

DOES SOCIAL STRUCTURE CHANGE IN A GROUP OF ZEBRA FINCHES, *TAENIOPYGIA GUTTATA*, BETWEEN TWO FEEDING CONTEXTS?

ABSTRACT

Social individuals interact with each other in populations of animal species, forming relationships that differ in strength, which in turn shapes the social structure of a group. However, the rigidity of animals' social structure when subject to environmental change is poorly investigated within the literature. My study aims to assess whether the social structure in a flock of zebra finches, *Taeniopygia guttata*, changed under two feeding contexts. This was achieved by changing the way in which food was presented in two experimental treatments, therefore providing different social feeding opportunity. The strength at which individuals associated within the flock was evaluated under these two contexts, and was used to infer social structure. I demonstrate that the social structure within the group is relatively flexible between the two treatments, where the organisation shows similarity between them, but is not restricted such that it remains identical. I suggest that potential pair and kin bonds remain stable across treatments, which contribute to the overall similarity between the structures under different contexts, while other relationships are much more variable, such as those involving juveniles. I also speculate that although preferential associations between pairs exist, a dominance hierarchy is unlikely to restrict the flexibility of the social structure across contexts. My conclusions suggest that the rigidity of social structures in zebra finch populations subject to environmental change will be dependable on the phenotypic and demographic-structure of the group, and further studies might reveal that hierarchical relationships are unlikely to control this flexibility.

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1. INTRODUCTION

Understanding the social structure of animal groups is a growing and important topic in sociobiology. Not only can it reveal information regarding the sociality of populations, but understanding social structure may also be a key determinant in the study of other related properties such as gene flow, spatial patterning and fitness consequences (Psorakis et al., 2015; Wey et al., 2008; Wilson, 1975).

Social structure is a synthesis of how individuals interact with each other that summarises the relationships between all members within a group (Whitehead, 2008). Robert Hinde (1976) developed particularly influential framework on the subject, outlining three levels of organisation when assessing social structure. He first stated that there are simple behavioural interactions between specific dyads within a group. In turn, the content and patterning of these interactions define the relationships between individuals. Finally, Hinde stated that the nature and patterning of these relationships determines the entire social structure among all dyads, and therefore the group. In short, interactions describe relationships, which in turn define social structure. This has led to perhaps the most widely cited definition of animal social structure as the “*nature, quality and patterning of relationships*” (Hinde, 1976).

The study of the social structure of populations is highly relevant in biological research. This is because an individual’s proximate conspecifics, as determined by the structure, are fundamental elements of its environment when living in a group. Such individuals may compete with each other, cooperate, mate, or provide parental care, among a number of different interactions that might influence reproductive success, mortality and dispersal. Therefore, social organisation has the potential to greatly affect the average fitness of individuals within a group, and therefore the persistence of said group. Furthermore, the form of social structure will influence the evolution of social traits of individuals within the group (Whitehead, 2008). This is because an individual’s interactions with related conspecifics may affect its inclusive fitness, thus driving social evolution (Alexander, 1974; Hamilton, 1964). Additionally, the form of social structure governs the network of relationships between all non-relatives within a group, thus playing a key role in the evolution of cooperation (Trivers, 1985).

Further to these more general and ultimate principles as to how social structure affects the evolution of populations, social structure also determines the transmission of anything that can be spread through a population by individual-to-individual association or interaction (Whitehead, 2008). For example, a number of studies on animal populations have related their social structure to the spread of information (Lusseau, 2003; Aplin et al., 2012; Allen et al., 2013) and disease transmission (Drewe, 2010; Godfrey et al., 2009; Weber et al., 2013).

One area of research regarding social structure is the understanding of how environmental features might cause the formation, and influence the specific nature, of within-species social organisation (Firth, 2016). Initial pioneer studies outlined the importance of ecological factors in the formation of non-kin social groups in mammalian species (e.g. Kruuk, 1978; Macdonald, 1989). It was identified that ecological variables such as abundance of food, level of competition and population density play a central role in shaping social structures. It has even been recognised that such factors could potentially trigger alternative social systems, and therefore structures, as an adaptive response of a population (Lott, 1984). Some more recent studies have involved experimentally manipulating ecological factors, such as food availability or dispersion, with results that have suggested social structure often responds flexibly to imposed external changes (e.g. Davies & Hartley, 1996; Verdolin, 2009).

Linked to this, the role of feeding behaviour in social structure is one that has prompted much empirical work. It raises interesting questions concerning the interplay between maximising fitness with regard to feeding and avoiding agonistic encounters during such behaviour, and maximising fitness in terms of maintaining social structure. Many early studies aimed to predict social individuals' decision-making when feeding by assuming that consumption was being maximised (Charnov, 1976; Pyke, 1984), therefore disregarding the changes in social structure. However, later work revealed that individuals forgo maximising their own food consumption in order to maintain social cohesion (Firth et al., 2015; Giraldeau & Beauchamp, 1999; Kazahari, 2014; Livoreil & Giraldeau, 1997). This means that despite not maximising personal food intake, they are advantaged by gaining benefits from social living. Such advantages may include predator vigilance and defence, food discovery and cooperation (Giraldeau & Caraco, 2000; Vásquez & Kacelnik, 2000; Krause & Ruxton, 2002).

Despite empirical studies that have predicted the feeding behaviour in groups with regard to maintaining social cohesion and structure, experiments that have specifically evaluated the change in social structure in a single group under different feeding contexts are lacking. Therefore, there is information missing as to how rigid population structures are in social species when subject to environmental change with regard to feeding.

In this study, I address the question of whether social structure in a group of social animals changes when foraging takes place under two different feeding contexts. I used a flock of highly social zebra finches, *Taeniopygia guttata*, as a model system. When in the wild, this species flocks throughout the year, feeding together in groups consisting mainly of adult pairs and fledged offspring (Zann, 1996). In this respect, flocks of the species are considered to have fairly stable social structures over short time periods. Studies have also shown evidence that

individuals within flocks of zebra finches show dominance over others, thus gaining preferential access to food when foraging (David et al., 2011), and such dominance ranking is likely to contribute in determining social structure in the species. I used the zebra finch as a model species due to these aspects of its sociality, as well as its regular use in studies of behaviour (e.g. Martins et al., 2007; Schuett & Dall, 2009). In the study, I used association indices and selected social network analyses to investigate the social structure in the study flock. By comparing the association patterns under the two treatments, I was able to explicitly determine the flexibility and difference in social structure when subject to external feeding changes.

2. MATERIAL AND METHODS

(a) *Social structure*

When assessing social structure in this study, I used Hinde's (1976) central framework. He stated that social structure, defined as the "*nature, quality and patterning of relationships*", is fundamentally determined by interactions between dyads, as they define the relationships which govern structure. Whitehead (1997) states that if the circumstances in which these interactions take place are known, then the presence of dyads in these circumstances, termed as an "association", can be used to infer relationships and thus the social organisation. In my study, an association was defined as when two birds were in contact with the same feeding dish, as they were in close enough proximity in these instances to interact.

