

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

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Abstract

1. Many animals live and breed in colonies, and yet, with just a few exceptions, the value of the social bonds between colony members has rarely been examined. Social ties are important for group coordination at collective tasks, and social coordination can facilitate synchronized reproduction among colony members. Synchronized reproduction in turn can amplify the benefits of coloniality, such as social foraging and predator avoidance.
2. We conducted a field study to investigate whether 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.
3. We PIT-tagged wild zebra finches (*Taeniopygia guttata*), monitoring their reproduction and social foraging over two consecutive years. We then used social network analysis to characterize the strength of social bonds among birds in the population.
4. We show that birds that are more synchronized in their reproductive timing (and breed in the same colony) had significantly stronger social ties both during and after reproduction than expected by chance. Our long-term sampling also revealed that the strong social ties between synchronized breeders were carried over across years.
5. Our study reveals a strong correspondence between synchronized breeding and the social structure of the breeding colony. This suggests that the synchrony between pairs is not a simple process based on opportunity, but a mechanism underpinned by more complex sociality, which could be carried over to other behavioural contexts. The maintenance of cross-contextual social ties across years

suggests that social structure could have extensive consequences on the overall life history of individuals in addition to playing a key role for the reproductive dynamics of colonial breeders.

KEYWORDS

avian sociality, colonial breeding, group foraging, reproductive synchrony, RFID tags, social bond, social network analysis, *Taeniopygia guttata*

1 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 (Evans, Votier, & Dall, 2016; 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 (Helm, Piersma, & van der Jeugd, 2006; Ims, 1990). 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, 1990). 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, Colgan, & Boag, 2005; reviewed in: Helm et al., 2006). Overall, the social interactions underlying the synchronization 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 (Webber & Vander Wal, 2019) in mammalian (Lusseau et al., 2003; Wolf, Mawdsley, Trillmich, & James, 2007) and avian societies (Moyers, Adelman, Farine, Moore, & Hawley, 2018; Silk, Croft, Tregenza, & Bearhop, 2014), 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 (Sorato, Griffith, & Russell, 2016). One notable exception is 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 (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 that 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 that 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 relates to social behaviour during the reproductive period.

One type of social behaviour during the reproductive period is to synchronize activity with other nearby breeders. Synchronizing the timing of reproduction with pairs in close proximity means that they will have a shared agenda of, for example, incubation and then offspring provisioning and similar energetic requirements. Foraging together can increase their food searching efficiency via information transfer (Bijleveld, Gils, Jouta, & Piersma, 2015) or food intake rate by reduced vigilance (Beauchamp, 1998; but see: Coolen, 2002), while the individual predation risk might be reduced by the 'encounter' and the 'dilution' effect (Bellinato & Bogliani, 1995; Inman & Krebs, 1987). If it is easier to synchronize breeding and engage in other collective activities when close (non-mating) associations exist, then maintaining social associations with conspecifics across contexts should be beneficial. Synchronized breeding could also reinforce the familiarity among individuals, which can provide further social benefits. For example, 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, Holleley, Mariette, Pryke, & Svedin, 2010). While mate choice in this species has been of long-standing interest (Pogány et al., 2018; Wang 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 (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 adaptation 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 (Zann, 1994; Zann, Morton, Jones, & Burley, 1995). Reproduction in zebra finches is not highly synchronized across a population, and nest initiations within a breeding bout are often staggered (Mariette & Griffith, 2012). An experimental study on a wild population demonstrated that they actively seek to initiate nests in close proximity to conspecifics that are at the same stage, presumably to synchronize their breeding (Brandl, Griffith, & Schuett, 2019). However, we have little information about correlates or consequences of breeding synchrony in populations, although it was 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 aimed to investigate whether zebra finches that are more reproductively synchronous within a colony are more likely to associate in a non-reproductive context: social foraging. We predicted a positive relationship between social association strength among individuals and their reproductive synchrony. Our analysis was explicitly focused on associations between, rather than within, breeding 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 whether the reproductive synchrony of colony members is associated with, and can predict, social ties across contexts; that is, whether birds from synchronously breeding pairs are also more likely to forage together. We then investigated the social structure of the population across seasons to test whether associations established during one breeding period were stable and persisted between periods of reproduction and into the next breeding event.

