed blue line with filled squares) between the beginning of September and end of December in 2015 (a) and 2016 (b), each divided by the number of nest boxes. The number of prospecting visits was divided by the number of nest boxes with active decoders in each week (2015: max. 50; 2016: max. 54); the number of hatching nests refers to the whole study site (i.e. all 6 areas) and was divided by the total number of nest boxes (2015: 180; 2016: 174), to account for the different numbers of available boxes between years. The data shown include both periods were boxes had active nests as well as inactive periods.
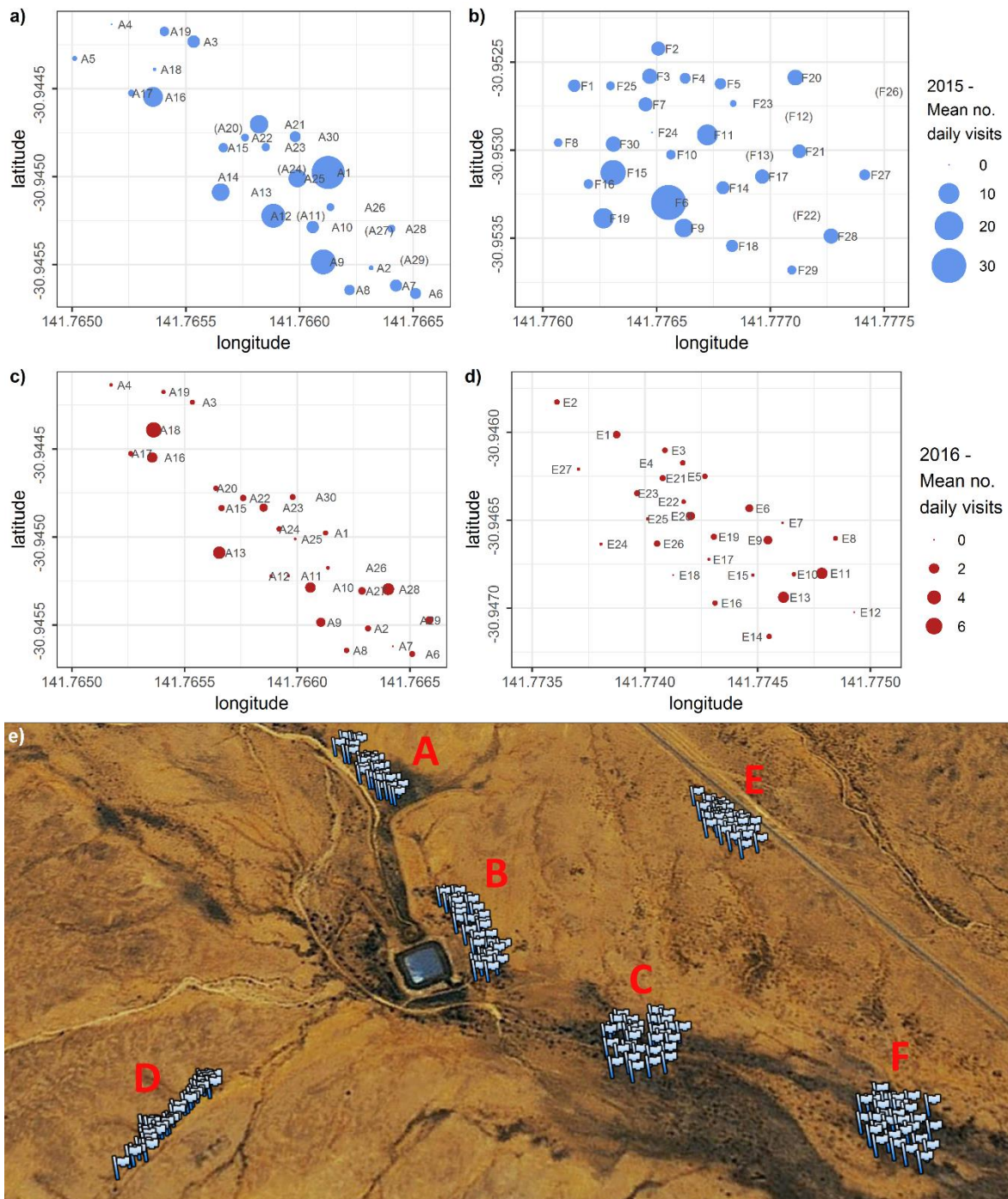
Figure 1.2. Spatial distribution of nest boxes and prospecting visits. Circle diameters indicate the mean number of prospecting visits per day at each nest box with decoders in 2015 (n = 50 nest boxes; a: area A; b: area F; blue circles) and 2016 (n = 54 nest boxes; c: area A; d: area E; red circles), respectively. The plotted areas (a-d) are each 134 x 175 m, the map area (e) is 1.17 x 1.80 km. The data shown include both periods were boxes had active nests as well as inactive periods. Nest box names start with the letter of the respective nest box area, which are repeated as red letters in the north-oriented map of the area (e; flags indicate nest boxes). Identical nest box names represent the same nest boxes in different years in figures (a) and (c); names of nest boxes which did not have working decoders are in parentheses. Copyright of Google Earth image (e): Google, CNES/Spot Image 2016. Fowlers Gap, NSW 2880, Australia. 30°57'05.41"S, 141°46'11.04"E, Eye alt 2.01 km, September 4, 2013.

Prospecting at active nest boxes

In 2015, the mean number of daily prospecting visits at nest boxes with active nests inside was 5.2 ± 12.2, the mean number of daily visitors was 2.6 ± 2.0. A maximum of 106 prospecting visits were made at a single box in one day; the maximum number of individuals at one box in the same day was 18. Nests during the chick rearing stage were prospected at a higher frequency than nests with eggs (Table 1.1; Fig. 1.3a, 1.4a). Further, the probability of a prospector visiting a nest significantly increased with clutch/brood size of the nest (Table 1.1; Fig. 1.4a).

In 2016, the mean number of daily visitors at active nest boxes was 0.6 ± 2.8 visits; the maximum was 75 prospecting visits at a single box in one day. On average 0.2 ± 0.6 individuals visited each nest per day, with a maximum of 5 different prospectors visiting the same nest in one day. Considering only the days in which nests were visited, the average number of visitors per day was 1.4 ± 0.7. In 2016, neither the brood size, nor stage of nests, or an interaction between the two variables affected the probability of prospecting visits at nests (Table 1.1; Fig. 1.3b and 1.4b).

Table 1.1. GLMM with binomial error structure assessing the effect of brood size at different nest stages (egg incubation or chick rearing) on the probability of prospectors visiting a nest box in 2015 and 2016, respectively. Data for the two years were analysed separately. Significant p-values are highlighted in bold. Values in brackets represent coefficients in full models. N represents the number of recording days, i.e. number of boxes x number of days with decoder data. The day of visit and the nest box ID were included as random intercepts in all models; area was additionally included in 2016. (coeff. = coefficients).

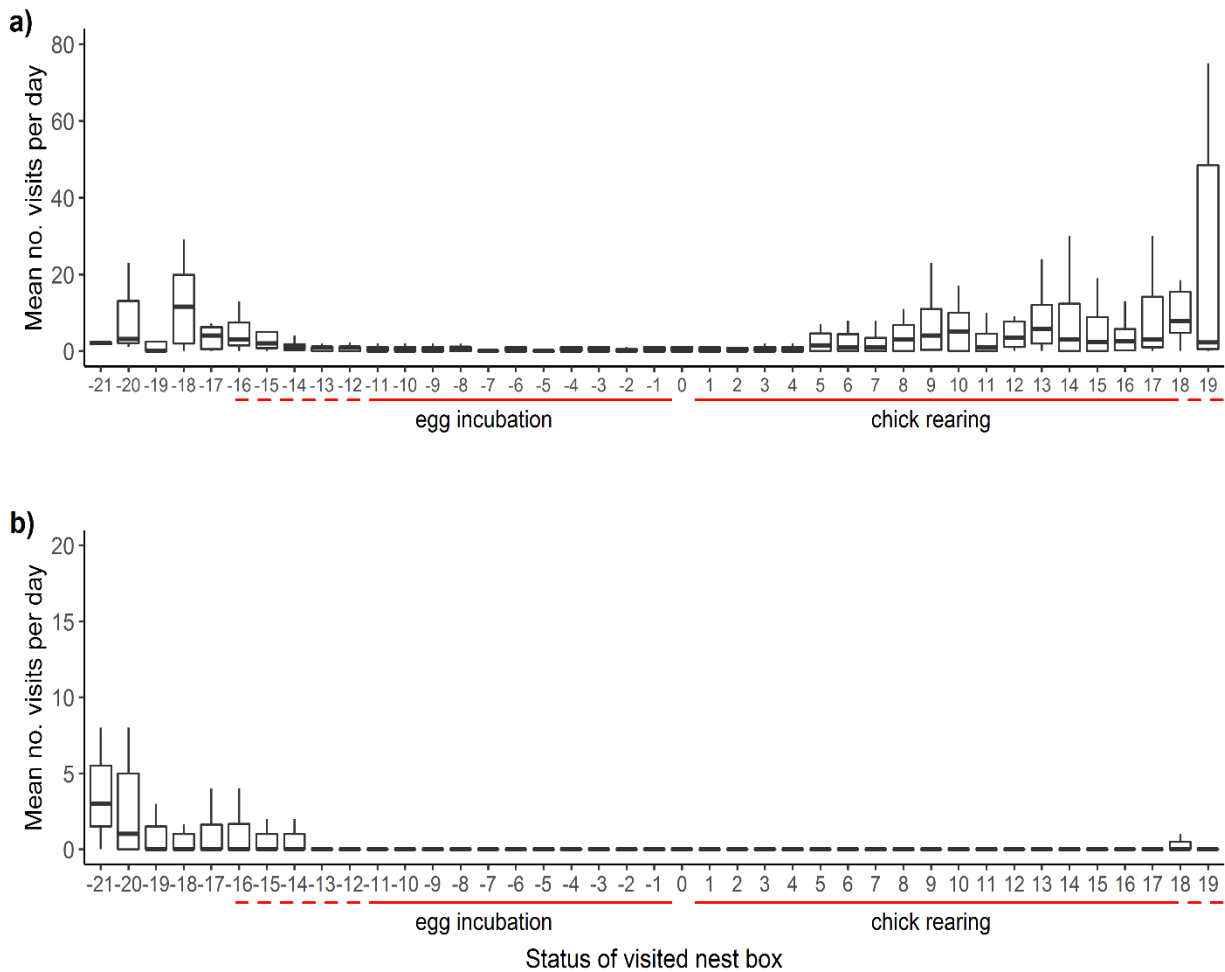|		**2015**				**2016**			
response	fixed effects	N	coeff.	X^2	p	N	coeff.	X^2	p
visit (yes/no)	intercept (stage [eggs])	708	-1.186 (-0.571)			1202	(-3.321)		
	stage [chicks]		1.373	50.50	**<0.001**		(1.378)	<0.01	0.983
	brood size		0.137	3.96	**0.047**		(0.140)	<0.01	0.930
	stage[chicks] *brood size		(0.220)	2.65	0.104		(-0.261)	2.40	0.121

Figure 1.3. Medians of the daily means of prospecting visits at each stage of the nesting cycle, in 2015 (a) and 2016 (b). The status of the nest box being visited is presented as a time scale of the nesting cycle, with 0 representing the hatch day. Hatching is preceded by the egg incubation (negative numbers counting down from hatch day), lasting 11-16 days (Zann, 1996). In the days prior to incubation nest building and egg laying occurs (one egg per day; i.e. duration of egg laying depends on clutch size). The positive numbers represent stages of chick rearing; age of chicks is increasing by one day with each number and fledging occurs between day 18 and day 19. Solid red lines indicate the minimum period of egg incubation and chick rearing, respectively; dashed red lines extend to the maximum duration of each stage. Due to the difference in the numbers of prospecting visits between years, the y-axes in (a) and (b) display different ranges. Box plots show the median and 25th and 75th percentiles, whiskers indicate values within 1.5 times the interquartile range; outliers (i.e. values beyond 1.5 times the interquartile range) were removed in the figure only, for the purpose of better graphical representation.
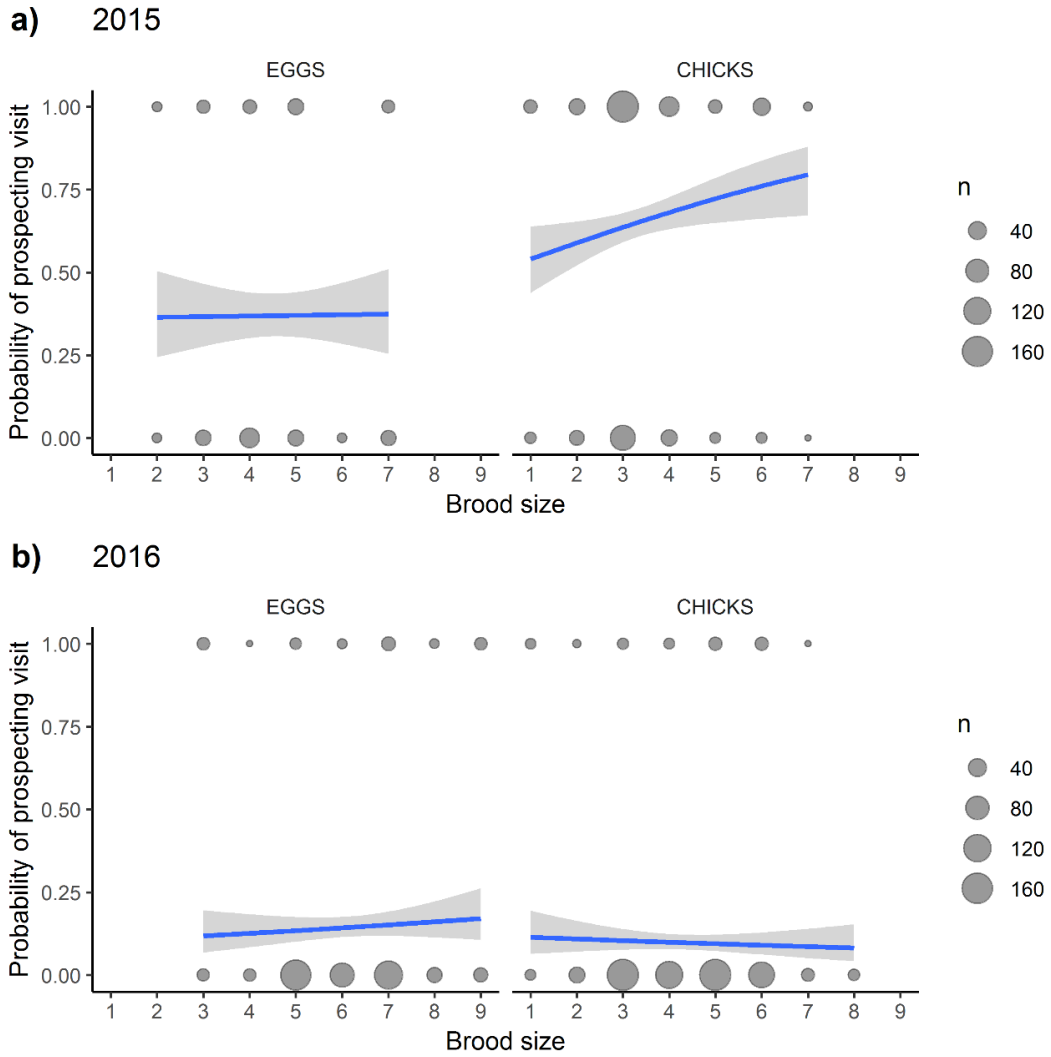
Figure 1.4. Probabilities of nests with different clutch/brood sizes being visited at the egg (left) or chick stage (right) in 2015 (A) and 2016 (B), respectively, with fitted logistic regression model. The line in the middle represents the predicted values for each brood size at both nest stages and the bands around are showing their 95% confidence intervals. Size of the dots represent the number of data points for each day at 0 (= no visits) or 1 (= visits).

Prospecting at empty nest boxes

In 2015, the mean number of prospecting visits per day at empty nest boxes was 15.9 ± 16.4 visits made by 3.0 ± 2.4 different individuals; the maximum was 56 visits at an empty box in one day, which were made by ten different individuals. Comparing the empty boxes with the active ones, the probability of prospecting visits was significantly lower across the five days

before nests fledged than at empty nest boxes (X^2_3 = 4.33; p = 0.038; N = 8 nest boxes with 51 recording days; Fig. 1.5a).

In 2016, the mean number of prospecting visits per day at empty nest boxes was 1.0 ± 4.9 visits, with a maximum of 75 visits in one day. On average, 0.2 ± 0.5 different zebra finches were prospecting at an empty box per day, with a maximum number of 4 different birds that visited the

same box in one day. Only considering the recording days of boxes that received prospecting visits, the mean number of visitors was 1.24 ± 0.6. The probability of prospectors visiting a nest box was significantly affected by the nest box status ($X^2_3 = 29.60$; p <0.001; N = 42 nest boxes with 371 recording days; Fig. 1.5b). Post hoc testing revealed a

significantly higher likelihood of prospecting visits when nest boxes were empty compared to the period five days before chicks fledged (p = 0.016). However, the likelihood of visits at newly initiated nests was even higher than at empty boxes (p = 0.033), and also higher than at nests just before fledging (p < 0.001) and higher than in the five days leading up to a nesting failure (p = 0.009)
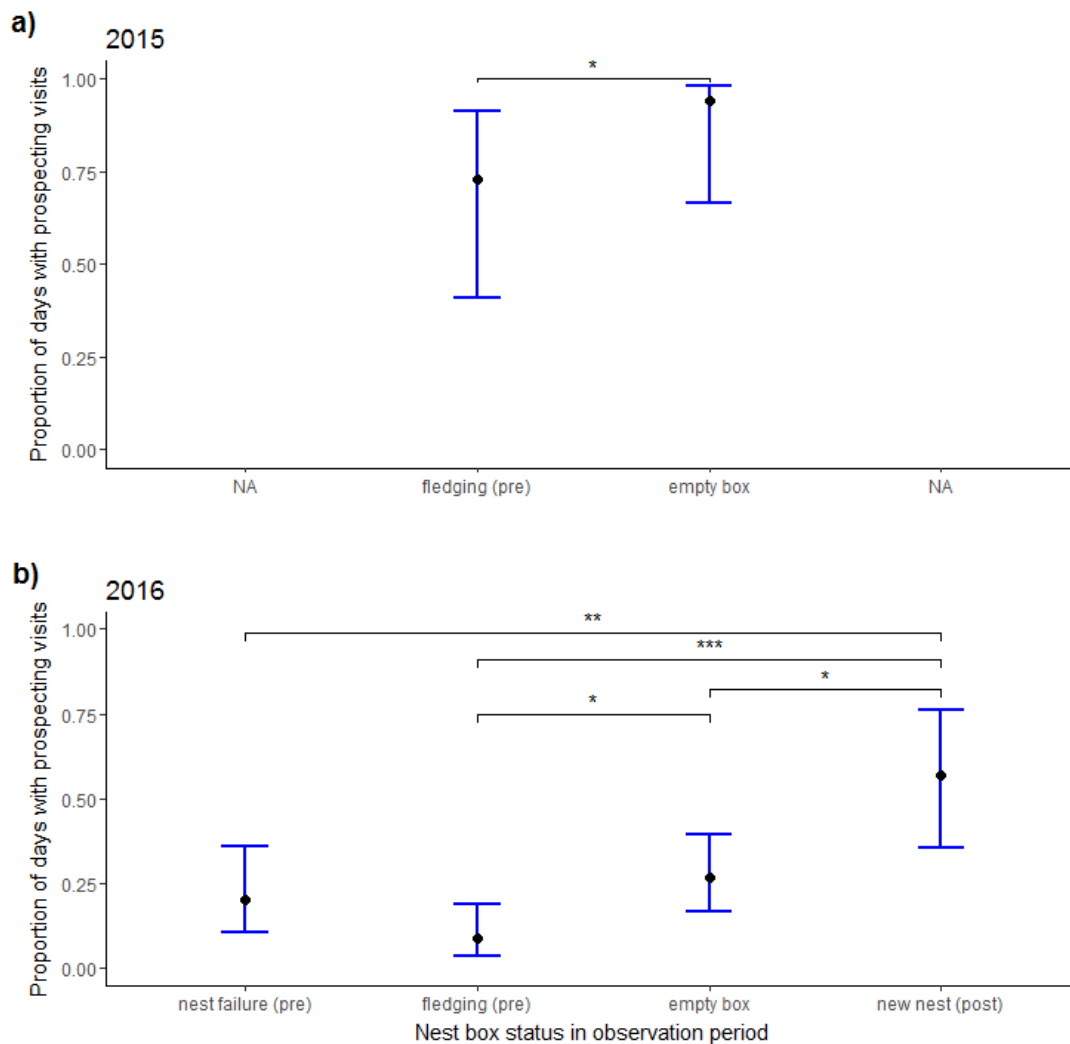

Figure 1.5. Probability of prospecting visits at nest boxes during the five days before (pre) and after (post) becoming vacant, and during the five preceding or subsequent days in which the boxes were empty (empty box). The periods before a nest box became empty (pre) was further divided by the cause that let up to it, i.e. nest failure (abandonment, predation or death of eggs or chicks) and fledging. The boxplots show the estimated probability (dots) of recording prospectors at boxes of each different state. The upper and lower whiskers show 95% confidence limits. Inverse logit back-transformed estimates from GLMMs are used.

DISCUSSION

With an automated PIT-tag detection system we have documented the prospecting behaviour of a wild zebra finch population. We have recorded a high number of prospecting visits to conspecific nests in this species, with 95% of monitored nests being visited by prospecting adults and in one year, over 45% of tagged adults were recorded visiting the nests of conspecifics. At its peak, on a single day we recorded over 300 prospecting visits to the monitored nests in our study population, with each nest receiving an average of five visits per day, and one nest being visited over one hundred times in one day. We have detected a very high rate of conspecific nest visitation that was previously quite unsuspected, considering the predictions on the strategy of nest prospecting in unpredictable habitats (e.g. Boulinier et al., 1996). The two consecutive years in which we conducted our study, were characterized by very different ecological conditions. The variation in the environmental conditions is reflected by differences in the prospecting behaviour and gives an insight into the wide range of flexibility the opportunistically breeding zebra finches employ to optimize their fitness in the highly fluctuating habitat of the Australian arid zone (Morton et al., 2011). To date, prospecting behaviour had only been thoroughly investigated in species of temperate climates, with breeding schedules that follow a relatively stark seasonality (e.g. Boulinier et al., 1996; Cadiou, Monnat, & Danchin, 1994; Doligez et al., 2004; Parejo et al., 2007; Schuett et al., 2012). The stability, and thus, predictability of a habitat can have considerable implications for the strategy of information use (e.g. Boulinier & Danchin,

1997; Erwin et al., 1998; Rafacz & Templeton, 2003). Thus, it is highly interesting to compare and contrast our findings with the state of knowledge on prospecting in other species.

The prediction we made regarding timing of prospecting and selection of nests to prospect on, building on previous studies (e.g. Boulinier et al., 1996; Parejo et al., 2008), were fulfilled in one study year, but not in the other. Only in 2015, we found the highest number of prospecting visits at nests at late stages (i.e. with chicks), which is the time when a nest should provide the most reliable information for prospectors (e.g. Boulinier et al., 1996). Similarly, only in 2015 did we find that prospecting levels were positively correlated with the reproductive output of a nest (e.g. Schuett et al., 2017), as expected if the aim of individuals is to locate nest sites of high quality and high reproductive output. Successful nests might be already identified before visiting, following cues from e.g. parental provisioning rate (Doligez et al., 2004; Pärt & Doligez, 2003) or chick begging calls or they might be revisited at a higher rate. However, neither of these predictions were met when we repeated the study in the following year in the same period and with comparable sampling effort.

Even though the number of successfully hatched nests in the nest boxes with decoders was identical in both years, this was not true across the whole study site. While reproductive output and breeding activity was similar across all areas in 2015, 2016 had much higher variation between sites; and while a similar number of nesting attempts were started in 2016, fewer succeeded until the point of fledging. In

2016, just by chance, the decoders had been installed in two areas with relatively high reproductive success compared to the other areas in the same year (not completely by chance, as one area with absolutely no breeding activity was specifically avoided). Overall, in 2016 reproductive output was lower than in the year before; the weekly number of hatching nests per box was higher in most weeks in 2015 (only week 38 and 39 were marginally higher in 2016) and in the last two weeks of 2016 no more nests hatched, indicating that the breeding activity had stopped.

The number of newly initiated nests in 2016 strongly declined in week 44, coinciding with a decline in prospecting activity. Even though we could not detect a statistically significant correlation overall, both behaviours declined in the same period (Fig. 1.1). We can assume that breeding activity had stopped because ecological conditions were no longer favourable, and it appears that the zebra finches thereupon reduced the rate at which they checked on the nests of their conspecifics. This suggests that the correct timing for the onset of breeding is first based on the personal information provided by environmental factors, before then perhaps being refined by social cues from conspecific nesting activity (Brandl et al., 2018), as otherwise we could expect them to continue to prospect continuously. This could also serve as a potential explanation why breeding activity in zebra finch colonies is not highly synchronised between pairs (Mariette & Griffith, 2012a; Zann, 1996), i.e. they might differ in their individual evaluation of the abiotic environmental cues (e.g. density and abundance of grass seeds), whereas, if the signal for the onset of breeding was

transmitted socially we would expect a fast spread and higher levels of synchrony within the population.

In European birds, prospecting usually peaks at the end of a breeding season, thus, allowing individuals to estimate the quality of a breeding site when fledglings are present and use this information in the following year (e.g. Boulinier et al., 1996). In the light of the unpredictable habitat and the opportunistic breeding strategy of zebra finches, it is very unlikely that the social information collected in one year will be used in the next year; but using it sooner, for another brood shortly thereafter, could still be very a very effective strategy, as temporal autocorrelation in the quality of a site might persist in the short-term (Schmidt, 2004). The reproductive system of the opportunistically breeding zebra finches is constantly activated (Wingfield et al. 1992; Perfito et al. 2007), allowing for multiple successive broods. This is very different to reproduction in temperate climates with mostly just a single reproductive event per season. The extended reproductive periods of zebra finches might, thus, reduce the trade-off between information gathering and reproduction that has often been suggested, i.e. individuals have to choose to either breed or prospect in one season (e.g. Boulinier & Danchin, 1997; Ward, 2005). Further, if this hypothesis is true, this would also mean that only the individuals which are planning to have another brood shortly thereafter should make prospecting visits to other nests, and this prediction is very well in line with the decline in breeding and prospecting towards the end of 2016.

The finding of the high rates of prospecting activity in the first days of a

newly initiated nest was unexpected, as this has, to our knowledge, not been described before in any other species. There is, however, one potential explanation for the increased prospecting activity at this stage, related to reproductive synchrony. It is possible that zebra finches which are about to initiate a new nesting attempt actively seek other pairs, which are also initiating a nest at the same time, to synchronize their reproduction with. Synchronizing reproduction with close neighbours can have many advantages, including opportunities for social foraging of both parents and fledglings, and enhanced predation avoidance mechanisms (e.g. Ims, 1990b; Westneat, 1992). We have shown that the higher number of prospecting visits at active nests, compared to empty ones, is not constituted by a higher number of prospecting individuals, but rather the same individuals visiting the box repeatedly. This observation fits in well with the hypothesis of prospecting for synchronised nests, as it means that certain prospectors (the ones trying to synchronize their reproduction) have an increased interest in the nest initiation of their neighbours, and particularly the timing of their egg laying. This hypothesis requires further testing, but is so far supported by our data, and if true, reveals a completely novel aspect of reproductive synchrony and in general, social information use in opportunistic breeders.