(b) *Study organism*

The zebra finch, *Taeniopygia guttata*, is a domesticated songbird native to Australia, and is a model species for the class Aves. The study flock consisted eight males and eight females, all of which were uniquely ringed and given an ID from *A-P*. Six of the individuals were bought from a reputable pet wholesaler in spring 2018. The remaining ten were bred within the flock, four in 2018 and six in 2019 (Table A1). I did not have information on the kin or mated pair relationships within the flock.

The birds were kept in an aviary which consisted of an outdoor enclosure of approximately $3.5 \times 1.0 \times 2.5$ m and an indoor enclosure of roughly the same dimensions. The birds were allowed to move between the two areas of the aviary freely. Prior to the experiment, they were provided *ad libitum* access to water and 'Foreign Finch Mix' from a multi-perched column feeder. Fresh spinach leaves and 'CeDe Egg Mix' were provided to the finches weekly.

(c) *Experimental feeding contexts*

During the experiment, the birds were provided access to food in two different contexts. In the *Single Dish* context, one ceramic brown dish of 130 mm diameter and 30 mm height was entirely filled with ‘Foreign Finch Mix’ and placed in the centre of the outdoor compartment. In the *Double Dish* context, two of the same types of dish were equally filled to the top with seed and placed in the centre of the enclosure, 60 cm apart from each other. I acknowledged that this meant there was twice as much food in the *Double Dish* context. However, halving the amount in each dish would have made the patch poorer, and so I decided that the former option was more appropriate for the procedure. For the duration of the experiment the birds were given free access to food.

(d) *Experimental procedure*

My experiment took place between 1st and 5th July 2019. During this five-day period there was no rain and the temperature remained within the range of 18°C – 25°C during the study periods. Each day, there were two set study periods, the first from 11.00 – 13.00, and the second from 14.00 – 16.00. There was a total of ten study periods that made up 20 hours overall. Five of both of the different feeding context treatments were randomly assigned to the ten periods prior to the experiment (Table 1).

Table 1. The ten study periods within the five-day experiment with their corresponding randomly assigned treatment, either *Single Dish* or *Double Dish*.

Study Period	Feeding Context Treatment
01/07/2019 11.00 – 13.00	<i>Double Dish</i>
01/07/2019 14.00 – 16.00	<i>Single Dish</i>
02/07/2019 11.00 – 13.00	<i>Double Dish</i>
02/07/2019 14.00 – 16.00	<i>Single Dish</i>
03/07/2019 11.00 – 13.00	<i>Single Dish</i>
03/07/2019 14.00 – 16.00	<i>Double Dish</i>
04/07/2019 11.00 – 13.00	<i>Single Dish</i>
04/07/2019 14.00 – 16.00	<i>Single Dish</i>
05/07/2019 11.00 – 13.00	<i>Double Dish</i>
05/07/2019 14.00 – 16.00	<i>Double Dish</i>

Prior to the experimental period, a black inconspicuous camera case of $80 \times 25 \times 110$ mm was placed approximately 50 cm in front of where the dish(es) were to be placed, so that the birds became habituated to it. Each morning during the experimental period, the column feeder and other foodstuffs were removed at 10.00, thus starving the birds an hour before the trials took place. At 11.00, either a single dish or two dishes were placed in the enclosure, as discussed above. A camera was placed in the case facing the dish(es) and recorded continuously until 13.00. The camera and food were then removed and the birds were left for an hour. At 14.00, the food and camera were then reintroduced to the enclosure, and again recording took place for two hours. The camera used was a *Canon Legria Mini Full HD Camcorder* which recorded at 1920×1080 , 24 Mbps², with a 160° angle of view. After the second study period of the day, the camera and dish(es) were taken out of the enclosure at 16.00, and the column feeder was restored. This method was then repeated for every day of the experimental period.

Following this five-day period, the footage was downloaded onto a *MacBook Pro* and watched using *QuickTime Player Version 10.4*. All feeding associations were therefore recorded, as well as their length and timestamp in the footage. Such pairwise feeding associations encompassed a number of different behaviours, whereby either both birds were feeding, both were perched, one was feeding and one was perched, or one bird was displaced by another. All associations were rounded to the nearest second, and any association less than a second was rounded to 1 second. The Pair ID, or the ID of both birds involved in the association, was also recorded. All of this information was logged across the 20 hours of footage and compiled in *Microsoft Excel* (Table A2).

(e) Statistical methods

The total time length (seconds) of feeding associations for each Pair ID in both the *Single Dish* and *Double Dish* treatments were used for statistical analysis. In order to address whether social structure changed between the two feeding contexts, the feeding association data in the two treatments was standardised using the Simple Ratio Index (Cairns & Schwager, 1987). This index is given by $r_{i,j} = \frac{x_{i,j}}{x_i + x_j}$ (Psorakis et al., 2015), where, in this experiment, $r_{i,j}$ is the association index for a Pair ID ij , $x_{i,j}$ is the total time of feeding association between i and j , x_i is the total time that a feeding association of i was observed for a given treatment, and x_j was the total time that a feeding association of j was observed under the same treatment. This gave an association index under both treatments (Table A3), where a value of 0 would indicate that a pair were never observed feeding together and a value of 1 would mean that a pair always

occurred together when feeding. This gives an exact answer of the frequency of a pair's association relative to all feeding associations that both members of the pair experience.

This data was imported from *Microsoft Excel* into *RStudio Version 1.2.1335* (RStudio Team, 2018) where all analysis was carried out. Firstly, a Wilcoxon signed-rank test, the non-parametric equivalent of a paired t-test, was undertaken on the association index data. Following this, the data was transformed into a symmetrical matrix for each treatment, and a two-tailed Mantel test (Mantel, 1967; Smouse et al., 1986) was run using the *ecodist* package (Goslee & Urban, 2007) to test the correlation of the two matrices.

The package *igraph* (Csardi & Nepusz, 2006) was used to visualise the social structure of the individuals based on their association indices. This was done by creating social network graphs under both treatments. Once plotted, potential subgrouping within the networks was also visualised using the analyses of modularity, or network division. Nodes were clustered into communities such that a high proportion of edge weight was within, rather than between, said communities. Newman's (2006) eigenvector modularity technique was used as it has been proven to work well and is the clustering method most commonly used with animal social networks (e.g. Ansmann et al., 2012; Farine & Whitehead, 2015). Modularity can be defined as the difference between the proportion of total association within the produced clusters, and the expected proportion, where Newman (2004) states that the divisions are "good" if the modularity is ≥ 0.3 . The clustering method works by successively dividing clusters into two by using the negative and positive elements of the leading eigenvector of the "*modularity matrix*", increasing modularity at each stage until further divisions would reduce the modularity (Newman, 2006; Whitehead, 2008).