2 MATERIALS AND METHODS

2.1 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 × 2 km has a dam with a relatively permanent water body in the centre and an established nest box population in its surrounding (Griffith, Pryke, & Mariette, 2008). Wooden nest boxes attached to metal stakes were provided: 207 nest boxes in 2015 and 236 nest boxes in 2016. The boxes were arranged in six colonies of 30 boxes each, with the remainder of the boxes scattered in the periphery of the colonies to allow for use by birds that preferred to nest in lower densities (for set-up of nest boxes, see maps in Figures S1–S3). In 2015, we conducted a clutch and brood size manipulation 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, Griffith, & Schuett, 2018). The manipulation did not affect the subsequent nest site choice of pairs. Zebra finch pairs with multiple successive broods mostly remained in the same colony, but always switched nest boxes between broods (Brandl et al., 2018).

2.2 Feeders and electronic monitoring system

Supplementary food (commercial finch seed mix) was provided in feeding stations (wire holding cage of 70 × 40 × 50 cm; for further details on feeders, see Mariette et al., 2011). Feeding stations were equipped with RFID decoders (RFIDRW-E-232; Priority 1 Design). 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 most of the study period, two additional feeders were added to each of the six colonies, making 18 feeders in total (see dates in Table 1; for set-up of the feeders, see maps in Figures 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 (one feeder placed in the centre of each colony again) and end of the breeding period (sixteen feeders placed in surroundings of the colonies; Table 1 and Figures S1–S3).

2.3 Bird capture and tagging

All reproductive activity in the area was monitored between 1 August and 20 December in both years. Adults were caught in the nest boxes using nest box traps between nestling days 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). 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

TABLE 1 Summary of the four study periods: *breeding2015*, *post2015*, *pre2016* and *post2016*

	<i>breeding2015</i>	<i>post2015</i>	<i>pre2016</i>	<i>post2016</i>
Period	23 October–21 November	22 November–26 November; 28 November–2 December	5 August–10 August	10 December–14 December; 16 December–19 December
No. of days	30	10	6	9
No. of feeders	6:23 October–25 October; 18:26 October–21 November	18	6	16
No. of feeder visits	115,430	69,442	10,301	15,954
No. of individuals detected at feeders	380	330	74 (40 of them tagged in 2015)	80 (28 of them tagged in 2015)
No of pairs/individuals in analysis	130 pairs	69 birds	24 birds	13 birds
Mean feeding duration	287.0 s	285.4 s	338.5 s	356.1 s
Mean flock size	3.1 birds	2.8 birds	2.4 birds	2.5 birds
Min–max percentage active nest boxes	85%–97%	86%–91%	<1%–3%	1%–12%
Breeding summary	High breeding activity	High breeding activity in November; declining during December	Start of breeding bout; first egg laid on 7 August	End of breeding bout; only three nests with eggs across study area

Notes: Dates, duration, number of feeders and feeder visits, number of visiting zebra finches, mean duration of feeding events and mean flock sizes (as determined by the Gaussian mixture model) and the range of minimum and maximum percentage of active nest boxes (i.e., with eggs or chicks) are given for each period and summarized across the six colonies. In *post2015* and *post2016*, the days on which feeders were moved to new locations (27 November 2015 and 15 December 2016) were not included in the data.

throughout October and early November 2015 and on two days in August 2016.

In total, we PIT-tagged 827 zebra finches (250 females, 331 males and 246 juveniles) in 2015: 655 were caught and marked at their nest box (431 adults and 224 nestlings), and 172 birds were caught in the feeders (138 adults and 34 juveniles). In 2016, we captured and tagged an additional 228 previously unmarked adults (113 females and 115 males): 194 were caught at nest boxes, and 34 were caught at the feeders at the beginning of the field season (on 8 August and 9 August).