Overall, it might seem counterintuitive at first, that prospecting occurs in a highly fluctuating habitat, because the theory on information use in unpredictable habitats suggests that social information is unreliable and prospecting cannot be used to predict habitat quality if this is not stable over time.

However, the high level of prospecting that we have detected, using the automated monitoring system we deployed, suggests that keeping an eye on the nests of other conspecifics within the broader population must be useful. While our findings partially comply with the predictions derived from the study of European birds breeding in a highly predictable habitat, it is also clear that information use in unpredictable habitats does diverge from that in temperate habitats. The non-random pattern of prospecting on nests over the different phases of their reproductive activity suggests that prospectors are collecting information from these visits and the motivation and consequences of this information should be the focus of further work. It is not really possible to directly compare the rate of prospecting visits to those seen in species of bird breeding in Europe, because the visits recorded will depend on the extent of nest monitoring and the proportion of tagged birds in the local area. However, our study has clearly demonstrated that nest prospecting also takes place in a very unpredictable ecological context, and varies significantly across different conditions. Expanding the study of information use to unpredictable habitats, to understand the full complexity and range of involved mechanisms and behaviours seems highly relevant, today more than ever, living in a world where extreme environmental fluctuations can be expected over the next decades, exacerbated by climate change.

CHAPTER 2

Begging calls provide social cues for prospecting conspecifics in wild zebra finches

ABSTRACT

Social information can spread fast and help animals adapt in fluctuating environments. Prospecting on the breeding sites of others, a widespread behaviour, can help to maximize reproduction by, for instance, settling in the same area as other successful breeders. Previous studies have shown that successful broods have the highest number of prospectors and that they are visited most when offspring in nesting sites are already old, making the information more reliable. In this field study, we experimentally tested how prospectors are attracted to successful nest sites. We presented wild zebra finches (*Taenopygia guttata*) with different visual or acoustic cues in nest boxes, simulating the presence of small or large clutches or broods. More zebra finches visited experimental nests that were associated with playback recordings of begging calls of large broods (7 chicks) as opposed to begging calls of small broods (3 chicks) and controls (white noise and silence). On the other hand, visual cues (nests with different number of eggs or rocks), representing nests at early stages, did not influence either the probability of visits, nor number or duration of visits. We present the first evidence that begging calls of chicks in the nest, a signal intended for kin communication, can also provide social information to unrelated prospecting conspecifics. This information could potentially be used for a fast initial assessment of the quality of a breeding site.

INTRODUCTION

The quality of the environment can be difficult for an individual to assess, and therefore continuously gathering information from conspecifics is a good way to stay up-to-date with breeding conditions in an ever-changing environment. The information that individuals can gain in this way will ultimately guide their decision-making (e.g., Danchin et al., 2004). Reducing uncertainty through this social information increases evolutionary fitness (e.g., McNamara & Dall, 2010). Individuals can collect personal information by directly sampling the environment (e.g., Dall et al., 2005; Danchin et al., 2004), but using social information should be favoured if personal information is costly or not available (e.g. Laland, 2004). Social information can be derived from observing interactions of others with the environment, comprising their actions, their decisions as well as their performance (Danchin et al., 2004). Social information use has been identified in many behaviours of adaptive significance, such as mate choice (e.g., Drullion & Dubois, 2011; White, 2004), foraging (e.g., Coolen et al., 2005; Templeton & Giraldeau, 1995), depredation avoidance (e.g., Ward, Herbert-Read, Sumpter, & Krause, 2011) and habitat and breeding-site selection (e.g., Doligez et al., 2002; Kelly, Chiavacci, Benson, Ward, & Koenig, 2018; Loukola, Seppänen, & Forsman, 2012). While experimental evidence suggests that social information can, in certain scenarios, even lead to maladaptive behaviour (Laland & Williams, 1998), it can also help animals to adjust more rapidly to changing conditions (e.g., Danchin et al., 2004; Jaakkonen, Kari, & Forsman, 2013). When discussing the costs and benefits of social information, the argument is often made that socially acquired knowledge might be less reliable and more prone to deception (e.g., Kendal et al., 2005; Koops, 2004). However, the same argument should not apply to social information derived from inadvertently produced signals. Such signals, not produced with the intention to serve as social cues, can be seen as reliable, because they have to maintain the value for the producer (e.g., Danchin et al., 2004). Begging calls of nestlings, for example, are honest indicators of offspring needs and used in both parent - offspring (e.g., Glassey & Forbes, 2002; Godfray, 1995) and also sib - sib communication (e.g., Dreiss, Lahlah, & Roulin, 2010; Roulin, Kölliker, & Richner, 2000). Eavesdropping predators can use these cues as inadvertent social information to locate nests (e.g., Haff & Magrath, 2011; McDonald, Wilson, & Evans, 2009). While begging calls of chicks serve as signals for the parents and siblings and (inadvertently) also as cues for heterospecific predators, it is unknown whether begging calls can also function as cues for non-kin conspecifics. What we know about the use of conspecific vocalizations as social information for breeders stems from studies focusing on the period after fledging (e.g., Betts, Hadley, Rodenhouse, & Nocera, 2008; Kelly & Schmidt, 2017; Waas, Colgan, & Boag, 2005).

A widespread strategy to obtain information on the reproductive performance of conspecifics (or even heterospecifics, reviewed in Seppänen, Forsman, Mönkkönen, & Thomson, 2007) is to visit their breeding sites (e.g., reviewed in Reed et al., 1999). Prospecting on the nest of others can help to assess potential breeding sites in advance (e.g. Doligez et al., 2004;

Pärt et al., 2011) or to decide how much to invest into one's own reproduction (e.g. Forsman, Hjernquist, Taipale, & Gustafsson, 2008; Forsman, Seppänen, & Nykänen, 2011). In collared flycatchers (*Ficedula albicollis*), for example, it was experimentally shown that local reproductive success predicts both immigration and emigration rates of conspecifics in forest patches (Doligez et al., 2002). If it is the aim of prospectors to find areas of high quality for their own breeding, we can expect that prospectors might visit successful nests at higher rates, spend more time there and choose the time where information is most reliable (Doligez et al., 2004). To date, several researchers found support for these predictions in both experimental and correlational studies. Several studies show evidence for higher prospecting activity at nests with larger broods (Schuett et al., 2017; Zicus & Hennes, 1989). Other studies found that prospecting activity was positively correlated with parental feeding rate (Doligez et al., 2004; Pärt & Doligez, 2003; but see: Schuett et al., 2017), suggesting that prospectors can preselect to visit successful nests preferentially, by cueing on the provisioning activity of parents (which in turn is associated with the intensity of nestling begging calls; e.g. Leonard & Horn, 2001; Ottosson, Bäckman, & Smith, 1997). Regarding the timing of prospecting visits, the highest frequency was observed at late stages of chick rearing, presumably because this is the time when nests provide the most reliable information on local reproductive success (e.g. Boulinier et al., 1996). Further evidence for this was found in a brood size reduction experiment on spotless starlings (*Sturnus unicolor*), which revealed that the

positive correlation between brood size and number of visiting prospectors was most pronounced at the latest stage of chick rearing (Parejo et al., 2008). This may indicate that nests with older chicks provide the most reliable information on reproductive success.

Zebra finches (*Taeniopygia guttata*) are monogamous, but social passerines living in loose colonies (Zann, 1996). They are granivorous birds with relatively low parental feeding rates of as little as one visit per hour and high synchrony between parents (Mariette & Griffith, 2012b). Hence, parental feeding rates of zebra finches might not serve as a sufficient indicator of their reproductive success. Wild zebra finches prospect on the nests of conspecifics (Mariette & Griffith, 2012a), but very little is known about the mechanisms of social information use in this species and whether the predictions from the numerous studies on species of temperate zones apply to them. Living in the arid and semiarid zones of Australia, zebra finches are faced with the distinct ecological challenges of a highly fluctuating environment (Morton et al., 2011). These ecological conditions lead to the opportunistic breeding pattern of the zebra finch. Opportunistic breeding means that whilst the zebra finches breed with some degree of seasonality, they breed over an extremely long potential breeding period, and can breed multiple times in a single year. This generates a number of additional challenges over the timing of and investment into reproductive events, relative to species in more predictable and seasonal environments. Opportunistic breeding is widespread throughout Australia (Duursma et al., 2017) and probably in other poorly studied parts of the world. The well-studied

zebra finch therefore provides a good model to investigate the mechanisms through which social information can be accessed by species living in ecologically challenging environments.

In a field experiment, we aimed to test which social cues from the nests of zebra finches attract prospecting conspecifics. We will thereby gain insight as to what social information zebra finches might use for their reproductive decisions in an unpredictable habitat. In 2 separate experiments, we presented wild zebra finches with either acoustic cues (playback of chick begging calls) or visual cues (eggs) of conspecifics with either small or large broods/clutches. Using playbacks of chick begging calls or nests with unhatched eggs, respectively, allowed us to completely discern clutch and brood size from parental activity. Previous studies suggest that playbacks of conspecific courtship calls can function as social cues affecting reproductive parameters (sexual and agonistic interactions in royal penguins, Eudyptes schlegeli: Waas, Caulfield, Colgan, & Boag, 2000; breeding schedule and clutch size in zebra finches: Waas et al., 2005). Similarly, fledgling calls of veeries (*Catharus fuscescens*) have been shown to function as social cues for conspecifics who are more likely to settle in patches where such calls were played, presumably because the calls of fledglings provide evidence for prior nest success (Kelly & Schmidt, 2017).We want to add to the small number of studies, which have demonstrated that begging calls can serve as inadvertently produced social information for non-kin conspecifics. Further, this is to our knowledge the first study investigating the direct reaction of prospectors to begging calls (i.e. do they affect which nests are

visited). If the presence of fledglings in an area alone, as simulated in the study on veeries (Kelly & Schmidt, 2017), would provide all relevant information for conspecifics, there would be no need to prospect on their nests beforehand. As zebra finches, however, visit the nests of their conspecifics frequently (Mariette & Griffith, 2012a), it is highly likely that nests already provide additional and or/different information at earlier stages. Additionally to giving cues on successful breeding sites (Doligez et al., 2002), nests at earlier stages could potentially provide information to help e.g. synchronize nesting (Emlen & Demong, 1975; Stempniewicz, Goc, Bzoma, Nteck, & Iliszko, 2000) or to adjust clutch size and egg mass (Forsman et al., 2011). We therefore believe that it is highly relevant to expand our understanding on conspecific social information use in the pre-fledging period.

With this field experiment, we tested the hypothesis that chick begging calls can serve as a source of social information for prospecting zebra finches. If this is the case, we predicted that zebra finches will visit nests with begging call playbacks more than controls (silence and noise). If the begging calls can also serve as indicators for breeding success, they should visit larger (and potentially more successful) clutches/broods of conspecifics more than small ones. Further, the acoustic cues (representing nests at later stages), may be perceived as more reliable (see e.g. Boulinier et al., 1996) than visual cues (i.e. nests at early stages) and hence the distinction between small and large broods should be more pronounced in the nests with chick calls as cues than with those with egg cues.

METHODS

Study species and field site

Zebra finches are small, sexually dimorphic passerines with a strong pair bond and biparental brood care (Mariette & Griffith, 2012b). The mean clutch size in zebra finches is 5 eggs, ranging from 2 to 8 eggs (Griffith et al., 2008). The study was performed at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31.086972°S,141.704836°E), New South Wales, Australia, between October 11 and November 27, 2016. The study site (~1.5 x 2 km in area) has a dam with a relatively permanent water body in the centre. In the surrounding of the dam 180 wooden nest boxes (12/18 cm front/back height, 9.3 cm width, 14 cm depth; entry hole 3 cm diameter) attached to metal stakes were installed, which are readily accepted for breeding (Griffith et al., 2008). The nest boxes were arranged in six areas of 30 nest boxes each (mean ± SE distance to nearest neighbouring area: 413.62 ± 63.62 m; mean distance to nearest neighbouring nest box within areas: 10.36 ± 1.98 m).

General experimental procedure

The experimental setup for each trial consisted of 4 wooden nest boxes attached to metal stakes (same as the ones provided for breeding). The 4 nest boxes were set up in a roughly square configuration (mean ± SE distance between experimental nest boxes = 47.91 ± 2.92 m, $n_{\text{nest boxes}}$ = 110; distances not measured in every trial) in the morning, within one of the 6 nest box areas (i.e. the experimental nest boxes were set up in between the permanent breeding boxes). The 2 different experiments (acoustic cues or visual cues, see below) were never conducted in the same area on the same day. The same experiment was never set up in the same area on consecutive days. In addition, each day only one trial per experiment was conducted. Thirty trials in total were run of each experiment, five trials per area.

All experimental nest boxes were erected south of a big bush or small tree. The nest box openings were facing towards the shrub with ~1 m distance in between and in a height of ~1.5 m. An action camera (GoPro, GoPro Inc., San Mateo, US; Rollei, GmbH & Co.KG, Norderstedt, Germany) was attached to a branch of the respective plant so that the nest box was in the centre of the camera's view. The nest boxes were then prepared according to the respective experiment and treatment (see below). Once the setup of all 4 boxes of an experiment was completed, the cameras were started. Each trial lasted as long as each camera would record (mean 2.5 ± 0.03 hr, $n_{\text{nest boxes}}$ = 232). Once all cameras had stopped recording, the complete setup including the stakes and nest boxes were removed. Trials of the experiment with acoustic cues, which were always started first, were always finished before 1pm, while the trials with visual cues finished latest at 2pm.

Experiment with acoustic cues

For the experiment with acoustic cues, a speaker (JBL Clip+, JBL by Harman, Northridge, U.S.; 3.2 watts, 160 Hz – 20 kHz) was placed inside each nest box. The speakers were covered with a thin layer of nest material that had previously been collected from abandoned zebra finch nests. An MP3-player (Intenso Video Scooter

Digital Player, Intenso International GmbH, Vechta, Germany) was attached to each speaker, each containing the sound file for one of the following 4 treatments: '3 chicks' (begging calls of 3 chicks); '7 chicks' (begging calls of 7 chicks); 'noise' (white noise) and 'silence' (no sound). The assignment to the nest boxes was randomized by blindly allocating the players to the nest boxes. Once all boxes and devices had been set up, all speakers, MP3 players and cameras were started. When the video recordings were analysed, we ensured that all playbacks were audible throughout and until the end of each trial.

White noise and silence files were both created using the respective function in the software Audacity (Audacity Team, 2014). The playback files were previously recorded with a Zoom H4n digital recorder (Zoom North America, New York, U.S.) in nests with 3 chicks ($n_{nests} = 4$) and 7 chicks ($n_{nests} = 4$). Chicks were recorded in their nest boxes between day 8 and day 10 after hatching. To ensure that chicks were hungry and hence very motivated to utter begging calls, we checked the state of their crops. Depending on the fill level, we then blocked the entrance of the nest boxes with a cloth for 10 – 90 min, to prevent parents from feeding, until crops were empty. To elicit begging calls from all chicks of the brood, we carefully touched the beaks of the chicks with a small stick before the start of recording and during the recording session if some of the chicks had stopped begging. Two recordings were made at each selected nest in one session. Each recording lasted for 2 min with a 2 min break in between where the lid of the nest box was closed. The recorder was held in a distance of 10 cm from the chicks, and we used the same

settings for all recordings. We edited the recordings with Audacity (Audacity Team, 2014). We copied and pasted different sequences of begging calls from the recordings to create the playback files. Three-hour playback files were assembled by alternating 45 s sequences of begging calls with 90 s sequences of silence. Each file was created using only the files from one recording session at one nest box (4 min). We cut the recordings in 45 s sequences with different starting points and randomly assembled them within the playback file. We measured the amplitudes of all sound files using a sonometer (A setting, 1m, SPL meter, Castle GA206 sound level meter). The mean ($\pm$ SE) amplitude of the treatments playing sound were: '3 chicks': 51.5 ± 1.55 dB, $n = 4$; '7 chicks': 56 ± 1.35 dB, $n = 4$; 'noise': 56 dB, $n = 1$). We did not modify the audio files in other ways than described here; the difference in amplitude between '3 chicks' and '7 chicks' recordings reflect the natural occurring difference. During the experiment, the eight different begging call playback files were paired in different combinations and used in random order. Begging call playback files were never used in the same area where they had been recorded.

Experiment with visual cues

In this experiment, we applied the same general procedure as described before. However, the following visual cues were presented inside the four nest boxes in each trial: '3 eggs' (a nest containing 3 zebra finch eggs); '7 eggs' (a nest containing 7 zebra finch eggs); '3 rocks' (a nest containing 3 rocks); and 'empty' (the nest box remained empty). The empty box and

the rocks served as controls. The purpose of the rocks was to present a visual stimulus other than the eggs. The nest material and eggs used in the experiment had previously been collected from abandoned nests of zebra finches breeding in nest boxes. We only collected nests that had been abandoned before chick rearing, i.e. nest material was relatively clean. For each trial, three nests were assembled inside the experimental nest boxes, while the fourth box stayed empty. In the centre of each of the three nests, we neatly arranged 3 eggs, 7 eggs, or 3 rocks, respectively. The rocks we selected for the experiment were of light colour and matched sizes of zebra finch eggs as closely as possible. Nest material, eggs and rocks were exchanged between trials, and treatments were shuffled between nest boxes.

Data analysis

Six different observers who were blind to the purpose of the experiment viewed the complete video material, coding the behaviour of the birds. Four behavioural categories were identified: 'at box' - a zebra finch appears in close vicinity to the nest box, but has no physical contact with it; 'sits' – a zebra finch sits on top of the nest box; 'hangs' – a zebra finch hangs at the entrance of a nest box with at least 50% of his body being outside; 'in box' – a zebra finch is inside the nest box with more than 50% of his body. The duration of each behaviour was noted. Each bird appearing in a video was assigned a unique ID code. As long as an individual was clearly identifiable, the same ID code was used. Once a bird left the camera's field of view, we assumed any bird reappearing to be a

new individual. Where a count of individuals is mentioned, throughout the manuscript, it refers to this approximated value. The mean number of individuals appearing per hour ('mean number of IDs per hr') was then calculated for each treatment by dividing the total number of individuals by the total duration of each trial [h]. In the same way, the mean duration of visit per individual ('mean duration of visit per ID [s]') was calculated to reflect how much time one zebra finch interacted with a nest box on average. Both variables were calculated for each of the four behavioural categories separately, as well as in total.

The data were analysed in two steps and separately for each experiment. Firstly, we fitted a generalized linear mixed effect model (GLMM) with binomial error structure to assess if the treatment affected whether boxes were visited at all during a trial. We used the binomial variable 'visitation' [one or more birds visited the box = 'yes'; no birds visited the box during the trial = 'no'] as response variable and the day of the experiment and the area where it was conducted as random effects. Tukey's post hoc test was performed for significant results.

For the further analysis comparing number and duration of visits between treatments, we did not run GLMMs because data were highly zero inflated. Instead, we conducted a Friedman rank sum test, using each variable (mean number of IDs per h and mean duration of visit per ID [s]) as response. In the Friedman test, treatment was used as the grouping factor; the day of the experiment was included as a blocking factor. When the result of the Friedman test was significant, we additionally conducted a

multiple pairwise comparison ('symmetry test'; Hedderich & Sachs, 2011) to establish which treatments significantly differed from each other. Kruskal-Wallis tests were performed to examine if the use of different playback files had an effect on the mean number of IDs per h or the mean duration of visit per ID [s] in each of the 2 treatments of the experiment with acoustic cues using chick begging calls as playback ('3 chicks' and '7 chicks').

In some of the trials, not all four treatments could be tested successfully, due to technical issues with the cameras or playback equipment (eight setups in four trials of the acoustic experiment; four setups in three trials of the visual experiment). Since the Friedman test requires a balanced complete block design, no data from these trials could be included in the analysis. For the Friedman test, we additionally removed trials where none of the four nest boxes had any visit at all (two trials of the experiment with acoustic cues and five trials with visual cues) from the data, as they contained no informational value.

All statistical analyses were conducted with R (R Core Team, 2014): for LMMs we used the package 'lme4' (Bates, Maechler, Bolker, & Walker, 2014); for multiple pairwise comparisons we used the packages 'multcomp' (Hothorn, Bretz, & Westfall, 2008) and 'coin' (Hothorn, Hornik, Van De Wiel, & Zeileis, 2008). Statistics are presented as mean ± SE (standard error of the mean) and median ± IQR (interquartile range).

RESULTS

Experiment with acoustic cues

The experiment using playbacks as acoustic cues for zebra finches consisted of 30 trials (112 nest box setups) that were included in the analysis, lasting a total of 287.09 hr. In this period, a total of 607 visits (2.11 visits per hr) of zebra finches were recorded at the experimental boxes across all treatments. Interactions with the nest boxes during these visits summed up to for 8.74 hr. The treatment significantly affected whether a nest box was visited by zebra finches during a trial or not (binomial GLMM: $\chi^2_3 = 15.78$, $P = 0.001$, $n_{trials} = 30$; Figure 2.1A). Tukey's post hoc tests revealed a significantly higher likelihood that a box with '7 chicks' playback had any visitors, compared to '3 chicks' ($P = 0.011$), 'noise' ($P = 0.003$) and 'silence' ($P = 0.001$, $n_{trials} = 30$). The probability of finding three statistically significant tests (with $P \leq 0.011$) of six due to chance alone (calculated via a Bernoulli process: Moran, 2003) is $P < 0.001$.

Further, also the mean number of IDs per h differed between treatments (Friedman test: $\chi^2_3 = 8.69$, $P = 0.034$, $n_{trials} = 24$; Figure 2.1B). Post-hoc pairwise comparisons for the mean number of IDs per hr showed a significant difference between the following treatment pairs: '7 chicks' playback boxes were visited more often than both '3 chicks' ($P = 0.010$), 'noise' ($P = 0.012$) and 'silence' playback boxes ($P = 0.044$, $n_{trials} = 24$). The probability of finding three statistically significant tests (with $P \leq 0.044$) of six due to chance alone is $P < 0.002$. No significant differences were found between the other treatment pairs. The mean duration of visit per ID [s] was not different between

treatments (Friedman test: $\chi^2_3 = 5.78$, $P = 0.12$, $n_{trials} = 24$) but the order of the

treatments was in accordance with mean number of IDs per h (Figure 2.1C).
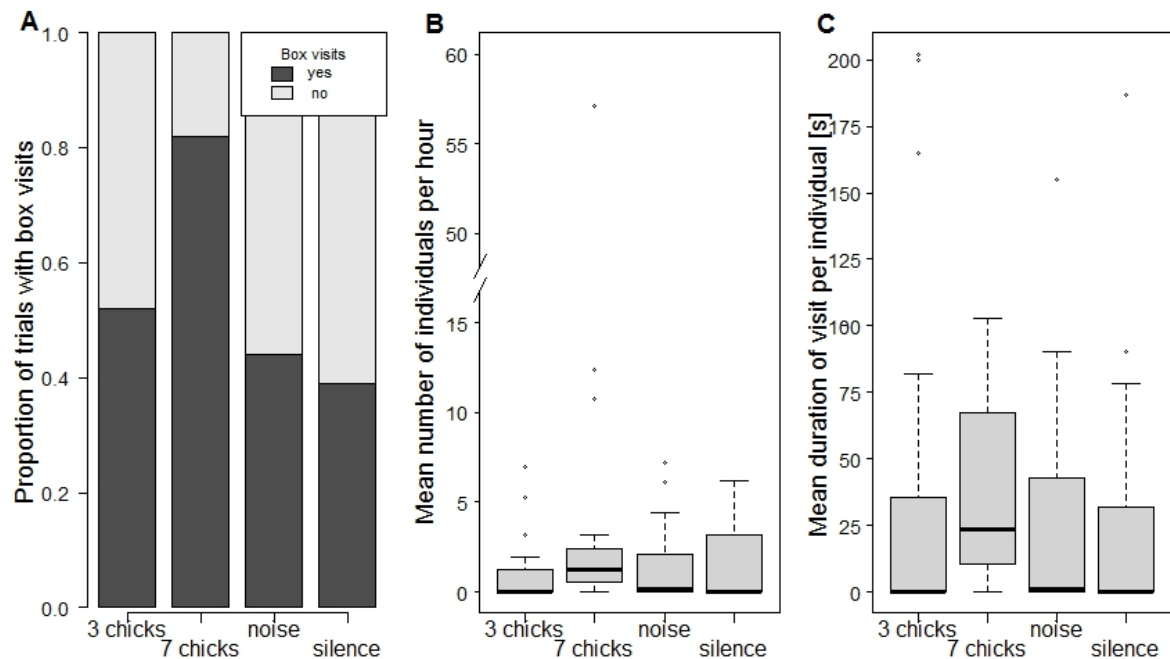

Figure 2.1. Proportion of trials in which the nest box of each treatment was visited by zebra finches (A), the medians of the mean number of individuals per hour (B), and the mean duration of visits [s] (C) at nest boxes playing different acoustic cues. The y-axis in plot B was truncated for plotting an extreme value.

Analysing the behavioural categories separately, only the birds being in close proximity to the box without touching it ('at box') differed significantly between treatments, in both number and duration of visits (Table 2.1). Post hoc testing revealed a significantly higher number of birds being 'at box' in the '7 chicks' treatment than in '3 chicks' ($P = 0.002$) and 'noise' ($P = 0.009$, $n_{trials} = 23$) treatment boxes. There was also a marginally non-significant trend for more birds being 'at box' in '7 chicks' boxes compared to 'silence' boxes ($P = 0.054$, $n_{trials} = 23$). The probability of finding two statistically significant tests (with $P \leq$

0.009) of six due to chance alone is $P < 0.002$. Furthermore, birds spent significantly more time per visit 'at box' at the '7 chicks' playback boxes than at the '3 chicks' boxes ($P = 0.010$), the 'noise' boxes ($P = 0.017$), and the 'silence' boxes ($P = 0.023$, $n_{trials} = 23$). The probability of finding three statistically significant tests (with $P \leq 0.023$) of six due to chance alone is $P < 0.001$.

Which playback file was used for the '3 chicks' or '7 chicks' begging call playback did not significantly affect the mean number of IDs per h ('3 chicks': $\chi^2_3 = 1.74$, $P = 0.70$, $n_{trials} = 24$; '7 chicks': $\chi^2_3 = 2.96$, $P = 0.47$, n

$_{\text{trials}}$ = 24) or the mean duration of visit per ID [s] ('3 chicks': χ^2_3 = 1.41, P = 0.70, n_{trials} = 24; '7 chicks': χ^2_3 = 2.96, P = 0.63, n_{trials} = 24).