3. RESULTS

Over the entire experimental period, a total of 201 feeding associations were recorded across 72 unique pairs. There were no observations of association in the 46 remaining possible pairs. The average observed feeding association was 16.61 ± 1.74 (mean \pm standard error of the mean seconds), where the shortest were 1 second and the longest was 159 seconds. 84 feeding associations were recorded in the *Single Dish* treatment, where the average length was 22.18 ± 3.57 (mean \pm SEM seconds), and 117 were recorded in the *Double dish* treatment, where the average length was 12.61 ± 1.43 (mean \pm SEM seconds). In *Single Dish* there were 46 unique pair associations, and in *Double Dish* there were 56.

There was no evidence that the social structure changed under the two feeding contexts, under the assumption that a lack of change in the strength of association of given pairs between

the two treatments means that the structure was not affected (Wilcoxon signed-rank test: $V = 1033$, $N = 72$, $p = 0.11$). This can be seen in a boxplot (Figure 1), where there is no obvious discernible pattern of change, and in a histogram showing the frequency of the differences between paired association indices (Figure 2). This shows that many of the differences in paired association strengths reside around zero, and therefore that under different feeding contexts there was no discernible difference in the strength with which pairs associate.

The correlation of pairs' strength of association between treatments, as opposed to the changes between them, suggests that there is a weak to mid-strength similarity in the social structures of the flock under different feeding contexts (Mantel test: $r = 0.27$, $p = 0.01$). The r value of 0.27 means there is similarity in the relative size of matrix elements of the same

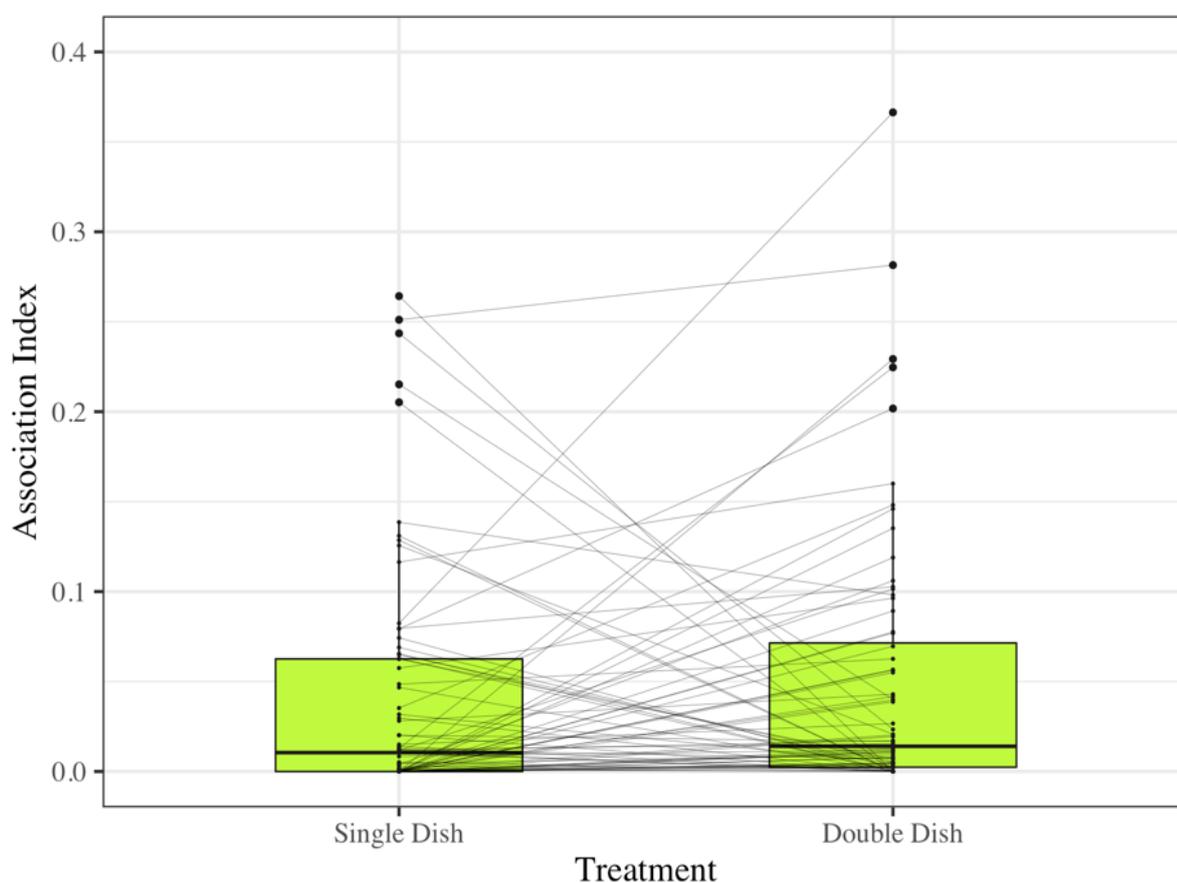


Figure 1. Paired association strengths of Pair IDs between the *Single Dish* and *Double Dish* treatments. There was no significant change between treatments.

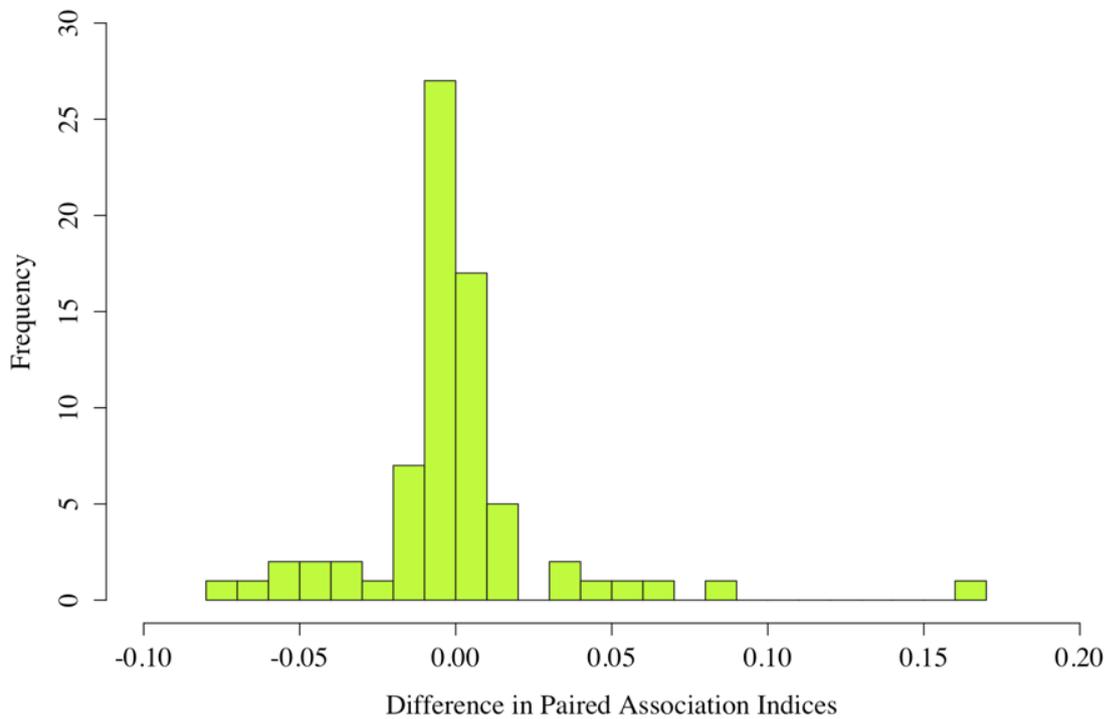


Figure 2. The frequency of the difference in paired association strengths between the two treatments, omitting all Pair IDs where the association index was 0 under both treatments.

position between the two treatments, where $r = 1$ would indicate perfect correlation, $r = -1$ would indicate inverse correlation, and $r = 0$ would indicate no correlation. Furthermore, the group retains some degree of similarity, due to the correlation in the magnitude of association indices for some pairs, between the *Single Dish* and *Double Dish* treatments.