2.4 Network construction

We quantified social association among all individuals in the population from the RFID data collected at feeding stations. We used a Gaussian mixture model to identify time windows in the temporal data stream (detections of individuals in time) corresponding to clusters of visits by individuals (Farine & Whitehead, 2015; Psorakis et al., 2015). The algorithm identifies temporal peaks of activity in the data stream corresponding to groups of individuals visiting the feeder and including all feeder visits (see mean duration of feeding events and mean flock sizes in Table 1). The individuals observed in the same feeding event were considered as flocking together, an approach called the ‘gambit of the group’ (Franks, Ruxton, & James, 2010). We used the repeated observations of individuals at the feeders together to construct the social networks, 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, 2018). Translating the rates of co-occurrences per unit time into an association index ranging from 0 (individuals never associate) to 1 (individuals always associate) is a way of avoiding the confounding effects coming from observing some individuals more often than others (Cairns & Schwager, 1987; Hoppitt & Farine, 2018).

We constructed separate social network analyses in four distinct time periods spanning multiple seasons (see dates in Table 1). The first period, (a) *breeding2015*, corresponds to the peak of the 2015 breeding season lasting 30 days. Breeding had already been ongoing for about three months before *breeding2015*, but we only collected RFID data after 50% of the birds in the population were tagged. For data during the breeding season, we constructed nest box-level networks (i.e., where the nest boxes/breeding pairs represent the nodes of the network). These nest box-level networks capture 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, to help account for the fact that one member of a pair often stayed in the nest or only one member of a pair entered the feeder. We calculated the edges in this network as the mean of the four possible between-nest box pairwise relationships. The next three periods represent intervals of data collection after the main part of the 2015 breeding season to investigate a potential carry-over of social ties. These three periods were defined as follows: (b) *post2015*: the last 10 days of data collection in 2015 with 18 feeders; (c) *pre2016*: six