Table 2.1. Effects of treatment on mean number of IDs per h and mean duration of visit per ID [s] calculated for different behaviours during the experiment with acoustic cues. Medians, IQRs and the results of Friedman tests are shown. Four different behaviours that zebra finches displayed at the experimental nest boxes were identified in the video material: 'at box', 'in box', 'sits' and 'hangs'. Number of trials (N) vary because trials with zero visits in all treatments are not included. Significant P-values are highlighted in bold.

behaviour	variable	median	IQR	n	χ^2	df	p
'AT BOX'	mean number of IDs per h	0.38	1.63	23	11.459	3	0.009
	mean duration of visit per ID [s]	1.00	1.20	23	8.866	3	0.031
'IN BOX'	mean number of IDs per h	0.00	0.64	7	0.509	3	0.92
	mean duration of visit per ID [s]	0.00	1.00	7	1.824	3	0.61
'SITS'	mean number of IDs per h	0.44	1.99	19	3.281	3	0.35
	mean duration of visit per ID [s]	7.50	15.65	19	6.671	3	0.08
'HANGS'	mean number of IDs per h	0.33	1.29	13	3.058	3	0.38
	mean duration of visit per ID [s]	1.57	9.75	13	1.835	3	0.61

Experiment with Visual Cues

We ran 31 trials of the experiment with visual cues in the nest boxes (120 nest box setups), which had a total runtime of 293.32 hr. During this time, 543 visits (1.85 visits per hr) were made at the nest boxes, for a total duration of 8.76 hr. Treatment did not significantly affect whether a nest box was visited at all or not (binomial GLMM: $\chi^2_3 = 1.40$, $P = 0.71$, $n_{\text{trials}} = 31$; Figure 2.2A). There was no significant difference in the mean number of IDs per hr (Friedman test: $\chi^2_3 = 2.65$, $P = 0.45$, $n = 23$; Figure 2.2B) or the mean duration of visit per ID [s] (Friedman test: $\chi^2_3 = 0.25$, $P = 0.97$, $n = 23$; Figure 2.2C) between treatments.
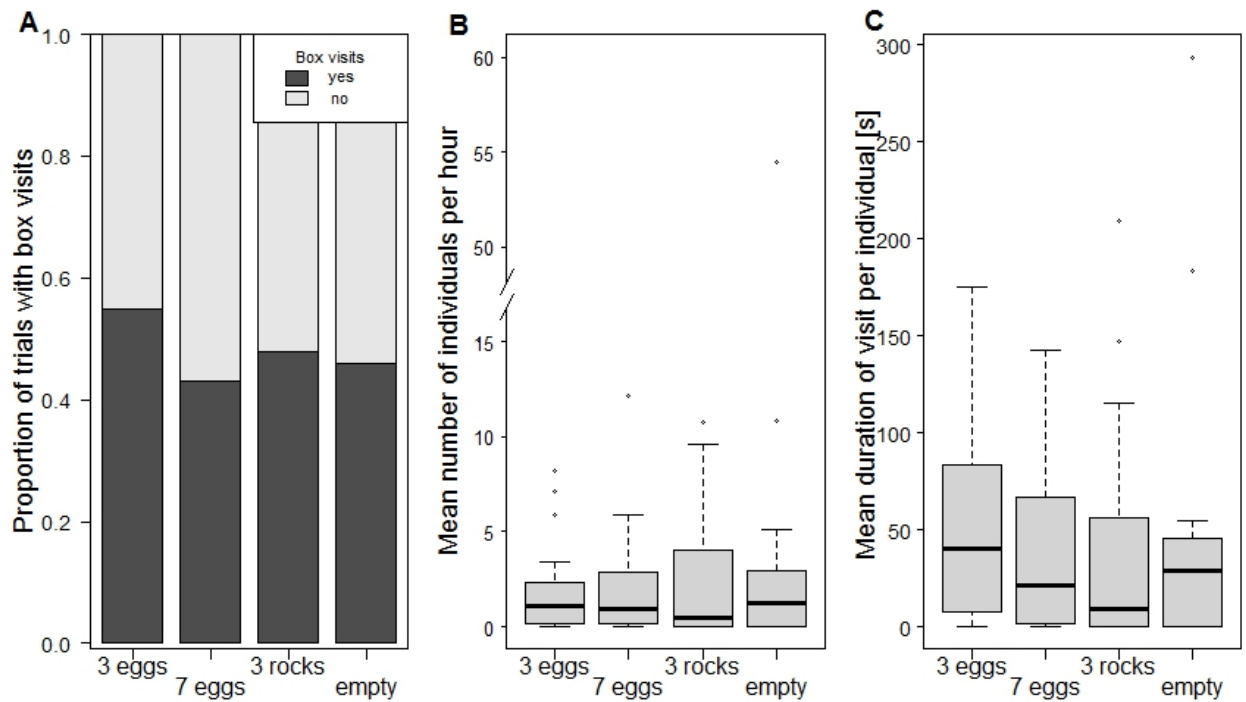

Figure 2.2. Proportion of trials in which the nest box of each treatment was visited by zebra finches (A), the mean number of individuals per hour (B), and the mean duration of visits [s] (C) at nest boxes containing different visual cues. The y-axis in plot A was truncated for plotting an extreme value.

Additionally, no significant differences were found in mean number of IDs per h or mean duration of visits between treatments in any of the four behaviours that zebra finches showed at the experimental nest boxes (Table 2.2).

Table 2.2. Effects of treatment on mean number of IDs per h and mean duration of visit per ID [s] calculated for different behaviours during the experiment with visual cues. Medians, IQRs and the results of Friedman tests are shown. Four different behaviours that zebra finches displayed at the experimental nest boxes were identified in the video material: 'at box', 'in box', 'sits' and 'hangs'. Number of trials (N) vary because trials with zero visits in all treatments are not included.

behaviour	variable	median	IQR	n	χ^2	df	P
'AT BOX'	mean number of IDs per h	0.70	1.91	22	1.894	3	0.56
	mean duration of visit per ID [s]	8.50	27.50	22	1.742	3	0.63
'IN BOX'	mean number of IDs per h	0.38	0.96	15	2.140	3	0.54
	mean duration of visit per ID [s]	18.00	65.00	15	1.209	3	0.75
'SITS'	mean number of IDs per h	0.39	1.54	17	1.571	3	0.67
	mean duration of visit per ID [s]	6.00	15.79	17	1.047	3	0.79
'HANGS'	mean number of IDs per h	0.53	2.28	22	2.436	3	0.49
	mean duration of visit per ID [s]	14.25	22.36	22	0.866	3	0.83

DISCUSSION

In this field study, we used two different experimental setups to test whether wild zebra finches react differently to neighbouring nest boxes, depending on different acoustic and visual cues. Our results demonstrate that the playback of large broods begging indeed attracted more visitors than the begging calls of small broods. This result is in accordance with the hypothesis that prospectors preferentially visit more successful broods (e.g. Cadiou et al., 1994; Schuett et al., 2017). The chick begging calls alone provided social information for unrelated conspecifics, which can potentially be used to infer on their breeding success. If the information obtained through prospecting is used to identify high quality breeding habitats (see e.g. Boulinier et al., 2008; Brown, Brown, & Danchin, 2000; Doligez et al., 2002), being able to identify them quickly will have energetic benefits. If birds can already assess the success of nests from a distance it will save time and energy, which can in turn be invested in other activities. Additionally,

having to visit fewer nests of low informational value will reduce the risk of becoming a victim of depredation and can potentially also minimize conflicts with conspecifics.

From the view of a breeding pair receiving prospecting visits, the prospecting activity and, in consequence, the chance of a prospecting pair settling in the area are unlikely to have strong adverse effects. Zebra finches, as a non-territorial, monogamous species, are likely to benefit from additional breeding birds around and the advantages associated with coloniality (e.g. predator detection, dilution effects, group foraging; Mariette & Griffith, 2012a; Møller, 1987; Waas et al., 2005). Hence, loud begging calls and the attracting of prospectors to nests is not likely to be a problem for conspecifics.

The amplitude of the playbacks of seven chicks begging and white noise were identical, which makes it highly unlikely that this was a contributing factor to why some boxes were visited more. The difference we observed between '7 chicks' and 'noise' treatment can, hence, be likely attributed to the character and informational value of the signal. Also in accordance with our predictions, the boxes of the '7 chicks' treatment were significantly more likely to be visited than the 'silence' boxes. The probability that '3 chicks' playback nest boxes were visited was not significantly higher than in the control treatments. This could be contributed either to the lower amplitude of the signal or the lower information value of these nests or potentially a mix of both. It is possible that the zebra finches visiting the nest boxes consisted of a mix of birds prospecting for

information at conspecific nests and looking for empty nest boxes to breed in, which would also explain a certain level of visits to the control boxes.

There is a possibility that prospectors would usually react differently to chicks of different hunger levels, which affects begging intensity (e.g. Ottosson et al., 1997). In our experiment, however, we were probably able to control for this by only recording chicks with empty crops, i.e. at an equally high level of hunger. Reactions to the recordings of chicks from different broods were similar. Nevertheless, prospectors sometimes also looked inside the nest boxes, which could be used to gain additional visual information on nestling hunger and overall condition.

We did not observe a difference in the number or duration of visits at the nest boxes containing only visual cues. Obviously, in this scenario birds could not preselect which box to visit, as they were identical from the outside and no other cues, such as parental activity, was available. However, birds that had already inspected the content of the nest box could have returned to the box more frequently or spend more time inspecting it, had they distinguished between more and less successful nests based on clutch size. Our finding follows the line of what can be predicted from another study, where a difference in prospecting rate between smaller and larger brood was only pronounced at late chick stages, presumably because information is more reliable then (e.g. Parejo et al., 2008). However, we cannot completely rule out that our result could have been different if the experimental trial had been running for longer time. Birds could have revisited certain boxes again at a

later point in time. Further, our method of video analysis did not allow for individual identification once an individual had left the field of view. The number of birds appearing at the box, which we used as a proxy for the number of individuals, might not be fine scaled enough in this context. Another point is that we do not know how a non-incubated clutch, as we presented it, was perceived. It could appear as an unfinished or abandoned nest, which might not provide very valuable information in this stage. We performed the experiment at non-incubated nests to dissociate all influence from parental activity, but this also brings along some restrictions. We therefore have to be careful with the interpretation of this negative result.

Overall, our study provides the first evidence that wild birds can use begging calls from chicks at the pre-fledging stage, an acoustic signal intended for kin communication, as social signal. This social information could be an important cue to infer on conspecific's breeding success. Even though the parental feeding activity at nests is a known indicator of breeding success in some species (Doligez et al., 2004; Pärt & Doligez, 2003; but see: Schuett et al., 2017), the value of the begging calls in the nest as inadvertent social information has previously not been demonstrated. Our findings highlight the importance to further expand research on social information use, in particular on mechanisms that might have been previously overlooked.

CHAPTER 3

Wild zebra finches do not use social information from conspecific reproductive success for nest site choice and clutch size decisions

ABSTRACT

Information about the quality of local habitat can greatly help to improve an individual's decision making and, ultimately, its fitness. Nevertheless, little is known about the mechanisms and significance of information use in reproductive decisions, especially in unpredictable environments. We tested the hypothesis that perceived breeding success of conspecifics serves as a cue for habitat quality and hence influences breeding decisions (nest site choice and clutch size), using the zebra finch (*Taeniopygia guttata*) as a model species. Zebra finches breed opportunistically in the unpredictable, arid zone of Australia. They often inspect the nests of conspecifics, potentially to prospect on conspecific reproductive success, i.e. to collect social information. We conducted a clutch and brood size manipulation to experimentally create the perception of high and low quality areas. In six areas, clutch sizes of almost 300 zebra finch nests were either all increased (N = 3 areas) or reduced (N = 3 areas) throughout one breeding season. The number of breeding pairs and sizes of newly laid clutches were not significantly affected by the manipulated reproductive success of the areas. Thus, zebra finches did not use social cues for their reproductive decisions, which contrasts with findings of species in temperate zones, and could be an adaptation to the high unpredictability of their habitat. Even the personal experience of rebreeding birds did not directly affect their clutch size. Our study suggests that zebra finches employ a high level of opportunism as a key strategy for reproduction. Further, this is the first study to our knowledge using an experimental approach in the wild to demonstrate that decision-making in unpredictable natural environments might differ from decision-making in temperate environments with seasonal breeding.

INTRODUCTION

Having reliable information about the environment can be key to survival and high reproductive success in animals, due to the way it can affect adaptive decision making. Gathering information is a continuous process and being informed about possible alternatives is a prerequisite for making optimal decisions in variable conditions (Dall et al., 2005). Often a variety of information sources is available to animals and different strategies can be used to exploit them. Individuals can acquire personal information through a trial-and-error approach and investment of their time and energy. Alternatively, social information can be obtained by observing the actions, decisions, and performance of other individuals (Danchin et al., 2004). Social information use is often thought to be less costly than gathering personally acquired information (Boyd & Richerson, 1988; Webster & Hart, 2006; Webster & Laland, 2008) and can lead to an increase in the fitness of the receiver (Boyd & Richerson, 1988; Danchin et al., 2004; Valone, 2007). However, as a trade-off, relying on social information can involve a loss of accuracy and reliability or give less up-to-date information (reviewed by Kendal et al., 2005). This was demonstrated, for example, in yellow warblers, (*Setophaga petechia*) which are hosts for the brood parasitic brown-headed cowbirds (*Molothrus ater)*. The frequency of nest parasitism by cowbirds underlie strong annual fluctuation and the hosts therefore rely on more current individually learned defense rather than social cues (Campobello & Sealy, 2011a). Reed warblers (*Acrocephalus scirpaceus*), on the other hand, which are very frequent victims of parasitism by the common cuckoo (*Cuculus canorus*) can enhance their nest defense by using social information (Campobello & Sealy, 2011b).

While the number of existing empirical studies on information use in general is high, the minority of them have addressed the use of social information with respect to breeding-site and habitat selection (Brown et al., 2000; Jaakkonen et al., 2013; Parejo, Oro, & Danchin, 2006) or reproductive investment decisions (Forsman et al., 2011; Schuett, Koegl, Dall, & Laaksonen, 2015). It has been suggested that the current reproductive success of conspecifics might give a more accurate prediction for the quality of a breeding habitat than other environmental parameters (Boulinier & Danchin, 1997). Depending on the context, some species can even switch between con- and heterospecific information use (e.g. pied and collared flycatcher, *Ficedula hypoleuca* and F. albicollis, switch depending on which have the higher density; Jaakkonen et al., 2014; Samplonius, Kromhout Van Der Meer, & Both, 2017). Indeed, individuals of many species 'prospect', i.e. visit breeding sites of other individuals (e.g. reviewed in Reed et al. 1999), likely to assess the quality of potential breeding sites in advance (e.g. Cadiou et al., 1994; Doligez et al., 2004; Pärt & Doligez, 2003). A good example of this behavior and its functional value was shown in an experimental study on collared flycatchers (Doligez et al., 2002). This European passerine reacted to patches of habitat with experimentally increased brood sizes with higher settlement of breeders in the following year, demonstrating the use of social information from conspecifics as a predictor for habitat quality (Doligez et al., 2002).

One important aspect that the collared flycatcher (Doligez et al., 2002) shares with most other avian species studied in this context (e.g. *Rissa tridactyla*: Boulinier et al., 1996; *Ficedula hypoleuca*: Schuett et al., 2017; *Corvus monedula*: Schuett et al., 2012) is that their breeding grounds are in temperate climates with an underlying annual periodicity, making the resources relatively predictable and the breeding schedules quite fixed. This means that the knowledge we have about information use and decision-making in a breeding context almost exclusively comes from studies conducted in rather stable and foreseeable environmental conditions. Other climatic regions, however, offer very different ecological conditions and challenges for animals. Arid zones, for example, are characterized by high spatial and temporal variability and are subject to drastic fluctuations of climatic elements (Morton et al., 2011), which is a stark contrast to the much more stable and certain conditions in the temperate zones. The difference in the predictability of environments is likely to affect how information is collected and used (Doligez et al., 2003; Feldman et al., 1996; Rafacz & Templeton, 2003), providing a basis for adaptive animal behavior (Dall et al., 2005). Therefore empirical studies on information use in highly unpredictable habitats will provide important insights into the more general importance of social information and its role in driving adaptive decisions (Schmidt, Dall, & Van Gils, 2010).

The zebra finch (*Taeniopygia guttata*) is a commonly studied passerine in the laboratory that is known to use social information in the context of foraging behavior (Farine, Spencer, & Boogert,

2015). In the wild, however, little is known about the importance of social information in this colonial species that is endemic to the arid zone of Australia. Confronted with a patchy habitat of varying quality it is conceivable that zebra finches would apply the same strategy of prospecting on the local reproductive success of conspecifics that has been seen in European passerines (e.g. Boulinier et al., 2008; Doligez et al., 2002; Doligez et al., 2004) to adjust their own choice of nesting site and investment in reproduction accordingly. Several models predict that social information could be perceived as an unreliable predictor for future reproductive success in an unpredictable environment, because of the lack of temporal autocorrelation in patch quality (Boulinier & Danchin, 1997; Doligez et al., 2003; Erwin et al., 1998). Attraction to breeding conspecifics, however, still seems to be a beneficial strategy in unstable environments (Mariette & Griffith, 2012a; Parejo et al., 2006). Additionally, data from a laboratory experiment on foraging starlings (*Sturnus vulgaris*), shows that social information can be perceived as more valuable in unpredictable conditions (Rafacz & Templeton, 2003).

Therefore, and in the light of the low number of empirical studies, it is currently not clear whether a social bird, such as the zebra finch living in an unpredictable environment, will disregard social information as predicted (Boulinier & Danchin, 1997; Doligez et al., 2003) and make decisions on the basis of personal information (Dall et al., 2005; Kendal, Coolen, & Laland, 2004; Kendal et al., 2005). The personal information can either be obtained directly through prior breeding

experience or from more recent indirect cues (Dall et al., 2005), such as rainfall, temperature or food availability (Zann, Morton, Jones, & Burley, 1995).

In this study, we used an experimental approach to test whether zebra finch reproductive decisions could be influenced by social information. We differentially manipulated perceived reproductive investment by creating three areas in which all laid clutches were artificially enlarged and three areas in which all clutches were reduced. Subsequent reproductive decisions were recorded to deduce what type of information was used. Zebra finches frequently prospect on the nests of conspecifics (Mariette & Griffith, 2012a) and we hence infer that individuals had the possibility to collect social information about the reproductive performance of conspecifics.

If zebra finches use social information for their reproductive decisions we expect them to settle primarily in perceived high quality patches and to lay larger clutches when breeding in those areas, as compared to the low quality patches. In the case that personal information on recent breeding success is preferred or outweighs the social cues we should observe a direct effect of the prior experience on the next brood. While breeding site choice and breeding investment should be random in the first brood, the subsequent brood would be affected by the respective personal breeding experience. Pairs that were only allowed to raise a small brood should be more likely to leave the area or lay a smaller clutch in the next breeding attempt, while their latency to rebreed might also be shorter. If neither social information nor personal breeding experience is exploited we may conclude that the birds relied on other environmental cues (Zann et al., 1995) or other social cues not measured in this study (e.g. acoustic cues: Waas et al., 2005).

METHODS

Study site and study species

Zebra finches are small passerines that live on a diet of grass seeds and employ a strategy of opportunistic breeding adapted to the harsh and fluctuating desert environment (Zann, 1996) Zebra finches show a high degree of mobility and presumably move over large distances to find patches of good condition in which to settle and breed (Zann, 1996). The often extended breeding periods are aseasonal and nest initiation is not strongly synchronized between pairs (Mariette & Griffith, 2012a; Zann, 1996). Zebra finches can have multiple successive broods if conditions are favourable and they are socially (Zann, 1996) and genetically monogamous (Griffith et al., 2010), with bi-parental brood care (Mariette & Griffith, 2012b). They live in loose colonies (Zann, 1996), which are held together by conspecific attraction (Mariette & Griffith, 2012a). Despite these aggregations in social groups, which also occur when drinking or foraging, zebra finches mostly move around in mixed-sex pairs, which thus seems to be the most important social unit (McCowan, Mariette, & Griffith, 2015).

The study was performed at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05'13.1"S 141°42'17.4"E), New South Wales,

Australia, between August and November 2015. The study site is a roughly rectangular area of 1.5 x 2 km with a dam in the centre that contains the only relatively permanent water body in the area. At this study site, 180 nest boxes were provided attached to metal stakes, which are readily accepted and even preferred as nesting locations over natural nesting sites (Griffith et al., 2008). Previous studies at the same site have shown that zebra finches move across the whole study area multiple times a day (Mariette & Griffith, 2012a; Mariette et al., 2011a), thus they should have access to information about the whole study site. Nests were monitored between August 1st and December 7th 2015. The first pairs had already commenced breeding by the beginning of August and birds continued breeding until March of 2016.

Clutch and brood manipulation

The manipulation of clutch and brood size was conducted for 80 days between August 28st and November 15th of 2015. Nest boxes were grouped in six clusters (mean distance to nearest neighbouring cluster = 41.4 ± SD 142 m) of 30 nest boxes each (mean distance to nearest neighbouring nest box within clusters = 10.4 ± SD 4.8 m). Three of these areas were randomly assigned to the 'high quality' (HQ) and three areas to the 'low quality' (LQ) treatment in pairs that were roughly equidistant from the central dam. Almost all clutches laid throughout the experiment were reduced or enlarged to a final clutch size of 3 eggs in the LQ areas and 7 eggs in HQ areas (mean clutch size in zebra finches = 4.9 ± SD 1.05 eggs; Griffith et al., 2008). Manipulations were conducted 6 days after clutch completion (± 2 days, as

necessary for matching eggs, see below), in the middle of the incubation period (incubation period ranging from 11-16 days; Zann, 1996). Zebra finches lay one egg per day (Zann, 1996) and clutches were considered complete when no new egg was added within a 24 hour period. All pairs that initiated breeding within the duration of the experiment started as focal individuals (and potential prospectors), before they became demonstrators (with manipulated clutch sizes) for later breeders. When an individual arrived at the study area it could collect information from individuals already breeding. At the time a breeding pair had decided where to build a nest and how many eggs to lay, the investment of these focal individuals, i.e. their natural clutch sizes, was recorded. Thereafter, the manipulations occurred and all previous focal individuals served as demonstrators for birds initiating nests at any later time point.

Eggs from clutches that were reduced were transferred to nests that were enlarged, matching the developmental stages of eggs in the respective nests. When not enough eggs at a certain stage were available, infertile eggs or eggs with hatching failure that had been collected from abandoned nests were used to increase clutch sizes (out of a total of 278 manipulated clutches: one non-viable egg was added to 23 clutches, two were added to 14 clutches, and three to 3 clutches). All nest box areas were regularly scanned for the occurrence of natural nests, which were removed immediately to prevent birds from gathering information from uncontrolled sources.

Nest box and bird monitoring

Nest boxes were routinely inspected every four days to monitor nest building and egg laying and then daily around the calculated approximate hatch date. Nesting attempts were only counted if the number of eggs was within range of natural clutch sizes (2-8 eggs; Griffith et al., 2008); any nests that did not meet the criteria, mostly cases of egg dumping and a few nests with one single egg, were excluded from the data. Besides the number of eggs laid (natural clutch size before manipulation), also the actual hatch date was recorded. Post manipulation, we counted the number of chicks on day 3 and day 11 (day 0 as hatch date). Between day 6 and 11 adults were caught in the nest boxes using nest box traps. We successfully trapped at least one adult at 236 out of 288 nests. All trapped adults and 11-day-old chicks were banded with a uniquely numbered metal band (Australian Bird and Bat Banding Scheme). We did not check nest boxes after day 11 to avoid the risk of premature fledging and assumed that they had fledged if the box was empty on day 19. Throughout the experiment we provided supplementary food by placing a permanent feeder in the centre of each area (for details on feeders see Mariette & Griffith, 2012a). Since it was not possible to quantify the availability of natural food, these feeders were used to ensure that the provision of artificial food was constant across the experimental areas and reduce the likelihood that food was a limiting factor when raising increased size broods. All feeders were checked daily and refilled with commercial finch seed mix when empty. Previous studies have shown that the distribution of food and water in the landscape determines the nest site choice of zebra finches on a larger scale (max. observed nest distance from water 25 km; Zann, 1996), but not on a small scale (in areas 1-2 km wide; Mariette & Griffith, 2012a).

Data analysis

To test for any potential bias before the start of the experiment, we ran a linear mixed effect model (LMM) with the clutch size of all nests that were laid in the monitoring period before the start of the experiment as response variable, and the prospective treatment (HQ, LQ) of the areas as fixed effect (Table 3.1, Model 1). The model included area as a random term (i.e. random intercept throughout). To assess whether the effects of our manipulation were sufficient to carry-over until chicks were close to fledging, we fitted an LMM with treatment as fixed effect and the number of chicks on day 11 after hatching as a response variable. Here, we only included nests that had hatched at least one chick. Area and nest box were included as random terms. The latter was included in the model, because up to four nests had been initiated in some nest boxes during the experiment.

We tested whether the total number of initiated broods in the HQ and LQ areas differed from one another with a χ^2-goodness-of-fit test, only including the first brood of each pair to exclude personal information effects. χ^2-tests of independence were conducted to compare the number of successful nests (i.e. nests that did/did not hatch at least one chick) and survival rates (i.e. number of chicks that survived/died between day 3 and day 11) between treatments.

We fitted another LMM to analyse the effect of our manipulation on breeding investment (Table 3.1, Model 2). We assessed the effects of treatment using the natural clutch size as response variable and day of experiment (days since beginning of experiment) and the two-way interaction between treatment and day of experiment as fixed effects. The interaction between treatment and day was included to control for the fact that the amount of manipulation increased over time (also see below). To further investigate whether an effect of the treatment was potentially only significant at a certain stage in the experiment we also fitted LMMs with the natural clutch size as response variable and treatment as fixed effect using data from three different stages of the experiment: 'early', i.e. day 1 - 27; 'mid', i.e. day 28 - 54; and 'late', i.e. day 55 - 80 of the experiment. We included nest box and area as random effects. Only the first breeding attempt of each pair within the experiment was included in these models to exclude the effect of personal experience.

The number of already manipulated nest boxes and thus, also the amount of social information that was currently available for breeding pairs increased throughout the experiment. Even though this factor is important, we did not include the total number of manipulated nest boxes at each day in any models to avoid multicollinearity: the number of manipulated boxes and day of experiment were strongly positively correlated (Spearman rank correlation: $r_s = 0.976$, N = 288, P < 0.001). Thus, we were not able to disentangle the effects of the number of manipulated boxes from other time dependent effects such as seasonal variation. Hence, we only used 'days of experiment' in

models to represent all time-dependent variation. The 'number of manipulated nest boxes' for each nest was calculated as the total number of boxes in the study site that were manipulated at the date the female approximately instigated egg laying (i.e. 22 days before hatch date; 5 days to make an egg, an average of 5 days for egg laying, plus around 12 days of incubation; Blount et al., 2006; Zann, 1996).

In two additional LMMs we tested the effects of personal experience through repeated breeding on breeding investment and in another LMM the effect on latency to rebreed (Table 3.2). Here we included only data of pairs that bred twice during the experimental phase (at least the first brood during manipulations, some bred again after). We tested whether birds that had experienced the treatment of their respective breeding area first-hand would use this information to make adjustments for their next brood. In a first model we analysed whether natural clutch size (response variable) changed with the brood order, i.e. first or second brood (also including treatment and days of experiment as fixed effects) to test for a general effect of repeated breeding (Table 3.2, Model 3). To analyse the impact of prior experience in more detail, we fitted another LMM focusing on the influence that the specific investment in the first brood has on the second brood (Table 3.2, Model 4). In this model we used natural clutch sizes of the second broods as a response variable and included the natural clutch size and the treatment of the corresponding first broods as fixed terms. Another LMM was used to assess whether personal experience affected the latency to rebreed between the start of the first brood and the start of the next brood

(Table 3.2, Model 5). Number of days between start of egg laying in consecutive broods was used as response variable in a model including clutch size, treatment and fledging success (yes/no, at least one chick fledged) of the first brood as fixed terms. In the first LMM we used pair ID, nest box and area as random terms, in the second model we included the area of the second brood and in the last model area of the first brood was used as random term.