During the experimental procedure and analyses, I noted that some associations were particularly strong and stable across treatments. When combined with personal observation and information of the phenotypes of the individuals involved, I inferred that such associations presented evidence of pair and kin bonds within the group (namely *BC*, *DI*, *FO*, *FP*, *GK*, *OF* and *OP*). When analytically removing these pairs, there is some evidence that the social structures correlate less between contexts than when they are included (Mantel test: $r = 0.12$, $p = 0.11$). Conversely, I noted that juvenile *P* was youngest in the group and showed high variability in its association data. I omitted this individual when assessing the change in social structure, and the correlation is much stronger between the two contexts than when *P* is included (Mantel test: $r = 0.47$, $p < 0.01$).

The social network graphs visually indicate that the distribution and magnitude of association indices between all pairs is different between the *Single Dish* and *Double Dish*

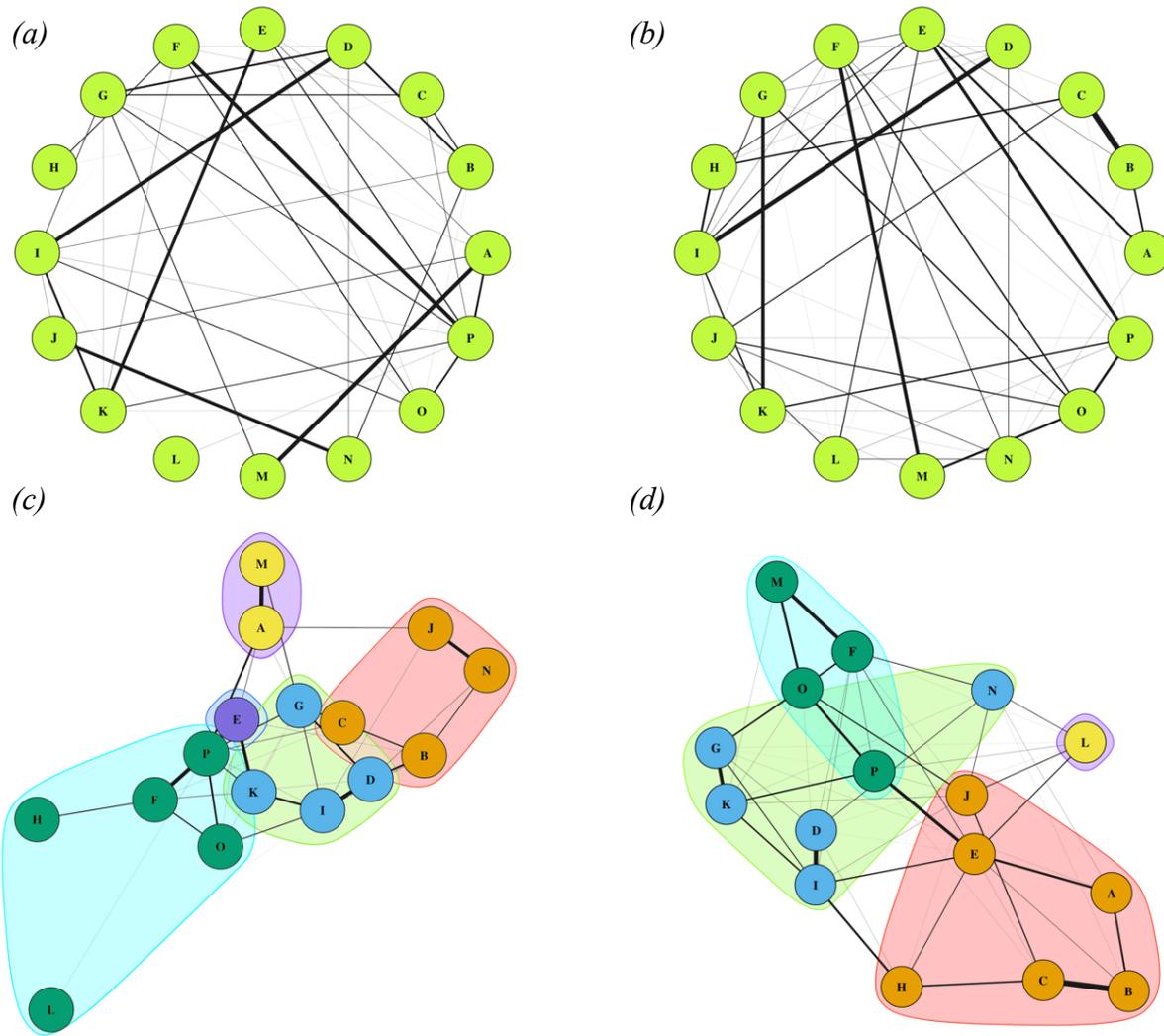


Figure 3. The network of the study flock under both treatments, where each node represents an individual ($A-P$) and the edge weights are determined by the association index between the two members of the pair. (a) The network in *Single Dish* treatment and (b) in *Double Dish* treatment, where the layout of the networks are the same to directly compare edge weights. (c) The network in *Single Dish* treatment where the individuals are clustered using the leading eigenvector method (Newman, 2006) and (d) the network in *Double Dish* treatment using the same clustering method. In the latter two plots, the nodes are not in the same positional layout and the colours of the clusters do not necessarily refer to the same communities.

treatments (Figure 3 *a* and *b*), giving the appearance of different social organisation in the two treatments. Despite this, it is clear that although the weights change, a number of nodes that are connected in *Single Dish* remain so in *Double Dish* (25.42% of Pair IDs), and similarly, there are a number of nodes that are not connected in either (38.98% of Pair IDs). The weights of some edges appear strikingly similar between the two graphs, such as those for the pairs *FO* and *DI*.

The social structure changes within the group between the two treatments in terms of the composition of subgroups within the flock that preferentially associate together under the different feeding contexts (Figure 3 *c* and *d*). The leading eigenvector method (Newman, 2006) depicts 5 distinct clusters in the *Single Dish* treatment and 4 in *Double Dish*. The composition of nodes within each community differs between the treatments. However, 10 out of the 16 nodes stayed in the same cluster as two or more other nodes between treatments: *B*, *C* and *J* (red cluster); *F*, *O* and *P* (light blue cluster); and *D*, *G*, *I* and *K* (light green cluster). The strength of association between birds within the communities, compared to with other individuals outside of their subgroup, did not significantly change across contexts (Modularity: $Q = 0.344$ for *Single Dish*; and $Q = 0.331$ for *Double Dish*).