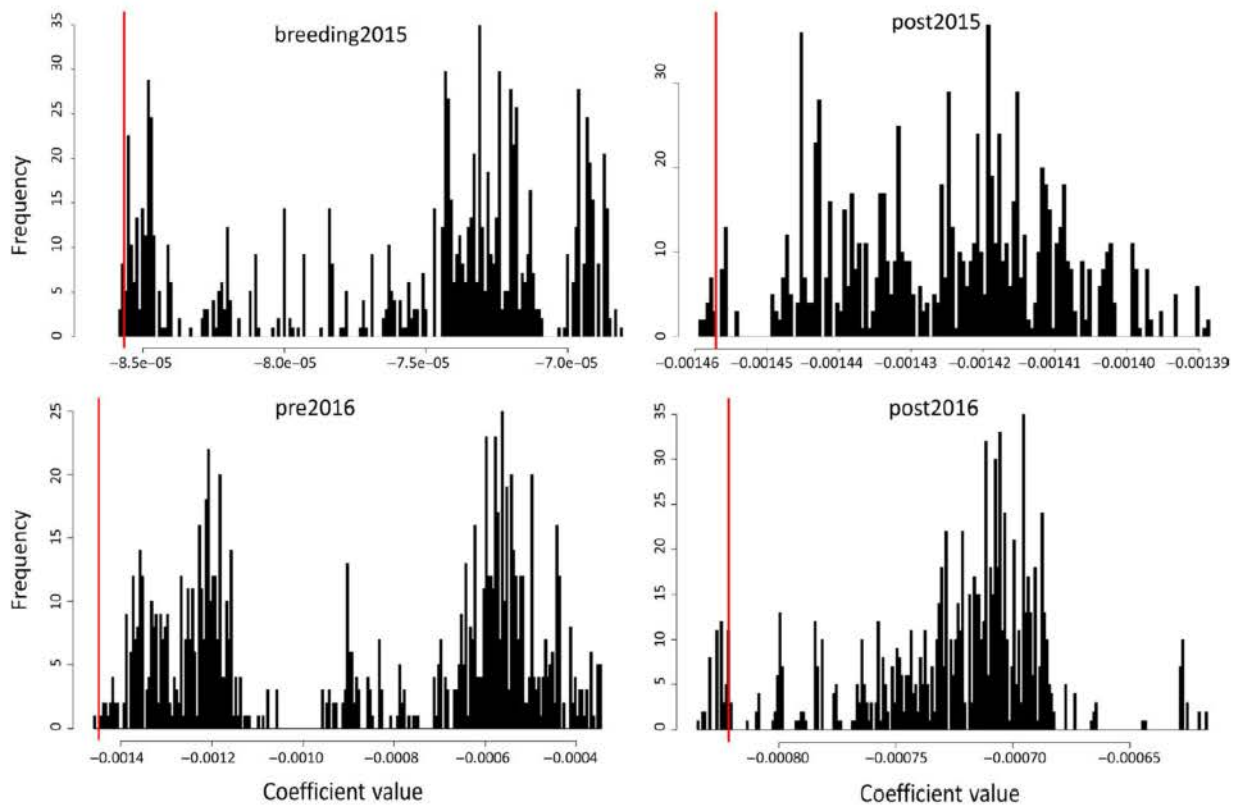


FIGURE 1 Histogram of the frequency distribution of the coefficient estimates for the fixed effect (association strength) calculated from the 1,000 pre-network data permutations (black bars). The model coefficient value for the change in association strength in relation to the level of breeding synchrony using the observed data is indicated by the red line. The p -value (p_{rand}) was obtained by comparing the observed coefficient to the distribution of coefficients from the permuted data, and thus gives the probability that the observed model coefficient sits within the expected random distribution

days with six feeders, at the beginning of the breeding period 2016; and (d) *post2016*: nine days with 16 feeders at the end of the breeding period 2016 (Table 1). *Post2015* was introduced to have a more similar time window (i.e., equal length and network construction) for comparison with the periods thereafter (*pre2016* and *post2016*). For these later periods (*post2015*, *pre2016* and *post2016*), we created individual-level social networks, but excluded associations between mated pairs.

To validate that the social structure in the constructed networks was meaningful, we compared edge weights between mated pairs with edge weights between individuals that were not mated with each other (with pairs identified by capture and RFID detection at nest boxes; Figure S4).

2.5 Data analysis

To quantify breeding synchrony, we created a matrix with dyadic comparisons of the breeding status between all breeding pairs (nest boxes) in 2015. To calculate the level of nesting 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

one for each day (with an active nest) leading up to it, and adding one for each day of the nestling rearing period thereafter. Breeding asynchrony between each possible dyad of pairs was then calculated as the absolute number of days difference in nest status (e.g., Nest A: hatch day = 0, Nest B: 7-day-old nestlings = 7; difference = 7). Thus, breeding synchrony was defined as a smaller difference in nest status.

We then conducted matrix regressions (multiple regression quadratic assignment procedure, using the package *asnipe* [version 1.1.11] (Farine, 2013)) fitting breeding synchrony and breeding location distance (derived from the GPS positions of the nest boxes using the package *geosphere* [version 1.5.7] (Hijmans, Williams, & Vennes, 2015)) as fixed effects, and the association matrices as the response variable. We obtained our P -values by comparing the coefficient estimates for the fixed effects obtained from the observed model with the coefficient estimates calculated using the same model applied to 1,000 networks on which we applied the pre-network permutations (such p -values are referred to as p_{rand} hereafter; Figure 1). The p_{rand} values give the probability by that observed model coefficients sit within the random distribution and thus the probability that the effect could be more extreme in a random network than in

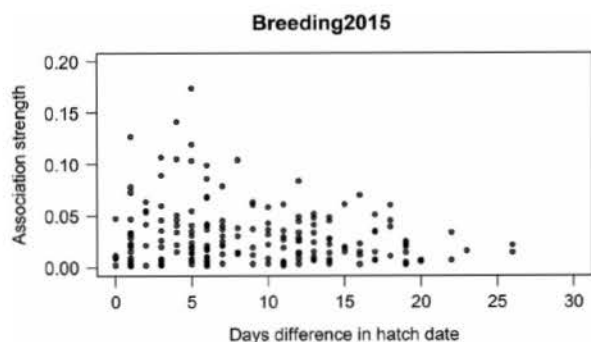


FIGURE 2 Strength of feeding associations between dyads of pairs in *breeding2015* in relation to their level of breeding synchrony during 2015

the observed (Farine & Whitehead, 2015). p_{rand} values were calculated using a two-tailed test. We used pre-network permutations on the flock membership data because we wanted to test whether birds breeding in synchrony had stronger associations than expected by chance (as in the randomized network), rather than comparing the association strength between different groups of birds in our study population (the latter would have been the test using network-level, or 'node', permutations).