Full models were always reduced by stepwise removing the least significant terms, as determined by likelihood ratio test between models (Crawley, 2007). Terms were only removed if the explanatory power of the simpler model was not significantly reduced, when compared to the more complex model with likelihood ratio tests (Crawley, 2007). Random effects were conservatively not reduced. We checked that model assumptions of LMMs were not violated using diagnostic plots and based on this selected normal error structure as the best fit. Profile likelihood ratio confidence intervals were calculated for all fixed effects (Colegrave & Ruxton, 2003). All statistical analysis were conducted with R (R Core Team, 2014). For LMMs we used the package 'lme4' (Bates et al., 2014). Statistics are presented as mean ± standard deviation (SD) throughout.

A total of 38 clutches were removed from the data because the eggs were found already abandoned before, or at the time the manipulation should have taken place, or the eggs disappeared from the nest (e.g. due to predation). These nests were then removed from the nest boxes and hence should not have strongly affected potential prospectors. It was not possible to record data blind because our study involved focal animals in the field.

RESULTS

Effect of manipulation on clutch size and brood success

The clutch sizes of the nests that were recorded in August, before manipulations started, did not differ between prospective treatment areas (Table 3.1, Model 1). We manipulated the size of 278 (of 288) clutches laid in 170 nest boxes by 273 zebra finch breeding pairs. After the manipulations mean clutch size was 6.88 ± 0.50 eggs in the HQ nests and 3.07 ± 0.36 eggs in the LQ nests. The effect of the manipulation was also carried over to the number of surviving chicks: on day 11 after hatching broods in the HQ areas were still larger (mean number chicks day 11: 4.13 ± 2.10 chicks) compared to broods in the LQ areas (mean number chicks day 11: 2.38 ± 1.06 chicks; $\chi^2_1 = 14.345$, N = 246, P < 0.001)

Effects of treatment on natural clutch sizes

There was no significant difference in the total number of broods initiated in HQ areas (140 broods; mean no. broods per area = 46.67 ± 1.53) compared to LQ areas (133 broods; mean no. broods per LQ area = 44.33 ± 5.51; $\chi^2_1 = 0.179$, $P = 0.672$) we recorded throughout the experiment (not including second broods some individuals had). Overall, 94% of the experimental nests hatched at least one chick with no significant difference between the treatment areas ($\chi^2_1 =$

Table 3.1. Summaries of LMMs to assess the differences in reproductive measures between treatment areas before the start of the experiment (Model 1) and to assess the effect of treatment (HQ, LQ) and day (days since start of the experiment) on the number of eggs laid by zebra finches in their first broods within the experiment (Model 2). Significant p-value is highlighted in bold. Estimates of coefficients and 95% confidence intervals (CI) are estimates for the variables in minimal adequate model; values in brackets represent coefficients and confidence intervals in full model. (exp. = experiment, manip. = manipulation, treatm. = treatment).

Model number	Response variable	Predictor variables	Estimates	CI	N	X^2	df	P
1 (before manip.)	*Natural clutch size*	(intercept)	4.145	3.78 – 4.55	34			
		treatment [LQ]	(0.263)	(-0.41 – 0.90)		1.19	1	0.275
2 (after start of manip.)	*Natural clutch size*	(intercept)	5.108	4.81 – 5.40	273			
		treatment [LQ] * day	(-0.002)	(-0.01 – 0.01)		0.17	1	0.679
		treatment [LQ]	(-0.092)	(-0.66 – 0.48)		1.23	1	0.268
		day	-0.007	-0.01 - <-0.01		5.87	1	**0.015**

0.015, *P* = 0.903). Likewise, the mean rate of surviving chicks from day 3 to day 11 was not significantly different between HQ (82 ± 34% of the nestlings on day 3 were still alive on day 11) and LQ areas (85 ± 33% nestlings survived; χ^2_1 = 2.207, *P* = 0.137). In 70% of the HQ broods and 81% of the LQ broods all chicks survived between day 3 and day 11. In 18% of the HQ broods 1 or 2 chicks died and in 11% of broods 3 - 7 chicks died.

The natural number of eggs laid per nest was not affected by the treatment or an interaction between treatment and day of experiment. However, clutch sizes decreased significantly over the duration of the experiment (Fig. 3.1; Table 3.1, Model 2). Also when the effect of treatment was analyzed separately for each of three different stages of the experiment it was non-significant ('early': χ^2_1 = 0.001, N = 73, *P* = 0.984, 'mid': χ^2_1 = 0.175, N = 98, *P* = 0.676; 'late': χ^2_1 = 1.398, N = 102, *P* = 0.237).
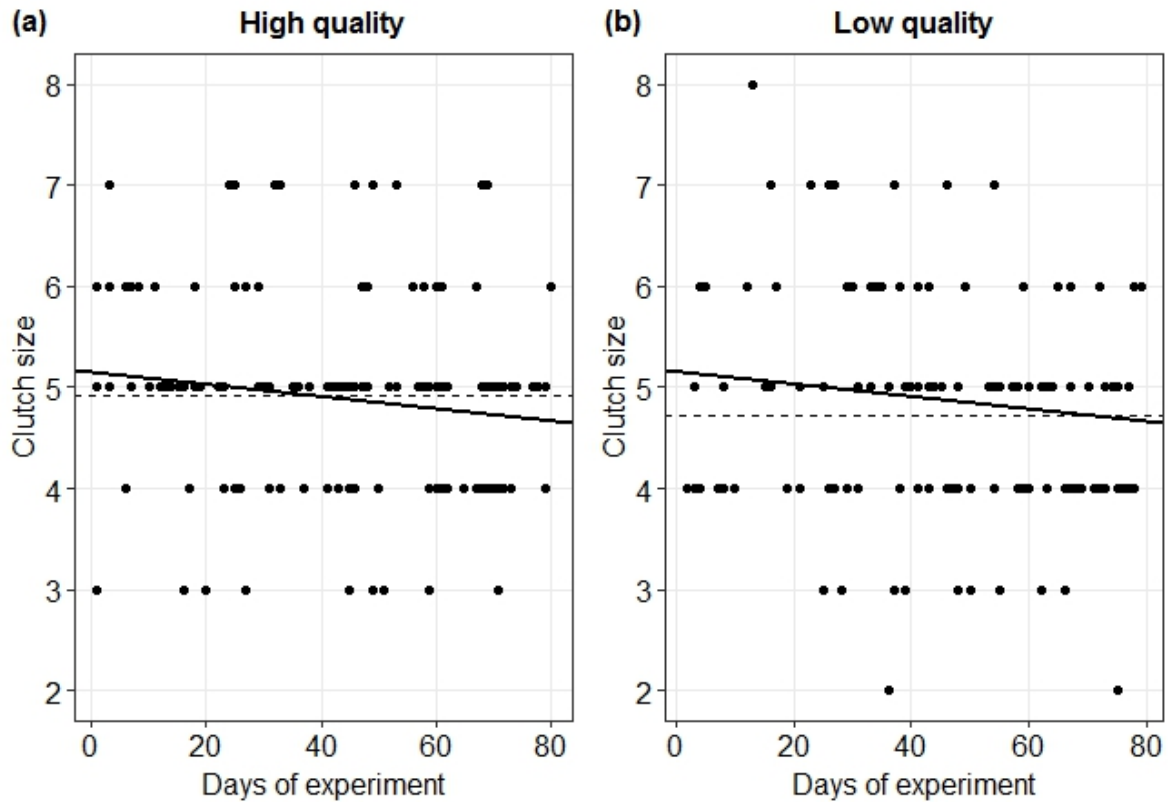
Figure 3.1. Number of eggs per clutch in (a) HQ and (b) LQ treatment areas laid at each day of the experiment, respectively. The dashed lines represent mean clutch sizes (calculated from raw data), the solid line predicts clutch sizes at each day of the experiment (based on the output of the minimal model, see Table 3.1, Model 2).

Effects of personal information through repeated breeding

During the monitoring period 24 breeding pairs bred multiple times (one pair three times, the others twice). However, eight of them laid their first clutch before the start of the experimental period, leaving 34 broods from 17 pairs for analyses of the effect of personal information. Most of these pairs with multiple broods did not move to another area after the first brood. They continued breeding in the same experimental area, but did not continue to use the same nest box. Only three pairs switched areas; two pairs raised their second brood in a HQ area after breeding in LQ area before and one pair moved from one LQ area to another LQ area. Including only pairs that had the experience of a first brood in the experiment (8 pairs in HQ, 9 in LQ), second clutches were significantly smaller than their first clutches reflecting the overall pattern in the broader dataset with declining clutch size as the season progressed. Treatment and lay date in relation to the duration of the experiment, however, did not predict clutch size (Table 3.2, Model 3). When analyzing the specific effect of prior experience on number of eggs in the second brood, neither clutch size nor treatment of the first brood had a significant effect on number of eggs laid in the second brood (Table 3.2, Model 4).

The time between the start of two consecutive breeding attempts of the same pair was not significantly affected by clutch size or treatment of the first brood (Table 3.2, Model 5). Only fledging success explained some of the variation, i.e. the interval between broods was significantly longer when at least one chick of the first brood fledged successfully. The mean time interval between the start dates of two consecutive breeding attempts of the same pair, as estimated in the model, was 53.7 ± 10.9 days in broods that fledged successfully and 31.3 ± 5.56 days in nests where all chicks died before fledging.

DISCUSSION

In this study we used an experimental approach to test the hypothesis that wild zebra finches exploit social information in making reproductive decisions. We manipulated clutch size in a relatively high number of zebra finch nests, creating the perception of a patchy environment, with respect to conspecific reproductive investment. The zebra finches in our experiment did not strongly rely on socially acquired information as shown by the results that clutch sizes were equal between treatments and areas of higher reproductive success were not preferred areas for new nesting activity.

The lack of evidence for social information use in our study is compelling, because it is in stark contrast to the findings of a series of other studies showing that social cues are successfully used as a predictor for reproductive success in birds (e.g. Danchin et al., 1998; Doligez et al., 2002; Parejo et al., 2007; Ward, 2005). These studies all offer substantive evidence for birds relying on social cues from conspecifics when breeding in a temperate climate where they can rely on relatively stable environmental conditions and seasonal predictability.

Table 3.2. Summaries of LMMs assessing the effect of personal experience for subsequent breeding attempts (Model 3 and 4) and the time interval till the next breeding event of the same pair (Model 5). The first model (Model 3) uses a general approach exploring effects of brood order, treatment (HQ, LQ) and day of experiment on clutch sizes, whereas the second model (Model 4) uses a more direct approach exploring effects of variables linked to the experience of the first brood on the clutch size of the second brood. Fledging success (fledge succ.) was coded as yes (at least one chick presumably fledged) or no (all chicks died before fledging). Significant p-values are highlighted in bold. Estimates of coefficients and 95% confidence intervals (CI) are estimates for the variables in minimal adequate model; values in brackets represent coefficients and confidence intervals in full model. (exp. = experiment, nat. = natural, treatm. = treatment).

Model number	Response variable	Predictor variables	Estimates	CI	N	X^2	df	P
3	*Nat. clutch size*	(intercept)	5.353	4.82 – 5.89	34			
		brood order [second]	-0.824	-1.48 – -0.17		5.78	1	**0.016**
		treatment [LQ]	(-0.130)	(-0.99 – 0.82)		0.12	1	0.725
		day	(0.015)	(-0.01 – 0.04)		1.14	1	0.285
4	*Nat. clutch size in 2nd brood*	(intercept)	4.529	4.01 – 5.05	17			
		nat. clutch size of 1st brood	(0.293)	(-0.12 – 0.71)		2.05	1	0.153
		treatment of 1st brood [LQ]	(-0.710)	(-1.65 – 0.23)		1.77	1	0.183
5	*Time between broods*	(intercept)	31.333	19.54 – 43.13	17			
		nat. clutch size of 1st brood	(3.751)	(0.56 – 6.43)		0.03	1	0.869
		treatment of 1st brood [LQ]	(0.450)	(-11.60 – 9.58)		2.60	1	0.107
		fledge succ. 1st brood [yes]	22.381	9.39 – 35.38		9.48	1	**0.002**

Social information in fluctuating and unpredictable conditions has mainly been dealt with in theoretical models, which have predicted a less frequent use with an increasing probability of environmental change (Boulinier & Danchin, 1997; Boyd & Richerson, 1988; Doligez et al., 2003; Feldman et al., 1996). This prediction is justified for certain scenarios and information needs to be up-to-date to be reliable. However, empirical studies in the field (e.g. Boulinier & Danchin, 1997; Doligez et al., 2002; Parejo et al., 2007; Ward, 2005) have all been based on the premise that information on patch quality is firstly always collected in the preceding season and secondly, that in this preceding season a trade-off between information gathering and reproduction exists. The first assumption is unlikely to be valid for zebra finches and the latter also needs to be put in question. Birds living in arid environments have greatly extended potential breeding seasons, compared with those in the more seasonally predictable northern hemisphere temperate zone (Duursma et al., 2017) and in any one year, can also breed multiple times. Shorter intervals between breeding attempts increase the chance that information is still valid for the subsequent brood. Also nest initiation in zebra finches is not strongly synchronized (Mariette & Griffith, 2012a). Hence zebra finches have conspecific cues available not only at the end of a breeding cycle and could potentially both collect information and initiate a brood shortly thereafter. Therefore, the trade-off between information gathering and breeding (if still existing) should be less pronounced.

While it is important to point out these ecological differences, the results of our study are still in line with theoretical predictions (Boulinier & Danchin, 1997; Doligez et al., 2003; Feldman et al., 1996). It is still plausible that the absence of social information use in our study might be due to the low predictability of the environment zebra finches live in. It is perhaps disadvantageous to take cues from others when conditions and hence the outcome is inconsistent even on a relatively short intra-annual timescale. Additionally, it is also possible that a mix of different sources of information is used and social information was over-ridden by personal information. Another study has demonstrated the opposite effect, with an experiment in which social cues outweighed personal habitat preferences of a migrant passerine usually breeding in very stable hardwood forests (Betts et al., 2008). In the context of defense against brood parasites combining personal and social information has been identified as a successful strategy (Thorogood & Davies, 2016). In our study, it appears that the social information was, if maybe not completely ignored, at least outweighed by other factors. The mechanisms are diverse and it becomes increasingly obvious that the specific ecological circumstances need to be regarded as a significant factor in the study of information use.

Two of the key variables defining what type of information will be used are the cost of obtaining information and its reliability (Dall et al., 2005). The cost of obtaining social information in the context of our study is mainly the time and energy invested in prospecting. The cost for personal experience, on the other hand, is a breeding attempt with potentially sub-optimal parameters. The acquisition of social information should therefore be the less costly strategy (Doligez et al., 2003;

Giraldeau, Caraco, & Valone, 1994; Laland, 2004). In our experiment, social information indicating either high or low reproductive success of conspecifics was readily available for individuals prospecting on neighboring nest boxes, which was frequently observed (see also Mariette & Griffith, 2012a). This behavior has also been described in many other bird species (e.g. Reed et al., 1999). Zebra finches are not territorial, and we have not observed any overt conspecific aggression around nest boxes. Furthermore, there are usually many nests within 100 m of a focal nest. Thus, there is unlikely to be a significant cost in finding and inspecting neighboring nests. We can assume that this investment of time and energy (probably also involving increased predation risk) also brings along benefits. Hence, it seems likely that prospecting is used to gather social information, but in different ways than tested by our hypothesis. For instance, social cues could be used for predation avoidance or to help with optimal timing. Such hypotheses will need to be tested in further experiments.

Our experiment did not include a treatment with average brood sizes as a control and thus did not test the response to the average brood size. Our manipulation, however, was within the range of natural clutch and brood sizes in this species and therefore was unlikely to have been perceived as unnatural. Even if zebra finches had a preference for an average brood size, it is reasonable to expect that offered a binary choice (smaller or larger brood), they would have been able to make a decision, given the likely fitness consequences of producing either too many, or too few offspring in the prevailing conditions (as

signaled by conspecifics, if this did serve as a source of information).

Our results showed quite clearly that social information was not the main cue used for reproductive investment decisions (at least for the parameters we measured), leaving personal information as an alternative source of information. Our experimental brood manipulation also affected the personal experience of breeding individuals. In the succession of multiple broods, it was possible for zebra finches to collect personal information on their own (manipulated) breeding success and make decisions accordingly in subsequent broods. When birds first entered the experiment, they had no personal experience with the treatment of the different nest box areas (breeding activity was very low in the area in the months before our experiment started, so most of the pairs in our experiment would have been breeding for the first time in this area). Decisions made at this point were either based on social cues from conspecifics (which we have largely excluded) or based on other sources of personal information (e.g. food availability or other environmental parameters). In any following brood, however, personal information on an individuals' own breeding success in a respective treatment area was existing. We found no indication that individuals altered their behavior or investment in relation to the component of personal information manipulated in our experiment. Pairs breeding multiple times did not alter their clutch size in response to the previously experienced treatment and movements between areas from one brood to the next were very rare, and not predicted by the experimental treatments. In a rapidly changing ecological situation, even the

personal information from a previous brood might be more outdated than the contemporary available personal information on the intrinsic quality of the habitat, such as food availability. Personal information obtained by monitoring other environmental parameters might give the most reliable representation of a quickly changing environment and hence allow for the best response. Once favorable conditions arise, zebra finches are able to time the hatching of the first chicks accordingly (Zann et al., 1995).

Our prediction for this experiment was that birds from LQ areas would move to HQ areas. However, birds rarely changed the area between breeding attempts at all. Our results confirmed a previous finding that zebra finches move to another box for a subsequent brood, but stay closer to the old one than expected by chance (Mariette & Griffith, 2012a). It is remarkable that this strategy is still valid for the birds even after we had manipulated their own brood and that of the conspecifics breeding nearby. Even in the LQ areas, where individuals suffered low reproductive success during the experiment, zebra finches mostly remained in that area. There may have been benefits of becoming familiar with the area, as shown in birds and lizards (Bruinzeel & van de Pol, 2004; Piper, 2011; Stamps, 1987). Another explanation could be that birds simply perceived all areas as equally high quality habitats due to the food supplementation. This would mean that they ranked the personal information on available resources higher than personal breeding success (or social information). Another study on the same population, however, has shown that zebra finches did not cluster their nests around either food or water (Mariette & Griffith, 2012a).

Our prediction that parents raising larger broods would have a longer interval between consecutive breeding attempts, as demonstrated in great tits (Parus major; Slagsvold, 1984), was not supported. Lemon (1993) showed that zebra finches with experimentally extended time required for foraging increased the time interval between successive broods. In our experiment, food availability was equal in both treatments, thus perhaps levelling some of these associated effects. Only the successful fledging of chicks led to a longer time interval between broods in our study. This is not surprising, since fledglings require a period of 15-20 days further care until full nutritional independence from parents (Zann, 1996). During this period where fledglings are still provisioned by parents the next breeding attempt cannot be initiated. The relative high survival rate throughout may also be explained by birds having sufficient food available. This could have enabled them to partially or fully compensate for the challenge of raising additional chicks. Studies have shown negative impact of increases in reproductive effort on future competitiveness, at least for species in temperate climates (Fokkema, Ubels, & Tinbergen, 2016, 2017). Unfortunately no such data are available for wild zebra finches and the extremely low return rate of individuals to the same site between years makes it hard to impossible to study this effect.

Zebra finches generally employ a high level of opportunism in their breeding strategy. They breed whenever conditions are favorable in terms of food availability,

which can be at any time of the year (e.g. Zann, 1996). As adaption to the unpredictability of breeding periods and in contrast to seasonally breeding vertebrates their reproductive system is constantly activated (Perfito et al., 2007; Wingfield, Hahn, Levin, & Honey, 1992). We were not able to change the breeding decisions of the birds in any obvious way with our manipulations. Thus, perhaps there is also a certain degree of opportunism involved in other reproductive aspects (e.g. nest site choice and clutch size), besides the timing. The factors involved in determining the clutch size of zebra finches are not fully understood, but nutritional aspects appear to be involved (Zann, 1996). While the energetic costs of foraging were not found to directly affect clutch sizes of immediate broods (Lemon, 1993), other studies showed that optimized female nutrition early in life (Haywood & Perrins, 1992) and in the pre-breeding period (Selman & Houston, 1996) increase clutch sizes. It is possible that zebra finches opportunistically maximize their reproductive output given their state and quality as soon as environmental conditions become favorable. Therefore, they might primarily rely on abiotic environmental cues (e.g. density and abundance of grass seed) rather than social cues or information obtained from previous breeding. Especially in quickly changing environments information on own or conspecific breeding success might be outdated quickly.

Our results suggest that species (or populations) reproducing in unpredictable environments might substantially differ in their information use from those living in more predictable environments, such as temperate environments with fixed and constrained schedules for reproduction.

More studies outside temperate environments are now needed to shore up our findings and to advance our understanding of information use under a range of environmental conditions.

CHAPTER 4

Wild zebra finches choose neighbours for synchronized breeding

ABSTRACT

Organisms should aim to time their reproduction to match the optimal ecological conditions. Nevertheless, the observed breeding synchrony within populations is often higher than can be explained by ecological conditions alone. Social cues have been identified as determinants of reproductive decisions in temperate habitats, where autocorrelation in patch quality allows using reproductive success of conspecifics as a predictor for the forthcoming season. Social information use in unpredictable habitats, where such predictions might not be reliable, is less well understood to date. In highly fluctuating environments, social information might possibly serve as an important cue for temporal rather than spatial coordination. To examine this idea, we conducted an experiment on wild zebra finches, breeding in the ecologically unpredictable arid zone of Australia. In the wild, they frequently visit the nests of conspecifics, potentially prospecting for information, but the value and consequences of such visits are currently unclear. We experimentally tested whether wild zebra finches preferentially seek to breed adjacent to conspecifics at early stages (nest building), to synchronize reproduction with them. We found that zebra finches were more likely to initiate egg laying in boxes close to conspecifics at an early stage of breeding, suggesting that they prefer highly synchronized breeders as neighbors over more advanced ones, even though the latter would provide better evidence of reproductive success. We thus provide new insight into the social ecology of an opportunistic breeder in an unpredictable environment and propose new aspects to be considered in the study of information use in such habitats.

INTRODUCTION

Individuals will optimize their reproductive output by timing their reproduction to match the best ecological conditions, resulting in high levels of reproductive synchrony across many plant (e.g. Franklin, 2004; Satake & Iwasa, 2000) and animal populations (e.g. Hodge, Bell, & Cant, 2011; Koenig & Liebhold, 2005; Youngflesh et al., 2018). Especially in temperate and highly seasonal climates, breeding seasons can be restricted to relatively short periods and are often driven by a variety of abiotic factors such as temperature, photoperiod, humidity (e.g. Ims, 1990a) in addition to food availability (e.g. Both, 2010; Seress et al., 2018). However, even in habitats with less pronounced seasonality, such as the tropics, reproduction is temporally much more clustered than would be expected by chance (e.g. Helm, Piersma, & van der Jeugd, 2006; Ims, 1990a). Following this observation, several other ecological (e.g. predation, pollination and seed dispersal) and sociobiological (e.g. mating system, density and communal breeding) factors have been identified, which might contribute to the timing of reproduction and promote synchrony across individuals within a population (or asynchrony; reviewed in Ims, 1990a).

One potential advantage of reproductive synchrony is postulated in the 'predator swamping hypothesis' (Fraser Darling, 1938). Predator swamping by saturating predators with high numbers of potential prey emerging at the same time can increase offspring survival rate (e.g. Ims, 1990b; O'Donoghue & Boutin, 1995; Sweeney & Vannote, 1982). Similar to the predator swamping hypothesis, but a more

general advantage of group living can be the 'encounter' and the 'dilution' effect, which describe the decreased likelihood of an individual being detected or attacked by predators with increasing group size (e.g. Bellinato & Bogliani, 1995; Inman & Krebs, 1987). Another advantage, of a synchronously breeding group of adults, is that it can help parents and offspring maximize the benefits of social foraging, i.e. collectively discover and visit food sources. As a consequence, when pairs within a population synchronize their breeding with each other, it can positively affect the number of offspring produced and reduce nest predation (e.g. Westneat, 1992). As breeding synchronization requires temporal coordination between groups (or at least pairs) of individuals, it is often found in species breeding in colonies. In the blue-black grassquit (*Volatinia jacarina*), for example, the reproductive synchrony was almost five times higher in females living in aggregations compared to those on solitary territories (Dias, Kuhlmann, Lourenço, & Macedo, 2009).

A multitude of different social interactions between individuals can directly affect aspects of reproductive timing, either by stimulating, or inhibiting reproductive activity (reviewed in birds: Helm et al., 2006). For example, an experimental playback of colony sounds, was demonstrated to stimulate breeding activity and to positively affect clutch size in zebra finches *(Taeniopygia guttata*; Waas et al., 2005). In colonially breeding species in particular, breeding synchronization might be strongly influenced by social information (Helm et al., 2006), as there are a lot of other individuals available from which to glean information about the local environment.

Social information use has been relatively well studied with regards to spatial aspects of breeding, i.e. breeding site choice, particularly in European birds (reviewed in Reed et al., 1999). In many species, individuals prospect at breeding sites to assess their quality and suitability for their own future reproductive attempts (e.g. Boulinier et al., 1996; Doligez et al., 2002). The variation in quality of an area or nest site may be correlated both spatially and temporally, and therefore nest prospectors may gather useful information that is relevant to both spatial and temporal decisions about reproduction (Helm et al., 2006).

Zebra finches are small, granivorous passerines living in the arid zone of Australia. They are socially (Zann, 1996) and genetically (Griffith et al., 2010) monogamous and exhibit biparental brood care (Mariette & Griffith, 2012b). They exhibit nomadic movement patterns in search of favorable conditions in which to breed (Zann, 1996). Adapted to an opportunistic breeding strategy, the reproductive physiology of zebra finches is in a permanently activated state which allows breeding at any time of the year (Perfito et al., 2007), and they can have multiple successive broods within an extended period of reproduction (Zann, 1996). On a larger scale, the distribution of food and water in the landscape determines the nest site choice (max. observed nest distance from water 25 km; Zann, 1996), but the distribution of resources does not appear to have an effect on a small scale (in areas 1-2 km wide; Mariette & Griffith, 2012a). While zebra finches form aggregations whilst foraging and visiting water, they mostly move around in small groups made up from a number of mixed-sex pairs, with the pair being the most important social unit (McCowan, Mariette, et al., 2015). Previous observational work has provided support for the idea that a pair starting a new reproductive attempt will preferentially choose to initiate that attempt near breeding conspecifics (i.e. conspecific attraction), and particularly successful ones (Mariette & Griffith, 2012a). These previous observational results suggested that there is some form of social information transfer across the population, and perhaps some level of coordination between pairs within the population.

Wild zebra finches regularly prospect at conspecific nests (Brandl et al., 2018; Mariette & Griffith, 2012a). Though, we can assume that this prospecting is driven by the potential to gather information, the experimental evidence so far suggests that it does not play a role in determining either the location of a nest, or the level of investment in a reproductive attempt (Brandl et al., 2018). These are two of the main benefits of nest prospecting in temperate breeding birds in the northern hemisphere (e.g. Doligez et al., 2004; Pärt et al., 2011). The unpredictable ecology of the arid zone (Morton et al., 2011), means that social information gathered at one time, is unlikely to be a good predictor of habitat quality a year henceforth, as it is in species in the temperate zone of Europe (e.g. Boulinier & Danchin, 1997; Erwin et al., 1998). As a result, nest prospecting might be focused on gathering social information at a more immediate temporal scale, and perhaps is primarily used to coordinate reproductive timing between pairs in close proximity. If this is true, then it opens up a new perspective on the benefits and determinants

of nest prospecting in birds, and will expand the focus of the work to date, that has been focused on studies of seasonal breeders in the northern hemisphere temperate zone.