4. DISCUSSION

(a) *Does social structure change between contexts?*

By assessing the strength of association within a flock of zebra finches under different feeding contexts, I demonstrate that there is no difference in the level at which pairs associate when food is available over greater space and thus provides different social feeding opportunity. This is due to the fact that many pairs did not change their strength of association between the two treatments. However, I cannot conclude with certainty that this means that the overall social structure was not changed, because other pairs did differ in their strength of association (Figure 2). My study also found that the social structures under both contexts weakly correlate (Mantel test: $r = 0.27$, $p = 0.01$). Although the analysis limits interpretation of which specific elements of the structure correlate, it suggests that the flock showed organisational flexibility in its social structure, but still retained similarity.

The social network graphs suggest that aspects of the social structure remained similar between the two contexts, despite visually appearing fairly different. Firstly, when discounting the strength of association and instead only inspecting which individuals are connected on the graphs, a fairly low proportion of potential pairs were observed to associate under one context without doing so in the other (35.59%). This means that the birds did not entirely change the social partners they fed with under the two treatments, which would have led to the social structure being very different. Secondly, some individuals remained with each other in the same subgroup across contexts (Figure 3 *c* and *d*). As per Newman (2006), the strength of association between individuals was taken into account when building these clusters, and therefore, the presence of these individuals in the same subgroups suggest that similarities within the social structure are retained between the two contexts. However, the finding that

subgroups are not identical in their composition between treatments suggests that the social structure showed a degree of flexibility.

(b) *Do pair and kin bonds restrict the social structure's organisational flexibility?*

A key feature in the organisation of zebra finch social systems are pair bonds (McCowan et al., 2015; Schuett & Dall, 2009). In the wild, these bonds are permanent and occur between one male and one female, which either intend to or have mated. The pairs coexist in proximity year-round at almost every instance (Zann, 1996). The bond in domesticated finches is also strong, although divorces and re-pairings may occur (Morris, 1954; Silcox & Evans, 1982). I expect such bonds to be present in my study flock, and that the bonds should be discernible from my data, as male-female pairs synchronise their activities (Zann, 1996), including when feeding, often viewed in the context of mate-guarding (Møller & Ninni, 1998). I suggest that the presence of such bonds can be detected by summing the two association indices across both treatments, and subsequently discerning which associating pairs have the highest value. It can then be assessed whether this is likely to present evidence of a pair bond by evaluating its stability across treatments, and also integrating it with knowledge of the individuals' phenotypes (Table A1) and behaviour.

I speculate that, among others, two pairs that show strong evidence of representing individuals in a pair bond are *BC* and *DI*. This is because the sum of the two association indices in both treatments are the highest in these pairs out of all 118 Pair IDs. This relatively high magnitude of association indicates that *BC* and *DI* associate with each other within their pairs much more than with other birds in the flock. Moreover, when the association indices from both the *Single Dish* and *Double Dish* treatments that sum to these two highest values are considered, they remain fairly consistent across contexts in their rank. Under both feeding contexts, the association indices for the aforementioned pairs are the highest recorded values (excluding *BC* in *B*, which is the second highest) out of the fifteen pairs under that context (Figure A1; Figure A2). This presents evidence that the association in these two pairs is fairly consistent, much like pair bonds which are highly stable (Zann, 1996), further suggesting the presence of a pair bond in *BC* and *DI*. When this association data is coupled with information regarding the sex and age of the individuals in the pair (Table A1), and personal observation of pairs' behaviour outside of feeding contexts (Author, 2019, personal observation), it is highly likely that these suggest evidence of pair bonds within the social structure of study flock under both contexts.

I additionally speculate that the data for the birds *F* and *O* and juvenile *P* may indicate preferential parent-offspring association in addition to a pair bond (Figure A3). From unpublished observations, Zann (1996) states that the age after hatching that a juvenile is likely to start foraging without its parents is 30 – 56 days. Individual *P* was bred within the flock, and its age at the start of the experimental period was 33 days (Table A1). This means that during the experiment it was likely to still be preferentially feeding with its parents. Although its parentage within the group of finches was not known, I suggest that it can be inferred from the data. Its parents must be a male and female, likely to show evidence of a pair bond, and not be any individuals that were hatched in 2019 (*A – E*) as they would most likely be too young to have successfully bred and fledged *P* (Zann, 1994). Having assessed the data and observed the pairwise behaviours (Author, 2019, personal observation), it is probable that the association values for the pair *FO* indicate a pair bond, and additionally, that they are the parents of *P*, and thus *FP* and *OP* designate parent-offspring associations. These higher-than-average associations for the relevant pairs are carried over between contexts, where the association indices for *FP* and *OP* are the first and third highest in *Single Dish*, and fourth and second highest in *Double Dish* respectively (Figure A3).

Although the exact association values of the pairs that I suggest are in pair bonds and parent-offspring associations change between treatments, they remain relatively consistent between contexts compared to other pairs' association indices. This suggests that they are more stable when subjected to different feeding contexts compared to other kin and non-kin relationships within the flock. Indeed, when analytically removing the associations between pairs that are likely candidates of pair bonds or parent-offspring associations (namely *BC*, *DI*, *FO*, *FP*, *GK*, *OF* and *OP*), I suggest some evidence that the social structures correlate less between the two contexts than when they are included (Mantel test: $r = 0.12$, $p = 0.11$). I therefore speculate that a key feature that maintained the flock's social structure between treatments were pair bonds and the parent-offspring association.

The disproportionate effect that the suggested pair and kin bonded birds have on maintaining the social structure presents an interesting finding, which is that pair bonds and parent-offspring associations might be vital relationships in maintaining rigidity in zebra finch social structures under different contexts. This would suggest that in natural populations that have non-biased even sex ratios and individuals of a similar age, the social structure might be more rigid when subject to environmental disturbances due to a high occurrence of pair bonds. This may hold important implications with regard to the response of natural populations of bird species that form lifelong bonds to habitat change and resource variability in their environment,

and how the structure of their social system might be more stable in such scenarios where there is a high frequency of pair bonds. Further studies that experimentally alter the ratio of bonded versus non-bonded pairs in flocks of birds, and assess how their overall social structure responds to perturbation, would help develop our understanding of whether such relationships in gregarious bird groups increase the rigidity of their social structure under environmental change.

(c) Do age demographics affect the social structure's organisational flexibility?

Individual *P* showed the least evidence of preferential feeding out of all individuals within the flock. It fed for a much greater proportion of the experimental period than any other individual (Author, 2019, personal observation) and was shown to associate with twelve different birds across the two treatments (mean \pm SEM number of birds an individual associated with: 9 ± 0.58). Although there was evidence of some preference, in the form of a potential parent-offspring bond as previously discussed, the pattern of *P*'s association indices across the two treatments was highly variable (Figure A4).