The pre-network data permutations (following the algorithm originally described by Bejder, Fletcher, & Bräger, 1998) swapped individuals' observations within the same day and within the same feeder (Farine, 2017; Whitehead, 2008). Using this method of data randomization controlled for many aspects of the data that can affect associations among individuals but were not central to our question. For example, we controlled for the number of observations of each individual at a given feeder (controlling for space) and when those observations were detected (controlling for time). That is, in every version of the random data against which our observed data were compared (and thus our hypothesis was evaluated) each individual was 'observed' exactly the same number of times at each feeder on each of the days as in the original data. The aim of this algorithm is to maintain key aspects of the data, such as variation in where individuals foraged and when constant. Any remaining differences between the observed and randomized data are therefore likely to be due to the social decisions that individuals made (i.e., precisely when, or more specifically in which flock, an individual foraged). Using this approach, our null model controlled for non-random patterns of observations across days (i.e., general differences in feeding patterns of individuals, which could relate to current breeding status) and across feeders (i.e., individuals breeding nearby were more likely to be detected at the same feeder). The fact that some feeders provided different food quality than others (see Section 2.2) and the number of feeders varied was thus inherently controlled for by the permutations. If some feeders were generally more frequented than others, this was also the case in the random data. The network permutations were also conducted with the package *asnipe* [version 1.1.11] (Farine, 2013). All data were analysed with R [version 3.5.0] (R Core Team, 2017),

and *igraph* [version 1.2.4] (Csardi & Nepusz, 2006) was used to create the network graphs.

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 binary predictor in the model instead of distance. In the *pre2016* analysis, we removed the edge between one dyad of individuals as it was much higher than average (association strength >0.8) and was most likely a newly formed pair that we had not identified as such (see Figure S3 for comparison of association strength within pairs).

3 RESULTS

We recorded 115,430 detections at feeders by 380 wild zebra finches during the *breeding2015* period (see summary in Table 1; network in Supporting information; Figure 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 *breeding2015* network ($N = 130$ breeding pairs), edge weights decreased by -0.00009 per day of difference in synchrony (intercept = 0.0064, $p_{rand} = 0.003$; Figure 2), and by -0.00001 per 100 m increase in distance between nests ($p_{rand} = 0.049$). In other words, the more similar the breeding status of two pairs nesting in the same colony, the more likely they were to also be present in the same feeder together at the same time. Above results allow the interpretation that pairs that were 10 days apart in their breeding cycle were seen feeding together 14% less often.

We also found positive relationships between breeding synchrony among individuals and their social association strengths in later seasons. In the *post2015* network (Figure S6a), the edge weight decreased by -0.00147 per day of difference in synchrony during

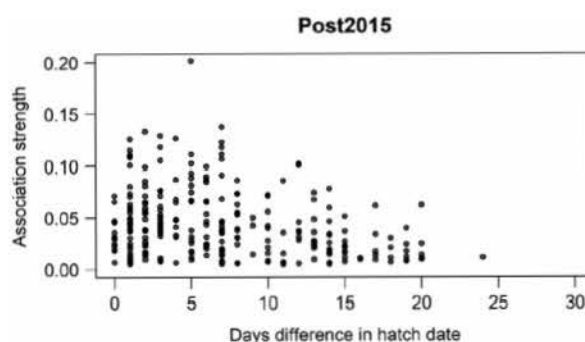


FIGURE 3 Strength of feeding associations between dyads of pairs in *post2015* in relation to their level of breeding synchrony during *breeding2015*