We conducted an experimental field study on wild zebra finches, attempting to bridge the knowledge gap on reproductive synchrony in the ecologically unpredictable Australian arid zone, where reproductive activity across species, each year, typically lasts across a period of time that is more than twice as long as in species breeding in the temperate zone of the northern hemisphere (Duursma et al., 2017). With an experimental approach, we offered zebra finches vacant nest boxes adjacent to conspecifics which were at an early (nest building), mid (egg incubation), or late stage (chick rearing) of the nesting cycle. If zebra finches try to synchronize breeding with close neighbors, we expect them to be more likely to choose to initiate breeding attempts next to zebra finch nests at the nest building stage than those at later breeding stages (eggs and chicks). This strategy would entail prioritizing the value of being spatially connected with another simultaneous breeding attempt, over the potential value of nesting near a successful conspecific (given that the presence of chicks in a nest provides a signal of success to that point). In addition to providing a new perspective on social information use in a highly flexible breeder in an unpredictable habitat, this study will also provide insight into the behavior of the zebra finch in the wild, which will be useful given the current focus on social information use in the this species in the laboratory (e.g. Farine, Spencer, et al., 2015).

METHODS

Study site

The experiment was conducted at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05'13.1"S 141°42'17.4"E), New South Wales, Australia, between August and December of 2016. The study site covers about 1.5 x 2 km and has an artificial dam in the center, holding a relatively permanent source of water for drinking. We provided 180 wooden nest boxes (12/18 cm front/back height, 9.3 cm width, 14 cm depth; entry hole 3 cm diameter), attached to metal stakes (further details: Griffith et al., 2008). Nest boxes were arranged in six clusters (mean distance to nearest neighbouring cluster = 413.6 ± SD 142 m) of 30 nest boxes each (mean distance to nearest neighbouring nest box within clusters = 10.4 ± SD 4.8 m) and are readily accepted for breeding (Griffith et al., 2008). An additional 45 nest boxes, which were positioned solitarily were not included in the study because they were spread out in the area peripheral to the study side at much lower density.

Experimental procedure

For each trial, three existing, occupied nest boxes were selected as stimulus boxes in one of the six nest box areas (mean distance between stimulus boxes within trials = 80.8 ± SD 41.9 m). The nests in stimulus boxes were at one of the following stages each: *nest building* (i.e. 5-50% nest material, no eggs at start of trial), *egg incubation* (i.e. clutch completed and being incubated), and *chick rearing* (i.e. post-hatching; N = 35 trials). Three empty nest boxes, the experimental boxes, were erected in close

proximity (2 – 4 m) to each one of the stimulus boxes for five days. The empty experimental boxes (which were identical in construction to the stimulus ones) were matched with the stimulus boxes in height and orientation, and were also attached to the same kind of metal post. During the five days of a trial, the experimental boxes were checked daily for the initiation of *nest building* (indicated by nest material in the box) or *egg laying*, which was each encoded as a binary variable (yes/no). The number of days it took for nest building and egg laying to begin was also recorded for each box.

Data analysis

We fitted two generalized linear mixed effect models (GLMMs) with binomial error structure to assess the effect of the treatment (i.e. nest stage of stimulus box at the initiation of trial; three levels: *nest building*, *egg incubation*, *chick rearing*) on the probability of zebra finches initiating nest building and egg laying during a trial, respectively, in the corresponding experimental boxes. Whether nest building or egg laying was initiated was evaluated only once per trial, i.e. the final outcome of a five-day trial. We used two additional GLMMs with Poisson error structure to test the effect of the treatment on the latency to the initiation of nest building and egg laying, this time only using the subset of the data where nest building and egg laying, respectively, had been initiated during the trials. All four models included *treatment* (nest building, egg incubation, chick rearing) and *nest continuation* of the stimulus nest as fixed terms. The variable *nest continuation* was introduced to account for the fact that the nests used as stimuli

appeared to vary in the success of their progression (see below).

In 20 of the 35 stimulus boxes at the *nest building* stage, egg laying commenced within the five-day duration of the trials. The other 15 nests remained at the *nest building* stage for five days without any apparent progress, in which case we suspected that the nesting attempt was aborted at some point. Further, in four stimulus nests of the *egg incubation* stage eggs appeared cold at the end of the trial and were presumably abandoned during the trial. Hence, to control for this variation in the stimulus nests, the binomial variable 'nest continuation' (yes/no; 'no' meaning that nests were presumably abandoned) was included into the models. Stimulus nests of the *chick rearing* treatment group were always coded as 'yes' for nest progress. In five stimulus nests of the *chick rearing* treatment the chicks died or were predated before the end of a trial, upon which this treatment was aborted and the data completely removed from the data set (N = 5 stimulus nests), leaving a total of 100 stimulus nests (35 trials á 3 stimulus nest boxes minus 5 failed nests at chick stage). All models included nest box, area and trial as random terms.

We obtained minimal adequate models by stepwise reducing full models; i.e. the least significant term, as determined by likelihood ratio test between models, was removed, one after another (Crawley 2007). Only terms that did not significantly reduce the explanatory power of a model, when compared to the more complex model, were removed (Crawley 2007). We conservatively did not reduce random effects. For significant terms with more than two levels Tukey's pairwise comparison

was performed with fdr-adjustment for the reported p-values (Benjamini & Hochberg, 1995). All statistical analyses were conducted in the R environment (R Core Team 2014). For GLMMs we used the package 'lme4' (Bates et al., 2014). Multiple pairwise comparison was performed with the package *multcomp* (Hothorn, Bretz, et al., 2008). The boxplots were created using estimated model predictions based on 1,000 simulations for each observation using the R package *merTools* (Knowles & Frederick, 2016); *ggplot2* (Wickham, 2010)*, ggsignif* (Ahlmann-Eltze, 2017) and *cowplot* (Wilke, 2017) were used for visualization. Statistics are presented as mean ± standard deviation throughout.

RESULTS

Nest building was initiated in 47 out of 100 experimental nest boxes (19 in the *nest building*, 14 in the *egg incubation* and 14 in the *chick rearing* treatment). Egg laying commenced in 27 of the experimental boxes (13 in *nest building*, 6 in *egg incubation* and 7 in the *chick rearing* treatment). Neither treatment nor nest continuation in the stimulus box had a significant effect on the likelihood of nest building being initiated in an experimental nest box (Table 4.1, Fig. 4.1a).

Table 4.1. Summaries of GLMMs with binomial error structure assessing the effect of *treatment* (nest building, egg laying or chick rearing in neighboring stimulus box) on initiation of nest building (yes/no) or egg laying (yes/no), respectively. *Nest continuation* (yes/no) refers to the stimulus nest box, i.e. whether nest building or egg laying was continued in the stimulus nest throughout the whole trial. N represents the total number of valid observations during 35 trials (consisting of three treatments; exception N = 5 trials where *chick rearing* treatment had to be removed because the chicks disappeared). Significant p-values are highlighted in bold. Values in brackets represent coefficients in full models. Coefficients are not back-transformed from model outputs.

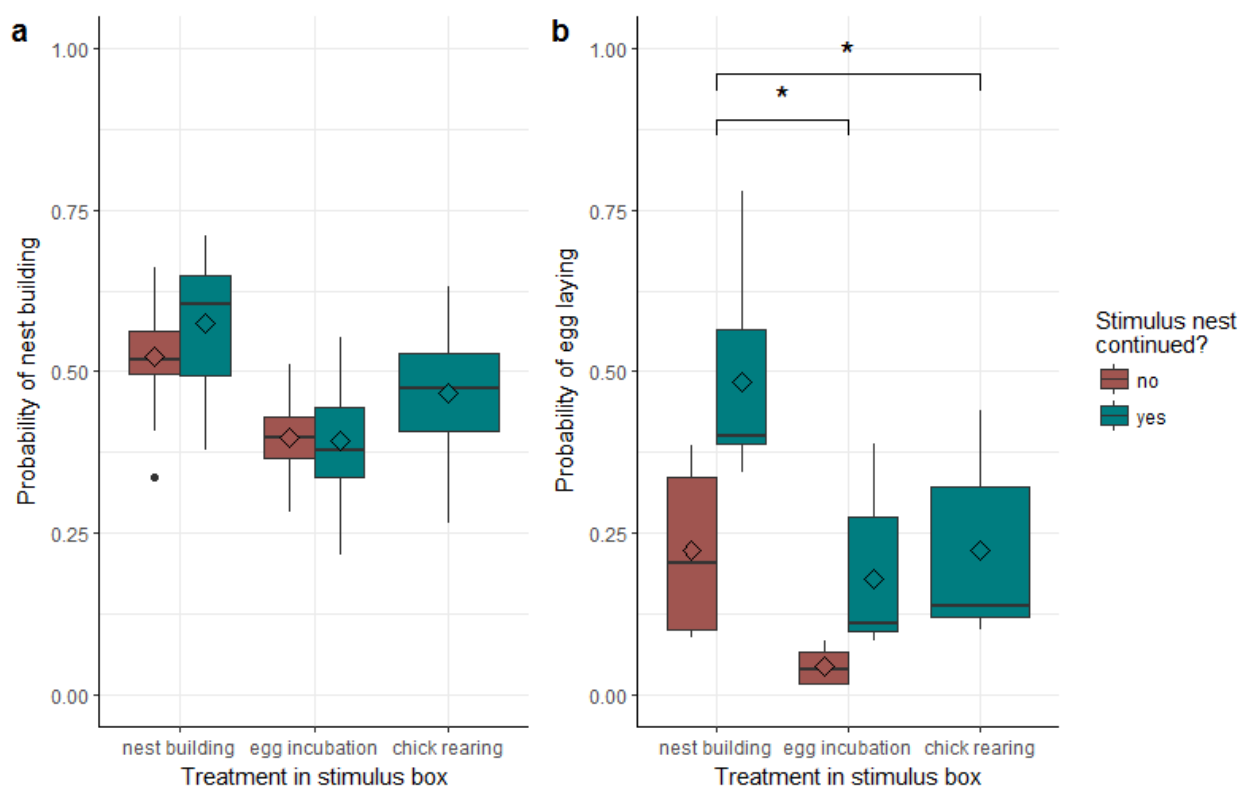| response variable	fixed effects	*N*	coefficients	X^2	df	*p*
nest building (yes/no)	(intercept) [nest building]	100	(0.160)			
	treatment [eggs]		(-0.694)	1.68	2	0.431
	treatment [chicks]		(-0.420)			
	nest continuation [yes]		(0.092)	0.02	1	0.883
egg laying (yes/no)	(intercept) [nest building]	100	-1.469			
	treatment [eggs]		-1.838	8.24	2	**0.016**
	treatment [chicks]		-1.596			
	nest continuation [yes]		1.773	5.25	1	**0.022**

Figure 4.1. Probabilities that nest building (a) or egg laying (b) was initiated in an experimental nest box adjacent to a stimulus nest box of one of three treatments: *nest building* (left), *egg incubation* (middle) or *chick rearing* (right), respectively. Horizontal lines in box plots indicate medians; diamonds (◊) indicate means. Teal colored box plots represent quartiles of trials where the stimulus nest continued to progress during trials; dark red box plots show quartiles for trials where nests in the stimulus boxes were not continued (i.e. they were abandoned), in the treatments *nest building* and *egg incubation*. Significant differences between treatments are marked with asterisks.

The probability of egg laying in an experimental box, however, was significantly affected by both the treatment and by whether a stimulus nest was continued throughout the trial (Table 4.1, Fig. 4.1b). The probability of egg laying was highest in boxes adjacent to the *nest building* stimulus and lowest close to boxes with the *egg incubation* stimulus. Post-hoc testing revealed that the probability of egg laying was significantly different between *nest building* and both *egg incubation* ($p = 0.038$; $N_{trials} = 35$) and *chick rearing* treatment ($p = 0.046$; $N_{trials} = 30$). Further, if the nest in the stimulus nest box continued successfully, there was a higher likelihood of egg laying in the corresponding experimental boxes (Table 4.1, Fig. 4.1b). In the experimental boxes where nest building was initiated, the mean latency to nest initiation was 2.89 ± 0.99 days; in the boxes where eggs were laid, this commenced on average after 3.85 ± 0.99 days. The number of days until the initiation of nest building and egg laying was not significantly different between treatments or affected by whether the nest in the stimulus box was continued (Table 4.2).

Table 4.2. Summaries of GLMMs with Poisson error structure assessing the effect of *treatment* (nest building, egg laying or chick rearing in neighboring stimulus box), and *nest continuation* (yes/no) in the stimulus box on latency to initiate nest building or egg laying, respectively. Values in brackets represent coefficients in full models. Coefficients are not back-transformed from model outputs.

response variable	fixed effects	N	coefficients	X²	df	p
days until nest building	(intercept) [nest building]	47	(1.223)			
	treatment [eggs]		(0.080)	0.84	2	0.656
	treatment [chicks]		(0.216)			
	nest continuation [yes]		(-0.194)	0.18	1	0.668
days until egg laying	(intercept) [nest building]	26	(0.916)			
	treatment [eggs]		(-0.182)	0.52	2	0.773
	treatment [chicks]		(0.047)			
	nest continuation [yes]		(0.182)	0.21	1	0.650

DISCUSSION

In a field experiment on wild zebra finches, we found that breeding pairs were significantly more likely to lay eggs in a nest box adjacent to a box that was at a very early stage (i.e. nest building and egg laying), compared to those neighboring boxes at later stages (i.e. egg incubation or chick rearing). This finding represents strong evidence that zebra finches try to synchronize their nesting schedule with that of conspecifics. The fact that individuals were not more likely to nest near individuals that had already achieved a level of reproductive success (by the ongoing presence of incubated eggs, or nestlings), suggests that in this species and context, the zebra finches were more motivated by the presence of simultaneously active conspecifics, than by the information on successful breeding by temporally slightly more advanced breeders. The advantage of temporal synchronization with a pair that is also just initiating its reproductive attempt, could be on one hand that the association between the neighboring nests (and all linked advantages) will last for a longer period (till fledging of both nests); and additionally, if the chicks fledge from the nests simultaneously they can further benefit. An increased number of fledglings will give individuals protection through the dilution effect and, additionally, they can forage together. Observations in the field have indeed confirmed frequent gatherings of fledglings at a similar age in higher numbers than one nest could produce.

Within a population of wild zebra finches, the pattern of reproduction overall appears to be rather staggered than highly synchronized and nest initiation in a population will regularly extend over periods of six to eight weeks, but the duration of breeding bouts can strongly vary within and between years (Griffith et al., 2008; Mariette & Griffith, 2012a). From this general pattern of reproductive timing in zebra finches, it appears that breeding synchrony within a population is low when compared to some other, particularly temperate species, with a much more fixed

breeding schedule e.g. in sand martins (Riparia riparia; Emlen & Demong, 1975) or lesser snow geese (Anser caerulescens caerulescens; Findlay & Cooke, 1982). However, theory suggests, that breeding synchrony in unpredictable habitats should be high, because of potentially short time windows for rearing offspring before conditions change again (Findlay & Cooke, 1982). While several studies reported a tendency for breeding asynchrony in tropical species (e.g. Moore, Bonier, & Wingfield, 2005; Stutchbury & Morton, 1995), no field studies from arid zones exist, to our knowledge.

A previous observational study had already suggested that zebra finches are more likely to initiate breeding in close proximity to already ongoing conspecific nests than would be expected by chance (Mariette & Griffith, 2012a), but the exact mechanism through which this was achieved was unclear. Building on the findings of our experiment, we can now conclude that stage of the neighboring nests is an essential aspect in the synchronization. It could possibly be argued, that nest synchronization might have occurred if nesting sites are scarce and hence, the new boxes we put up during the experiment were simply attractive nesting locations. However, the maximum number of occupied nest boxes at our study site was 115 out of 180 at any one point during the experiment; hence, there would have always been other, unoccupied nest boxes available. Additionally, this could not explain the differences we found between treatments. The nest box locations of the *egg incubation* and *chick rearing* stimulus boxes were unlikely to have been inherently worse than the *nest building* ones, as all of the stimulus boxes had equally been chosen by zebra finches to breed in.

As breeding synchrony requires social coordination, we believe that is highly likely that social cues are involved in the behavioral process. Wild zebra finches often make prospecting visits to the nests of conspecifics (Mariette & Griffith, 2012a). So far, both the unpredictable conditions of the habitat (Boulinier & Danchin, 1997; Erwin et al., 1998) and the experimental evidence (Brandl et al., 2018) suggest that social information is not used in the same way as it is known from temperate habitats (e.g. Doligez et al., 2002). Alternative explanations are needed, and we thus propose that it is highly perceivable that prospecting visits could be used to gather information on the reproductive timing of conspecifics. While further experimental work is needed to investigate this link, it could be an important step in the understanding of information use in fluctuating habitats.

Breeding synchrony undoubtedly offers many advantages (e.g. lower individual predator risk; social foraging; avoidance of unwanted extrapair copulations; reviewed in Ims, 1990a). Also, disadvantages through a high number of synchronized nests are possible (e.g. offspring competition for resources, increased predator attraction and other density-related effects). Thus, overall, the optimal level of breeding synchrony might often be a trade-off of various benefits and disadvantages. Our study provides evidence that nest synchronization is actively initiated in an opportunistic breeder of the arid zone. This study thus contributes to the limited understanding of the breeding ecology of unpredictable habitats. We

propose a potential link to a different strategy of information use in fluctuating environments that will need to be further explored. And last but not least, we want to fill some gaps in the understanding of the breeding ecology of a bird that is one of the most frequently studied species in the laboratory, but has received so little attention in the wild.

CHAPTER 5

Wild zebra finches that nest synchronously have long-term stable social ties

ABSTRACT

Social ties are important for group coordination at collective tasks, yet their value in colonial breeders has rarely been examined. Social coordination can facilitate synchronized reproduction among colony members, which in turn can amplify the benefits of coloniality. We conducted a field study to investigate if synchronized reproduction among individuals in replicated colonies is linked to the strength of their social bond, and whether these strong bonds are maintained beyond the reproductive period. We PIT-tagged wild zebra finches (*Taeniopygia guttata*), monitoring their reproduction and social foraging over two consecutive years. Using social network analyses, we show that birds from nests with synchronized reproduction had significantly stronger social ties both during and after reproduction than expected. We then demonstrate that strong social ties were carried over across years. The maintenance of social ties across years suggests that sociality plays a larger role in the synchrony of colonial breeders than previously thought.

INTRODUCTION

Living and reproducing in close proximity to conspecifics can have numerous advantages. Colonial breeders can benefit from increased predation avoidance strategies, group foraging, access to (extra-pair) mating partners, and public information (e.g. Krause & Ruxton, 2002). Further, the observed levels of synchrony between individuals within a colony or population are often much higher than would be predicted from the environmental conditions and food availability alone, which has been ascribed to enhancing the benefits of coloniality (e.g. Helm et al., 2006; Ims, 1990a). For example, communal foraging in bank swallows (*Riparia riparia*) is more effective when breeding synchrony is high, and can bring a great advantage for fledglings (Emlen & Demong, 1975; Ims, 1990a). Some degree of social coordination is presumably required to reach such a level of reproductive synchrony, beyond the influence of environmental factors. However, only few social factors have been identified as potential proximate causes leading to synchrony among conspecifics (e.g. colony sound: Waas et al., 2005; reviewed in: Helm et al. 2006). Overall, the social interactions underlying the synchronisation of reproduction within and across colonies are poorly understood.

Maintaining established social bonds among individuals may be one route through which social synchrony is achieved. Animals with strong social bonds should be able to more rapidly resolve disputes, or have greater tolerance for breeding in close proximity (sensu the 'dear enemy' hypothesis; Fisher, 1954). However, while social interactions have been widely investigated in mammalian (e.g. Lusseau et al., 2003; Wolf, Mawdsley, Trillmich, & James, 2007) and avian (e.g. Moyers, Adelman, Farine, Moore, & Hawley, 2018; Silk, Croft, Tregenza, & Bearhop, 2014) societies (Webber & Vander Wal, 2018), we have little knowledge about the social structure beyond the mating season in colonially-breeding species. Further, relatively few examples are known of prolonged associations between non-paired individuals in avian species that have open group membership; that is outside of cooperatively breeding birds, which typically form year round social aggregations (e.g. Sorato, Griffith, & Russell, 2016). One notable exception are corvids, which have been suggested to have similar complex societies as some social mammals, with long-term individual recognition of conspecifics outside of their kin (e.g. Boucherie, Mariette, Bret, & Dufour, 2016; Clayton & Emery, 2007).

With the rise of animal social network analysis as a tool for quantifying the structure of animal societies, there has been growing evidence that social ties can be persistent and have consequences for multiple behavioural aspects in a broader range of species. A study on great tits (*Parus major*) found that individuals which were experimentally segregated during feeding also ceased to have prospecting associations (Firth & Sheldon, 2015), and new 'experimentally-strengthened' social ties became more important for information transmission (Firth, Sheldon, & Farine, 2016). This experimental evidence suggests that social structure might be involved and interconnected across many behavioural aspects where it has previously been ignored. Another study, on the same

population of great tits, also demonstrated that individuals established nest sites (in the spring) close to individuals which had previously been members of their winter flock (Firth & Sheldon, 2016). Finally, one study on a long-lived colonial seabird found that colony membership was maintained across years even when the colony changed breeding site between years (Francesiaz et al., 2017). This study also found that colony membership was only maintained when reproduction was successful, providing some suggestion that between-year sociality could be tied to benefits arising from coloniality. Thus, while there is clear indication that social ties can be important in a wide range of contexts beyond reproduction, and potentially persist over different seasons, we still lack any data on how broader sociality ties in to social behaviour during the reproductive period.

One type of social behaviour during the reproductive period is to synchronise activity with other nearby breeders. Synchronizing the timing of reproduction with pairs in close proximity means that they will have a shared agenda of incubation and then offspring provisioning and similar energetic requirements. Thus, foraging together should increase their efficiency and reduce predation risk (Bijleveld, van Gils, Jouta, & Piersma, 2015). If it is easier to synchronise breeding and engage in other collective activities when close (non-mating) associations exist, then social associations between individuals can be beneficial across contexts. Synchronised breeding could also reinforce the familiarity among individuals, which can provide further social benefits. There could be multiple advantages to being surrounded with familiar individuals, such as tolerance

and cooperation in mobbing (Grabowska-Zhang, Sheldon, & Hinde, 2012) or an increase in reproductive success by being able to attract more mating partners (Beletsky & Orians, 1989). Thus, there could be several reinforcing mechanisms that maintain strong social ties across time, resulting in trans-seasonally linked social structure.

Zebra finches (*Taeniopygia guttata*) are colonial breeders that are well known for having a strong pair-bond between the socially and genetically monogamous partners (Griffith et al., 2010). While mate choice in this species has been of longstanding interest (Pogány et al., 2018; Wang, Forstmeier, Ihle, Khadraoui, Jerónimo, et al., 2018), we know little about the broader social structure in colonies, including any social associations beyond the pair-bond. Zebra finches are an iconic model species in laboratory studies (Griffith & Buchanan, 2010), but studies of social structure in the laboratory are relatively few (e.g. Boogert, Farine, & Spencer, 2014) and in general have limited ability to test questions involving ecological processes. In the wild, zebra finches breed opportunistically, as an adaption to the unpredictable conditions of the Australian arid zone. This means that they can reproduce at any time of the year when environmental conditions become favourable (e.g. Zann, 1994; Zann et al., 1995). However, reproduction in zebra finches is not highly synchronized across a population; and nest initiations within a breeding bout are often staggered (Mariette & Griffith, 2012a). Nevertheless, evidence from a wild population suggest that they actively seek to initiate nests close to conspecifics that are at the same stage,

presumably to synchronize their breeding (Mariette & Griffith, 2012a). However, we have little information about correlates or consequences of breeding synchrony in populations, although it has been proposed that the synchrony of nests that were in close proximity to one another might be the result of stable links between pairs (Mariette & Griffith 2012).

In this study, we investigated the social ties among wild zebra finches during breeding, and whether these are maintained into following years, to test if the social structure was linked to breeding synchrony between pairs. Our analysis is explicitly focused on associations between, rather than within pairs. We achieved this by first constructing social networks of individuals from the same colony co-foraging at feeding stations while simultaneously monitoring their reproduction. This allowed us to test if the reproductive synchrony of pairs is linked to, and can predict, social ties across contexts, i.e. if synchronously breeding pairs are also more likely to forage together. We then investigated the social structure of the population across seasons to test if associations established during one breeding period were stable and persisted between periods of reproduction and into the next breeding event.

METHODS

Study site

The research was conducted at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05'13.1"S 141°42'17.4"E), New South Wales,

Australia, in 2015 and 2016. The area of about 1.5 x 2 km has a dam with a relatively permanent water body in the centre. Wooden nest boxes attached to metal stakes were provided in the area surrounding the dam: 207 nest boxes in 2015, 236 nest boxes in 2016. The boxes were arranged in six colonies of 30 boxes each, with the remainder of the boxes were scattered in the periphery of the colonies to allow for use by birds that preferred to nest in lower densities (for setup of nest boxes see maps in Fig. S1-S3 in Supporting Information). In 2015, a clutch and brood size manipulation was conducted, as part of another study, by adjusting all clutches laid to three eggs in three of the colonies, and to seven eggs in the remaining three colonies (for details on the manipulation see: Brandl et al., 2018).

Feeders and electronic monitoring system

Supplementary food (commercial finch seed mix) was provided in feeding stations (wire holding cage of 70 x 40 x 50 cm; for further details on feeders see: Mariette et al., 2011a). Feedings stations were equipped with RFID decoders (RFIDRW-E-232; Priority 1 Design, Melbourne, Australia). Antennas connected to the decoders were attached to the circular entrance (20 cm diameter) of the feeders to detect and log the PIT-tag identity of tagged birds visiting the feeders (along with the date and time to the nearest second).

In 2015, one feeder was permanently positioned in the centre in each of the six nest box colonies between the end of September and beginning of December; for a shorter period, two additional feeders were added to each of the six colonies, making 18

feeders in total (see dates in Table 5.1; for setup of the feeders see maps in Fig. S1-S3). The additional feeders were relocated within the colonies every five days and contained different food qualities (different husk-to-seed ratios), as part of another experiment. In 2016, feeders were only provided at the beginning (feeders placed in the centre of each colony again) and end of the breeding period (feeders placed in surroundings of colonies; Table 5.1, Fig. S1-S3).

Bird capture and tagging

All reproductive activity in the area was monitored between August 1st and December 20th in both years. Adults were caught in the nest boxes using nest box traps between nestling day 6 and 11 (hatching day = day 0). All captured adults were banded with a uniquely numbered metal band (Australian Bird and Bat Banding Scheme) and subcutaneously injected (Ratnayake et al. 2014) with PIT-tags (Minichip; Micro Products Australia, Perth, Australia). In 2015, chicks were also banded in nest boxes and two chicks per nest received PIT-tags. Birds were additionally caught at feeding stations with walk-in-traps throughout October and early November 2015 and on two days in August 2016.

In total we PIT-tagged 817 zebra finches (250 females, 331 males and 246 juveniles) in 2015: 655 were caught and marked at their nest box (431 adults, 224 nestlings) and 172 birds were caught in the feeders (138 adults, 34 juveniles). In 2016, we captured and tagged an additional 228 previously unmarked adults (113 females, 115 males): 194 were caught at nest boxes and 34 were caught at the feeders at the beginning of the field season (on August 8th and August 9th).