This variability is likely to be linked to its age for a number of reasons. Firstly, because *P* was relatively newly fledged, it would have been experiencing high rates of growth as it would not yet have reached its adult weight or maturity (Zann, 1996). Due to its higher energy demand, this would have required it to feed more often, and thus with more individuals, compared to other members of the flock. As well as this, it was not likely to have yet established the same relationships within the flock compared to other individuals. For example, it was unlikely to have formed a pair bond, with the earliest bonds forming between 50 – 60 days of age (Zann, 1994), and it may have not established a rank in the potential dominance hierarchy.

The variability in feeding association that *P* displayed under the two contexts might disproportionately contribute to the flexibility observed in the organisation of the flock's social structure. Indeed, if *P* is omitted when assessing the change in social structure, the correlation is much stronger between the two contexts than how they actually compare when *P* is included in the analysis (Mantel test: $r = 0.47, p < 0.01$). I speculate that this suggests that the plasticity of the social structure under different contexts is increased by the presence of a juvenile, prompting wider implications with regards to age demographics in wild populations. It indicates that natural populations with a high proportion of newly fledged juveniles within the group might be expected to have more flexible social structures. If groups with a high proportion of juveniles were more flexible, whereby young birds interact with more individuals and with higher variability under different environmental contexts, transmission events would

diffuse more quickly across the entire population. This could be advantageous or damaging to the group, in the case of information transfer (Aplin et al., 2012; Wey et al., 2008) or disease transmission (Drewe, 2010; Weber et al., 2013). For example, a specific suggestion of this finding is that introduction of a communicable disease to wild zebra finch populations might have the greatest impact when the proportion of newly fledged birds is at its highest following a breeding season.

(d) Does a dominance hierarchy control the change in social structure under different feeding contexts?

Some literature supports the hypothesis that zebra finch social structures are somewhat organised in a hierarchical nature (Beauchamp, 2006; Zann, 1996). Studies that predict this take an individual-behaviour approach under one experimental context, whereby the dominance hierarchy was inferred depending on various measures relating to agonistic behaviour (Bonoan et al., 2013; David et al., 2011). I speculate that despite not collecting dominance data, my study can be used to suggest the absence of a robust hierarchy by comparing how you would expect the structure to have changed if a rigid hierarchy were present to how it actually changed.

Wild zebra finches compete for various resources, including food, which accounts for the difference in dominance rank among individuals (Bonoan et al., 2013). During these competitive encounters, such as feeding, the potential hierarchical nature of zebra finch social structures help individuals avoid costly energy expenditure and injuries, whereby an individual recognises another bird's dominance status, predicts the outcome of the competition, and decides whether or not to interact (Emery, 2006). Within my study flock, there were few incidences of dominant behaviour both prior to and during the experiment (Author, 2019, personal observation), but such pairwise interactions that did occur led to one member of the pair undertaking unnecessary and potentially costly behaviour as it was driven from the food source. Therefore, it would follow that zebra finches of a similar social status within my study flock would preferentially feed together in subgroups such as to avoid these encounters (Bonoan et al., 2013), as is the case in other avian species (Emery & Clayton, 2004; Paz-Y-Miño et al., 2004). Consequently, although I did not collect dominance data, I speculate that the clusters produced in my network analyses (Figure 3 *c* and *d*) might indicate individuals of a similar rank in terms of their dominance status, because they are more often associated together than with other members of the group. Moreover, some individuals remained clustered together across treatments, which could imply that they occupy the same rank across

treatments. Thus it can be speculated that dominance hierarchy somewhat controls which birds feed together, but individuals are fluid within this hierarchy such that they are not restricted to associating with highly specific individuals.

It follows that when given more ‘choice’ of where to feed (as is the case in the *Double Dish* treatment), it would be expected that the birds would associate less often with individuals that are not social partners, and therefore, birds that are potentially of a different dominance rank. However, this is not the case, as there is no evidence of greater modularity under the *Double Dish* feeding context. This tells us that although communities of birds that feed preferentially together do exist (Ansmann et al., 2012; Newman, 2004), greater opportunity for birds to ‘choose’ their feeding partners does not result in a social structure in which communities of social partners, potentially of the same dominance rank, are tighter. This is speculative, and in order to test precisely how the dominance ranking changes under the different feeding contexts, and therefore the fluidity of the hierarchy and whether there is enough evidence to say it exists, the types of interactions that make up associations should be assessed. This would require collecting asymmetric interaction data within the group where food is not supplied *ad libitum*, and then comparing dominance indices (Bayly et al., 2006).

Although caution should be taken when drawing implications from lab studies and applying them to wild populations, I speculate that the social structures of zebra finches might not be as constrained by dominance hierarchies as perhaps expected. As aforementioned, zebra finch sociality in the wild is widely reported on (Zann, 1996). Group-living might be selected for due to patchy resources, as is the case with other vertebrates (Rubenstein & Lovette, 2007; Silk, 2007), such that social coordination of knowledge is beneficial for the entire population for foraging (Beauchamp & Kacelnik, 1990; Benskin et al., 2002; Mariette & Griffith, 2013). It might be that while there are some incidences of differential dominance and avoidance of agonistic encounters, the maintenance and importance of sociality overcomes formation of rigid hierarchies. Under this notion, birds would not necessarily preferentially feed within small subgroups of the same dominance rank when presented with more environmentally-imposed ‘choice’ to do so, such as if a grass seed food patch was more dispersed. Instead, birds would feed with a range of individuals within the group to maintain social cohesion. Experiments that assess both the association of individuals, and the types of behaviour that compose the interactions, in different feeding contexts in the wild would enable more understanding into the relative importance of reducing costly agonistic encounters versus maintaining sociality during foraging behaviour.

5. CONCLUSION

In this study, I have demonstrated that the social structure in a group of zebra finches is relatively flexible between two feeding contexts, where there is a difference in the ‘choice’ of which individuals to associate with when foraging. I have shown evidence that the social structure changes in the group, but that some relationships remain similar under the different contexts, that I suggest might represent pair bonds and parent-offspring associations. This suggests that the social structure is somewhat flexible when the group is subjected to environmental change, but birds will still preferentially associate with certain individuals, thus retaining organisation between treatments to some degree. I have proposed that the frequency and strength of such preferential pairings during foraging, and therefore flexibility of structure, is related to individual phenotypes and demographics, such as age and sex, which may hold important implications regarding the relationship between the rigidity of social structure and population heterogeneity.

Further to this, I have suggested that previous studies that have investigated the existence of dominance hierarchies in zebra finch populations may overestimate their role in determining the social structure. My experiment has shown evidence that preferential pairings exist within the population, but I speculate that hierarchical structure is unlikely to control which individuals associate during foraging such that flexibility of the social structure is significantly restricted. Further experiments targeting this specific hypothesis in the field will enable explicit assessment of the relative importance of avoiding agonistic encounters versus maintaining social cohesion within wild zebra finch groups, as well as its links to wider processes with regards to the sociality of such populations.