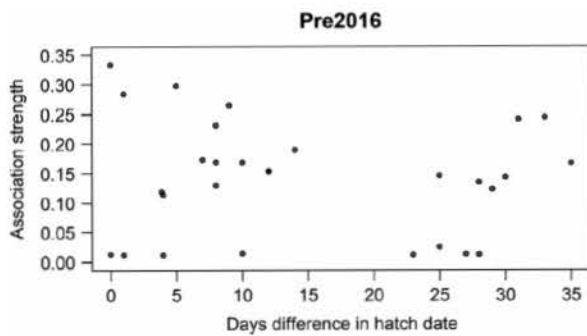


FIGURE 4 Strength of feeding associations between dyads of pairs in *pre2016* in relation to their level of breeding synchrony during 2015

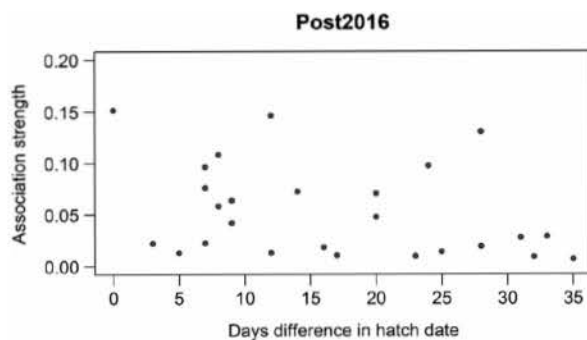


FIGURE 5 Strength of feeding associations between dyads of pairs in *post2016* in relation to their level of breeding synchrony during 2015

the preceding breeding season (intercept = 0.04317, $p_{\text{rand}} = 0.015$; Figure 3). If individuals were breeding 10 days apart, their association strength was thus reduced by 34%. Breeding was still ongoing in this period (see percentage of active nest boxes in Table 1), but the number of new nests being initiated strongly declined in December and most individuals in the network had finished breeding (41 individuals of the *post2015* network had active nests on 19 December; that is, 19.8% of the nest boxes were still active).

More than eight months later, in the *pre2016* network ($N = 24$ individuals; see Figure S6b), 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; edge weights decreased by -0.00145 per day of difference in synchrony (intercept = 0.1414, $p_{\text{rand}} = 0.001$; Figure 4). Assuming a difference of 10 days in the nest status between individuals, their association strength was reduced by 10% compared to fully synchronized individuals.

By the time we collected data for the period *post2016* network (Figure S3c), breeding had almost stopped (with only three active nests with eggs across study area). Only 13 individuals were still present (and tagged) from the original 2015 cohort, and birds that were more synchronized in 2015 still had a greater, albeit non-significant, tie strength in the *post2016* network. The edge weight (intercept = 0.023) among

synchronized pairs decreased by -0.0008 per day of difference in synchrony ($p_{\text{rand}} = 0.05$; Figure 5). If individuals were breeding 10 days apart, they were 35% less likely to feed together. Thus, despite a small sample, the patterns show a consistent effect to the previous seasons. Further, in this model we could not control for distance, and instead were limited to using shared colony (0 or 1) as a binary predictor (birds from the same area had, statistically non-significant, more than three times higher association strength: increase when breeding in same colony = 0.0489, $p_{\text{rand}} = 0.277$), which could have affected our ability to detect a significant relationship with breeding synchrony as the two effects were strongly correlated.

Across the four study periods, two pairs (or individuals) breeding 10 days apart would on average have a quarter (24%) less social feeding interactions with each other than if they were breeding in complete synchrony (ranging from 10% to 36%).

4 DISCUSSION

We have demonstrated that pairs of wild zebra finches that bred synchronously in the same colony had stronger social associations in a foraging context and maintained these stronger associations across a period of more than eight months. Our findings raise new questions about the adaptive value of social ties outside of the reproductive context, and the role they play in colonial breeding. 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, 2012), social learning (Boogert, Lachlan, Spencer, Templeton, & Farine, 2018) 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, day length or temperature).