Data analysis

We used a Gaussian mixture model to identify time windows where clustering of individuals occurred in the RFID data and statistically infer appropriate temporal boundaries for visits by flocks of zebra finches (Farine & Whitehead, 2015a; Psorakis et al., 2015). Social networks were constructed based on repeated encounters of individuals in the feeders using the simple ratio association index (i.e. edge weight: the proportion of times dyads of individuals were observed together divided by the number of times they occurred alone; Hoppitt & Farine, 2018b).

We constructed separate social network analyses in five distinct time periods spanning multiple seasons (see dates in Table 5.1). The first period was the 2015 breeding season, which we split into: (1) *breeding1 2015*: the first 21 days, and (2) *breeding2 2015*: the last 22 days. Using shorter periods for the analysis allowed us to more accurately compare the synchrony of currently active breeders. Breeding had already been ongoing for about three months before *breeding1 2015*, but we only collected RFID data once the majority of birds was tagged. For data during the breeding season, we constructed nest box-level networks, capturing the propensity to detect any member of a pair breeding in a nest box with any member of a pair breeding at other nest boxes (using the simple ratio index), to help account for the fact that one member of a pair often stayed in the nest. The next three periods represent intervals of data collection after the 2015 breeding season to investigate a potential carry-over of social ties. These three periods were defined as follows: (3) *post2015*: the last 10

days of data collection in 2015 with 18 feeders (overlapping with *breeding2 2015*); (4) *pre2016*: six days with six feeders, at the beginning of the breeding period 2016; and (5) *post2016*: nine days with 16 feeders, at the end of the breeding period 2016 (Table 5.1). For these periods, we created individual-level social networks, but excluded associations between mated pairs.

For the analyses of the effect of breeding synchrony on network ties, we created a matrix with dyadic comparisons of the breeding status between all breeding pairs in 2015. To calculate the level of nesting (a)synchrony at each day throughout the season, we created an index by assigning values to each nest stage: hatch dates were set as zero, subtracting 1 for each day (with an active nest) leading up to it, and adding 1 for each day of the nestling rearing period thereafter. Breeding asynchrony, as the absolute number of days difference in nest status, between each possible dyad of pairs was then calculated (e.g. Nest A: hatch day = 0, Nest B: 7-day old nestlings = 7; difference = 7). Inversely, breeding synchrony was defined as a decrease of the difference in nest status.

To test each hypothesis, we created a null model by performing pre-network data permutations (following the algorithm originally described by Bejder, Fletcher, & Bräger, 1998), restricting swaps to only occur between individuals observed on the same day and at the same feeder (Farine, 2017). We then conducted matrix regressions (multiple regression quadratic assignment procedure) fitting breeding synchrony and breeding location distance (derived from the GPS positions of the nest boxes) as fixed effects. We obtained our P-values by comparing the coefficients obtained from the observed model with the null model calculated in 1000 pre-network permutations (referred to as $P_{rand,}$ hereafter). We used pre-network permutations because we wanted to test whether birds breeding in synchrony had stronger associations than expected by chance, rather than testing whether they had stronger associations than birds that were not synchronous (the latter would have been the test using network-level, or 'node', permutations). Our foraging data were collected across all colonies simultaneously and birds regularly visited feeders in other colonies. However, we did not expect any relationship between breeding synchrony and social tie strength in birds from different colonies, so we restricted the comparison of breeding synchrony with association strength to pairs breeding in the same nest box colony only. In the *post2016* period, the sample of individuals which had bred in 2015, and were still present, was too small for subsetting per area, and we thus pooled the data from the entire study site and fit 'same colony' as a covariate in the model instead of distance.

To first validate that the social structure in the constructed networks was meaningful, we compared edge weights between mated pairs to edge weights between individuals which were not mated with each other (with pairs identified by capture and RFID detection at nest boxes; Fig. S4). All data was analysed with R (R Core Team, 2014) using the packages *asnipe* (Farine, 2013b), *igraph* (Csardi & Nepusz, 2006) and *geosphere* (Hijmans, Williams, & Vennes, 2015).

RESULTS

We recorded 214,688 detections at feeders by 446 wild zebra finches during the *breeding1 2015* and *breeding2 2015* periods combined (see summary in table 5.1; network in supplementary material; Fig. S5). We found a significantly positive relationship between the strength of foraging synchrony (edge weight) and breeding synchrony among breeding pairs across nest boxes in the same colony. In the *breeding1 2015* network (N = 89 breeding pairs), the mean edge weight of 0.0035 increased by 0.0002 per day increase in synchrony (P_{rand} = 0.026), with edge weights decreasing by 0.0004 per 100 meters of distance between nests (P_{rand} = 0.062). In the *breeding2 2015* network (N = 58 breeding pairs), the mean edge weight of 0.0218 increased by 0.0005 per day increase in synchrony (P_{rand} = 0.030), with edge weights decreasing by 0.0001 per 100 meters of distance (P_{rand} = 0.083). In other words, the more similar the breeding status of two pairs nesting in close proximity, the more likely they were to also be present in the same feeder together at the same time.

We also found positive relationships between breeding synchrony among individuals and their social association strengths in later seasons. In the *post2015* network (N = 261 individuals, see Fig. 5.1a), the mean edge weight of 0.0022 increased by 0.00016 per day increase in synchrony during the preceding breeding season (P_{rand} < 0.001). Breeding was still ongoing in this period (41 individuals of the *post2015* network had active nests on December 19th), but the number of new nests being initiated had declined considerably and most individuals in the network had finished
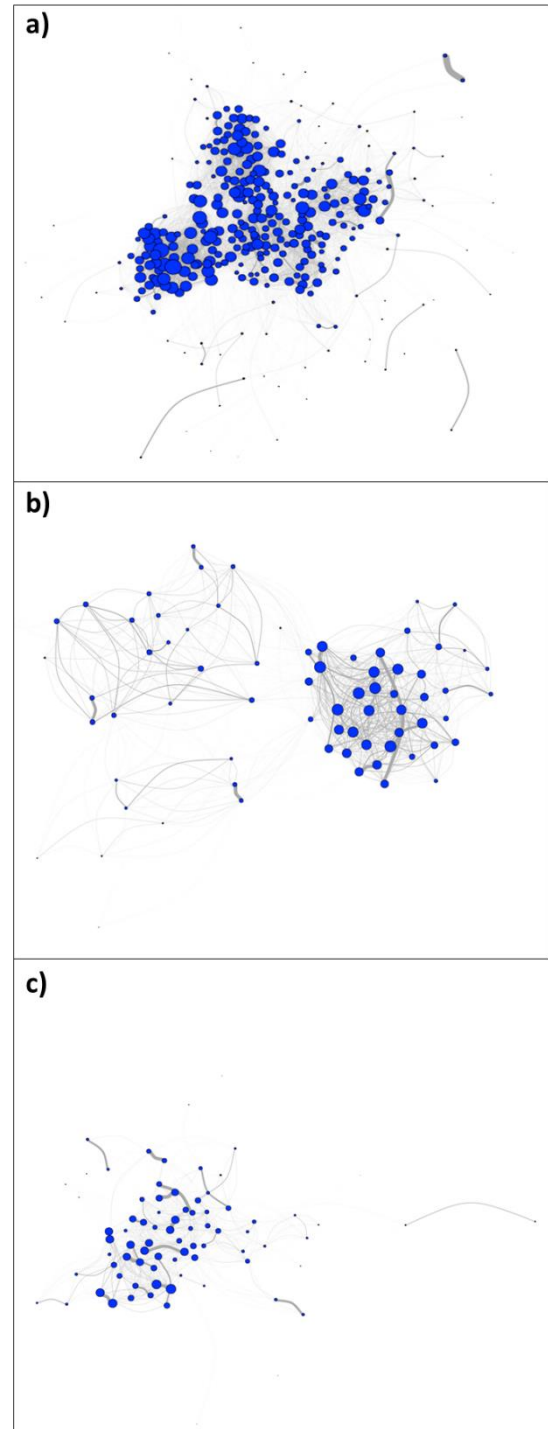
Figure 5.1. Social networks of PIT-tagged wild zebra finches co-occurring in feeding stations in *post2015* (a), *pre2016* (b), and *post2016* (c). Each node represents one individual, the size of a node indicates its detection frequency; edges connect individuals which were recorded in the feeder together and width of edges indicate frequency of co-occurrences

breeding. More than eight months later, in the *pre2016* network (N = 23 individuals, see Fig. 5.1b), the pairs that had bred more synchronously during *breeding2015* had significantly stronger ties in the network than expected if the composition of the groups detected at the feeders were random. The mean edge weight of 0.1454 increased by 0.0013 per day increase in synchrony (P_{rand} = 0.025). The *pre2016* network coincided with the beginning of a breeding period (the first egg was laid on August 7th; see network: Fig.5.1b). By the time we collected data for the period *post2016*

network, breeding had almost stopped (with only three active nests with eggs across study area; see Fig. 5.1c). Of the individuals originally present in the 2015 breeding data, 12 were still present. Although we could not detect a significant effect of the level of synchrony during *breeding2015* on strength of ties between pairs in the *post2016* network, the mean edge weight of 0.017 increased by 0.0002 per day increase in synchrony (P_{rand} = 0.133), a very similar effect to the previous seasons. Further, in this model we could not control for distance, and instead were limited to using shared

Table 5.1. Summary of the five study periods: *breeding1 2015*, *breeding2 2015*, *post2015*, *pre2016*, and *post2016*. Dates, duration, number of feeders at the study site, number of feeder visits and number of visiting zebra finches are given for each period. In *post2015* and *post2016* the days on which feeders were moved to new locations (27 Nov. 2015 and 15 Dec. 2016) were not included in the data.

	breeding1 2015	*breeding2 2015*	*post2015*	*pre2016*	*post2016*
period	23 Oct. - 12 Nov.	13 Nov. - 4 Dec.	22 - 26 Nov.; 28 Nov. – 2 Dec.	5 - 10 Aug.	10 - 14 Dec.; 16 - 19 Dec.
no. days	21	22	10	6	9
no. feeders	6: 23 - 25 Oct.; 18: 26 Oct. - 2 Dec.	18: 13 Nov - 2 Dec.; 6: 3 - 4 Dec.	18	6	16
no. feeder visits	52,553	162,135	69,442	10,301	15,954
no. individuals[*]	286	372	330	74 (40 of them tagged in 2015)	80 (28 of them tagged in 2015)
breeding summary	high breeding activity	high breeding activity; slowly declining during December	high breeding activity; slowly declining during December	start of breeding bout; first egg laid on 7 Aug.	end of breeding bout; three active nests with eggs across study area

[*]Total number of individuals detected at feeders. Number of breeding pairs (columns 1-2) and individuals (columns 3-5) used in the analyses are given in the text.

colony (0 or 1) as a covariate (birds from the same area had an increase in strength of 0.0116, P_{rand} = 0.211), which could have affected our ability to detect a significant relationship.

DISCUSSION

We have demonstrated that pairs of wild zebra finches that breed synchronously in the same colony had stronger social associations in other contexts and maintained these stronger associations across a period of more than eight months and two breeding periods. Our findings raise new questions about the adaptive value of social ties outside of the reproductive context. Social ties between neighbouring pairs in breeding colonies are rarely considered in behavioural and ecological studies. However, such associations could be highly relevant for the transfer of social information (Aplin, Farine, Morand-Ferron, & Sheldon, 2012b), social learning (Boogert, Lachlan, Spencer, Templeton, & Farine, 2018b), and foraging strategies (Aplin, Farine, et al., 2015; Firth, Voelkl, Farine, & Sheldon, 2015; Jones et al., 2018), and therefore could have consequences in many aspects of population dynamics. Social behaviour is in fact involved in the fine-tuning of most stages of the avian life history (Helm et al., 2006). Therefore, social bonds between individuals could also be involved in the coordination of synchronized breeding, especially when the phenology does not simply follow environmental stimuli (e.g. food availability or temperature).

We presently do not know in which context the social ties we have characterised were established. It is possible that birds opportunistically start to breed close to individuals at a similar stage, which in turn leads to increased joint foraging trips and, thus, stronger association. Alternatively, it is also possible that the foraging associations we detected during reproduction had previously been established, and familiar pairs then bred in close proximity and synchronously. From observations in the wild, we know that, besides individuals moving around in pairs, small group of 3-10 individuals are common and they often aggregate in 'social trees' near food or water (McCowan, Mariette, et al., 2015); such aggregations of individuals might then result in group foraging and possibly also breeding associations. Our data provide strong evidence that associations among birds that bred synchronously were strongly maintained in following seasons, though unfortunately we did not have sufficient numbers to test whether they again synchronised their breeding as breeding activity was severely depressed in 2016 due to poor conditions.

The use of social networks to study wild bird populations has increasingly revealed significant social structure in both wintering and breeding populations. Work on wintering great tits suggests that individuals can have consistent positions in their social network that can be maintained over years (Aplin, Firth, et al., 2015b), while populations are significantly assorted by traits such as personality, both in the winter (Aplin et al., 2013) and during the breeding season (Johnson et al., 2017). The mechanisms underlying these patterns are completely unknown. One thing that is

important, not only in great tits, but among all bird species, is the timing of breeding (Both, 2010; Ims, 1990a; Perrins, 1970). If maintaining specific associations during the winter (or non-breeding periods, in general) enhances the timing and temporal coordination of breeding, and ultimately the reproductive success of birds in the following season, then this could act as a strong agent of selection on social traits (McDonald, Farine, Foster, & Biernaskie, 2017).

Overall, our results can be seen as strong evidence that synchronised breeding is not merely a random and opportunistic interaction, but potentially one that has underlying causes in, or consequences on, social structure. If the only purpose of synchronising reproduction with neighbouring breeders was the immediate benefits for predator-avoidance and

potential advantages for the fledglings, we would expect the observed social ties between these pair should have subsided very quickly after fledging of the chicks. However, our results suggest that there are likely to be additional advantages in maintaining social bonds with familiar individuals, perhaps because they are beneficial in multiple contexts, or because strong bonds enhance factors such as survival until the next opportunity for reproduction. Our work has demonstrated that the application of new tools can elucidate unknown social ties between members of a population that indicate previously unknown levels of social cohesion operating. Further work in this and other species remains to understand how widespread such formerly cryptic social ties are, and how important they are in determining the reproductive success of individuals and populations.

SUPPORTING INFORMATION
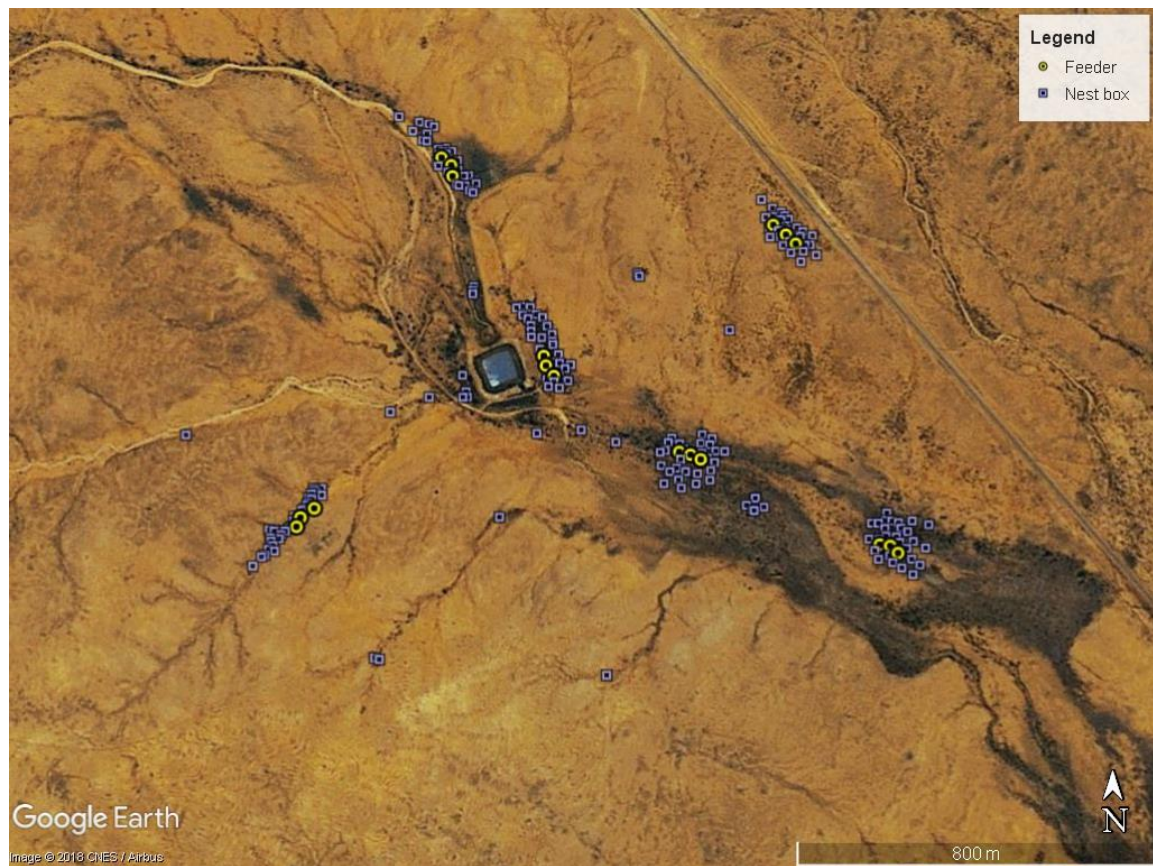
Figure S1. Map of feeders (yellow circles) and nest boxes (purple squares) at the study site in 2015 (during *breeding1* and *breeding2 2015* and *post2015*). One feeder in the centre of each nest box colony was stable; the other two feeders were relocated four times during the period of data collection, but remained within their colonies and in a similar setup (i.e. 50 m apart from each other and about 25 m away from the feeder in the centre). The two additional feeders per colony were only present between October 26th and December 2nd. The area depicted in the map is 3.12 x 1.98 km. Copyright of Google Earth image: Google, CNES/Airbus 2018. Fowlers Gap, NSW 2880, Australia. 30°57'3.15"S, 141°46'9.13"E, Eye alt 2.82 km; [July 19th, 2018].
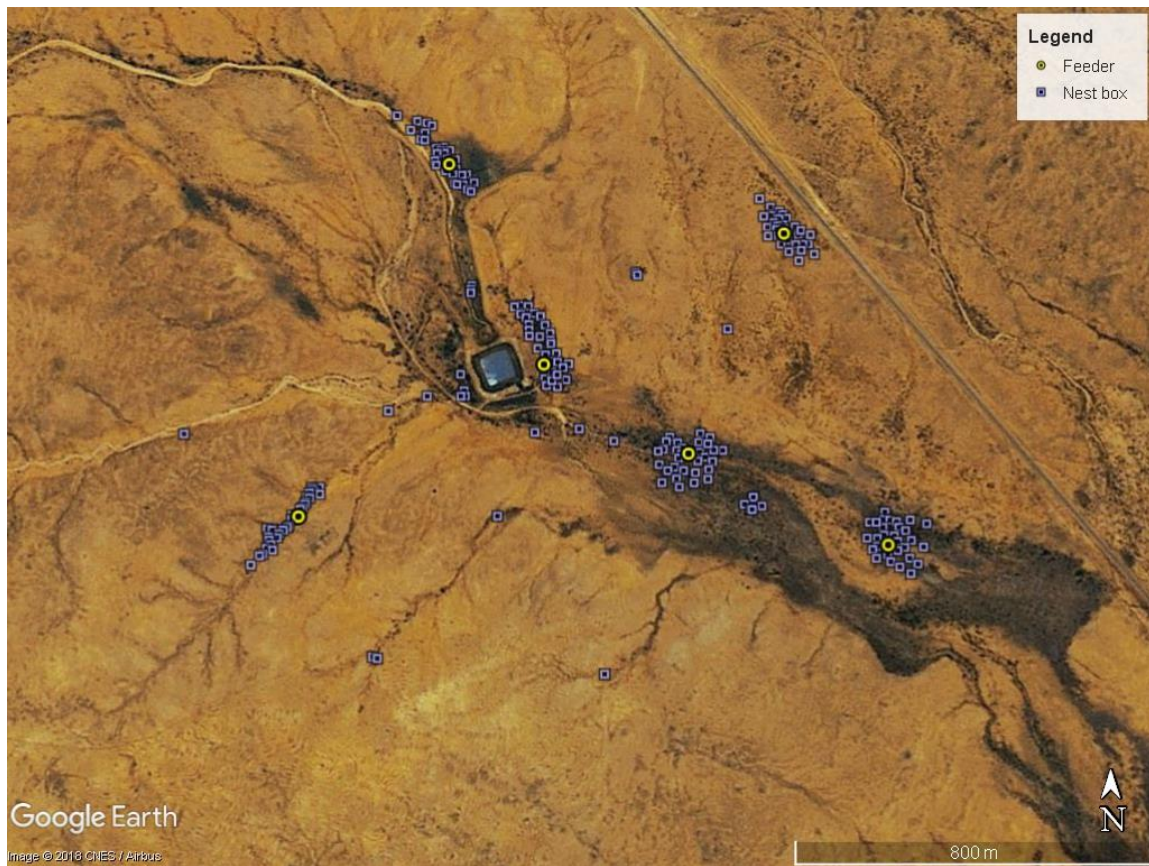
Figure S2. Map of feeders (yellow circles) and nest boxes (purple squares) at the study site in *pre2016*. One feeder was located in the centre of each colony. The area depicted in the map is 3.12 x 1.98 km. Copyright of Google Earth image: Google, CNES/Airbus 2018. Fowlers Gap, NSW 2880, Australia. 30°57'3.15"S, 141°46'9.13"E, Eye alt 2.82 km; [July 19th, 2018].
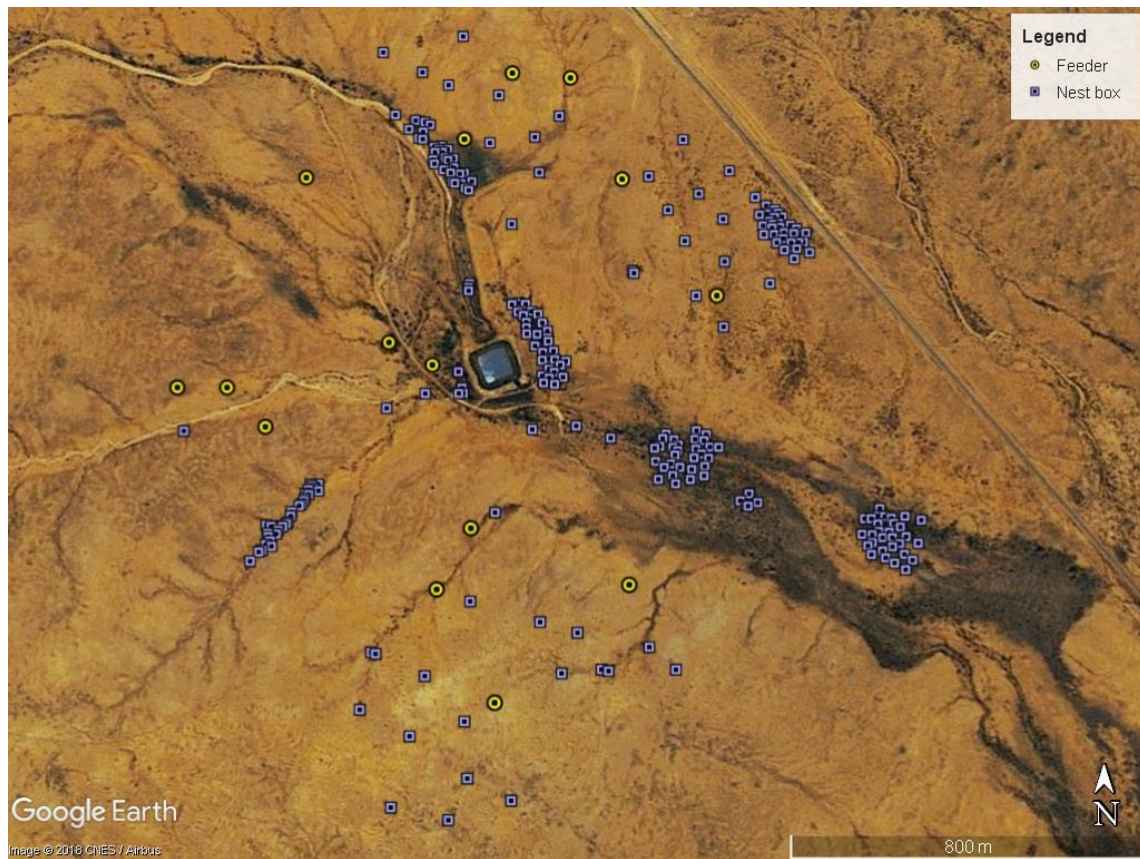
Figure S3. Map of feeders (yellow circles) and nest boxes (purple squares) at the study site in *post2016*. Feeders were relocated once on December 15th to a similar setup (not depicted) following the same criteria: feeders were placed ≥50 m away from the nearest nest box and ≤800 m away from the central dam. The area depicted in the map is 3.12 x 1.98 km. Copyright of Google Earth image: Google, CNES/Airbus 2018. Fowlers Gap, NSW 2880, Australia. 30°57'3.15"S, 141°46'9.13"E, Eye alt 2.82 km; [July 19th, 2018].
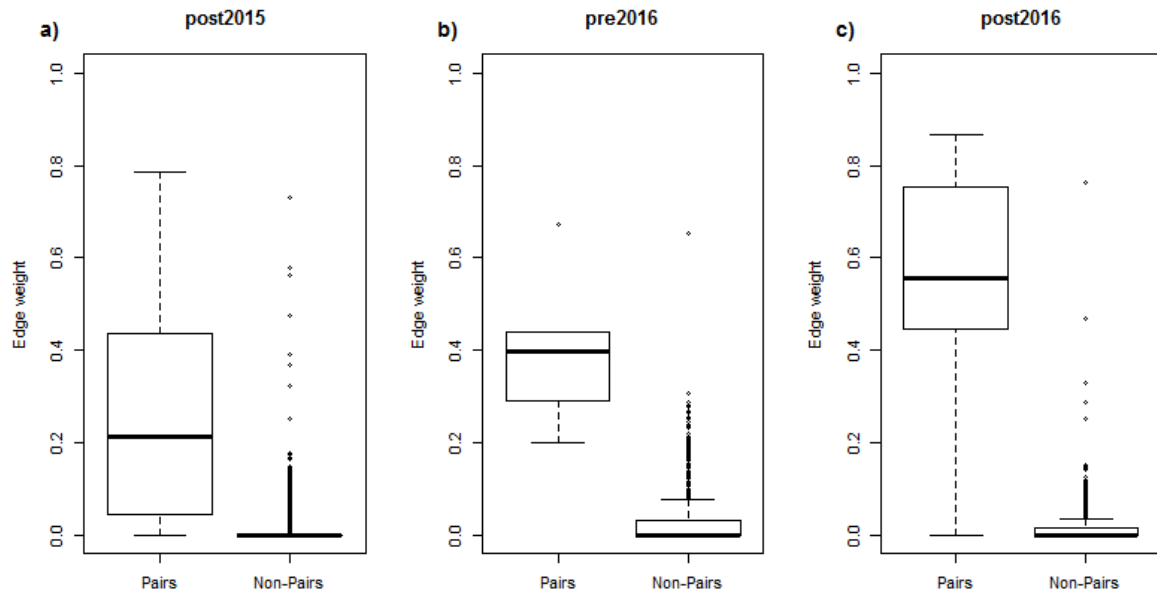
Figure S4. Edges between breeding pairs were stronger compared to non-paired individuals in the three different time periods: (a) *post2015*, (b) *pre2016*, and (c) *post2016*.
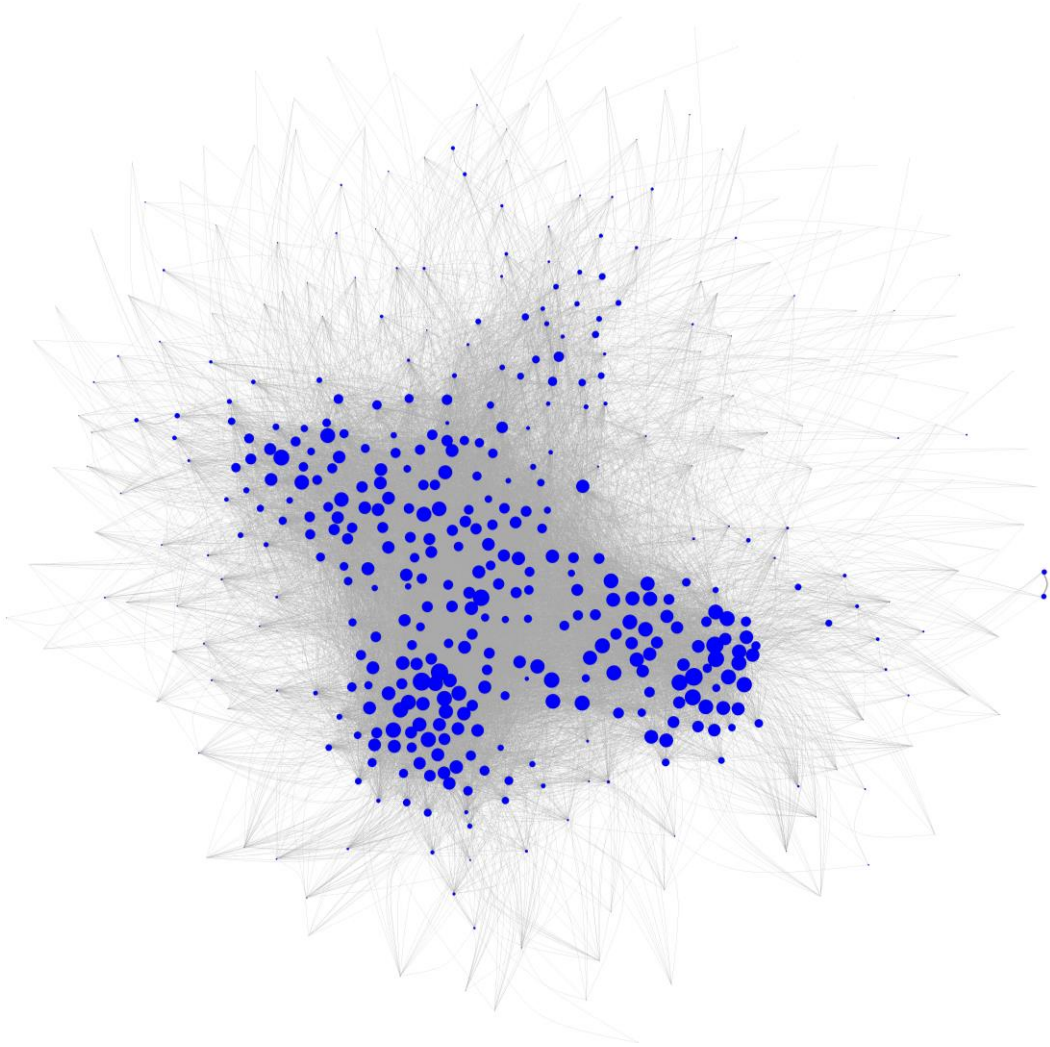
Figure S5. Social network of PIT-tagged wild zebra finches co-occurring in feeding stations during the periods *breeding1 2015* and *breeding2 2015* combined. Each node represents one individual, the size of a node indicates its detection frequency; edges connect individuals which were recorded in the feeder together and width of edges indicate frequency of co-occurrences.