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REFERENCES

- Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, 5(1), 325–383. <https://doi.org/10.1146/annurev.es.05.110174.001545>
- Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales. *Science*, 340(April).
- Ansmann, I. C., Parra, G. J., Chilvers, B. L., & Lanyon, J. M. (2012). Dolphins restructure social system after reduction of commercial fisheries. *Animal Behaviour*, 84(3), 575–581. <https://doi.org/10.1016/j.anbehav.2012.06.009>
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, 279(1745), 4199–4205. <https://doi.org/10.1098/rspb.2012.1591>
- Bayly, K. L., Evans, C. S., & Taylor, A. (2006). Measuring social structure: A comparison of eight dominance indices. *Behavioural Processes*, 73(1), 1–12. <https://doi.org/10.1016/j.beproc.2006.01.011>
- Beauchamp, G. (2006). Phenotypic correlates of scrounging behavior in zebra finches: Role of foraging efficiency and dominance. *Ethology*, 112(9), 873–878. <https://doi.org/10.1111/j.1439-0310.2006.01241.x>
- Beauchamp, G., & Kacelnik, A. (1990). Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata*. *Animal Behaviour*, 41, 247–253.
- Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, 64(5), 823–828. <https://doi.org/10.1006/anbe.2002.2005>
- Bonoan, R., Clodius, F., Dawson, A., Caetano, S., Yeung, E., & Paz-y-Miño-C., G. (2013). Dominance hierarchy formation in a model organism, the zebra finch (*Taeniopygia guttata*), and its potential application to laboratory research. *Bios*, 84(4), 201–209. <https://doi.org/10.1893/0005-3155-84.4.201>
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35(5), 1454–1469. [https://doi.org/10.1016/S0003-3472\(87\)80018-0](https://doi.org/10.1016/S0003-3472(87)80018-0)
- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9(2), 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X)
- Csàrdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695. Retrieved from <http://igraph.sf.net>

- David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*(1), 219–224. <https://doi.org/10.1016/j.anbehav.2010.10.008>
- Davies, N. B., & Hartley, I. R. (1996). Food Patchiness, Territory Overlap and Social Systems: An Experiment with Dunnocks *Prunella modularis*. *The Journal of Animal Ecology*, *65*(6), 837. <https://doi.org/10.2307/5681>
- Drewe, J. A. (2010). Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1681), 633–642. <https://doi.org/10.1098/rspb.2009.1775>
- Emery, N. J. (2006). Cognitive ornithology: The evolution of avian intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1465), 23–43. <https://doi.org/10.1098/rstb.2005.1736>
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, *306*(5703), 1903–1907. <https://doi.org/10.1126/science.1098410>
- Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163. <https://doi.org/10.1111/1365-2656.12418>
- Firth, J. A. (2016). *Carry-over and consequences of social connections amongst wild birds (PhD thesis)* (University of Oxford). Retrieved from <https://search.proquest.com/docview/1999216481?accountid=14169>
- Firth, J. A., Voelkl, B., Farine, D. R., & Sheldon, B. C. (2015). Experimental evidence that social relationships determine individual foraging behavior. *Current Biology*, *25*(23), 3138–3143. <https://doi.org/10.1016/j.cub.2015.09.075>
- Giraldeau, L. A., & Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Trends in Ecology & Evolution*, *14*(3), 102–106.
- Giraldeau, L. A., & Caraco, T. (2000). *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Godfrey, S. S., Bull, C. M., James, R., & Murray, K. (2009). Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behavioral Ecology and Sociobiology*, *63*(7), 1045–1056. <https://doi.org/10.1007/s00265-009-0730-9>
- Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, *22*(7), 1–19.

<https://doi.org/10.18637/jss.v022.i07>

- Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52. [https://doi.org/10.1016/0022-5193\(64\)90039-6](https://doi.org/10.1016/0022-5193(64)90039-6)
- Hinde, R. A. (1976). Interactions , Relationships and Social Structure. *Man*, 11(1), 1–17.
- Kazahari, N. (2014). Maintaining social cohesion is a more important determinant of patch residence time than maximizing food intake rate in a group-living primate, Japanese macaque (*Macaca fuscata*). *Primates*, 55(2), 179–184. <https://doi.org/10.1007/s10329-014-0410-x>
- Krause, J., & Ruxton, G. (2002). *Living in groups*. (Oxford series in ecology and evolution). Oxford.
- Kruuk, H. (1978). Foraging and Spatial Organisation of the European Badger, *Meles meles* L. *Behavioral Ecology and Sociobiology*, 4(1), 75–89.
- Livoreil, B., & Giraldeau, L. A. (1997). Patch departure decisions by spice finches foraging singly or in groups. *Animal Behaviour*, 54(4), 967–977. <https://doi.org/10.1006/anbe.1997.0489>
- Lott, D. F. (1984). Intraspecific Variation in the Social Systems of Wild Vertebrates. *Behaviour*, 88(3), 266–325.
- Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proceedings of the Royal Society B: Biological Sciences*, 270(SUPPL. 2), 186–188. <https://doi.org/10.1098/rsbl.2003.0057>
- Macdonald, D. W. (1989). The ecology of carnivore social behaviour. *Trends in Ecology & Evolution*, 4(2), 60. [https://doi.org/10.1016/0169-5347\(89\)90147-x](https://doi.org/10.1016/0169-5347(89)90147-x)
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27, 209–220.
- Mariette, M. M., & Griffith, S. C. (2013). Does coloniality improve foraging efficiency and nestling provisioning? A field experiment in the wild Zebra Finch. *Ecology*, 94(2), 325–335. <https://doi.org/10.1890/12-0572.1>
- Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R., & Evans, M. R. (2007). Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Hormones and Behavior*, 52(4), 445–453. <https://doi.org/10.1016/j.yhbeh.2007.06.007>
- McCowan, L. S. C., Mariette, M. M., & Griffith, S. C. (2015). The size and composition of social groups in the wild zebra finch. *Emu*, 115(3), 191–198. <https://doi.org/10.1071/MU14059>
- Møller, A. P., & Ninni, P. (1998). Sperm competition and sexual selection: A meta-analysis