Our data provide support for the idea that associations among birds that bred synchronously were maintained in following seasons. Even though the sample size was lower in 2016 reducing the power of our analyses, we nevertheless observed significantly stronger associations in the *pre2016* period, suggesting that a carry-over of social associations is likely to exist. Unfortunately, we did not have sufficient numbers to test whether the same pairs again synchronized their breeding as breeding activity was severely depressed in 2016 due to poor ecological conditions, and we could not conclusively test whether the associations from 2015 were maintained until *post2016*. Alternatively, it is possible that with newly arriving breeders, new associations will be formed and the fission–fusion dynamics in the colony will result in a changed social structure at the end of the second breeding period. Collecting data on more individuals to explore the carry-over effect in more detail would be desirable, but difficult to

achieve in the unpredictable conditions of the Australian arid zone. Nevertheless, we report consistent effect sizes across all four study periods, based on social data from multiple study years.

We presently do not know in which context the social ties we have characterized were established. It is possible that birds opportunistically start to breed close to individuals at a similar stage (Brandl, Griffith, & Schuett, 2019), 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 small groups of 3–10 individuals, likely to contain multiple breeding pairs, are common and they often aggregate in trees near food or water, which might also function as social hubs (McCowan, Mariette, & Griffith, 2015). Such aggregations of individuals moving and foraging together might then result in breeding associations.

The exact mechanisms underlying the pattern we have observed are currently not clear, although with our approach we can discount some alternative hypotheses. It is, for example, possible that birds at a certain stage of reproduction (e.g., with newly hatched chicks) would have more similar foraging needs (e.g., visit feeders more often than incubating birds or non-breeders), and therefore would be observed together more often. However, our null model accounts for individual variation in visits to feeders on each day, meaning that the strong effects we observed (cohesion on a minute-by-minute basis) were unlikely to have arisen from such a passive process. We thus believe that the variation in feeder use on a finer scale is more likely to be the result of active decisions by individuals guided by their social relationships. It is also possible that associations could have been driven by a third, unmeasured, causal effect. For example, phenotypes (e.g., personality) might respond to (unmeasured) environmental factors (e.g., rainfall or food availability) in a similar way, which could lead to a more synchronized reproduction between them, even on a long-term basis. Such phenotypic similarities could also drive foraging associations (such as assortment by boldness measured in other species; Aplin et al., 2013; Croft et al., 2009; Snijders et al., 2014). However, a recent experimental study on the same population has demonstrated that zebra finches prefer to actively settle directly next to breeders at the same stage (Brandl, Griffith, & Schuett, 2019). Therefore, it is unlikely that the breeding synchrony is only an unintentional side effect of individuals having similar phenotypes (which would also require assortative mate choice). Another possibility is a process involving age and experience. If younger, or less experienced, birds associate with older ones by synchronizing their foraging behaviour to acquire information about breeding, then copying reproductive decisions would lead to birds that forage together to breed more synchronously. This mechanism could lead to the patterns we have observed during the reproductive season but would be unlikely to explain the carry-over effects we observed post-breeding. Our study does, however, highlight the need for further studies on this topic. For example, artificial segregation at feeding stations, as previously done in wild bird

populations (Firth & Sheldon, 2015), could be used to test whether preventing foraging associations disrupts nesting synchrony.

Identifying the mechanisms that underlie nesting synchrony and carry-over effects across seasons remains an important goal. Studies of social networks in wild bird populations have repeatedly found 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., 2015), 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). Winter social networks also predict breeding neighbourhoods in the following spring (Firth & Sheldon, 2016). The processes underlying such patterns are completely unknown. One thing that is important, not only in great tits, but also among all bird species, is the timing of breeding (Both, 2010; Ims, 1990; 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, we present evidence that synchronized breeding has underlying causes in, or consequences on, social structure. Combining the indirect evidence from this study, and the results from a previous study showing experimental evidence for active synchronization (Brandl, Griffith, & Schuett, 2019), it becomes clear that breeding synchrony is not random or fleeting, but part of a complex interlinked social network that spans across different contexts. If the only purpose of synchronizing 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.

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AUTHORS' CONTRIBUTIONS

S.C.G., W.S., D.R.F. and H.B.B. conceived the study. H.B.B. collected the field data. D.R.F. and H.B.B. performed the data analysis. H.B.B. wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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