GENERAL DISCUSSION

General Discussion

Information use is widely recognized as an important key mechanism underlying adaptive behaviour and can be seen as a unifying framework for all processes involving decision-making (Dall et al., 2005; Danchin et al., 2004). The central relevance of information use in organismic biology has led to numerous studies in the field, often exploring information use in the context of foraging (e.g. Galef Jr & Whiskin, 2006; Templeton & Giraldeau, 1996), mate choice (Drullion & Dubois, 2008; Mery et al., 2009), and habitat selection (Doligez et al., 2002; Pärt et al., 2011). Social information is of particular interest because it can lead to cultural evolution (Aplin, Farine, et al., 2015; Danchin et al., 2004), is intertwined in complex group dynamics (Battesti, Moreno, Joly, & Mery, 2012; Firth & Sheldon, 2015), and might be involved in the formation of colonies (Evans, Votier, & Dall, 2016). Despite its high relevance, the multitude of studies investigating the mechanisms and function of social information use (e.g. Parejo et al., 2007; Thorogood & Davies, 2016; Webster & Laland, 2008) have remained restricted to relatively predictable environments, underlying a stable periodicity.

Hence, the main aim of this thesis was to gain novel insights into the role and mechanisms of social information use in an unpredictable habitat, using wild zebra finches in the Australian arid zone as a model. I particularly focused on the nest prospecting activity of the birds, as it represents a conspicuous way of acquiring social information, which can be easily monitored, and is widely unexplored in unpredictable habitats. Further, I also examined reproductive synchronisation in the population, a behavioural strategy that usually does not find much attention in the study of information use, but as I propose throughout this thesis, might be strongly linked to social information transfer.

In Chapter 1, I described the patterns in the timing of prospecting visits, to draw inferences on the potential informational value and contrast the findings with our knowledge on species in temperate habitats. My results revealed high levels of prospecting activity, but also showed a high level of variation and flexibility in this behavioural strategy. In the next chapter, Chapter 2, I could demonstrate that the playback of begging calls of chicks in large broods attracted prospectors more strongly than begging calls of small broods. This result gives an insight into the mechanism of how prospectors select nests to visits: begging calls might potentially help them to locate particularly successful nests. In Chapter 3, I described a brood size manipulation experiment, which I conducted to test the hypothesis that prospecting is used to assess the quality of a breeding site. However, my results did not support this hypothesis, and strongly suggest that social information, at least in the form acquired by nest prospecting, is not the main driving factor for nest site selection and clutch size determination. Chapter 4 presented the result of an experiment, demonstrating that zebra finches preferentially breed with synchronised neighbours and might actively seek the nests to synchronise with. While I did not explicitly test the link between the breeding synchrony and social information exchange, I suggest that such a link is highly plausible, based on the current evidence. Thus, prospecting for social information to coordinate reproductive synchrony can be seen as an alternative hypothesis to the nest site choice hypothesis presented in Chapter 3. To further explore the connection

between reproductive synchrony and sociality in zebra finches, I presented the results of a social network analysis following the social ties of synchronous breeders over two years, in Chapter 5. The discovery that an opportunistic breeder maintained long-term stable social ties between synchronised pairs is remarkable and gives much room for hypotheses on the role of sociality for reproduction and information transfer in unpredictable habitats.

Throughout this thesis, I have only investigated prospecting activity in adult individuals. The reason for this being, that the juveniles with PIT-tags only made few visits to nest boxes, mostly at the box, or in close surrounding of the box, they had fledged from and the amount of available data was too low to establish a meaningful hypothesis. This could further be attributed to the fact that extremely low numbers of PIT-tagged fledglings (less than 2%) were recaptured in the year after they had been banded in the nests, and that it is not possible to determine the age of individuals caught once they have reached physiological and morphological maturity (between 8 to 12 weeks after hatching; Zann, 1996). Further, high numbers of fledglings die before reaching adulthood and we have very limited understanding of juvenile dispersal (Zann, 1996), a period during which prospecting was observed in other species (Cox & Kesler, 2012; Fasciolo, Delgado, Cortés, Soutullo, & Penteriani, 2016).

My detailed observation of the prospecting activity in the zebra finch population monitored across two years has revealed that the levels of nest prospecting can be very high in certain environmental conditions, and is aimed at certain nest phases, rather than being distributed randomly across all nests (Chapter 1). Regarding the nest phase, I have shown that nests are visited more by prospectors when they have chicks, than when they are incubating eggs. The proximate cause for this might be found in the conspicuous begging calls the chicks elicit (Chapter 2), which start around day 3 or 4, and increase in frequency and intensity with age (Muller & Smith, 1978). There is a possibility, that the prospecting visits at the stage before chicks fledge are mainly attributed to the conspicuous audibility of the nests at that time. This would mean that zebra finches in the surrounding are drawn to the nests by curiosity or because the sound of hungry chicks triggers a strong innate response that attracts them to the nests.

Alternatively, the nests with fledglings could provide fitness enhancing social information on the habitat quality (Valone, 2007), as it was often suggested in species breeding in the Northern hemisphere (e.g. Brown et al., 2000; Doligez et al., 2002). However, the experiment I conducted to test this hypothesis, creating an environment with patches of varying reproductive success, could not find any indication that social information from conspecifics' nests was used to assess the environment and make reproductive decisions based on it (Chapter 3). Nevertheless, it is possible that social information is collected from prospecting visits at this stage, but the information might be overwritten by other sources of information, which can particularly happen if information from different sources is conflicting. The brood size manipulation artificially increased and decreased the reproductive success of nests in certain patches, but this difference in patch qualities was not reflected by environmental factors, for example, the availability of resources, which can be sampled individually (i.e. personal information).

Conflicting social and personal information is an interesting paradigm and experimental evidence in the context of foraging suggests that private information often dominates over contradicting social information, as shown in ants (Lasius niger; Grüter, Czaczkes, & Ratnieks, 2011), guppies (Poecilia reticulata; Kendal et al., 2004) and budgerigars (Melopsittacus undulatus; Valone & Giraldeau, 1993). However, social information can also prevail over personal information in other scenarios, depending on various factors, including group size (King & Cowlishaw, 2007), personality (Kurvers et al., 2010), the costs involved (Webster & Laland, 2008), and reliability (van Bergen, Coolen, & Laland, 2004).

Last but not least, the stability of environmental conditions is a crucial factor in determining how reliable information about environmental parameters can be, and thus, which strategy of information use can be most advantageous for an individual (Feldman et al., 1996). In the case of the wild zebra finches, it is possible that the low level of environmental stability does not make social information the prevalent strategy for the assessment of environmental conditions. The often rapidly changing conditions do not allow for reliable long-term predictions regarding the quality of a habitat. This is the most obvious difference to temperate habitats, underlying strong seasonal periodicity, which we can expect to impact decision making. Nevertheless, zebra finches are also highly adapted to their harsh and unpredictable desert environment. Their opportunistic breeding strategy allows for long periods of almost continuous reproduction (Duursma et al., 2017), and using social information from the nests of conspecific for reproductive decisions could still be a successful approach, if used for a brood following directly thereafter. In this way, the often postulated trade-off between information gathering and own reproduction (e.g. Boulinier & Danchin, 1997; Ward, 2005) could be strongly reduced. Nevertheless, I could not detect social information use in this form in the studied zebra finch population. Thus, it is likely that the social information might be perceived as unreliable, particularly if it contradicts other information an individual has, and might thereupon be completely disregarded or only be used in addition to the personal information. The latter could mean that the zebra finches only used the social information for behavioural adjustments on a fine scale, for example subtle adjustments to the reproductive investment in form of the clutch size, which might not be so easily detectable.

Another aspect is that visiting nests shortly before fledging (Chapter 1) could also provide information about when the nest box becomes empty or provide valuable information about the reproductive success of other pairs in the population, which could be relevant in social relationships between individuals (see Chapter 5). Regarding the former hypothesis, the fact that the probability of a nest box receiving a prospecting visit increased in the first days of becoming vacant after a nesting attempt, supports the hypothesis that at least some individuals might simply be looking for empty nest boxes. Predation risk in zebra finch nests is extremely high (Zann, 1996) and nest boxes are a highly valued and preferred breeding location for zebra finches, as they significantly lower the predation risk compared to natural nests (Griffith et al., 2008). Nevertheless, it is rather unlikely that finding an empty nest box is the sole and main purpose of nest prospecting and the hypothesis does not align well with other findings, such as repeated

prospecting visits to active nests by the same individuals, while many other nest boxes are empty. In the context of predation, the prospecting visits in the days after fledging of a nest could also be interpreted as a strategy of assessing predation risk and investigating whetherall chicks fledged successfully.

Another main discovery from the analysis of the prospecting patterns in Chapter 1 was the high prospecting probability during the first days of newly initiated nests, which was even higher than that at nests before fledging and at empty nest boxes. This result was highly unexpected, as the informational value of nests during the building and egg laying phase did not seem obvious at the first glance. This phase, however, might give valuable cues for reproductive timing. On one hand, the nests could provide social cues indicating that other pairs are still breeding, i.e. the environmental conditions still allow for reproduction. The inherent mechanism could be, for example, that birds prospect at multiple nest locations at a breeding site and then decide, depending on the number of newly established nests they find, if they start a brood themselves.

On the other hand, information on new nests of conspecifics could also be used to reach reproductive synchrony or asynchrony. Particularly in highly seasonal habitats, the level of reproductive synchrony within a population is often mainly determined by abiotic factors (Ims, 1990a) and, directly linked to that, the food availability (Both, 2010). Nevertheless, also sociobiological factors have been identified and discussed as driving factors underpinning reproductive synchrony, and this should be particularly prevalent in colonial species (reviewed in Helm et al., 2006). That nest prospecting could be used for not only spatial, but also temporal breeding decisions has been proposed (Helm et al., 2006), but has not yet been put to a test.

The theory predicts, that reproductive synchrony should be high, if the time window for reproduction is low (Findlay & Cooke, 1982). In unpredictable environments, however, the length of breeding periods varies considerably between locations and between years. In wild zebra finches, reproductive synchrony across a population is rather low and brood initiation appears staggered (Mariette & Griffith, 2012a). In Chapter 4 of this thesis, I presented results of a field experiment, demonstrating that zebra finches do synchronize their reproduction with conspecifics breeding in close vicinity. The experiment showed that a breeding pair preferred to establish a nest next to a pair, which is also at the stage of nest initiation, strongly suggesting that the synchronization is an active process. Synchronising reproduction can bear considerable fitness benefits by further facilitating group advantages, such as predation avoidance mechanisms and social foraging (e.g. Ims, 1990a, 1990b; Westneat, 1992), by aligning the needs of the parents and the simultaneously fledging offspring of the synchronized nests. Hence, prospecting at nests to locate another breeding pair at the same stage and to breed synchronously with, could be an adaptive behaviour.

If social information acquired through prospecting visits on conspecific nests is used for the reproductive timing, this could be a mechanism unique to species breeding in aseasonal and unpredictable habitats. If seasonality periodicity is high and restricts reproduction to one well-defined breeding season per year, it is unlikely that the breeding activity of others serves as a

strong cue, because the environmental factors will probably dominate and there is not much room for temporal variability. This could also be the reason why such a mechanism has not been described in the wild before, as the majority of studies target species of temperate, and seasonal habitats, particularly in the study of information use. However, extending the research to other species in unpredictable habitats would be highly relevant to further explore this new hypothesis of social information use to synchronize reproduction.

It is not fully clear, why the reproductive synchrony across the zebra finch population was not higher overall. Reasons for low synchrony can be avoidance of extra pair-copulations (e.g. Stutchbury & Morton, 1995) or a scarceness of space and other resources (reviewed in Ims, 1990a). However, none of these theories seem very plausible in zebra finches. They are highly monogamous, seeds are a very well divisible resource and while vegetation offering nesting locations can be scarce, zebra finches do not require large space for breeding and can easily cram in a small bush with numerous nests, if necessary. One advantage of a staggered reproduction could be, however, that also social information from nests at later stages is available at most times. That means that a breeding pair ready to start a new nest could potentially acquire social information from nests at different stages; they could prospect at nest which currently have fledglings to fine-tune their reproductive investment, and they could also prospect at nests at early stages to find pairs with similar requirements and initiate a nest in close vicinity. Furthermore, social information can never be successfully used by all individuals at the same time and thus, reproductive asynchrony might facilitate a better spread of individuals with different informational states across a population.

The results presented in the final chapter of this thesis, Chapter 5, suggest that the associations between the synchronous breeding individuals is not random. Individuals which bred together, also foraged together significantly more often than expected per chance. These social bonds between individuals, spanning different behavioural contexts, persisted over a long period of low reproductive activity and where still maintained in the following year. Only a low number of recent studies (Dhanjal-Adams et al.; Firth & Sheldon, 2015, 2016; Francesiaz et al., 2017) has started to address the importance of stable long-term associations, outside of mating bonds, and in species where it had previously not been considered, in contrast to, for instance,. cooperative breeders (e.g. Sorato, Gullett, Griffith, & Russell, 2012). The growing evidence suggests that stable social ties between individuals might be much more strongly interconnected and involved in more different behavioural aspects than had previously been assumed.

In the example of the colonially breeding zebra finches, the stable associations could also play a key role in the transfer of social information, as it could determine which individuals exchange information. A study on great tits *(Parus major*; Firth & Sheldon, 2015) has provided evidence, that an experimentally induced segregation between individuals at feeding station strongly affected their prospecting relationships.

I have demonstrated, that social associations at feeding stations are reflected in the synchronous breeding patterns in wild zebra finches (Chapter 5). I have suggested that social information acquired through prospecting might be involved in the coordination of the breeding

synchrony (Chapter 4). Hence, using the findings from the great tit study (Firth & Sheldon, 2015) as a linking puzzle piece, the stable social ties between the zebra finches might also be connected to their prospecting associations, creating a complex network of social information transfer. This suggests that the social information transfer between individuals is not random and purely opportunistic but guided by stable social bonds between individuals.

In summary, the evidence I have presented throughout my thesis suggests that nest prospecting could serve multiple purposes for the zebra finches. Prospecting to assess habitat quality, prospecting to synchronize the reproduction with other pairs, and perhaps occasionally prospecting for an empty nest box to breed in are not mutually exclusive strategies. Further, also individually sampling environmental conditions to acquire personal information can be used as a complementary strategy.

Also, the research on European breeding species has not solely focused on the already well-established hypothesis of prospecting for the assessment of habitat quality. A recent study on great tits (*Parus major*) has suggested a role of territoriality and extra-pair mating in nest prospecting (Firth, Verhelst, Crates, Garroway, & Sheldon). However, these behavioural aspects are not very relevant for a monogamous and colonial species like the zebra finch. Nevertheless, it is interesting that also in the research on the well-studied species of the Northern hemisphere, new perspectives for the adaptive value of prospecting behaviour are being opened up.

Overall, the results I have presented in this thesis have given new insights into the role of social information use in unpredictable habitats, have led to new hypotheses, and paved the way for more targeted research in the future. The ecology of animals strongly affect how information is gathered and processed, how decisions are made, and which strategies are ultimately successful. Zebra finches need to have very well adapted behavioural mechanisms to survive in the harsh and unpredictable environment of the arid zone. My findings highlight that social information use is a highly complex and presumably successful strategy in the unpredictable conditions of the arid zone. In the light of the significant and persisting importance of zebra finches as a model species, I hope that my results from the wild, giving new ecologically relevant insights, will help to improve and inspire new research on this highly interesting species, particularly in the field of information use. Furthermore, comparative studies targeting other avian and non-avian species are needed to understand the evolutionary history and adaptive value of information use in unpredictable environments.

DECLARATION

Certificate of originality

I hereby declare that the contents of this thesis entitled "Social information use in an unpredictable environment – a case study on wild zebra finches" are a record of my own original work, except where other contributors are named. In detail, my contributions and those of others are listed in the below statement.

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen verwendet habe.

Hanja B. Brandl

Hamburg, August 2018

Contribution Statement

General introduction

I, Hanja B. Brandl, wrote the general introduction. Wiebke Schuett and Simon C. Griffith helped to improve it by editing it.

Chapter 1 | Nest prospecting in an opportunistic breeder – acquiring social information on reproduction in an unpredictable habitat

Hanja B. Brandl • Simon C. Griffith • Wiebke Schuett
(Submitted)

I collected the field data, analysed the data and wrote the manuscript. Wiebke Schuett and Simon C. Griffith contributed to the conceptual design of the study and the manuscript and provided feedback on the statistics and wording of the manuscript. Anika Immer, Kathryn Peiman and André Pinheiro provided assistance as field assistance, which helped with the data collection. Further, Marie Hardenbicker, Corinna Adrian and Caterina Funghi helped with the capture and tagging of the zebra finches.

Chapter 2 | Begging calls provide social cues for prospecting conspecifics in wild zebra finches

Hanja B. Brandl • Simon C. Griffith • Toni Laaksonen • Wiebke Schuett
(Submitted)

The field experiment presented in this chapter was conducted by me, with the help of my field assistant André Pinhéiro. I performed the statistical analysis, with improving comments from Wiebke Schuett and Toni Laaksonen. Simon C. Griffith, Toni Laaksonen and Wiebke Schuett all contributed to the design of the experiment and edited the manuscript which was written by me. Milena Markwart, Silja Blechschmidt, Hasan Karabacak, Olivia Rothberg, Baptiste Averly and Camille Delaby helped in the analysis of the video material.

Chapter 3 | Wild zebra finches do not use social information from conspecific reproductive success for nest site choice and clutch size decisions

Hanja B. Brandl • Simon C. Griffith • Wiebke Schuett
Published in Behavioral Ecology and Sociobiology 72:114, doi: 10.1007/s00265-018-2533-3
June 2018

I conducted the field work and data collection for this experiment, with the help of my field assistants Anika Immer and Kathryn Peiman. The MSc student Marie Hardenbicker also contributed by catching birds and monitoring nests. I wrote the manuscript and conducted the statistical analysis. Wiebke Schuett provided guidance for the statistical analysis. Wiebke Schuett and Simon C. Griffith both contributed to the conceptualization of the study and to the editing of the manuscript. Further, two anonymous reviewers gave constructive comments which helped to improve the quality of this manuscript.

Chapter 4 | Wild zebra finches choose neighbours for synchronized breeding

Hanja B. Brandl · Simon C. Griffith • Wiebke Schuett
(Submitted)

The experiment presented in Chapter 4 was conducted by me, with the support of my field assistant André Pinhéiro. I conducted all statistical analyses and wrote the manuscript. Wiebke Schuett and Simon C. Griffith gave input to for design of the experiment and the wording of the manuscript.

Chapter 5 | Wild zebra finches that nest synchronously have long-term stable social ties

Hanja B. Brandl · Simon C. Griffith • Damien R. Farine • Wiebke Schuett
(Submitted)

This study is based on data collected by me, Marie Hardenbicker (data from RFID-feeding stations in 2015), and Luke Mc Cowan (data from RFID-feeding stations in December 2016).

Damien R. Farine contributed his expertise in conducting the social network analysis. Simon C. Griffith, Wiebke Schuett and Damien R. Farine all contributed to the design of the study and helped to improve the manuscript, which I wrote.

General discussion

I wrote the general discussion and Wiebke Schuett helped to improve it by commenting and editing it.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in the studies were in accordance with the ethical standards of the institution or practice at which the studies were conducted. The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme.

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PROFESSOR SIMON C. GRIFFITH
DEPARTMENT OF BIOLOGICAL SCIENCES
FACULTY OF SCIENCE & ENGINEERING

22nd August 2018

To Whom It May Concern:

I am writing to confirm that I have read the thesis written by Hanja Brandl, entitled "Social information use in an unpredictable environment – a case study on wild zebra finches", and that the English is of a good standard throughout.

I am a native English speaker originally from the UK and now living in Australia.

Yours faithfully

Simon Griffith

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APPENDIX I

Early-life social environment predicts social network position in wild zebra finches

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ABSTRACT

Early-life experience can fundamentally shape the life history trajectories of individuals. Previous research has suggested that exposure to stress hormones during development is linked to marked differences in social behaviour later in life. In captivity, juvenile zebra finches exposed to elevated levels of corticosterone were less socially choosy and more central in their social networks when compared to their untreated siblings. These differences extended to other aspects of social life, with 'stress-exposed' juveniles switching social learning strategies from copying parents to copying only unrelated adults, and juvenile males less faithfully learning their father's song. However, while this body of research suggests that the impacts of early-life stress could be profound, it remains unknown whether such effects are strong enough to be expressed under natural conditions. Here, we collected data on social associations in a population of zebra finches in the Australian desert, after experimentally manipulating brood sizes. Juveniles from enlarged broods were likely to have experienced heightened sibling competition, and we predicted that they would express similar patterns of social associations to stress-treated birds in the previous captive study. We show striking support for the suggested consequences of developmental stress on social network positions, with our data from the wild replicating the same results in 9 out of 10 of the hypotheses previously tested in captivity. Our results confirm that the natural range of variation in early-life experience can be sufficient to predict individuals' social trajectories.

INTRODUCTION

The social component of the environment represents a unique aspect among the factors that contribute to differences in fitness. The population-level patterns of social connections that are formed from the interactions among individuals, and where individuals are positioned within this web of interactions, often captured using social network analysis (Farine & Whitehead, 2015b; Whitehead, 2008), are of increasing interest for a number of reasons. First, most social interactions are often only manifested physically for brief moments, but their consequences can extend well beyond this time. For example, in primates, rare grooming partners can be important for individual's survival (McFarland et al., 2017; Silk, Seyfarth, & Cheney, 2018), while a vampire bat *Desmodus rotundus*, donating food to an unrelated conspecific can represent a future investment that may be life-saving in case it later goes hungry (Carter, Farine, & Wilkinson, 2017). Second, the position of individuals within their social environment (i.e. in their social network) can be dependent on both their, and others', social interactions. For example, an individual's exposure to disease may not only depend on its own social gregariousness, but also on the gregariousness of its associates (see Brent, 2015).

There is now clear evidence that individuals can exhibit consistent differences in their social position within their social network (Aplin, Firth, et al., 2015a; Blumstein, Petelle, & Wey, 2013; Formica, Wood, Cook, & Brodie, 2017; Jacoby, Fear, Sims, & Croft, 2014), and that these differences can translate to consequences for fitness (Barocas, Ilany,

Koren, Kam, & Geffen, 2011; Farine & Sheldon, 2015; Formica et al., 2012; Ryder, McDonald, Blake, Parker, & Loiselle, 2008). For example, being more central in a network has been linked to having access to more information (Aplin, Farine, Morand-Ferron, & Sheldon, 2012a), but also being more exposed to disease (Adelman, Moyers, Farine, & Hawley, 2015; Fowler & Christakis, 2008). The composition of the social environment can also impact the strength and direction of selection that individuals experience (Farine, Montiglio, & Spiegel, 2015; McDonald et al., 2017), while the density of connections can determine at what level of social organization selection on traits is likely to operate most strongly (Montiglio, McGlothlin, & Farine, 2018). Yet despite over a decade of research on animal social networks, little is known about the mechanisms that underlie inter-individual differences in social relationships and network position (Boogert et al., 2014).

Three recent, and complementary, studies (Boogert et al., 2014; Boogert, Lachlan, Spencer, Templeton, & Farine, 2018a; Farine, Spencer, et al., 2015) suggest that the conditions that individuals face during their development can shape many aspects of their later social life. All three studies used the same nestlings, from two captive colonies of zebra finches, *Taeniopgygia guttata*, that were allocated to two treatments. Approximately half of each brood were exposed to physiologically relevant doses of the avian stress hormone corticosterone (stressed juveniles) while the other half were manipulated in the same way but without the active hormone (control juveniles). Once the chicks fledged, the

social affiliations among all colony members (including both adults and juveniles) were recorded by detecting the co-membership of individuals fitted with passive integrated transponder (PIT) tags in foraging flocks at feeders using radio frequency identification (RFID) loggers. In the first study, Boogert et al. (Boogert et al., 2014) found that stressed juveniles formed less exclusive (or more random) social associations, which resulted in a higher total number of social associates (higher binary network degree) and higher network centrality (higher network betweenness). The two following studies investigated how early-life stress influenced social learning strategies, finding that stressed juveniles switched from acquiring novel foraging behaviours from their parents to acquiring them from unrelated adults (Farine, Spencer, et al., 2015), and that stressed juvenile males were less faithful in copying their father's song, although the mechanism there seemed to be linked to variation in association strengths between father and sons (Boogert et al., 2018a). Studies of the zebra finch in captivity have thus provided some of the best support to date for the importance of the environment in the development of animal social behavior, and its influence on the acquisition of skills relating to fitness (song and foraging behaviour). Whilst the amenability of the zebra finch as a focus of behavioural research in the laboratory has permitted insightful studies such as those above, an important challenge remained about the extent to which such studies might reflect natural variation in an appropriate ecological context (Boogert et al., 2014). There appears to be extensive variation in the sociality of different individuals in a wild population (reviewed in (Dall & Griffith, 2014)), but the ontogenetic source of that variation remains unclear.

In the current study, we conduct a replication of the Boogert et al. (Boogert et al., 2014) study in a wild population of zebra finches using a natural source of developmental stress—brood size. Boogert et al. (Boogert et al., 2014) called for replication in the wild using a natural stressor, and in this study we experimentally increased and decreased the size of broods, predicting that nestlings from enlarged broods would experience higher sibling competition (as shown in the wild by (Mariette & Griffith, 2015)), causing these juveniles to respond in a similar way to juveniles that were exposed to the corticosterone stress hormones as nestlings in the original study. We then collected data on foraging associations among individuals (both adults and juveniles, each fitted with a PIT tag) at RFID-equipped feeders located in the surroundings of six breeding colonies. Finally, we conducted the same statistical tests as the original study, therefore producing almost exact experimental replication, but importantly in a very different context and under completely natural conditions.

METHODS

Study site

The study was conducted at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05'13.1"S 141°42'17.4"E), New South Wales, Australia, between September and December 2017. The roughly rectangular

area of about 4 km² holds a dam with a relatively permanent water body in the centre. We provided 180 wooden nest boxes arranged in six colonies (mean distance to nearest neighbouring colony ± SE = 413.62 ± 63.62 m) of 30 boxes each (mean distance to nearest neighbouring nest box within clusters ± SE = 10.36 ± 1.98 m; (Brandl et al., 2018)), and an additional 64 boxes scattered in the periphery of the colonies.

Brood size manipulations

Brood manipulations were conducted when nestlings were 3 days old (hatching date = day 0). Nestlings were measured (tarsus length, measured to an accuracy of 0.01 mm), weighed (to an accuracy of 0.2 grams), and then swapped between pairs of nests (triplets, if necessary), bi-directionally, i.e. all nests received at least one chick from another brood. In each nest pair, we created a reduced brood with 2 nestlings (N = 15 nests; i.e. low stress) and an enlarged brood with 5 to 8 nestlings (mean number chicks ± SE: 6.00 ± 0.18; N = 16 nests; i.e. high stress). All nests were manipulated, except for five nests where no other nest with nestlings at the same age was available for swapping (juveniles from these nests were included when generating the social networks but not used in the analyses comparing juveniles across treatments). A number of studies have previously shown that brood size manipulations can lead to differences in growth rates and body size (Mariette & Griffith, 2015); increased levels of plasma corticosterone (Saino, Suffritti, Martinelli, Rubolini, & Moller, 2003), and negatively affect the immunocompetence (Naguib, Riebel, Marzal, & Gil, 2004), and survival (DeKogel, 1997) of the offspring raised in enlarged broods.

Social network data

We collected data on social associations in almost exactly the same way as the Boogert et al. (Boogert et al., 2014) study. We caught adults with mist-nets, with walk-in feeder traps and at the nest boxes when nestlings were between 6 and 11 days old, whereupon we fit each individual with a unique ABBBS metal ring and subcutaneously injected each with a uniquely coded PIT tag (Minichip; Micro Products Australia, Perth, Australia). Nestlings were weighed, measured (tarsus length), and tagged on day 11. For practical reasons we did not tag all nestlings, but a number proportional to the manipulated brood size (mean proportion of tagged nestlings in small broods: 0.9 ± 0.05 SE, and in large broods: 0.7 ± 0.08 SE). This amounted to a total of 64 nestlings from enlarged broods, 27 from reduced broods, and 14 from unmanipulated broods.

We provided 16 feeders (a wire cage of 70 x 40 x 50 cm, see (Mariette et al., 2011b)), each fitted with an RFID antenna (ca. 20 cm diameter) at its entrance, connected to an RFID decoder (RFIDRW-E-232; Priority 1 Design, Melbourne, Australia). These allowed us to detect the presence of individuals as they entered and exited the food source (a very similar design to the original study). Feeders were located in a min. distance of 200 m from the dam and from each other, min. 100 m away from the nest box colonies and within a maximum of 800 m from the relatively central water (dam). The feeders were all refilled daily with commercial finch seed mix from the 22nd of September until October 1st. From October 2nd to December 6th, eight of the feeders were kept always filled with food (stable feeders), while the remaining eight

feeders were provisioned as an ephemeral food source, as part of another experiment (only half of them filled for 10 hours every other day with egg and biscuit formula mixed in with the seeds; all eight feeders were empty every third day). From December 7th to 17th eight of the feeders were removed and the other eight were filled daily. We used the social association data from all feeders from the entire period, as any co-visitations still represent social associations while foraging, even if no food was present. In terms of breeding, the establishment of the first broods (first egg laid) was on 15th of September, and reproduction continued through to the end of the final brood (last egg laid on 20th of November).

Statistical analyses

We used the same Gaussian Mixture Model approach as Boogert et al. (Boogert et al., 2014) to infer co-feeding events. This algorithm identifies temporally clustered detections of PIT tags in non-uniform data streams at a given feeder on a given day (Psorakis, Roberts, Rezek, & Sheldon, 2012; Psorakis et al., 2015). We combined the data from the feeding events detected across all of the feeders on all days to construct one population-level social network. As with the previous study, associations between individuals, or 'edges', in this social network were calculated using the simple ratio index (see (Hoppitt & Farine, 2018a)), which represents the probability of observing two individuals in the same event given that at least one was observed. Unlike the original study by Boogert et al. (Boogert et al., 2014), we did not create daily networks, as the wild population had a much

lower density of social associations given the greater freedom of movement and higher number of potential food sources (see (Farine, 2018) for more details on why replicated, or daily, networks are often required in captive populations). Further, because birds regularly visited multiple feeders spanning different local colonies, we did not create a separate network for each colony as the population-level network was overall well-connected (see Figure 1). The Gaussian Mixture Model and network construction were done using the *asnipe* package (Farine, 2013a) in R (R Development Core Team, 2017).

We then implemented the same set of 10 analytical tests as performed by Boogert et al. (Boogert et al., 2014). We (1) tested whether mated adults had stronger associations than non-paired adults, and (2) tested whether the association strengths among families were stronger than among non-families. We also tested whether birds from enlarged broods differed to birds from reduced broods in terms of (3) the size of their foraging groups or (4) the number of foraging groups joined. Having completed these baseline tests, we then investigated the relationship between brood size and social network position. Specifically, we tested whether juveniles from enlarged broods had (5) any difference in weighted degree, (6) a higher unweighted degree, (7) a higher (weighted) betweenness, and (8) any difference in (weighted) eigenvector centrality compared to those juveniles from reduced broods. Unweighted degree is simply the count of the number of connections to distinct individuals, while weighted degree is the sum of the association strengths that an individual has. Betweenness is the number of shortest paths

between pairs of individuals that include the focal individual. Eigenvector centrality captures how well connected individuals are to individuals with a high degree (here weighted degree as we used a weighted measure of eigenvector centrality). We also (9) tested whether juveniles from larger broods had less differentiated relationships (associated more randomly) by calculating the coefficient of variation (CV) of edge weights for each individual. A higher CV suggests that individuals have a mix of both strong and weak connections, whereas a lower CV suggests that individuals associate more equally with all conspecifics. Finally, we (10) tested whether juveniles from larger broods had weaker association with their parents.

We used the weighted assortment coefficient from the *assortnet* (Farine, 2014) package in R to test hypotheses 1 and 2. We then used linear mixed models to test hypotheses 3 to 10, fitting the response variable (number of groups, mean size of groups, unweighted degree, etc.) with treatment being the only predictor, and family and colony fitted as random effects. Because we did not have replicated networks, we did not need to fit time as a fixed effect or individual identity as random effect. However, because network data are inherently non-independent (see (Croft, Madden, Franks, & James, 2011)), the significance of each coefficient in each model (herein P_{rand}) was calculated by comparing the observed data to 10,000 coefficients calculated by fitting the same model to permuted versions of our data (see (Farine, 2017)). We used a standard pre-network permutation procedure (originally described by (Bejder, Fletcher, & Brager, 1998), see also (Whitehead, 2008)), in which pairs of observations of two individuals

observed at the same feeder on the same day were swapped between groups. After each swap, we recalculated the network, thus producing 10,000 random networks. Significance was calculated by comparing the observed coefficient value to the distribution of coefficient values from the randomised networks (following (Farine, 2017), see also (Manly, 1997)). For effects that were significant in Boogert et al. (Boogert et al., 2014), we used a one-tailed significance test, whereas we used a two-tailed test for effects that were not significant in Boogert et al. (Boogert et al., 2014).

Given that birds entered and left the population during the course of the study, our permutation test specifically controlled for any differences in the locations, number of foraging events joined, and temporal patterns of presence across individuals in the population. That is, if a chick fledged early in the season, it would have had more opportunity to forage with others. When generating the distribution for the null hypothesis (using pre-network permutations of the data), the observation of that juvenile on a given day could only be swapped with observations of other juveniles on the same day and at the same location. This means that any patterns arising because of an individual had more opportunity to forage with more conspecifics (it was present on more days) were maintained in the randomised data (meaning it had an equal opportunity to forage with many conspecifics in the distribution for the null hypothesis). For this reason, the standard errors of the coefficients from the linear models can sometimes be large despite the permutation test generating a significant P value (i.e. because variation among individuals pertaining to their general

differences in when and where they were detected are maintained in the permutation test, but contribute towards calculating standard errors).

RESULTS

Brood size manipulations had a strong effect on nestling weight. We detected no difference in weight (day 3, weight ~ numerical brood size after swapping: $\beta\pm SE=0.037\pm0.041$, $t=0.902$, see Supplemental Table S1 for full results) or tarsus length (day 3, tarsus length ~ numerical brood size after swapping: $\beta\pm SE=0.065\pm0.054$, $t=1.194$, see Supplemental Table S2 for full results) among chicks according to their end brood size on the day of manipulation. However, by day 11, every additional nestling in a nest reduced a nestling's weight by 1.6%, or approximately 10% between the smallest and largest manipulated broods (numerical brood size: $\beta\pm SE=-0.154\pm0.058$, $t=-2.660$, see Supplemental Table S3 for full results). However, we found no effect of brood size manipulations on body size on day 11 (tarsus: $\beta\pm SE=-0.017\pm0.037$, $t=-0.480$, see Supplemental Table S4 for full results).

We detected a total of 200 adults, 69 juveniles, and 14 individuals of unknown age at the RFID-equipped feeders, from which we constructed the social network (N=283 in total). Of the juveniles, 40 were from experimentally-enlarged broods (0.63 of those tagged), 16 were from reduced broods (0.59 of those tagged), 8 were from un-manipulated broods (0.57 of those tagged), and 5 were caught as juveniles from

unknown sources (the last two categories were not used in the analyses).

Our data on juveniles from enlarged and reduced broods supported 9 of the 10 statistical tests performed in Boogert et al. (Boogert et al., 2014) (see Table 1 for summary results). More specifically, we found our network captured the strong familial structure in the population. The strong connections between paired birds resulted in significant assortment in the social network by pair, while strong within-family links produced significant assortment by family. We found no evidence that birds from enlarged broods differed to birds from reduced broods in the size or number of foraging groups they joined, or in their weighted degree. However, birds from enlarged broods had a significantly higher unweighted degree, meaning that they had foraged with a greater number of conspecifics than birds from smaller broods. Although this might be the effect of living in larger families, the effect size was also significant if we removed each juvenile's connections to its family members. They also had a significantly higher betweenness, suggesting that they were potentially more important in the global connections of individuals across the whole population. We found no significant difference in eigenvector centrality, but birds from enlarged broods had a higher CV, meaning that they had more differentiated relationships. Finally, we found no evidence for a difference in the strength of relationships that juveniles from enlarged broods had with their parents when compared to juveniles from reduced broods.
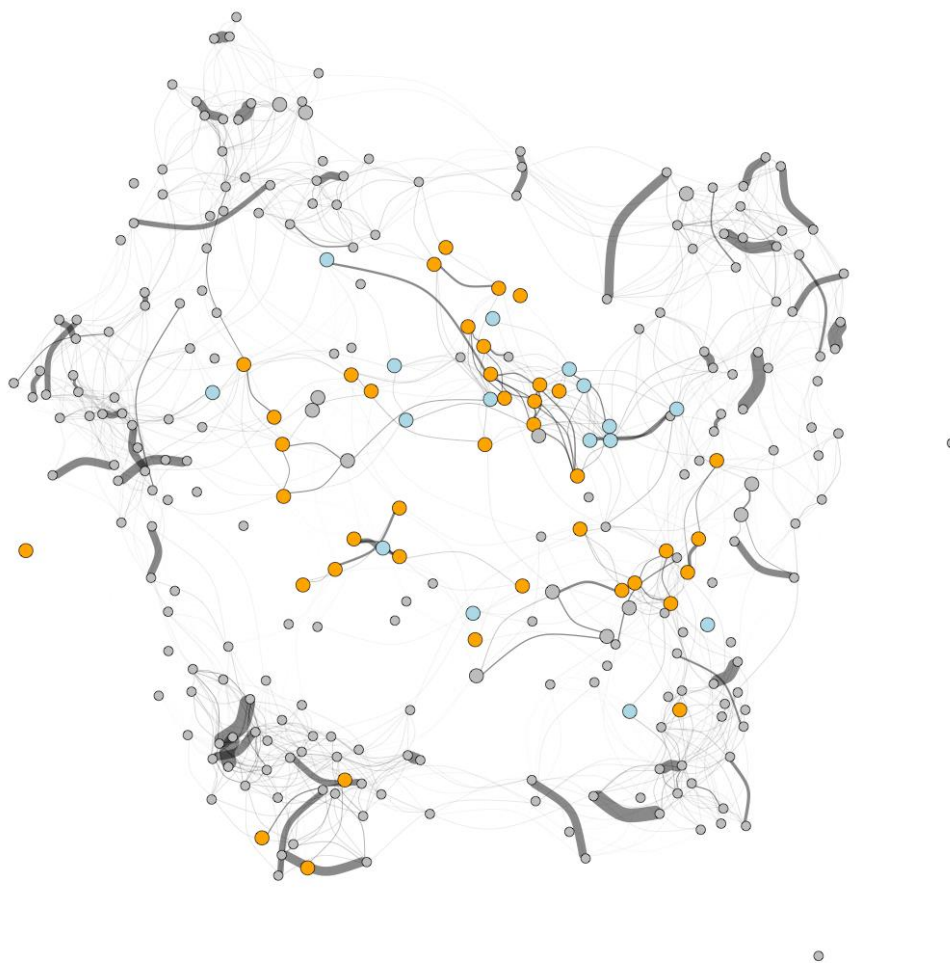
Figure 1. Social network from data collected from a population of wild zebra finches between September and December 2017 at feeders in the Australian desert. Small nodes represent adults, with the many wide edges showing the high association strength between pair-bonded individuals. Large nodes represent juveniles, with juveniles from enlarged broods shown in orange and juveniles from reduced broods shown in blue. Large grey nodes are juveniles not part of the experimental treatment groups. Network is plotted based on each individuals' 6 strongest edges only, although all edges were used in the analyses.

Our data strongly support the prediction that developmental conditions can underlie consistent differences in social network position. The social network of wild zebra finches captured several aspects of social structure that we expected from birds that form life-long breeding pairs where both parents contribute to the raising of the offspring, and forage together in a coordinated way (Mariette & Griffith, 2012b, 2015). The social network was significantly assorted by breeding pair, meaning that the density of connections (sum of edges divided by the number of possible edges) between pairs of individuals that bred together was disproportionately higher than expected by chance, and also reflected a high degree of assortment by family.

Table 1. Summary of the statistical results, including the predictions based on results from Boogert et al. [21]. Coefficients from linear models (β) are given for juveniles from enlarged broods relative to individuals from reduced broods for the results from the current data. P_{rand} values are calculated by comparing the observed coefficients to a distribution drawn from 10,000 permutations of the data. We used one-tailed tests when the prediction involved a directional effect, and two-tailed tests when no difference was predicted. For non-network tests, we relied on interpreting the t statistic. Complete results tables, including random effects, are provided as supplementary tables (the number is given in the Supp. Table column).

	Test	Prediction	Observed (coef±se)	Signif.	Match	Supp. Table
1	Pair bonds	Positive assortment	r=0.163±0.015	P_{rand}<0.001	Y	-
2	Family structure	Positive assortment	r=0.211±0.033	P_{rand}<0.001	Y	-
3	Size of foraging groups	No difference	β=-0.160±0.443	t=0.362	Y	5
4	Number of foraging groups	No difference	β=44.36±61.74	t=0.718	Y	6
5	Weighted degree	No difference	β=0.143±0.411	P_{rand}=0.196	Y	7
6	Unweighted degree[1]	Stressed chicks higher	β=9.514±20.301	P_{rand}=0.014	Y	8
7	Betweenness	Stressed chicks higher	β=218.1±202.3	P_{rand}=0.049	Y	9
8	Eigenvector centrality	No difference	β=0.018±0.090	P_{rand}=0.280	Y	10
9	Coefficient of variation of edge weights	Stressed chicks lower	β=-0.007±0.064	P_{rand}=0.001	Y	11
10	Strength of bonds to parents	Stressed chicks weaker	β=0.000±0.007	P_{rand}=0.257	N	12

[1]see Supplemental Table S8a for results without connections to family members, which are qualitatively identical.

In fact, nearly 20% of the total sum of edge weights was between individuals from the same family, despite these representing only 6% of the total possible edges in the network. However, not all these families were created equal, and by manipulating the early-life social environment of chicks, through brood size manipulations, we found that being raised in a nest containing more 'siblings' resulted in marked differences in social network position later in life. In particular, juveniles who grew up in

experimentally enlarged groups foraged with a greater number of conspecifics, were less 'choosy', and were more central in the overall social network.

We found support for 9 of the 10 hypotheses we replicated from the original study. Of these, we could directly compare the coefficients from three tests: assortment by pair, assortment by family, and the relationship of juveniles to their parents. In both tests of assortment, we found that the network of wild zebra finches was much more strongly assorted than the networks of captive zebra finches (pair bond: $r_{captive}$=0.111 vs r_{wild}=0.163; family: $r_{captive}$=0.091 vs r_{wild}=0.211). This result is, in large, expected because the wild birds were spread over a much larger area and had access to a larger number of feeders, but reflects the importance of foraging in family groups for wild zebra finches. Captive birds, on the other hand were confined to always remain in close spatial proximity which could lead to more unpaired and unrelated dyads being observed in the feeder, which is less likely to occur in the wild. The relationship of juveniles to parents was the only test where our results did not support the results of Boogert et al. (Boogert et al., 2014). However, we found that the direction (birds from enlarged broods had lower connection strength to their parents) and size ($\beta_{captive}$=-0.008 vs β_{wild}=-0.007) of the coefficients was very similar, which raises the possibility that future studies may find support for this particular prediction. Unfortunately, because the other network metrics are strongly influenced by the size of the networks, which were different between the captive and wild studies, this makes direct comparison of effect sizes challenging (see (Croft, James, & Krause, 2008; Farine & Whitehead, 2015b)).

Our current study is a relatively unique example of direct replication of a captive study in the wild (see also studies on personality in zebra finches in the wild and captivity by (McCowan, Mainwaring, Prior, & Griffith, 2015; McCowan, Rollins, & Griffith, 2014), and a recent study of sexual coloration in wild guppies by (Kemp, Batistic, & Reznick, 2018)). The value of our replicate experiment is enhanced by having used a naturally-occurring stressor, here variation in the brood size that juveniles have experienced. This means that we can realistically expect our findings to translate directly to natural situations. Further, although the original study by Boogert et al. (Boogert et al., 2014) suggested that the close confines of captivity made it potentially difficult to detect individual differences in some network metrics, such as eigenvector centrality, our data generated almost exactly the same results. This support for the original study suggests that well designed captive experiments can produce meaningful insights into the natural, free-ranging, social behaviour of zebra finches. Whether this is more broadly applicable or mostly true for zebra finches only (which naturally live and reproduce in small colonies) remains to be determined. Further, the design of the data collection (using PIT tag readers that produce large numbers of observations) and analysis (using daily networks to avoid being swamped by noise) in the original study, and similarity of data collection in the current study, may have also played a role in producing results that could be replicated in the wild.

There is clear body of evidence linking differences in early-life developmental conditions to the social behaviour, and resulting social structure, of individuals in populations. Developmental history appears

to be a potentially important factor underlying consistent differences in individual behaviour (Andrews et al., 2015; Bolton, Molet, Ivy, & Baram, 2017; Grace & Anderson, 2018; Sewall, Anderson, Soha, Peters, & Nowicki, 2018; Spencer, 2017; Szasz, Szollosi, Hegyi, Torok, & Rosivall, 2017), and brood size effects can carry over into following generations (Naguib & Gil, 2005). However, we still know relatively little about why stress appears to program individuals to be more socially gregarious and less choosy. Captive experiments in which finer details about the directionality of inter-individual interactions can be captured, facilitated by recent innovations in long-term high-resolution tracking individuals (Alarcon-Nieto et al., 2018), could provide new insights into the mechanisms—how do stressed individuals end up being more central and well-connected?—thus allowing us to determine whether the differences that have been observed are caused by the decisions of the stressed individuals themselves or the behaviour of others towards them.

AUTHORS' CONTRIBUTIONS

All authors contributed to the ideas of this study; HBB and CF collected the data; DF and HB conducted analyses and wrote the initial draft of the manuscript; all other authors provided substantial feedback. All authors gave final approval for publication.

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DATA ACCESSIBILITY

Raw and processed data, as well as R scripts to replicate the full analysis (from raw PIT tag detections or from the network data) are available to download from: https://edmond.mpdl.mpg.de/imeji/collection/k6_HOhUn546Uu4c

SUPPLEMENTAL TABLES

SUPPLEMENTAL TABLE S1. No difference in nestling weight on the day of manipulation (day 3) as a function of the brood size after manipulation. (N=146).

Fixed effect	β	SE	t
Intercept	2.450	0.204	11.990
Brood size	0.037	0.041	0.902

Random effects	Variance	SE	
Family	0.156	0.395	
Colony	0.041	0.201	
Residual	0.300	0.548	

SUPPLEMENTAL TABLE S2. No difference in tarsus size on the day of manipulation (day 3) as a function of the brood size after manipulation. (N=145).

Fixed effect	β	SE	t
Intercept	5.205	0.262	19.873
Brood size	0.065	0.054	1.194

Random effects	Variance	SE	
Family	0.291	0.539	
Colony	0.055	0.235	
Residual	0.422	0.649	

SUPPLEMENTAL TABLE S3. Brood size influenced nestling body weight on day 11. (N=121).

Fixed effect	β	SE	t
Intercept	9.425	0.287	32.79
Brood size	-0.154	0.058	-2.66

Random effects	Variance	SE	
Family	0.212	0.461	
Colony	0.000	0.000	
Residual	0.782	0.884	

SUPPLEMENTAL TABLE S4. No difference in nestling body size on the day 11 as a function of the brood size after manipulation. (N=121).

Fixed effect	β	SE	t
Intercept	13.282	0.199	66.84
Brood size	-0.018	0.037	-0.48

Random effects	Variance	SE
Family	0.010	0.010
Colony	0.025	0.160
Residual	0.516	0.719

SUPPLEMENTAL TABLE S5. No difference in foraging group size that individuals were detected in as a function of treatment.

Fixed effect	β	SE	t
Intercept	8.043	0.445	18.087
Large brood	-0.160	0.443	-0.362

Random effects	Variance	SE
Family	0.247	0.497
Colony	0.496	0.704
Residual	1.558	1.248

SUPPLEMENTAL TABLE S6. No difference in the number of foraging groups that individuals were detected in as a function of treatment. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t
Intercept	234.50	63.46	3.695
Large brood	44.36	61.74	0.718

Random effects	Variance	SE
Family	0.000	0.000
Colony	9251	96.18
Residual	41230	203.0

SUPPLEMENTAL TABLE S7. No difference in weighted degree of juveniles as a function of treatment. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	2.143	0.427	5.023	0.015
Large brood	0.143	0.411	0.347	0.196

Random effects	Variance	SE
Family	0.000	0.000
Colony	0.439	0.663
Residual	1.821	1.350

SUPPLEMENTAL TABLE S8. Effect of treatment on unweighted degree of juveniles. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	141.698	20.141	7.035	0.997
Large brood	9.541	20.301	0.471	0.014

Random effects	Variance	SE
Family	0.000	0.000
Colony	766.7	27.69
Residual	4494	67.04

SUPPLEMENTAL TABLE S8a. Effect of treatment on unweighted degree of juveniles after removing associations with family members. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	138.49	20.71	6.687	0.997
Large brood	7.57	20.44	0.370	0.014

Random effects	Variance	SE
Family	0.000	0.000
Colony	913.9	30.23
Residual	4535.7	67.35

SUPPLEMENTAL TABLE S9. Effect of treatment on betweenness of juveniles. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	388.4	171.0	2.272	0.009
Large brood	218.1	202.3	1.078	0.494

Random effects	Variance	SE
Family	0.000	0.000
Colony	0.000	0.000
Residual	467837	684

SUPPLEMENTAL TABLE S10. No difference in eigenvector centrality of juveniles as a function of treatment. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	0.408	0.102	4.002	0.982
Large brood	0.019	0.090	0.208	0.280

Random effects	Variance	SE
Family	0.000	0.000
Colony	0.034	0.185
Residual	0.087	0.294

SUPPLEMENTAL TABLE S11. Effect of treatment on social differentiation (coefficient of variation of edge weights) of juveniles. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	0.486	0.068	7.159	0.999
Large brood	-0.007	0.064	-0.116	0.001

Random effects	Variance	SE
Family	0.002	0.043
Colony	0.013	0.113
Residual	0.040	0.200

SUPPLEMENTAL TABLE S12. No difference in association strength of juveniles to their parents as a function of treatment. ($N_{enlarged}$=40, $N_{reduced}$=16).

Fixed effect	β	SE	t	P_{rand}
Intercept	0.026	0.007	3.935	<0.001
Large brood	0.0001	0.007	0.015	0.257

Random effects	Variance	SE
Family	0.000	0.012
Colony	0.000	0.009
Residual	0.000	0.017

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