- of paternity studies of birds. *Behavioral Ecology and Sociobiology*, 43(6), 345–358.
<https://doi.org/10.1007/s002650050501>
- Morris, D. (1954). The Reproductive Behaviour of the Zebra Finch (*Poephila Guttata*), With Special Reference To Pseudofemale Behaviour and Displacement Activities. *Behaviour*, 6(1), 271–322. <https://doi.org/10.1163/156853954x00130>
- Newman, M. E. J. (2004). Analysis of weighted networks. *Physical Review E - Statistical Physics, Plasmas, Fluids, and Related Interdisciplinary Topics*, 70(5), 9.
<https://doi.org/10.1103/PhysRevE.70.056131>
- Newman, M. E. J. (2006). Finding community structure in networks using the eigenvectors of matrices. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, 74(3), 1–19. <https://doi.org/10.1103/PhysRevE.74.036104>
- Paz-Y-Miño-C., G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. *Nature*, 430(7001), 778–781.
<https://doi.org/10.1038/nature02723>
- Psorakis, I., Voelkl, B., Garroway, C. J., Radersma, R., Aplin, L. M., Crates, R. A., ... Sheldon, B. C. (2015). Inferring social structure from temporal data. *Behavioral Ecology and Sociobiology*, 69(5), 857–866. <https://doi.org/10.1007/s00265-015-1906-0>
- Pyke, G. H. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology, Evolution, and Systematics*, 15, 523–575. <https://doi.org/10.1016/B978-0-08-045337-8.00210-2>
- RStudio Team. (2018). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA
 URL <http://www.rstudio.com/>
- Rubenstein, D. R., & Lovette, I. J. (2007). Temporal Environmental Variability Drives the Evolution of Cooperative Breeding in Birds. *Current Biology*, 17(16), 1414–1419.
<https://doi.org/10.1016/j.cub.2007.07.032>
- Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77(5), 1041–1050.
<https://doi.org/10.1016/j.anbehav.2008.12.024>
- Silcox, A. P., & Evans, S. M. (1982). Factors affecting the formation and maintenance of pair bonds in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, 30(4), 1237–1243.
[https://doi.org/10.1016/S0003-3472\(82\)80216-9](https://doi.org/10.1016/S0003-3472(82)80216-9)
- Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 539–559.
<https://doi.org/10.1098/rstb.2006.1994>

- Smouse, P. E., Long, J. C., & Sokal, R. R. (1986). Multiple regression and correlation extensions of the mantel test of matrix correspondence. *Systematic Zoology*, 35(4), 627–632. <https://doi.org/10.2307/2413122>
- Trivers, R. (1985). *Social evolution*. Menlo Park, Calif.: Wokingham: Benjamin/Cummings.
- Vásquez, R. A., & Kacelnik, A. (2000). Foraging rate versus sociality in the starling *Sturnus vulgaris*. *Proceedings of the Royal Society B: Biological Sciences*, 267(1439), 157–164. <https://doi.org/10.1098/rspb.2000.0981>
- Verdolin, J. L. (2009). Gunnison's prairie dog (*Cynomys gunnisoni*): Testing the resource dispersion hypothesis. *Behavioral Ecology and Sociobiology*, 63(6), 789–799. <https://doi.org/10.1007/s00265-009-0712-y>
- Weber, N., Carter, S. P., Dall, S. R. X., Delahay, R. J., McDonald, J. L., Bearhop, S., & McDonald, R. A. (2013). Badger social networks correlate with tuberculosis infection. *Current Biology*, 23(20), R915–R916. <https://doi.org/10.1016/j.cub.2013.09.011>
- Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, 75(2), 333–344. <https://doi.org/10.1016/j.anbehav.2007.06.020>
- Whitehead, H. (1997). Analysing animal social structure. *Animal Behaviour*, 53(5), 1053–1067. <https://doi.org/10.1006/anbe.1996.0358>
- Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. Chicago; London: University of Chicago Press.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, Mass.; London: Belknap Press of Harvard University Press.
- Zann R. A. (1994). Reproduction in a Zebra Finch Colony in South-eastern Australia: the Significance of Monogamy, Precocial Breeding and Multiple Broods in a Highly Mobile Species. *Emu*, 94, 285-299. <https://doi.org/10.1071/MU9940285>
- Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies* (Oxford ornithology series; 5). Oxford: Oxford University Press.

APPENDIX

Table A1. Table to show details of the sixteen birds used in the experiment, including: the ID assigned to each bird; the colour of their ring(s) (where *colour X + colour Y* indicates two rings on separate legs and *colour X/colour Y* indicates two rings on the same leg); their sex (where *M* is male and *F* is female); descriptive notes to help with identification; and their date of birth/hatching.

ID	Ring colour(s)	Sex	Descriptive notes	DOB
A	Pink + Purple	F	No stripe under eyes at all and entirely grey/beige plumage.	14.02.2019
B	Yellow + Orange	F	Grey head and chest lighter grey, white under eye surrounded by thin black bars. No orange on cheeks.	14.02.2019
C	White + Black	M	Orange cheeks, black bar on chest and more speckles than stripes.	14.02.2019
D	Pale blue + Yellow	M	Large orange cheeks with no black between it and white under eyes, big black bar on chest and mottled on side.	14.02.2019
E	Red	M	Orange cheeks, white under eye, stripy chest with black bar under. Red tag on its left leg.	14.02.2019
F	Lilac	M	Grey head with orange cheeks, quite stripy neck with black downward facing crescent moon	2018

			shaped bar. Thinner neck than H.	
G	Yellow	M	Orange cheeks, quite stripy chest with relatively small semi-circular black bar.	2018
H	White	M	Grey head with orange cheeks, black bar on chest with more speckles than stripes. Eye slightly more brown and orange cheek slightly more circular than F. Grey penetrates in triangle slightly more into brown speckles on side. Bigger.	2018
I	Black	F	Entirely gold/beige with thin black bar under eyes.	2018
J	Pink	F	White between black stripe under eyes and beak, quite dark head and grey body. No orange on cheeks. Similar to K.	2018
K	Green	F	Grey. No orange on cheeks.	2018
L	Blue	M	No orange on cheeks, just huge black cheeks, black bar and speckles.	06.2018
M	Green	M	Orange cheeks and very stripy chest with black bar, sometimes struggles to walk on right foot.	06.2018

N	Pink/ White	F	Entirely white/silver, thin black bars under eyes.	06.2018
O	Orange/ White	F	Completely white/silver.	06.2018
P	Orange	F	More mottled/greyish brown with dark cheeks.	29.05.2019

Table A2. Table of all 201 recorded associations, where an association was defined as any incidence of two birds making contact with the same dish. The table shows: the IDs of the birds; the timestamp of the association within the footage; the length of the association; which dish it took place on (where *L* is left, *R* is right, and *n/a* is during the *Single Dish* treatment); what time of day the treatment was applied (where *AM* is between 11.00 – 13.00 and *PM* is between 14.00 – 16.00); and whether the *Single Dish* or *Double Dish* treatment was applied.

Bird1	Bird2	Timestamp (s)		Length of Association (s)	Dish	AM/PM	Treatment
		Start	End				
F	J	00 15	00 17	2	R	AM	<i>Double Dish</i>
F	N	00 17	00 27	10	R	AM	<i>Double Dish</i>
F	N	00 38	00 39	1	R	AM	<i>Double Dish</i>
J	N	00 42	00 46	4	R	AM	<i>Double Dish</i>
G	I	00 00	00 07	7	R	AM	<i>Double Dish</i>
F	G	00 10	00 17	7	R	AM	<i>Double Dish</i>
C	J	00 21	00 42	21	L	AM	<i>Double Dish</i>
G	O	00 38	00 45	7	R	AM	<i>Double Dish</i>
F	M	00 11	00 29	28	R	AM	<i>Double Dish</i>
I	K	00 00	01 00	60	R	AM	<i>Double Dish</i>
G	I	00 26	00 44	18	R	AM	<i>Double Dish</i>
G	K	00 26	00 44	18	R	AM	<i>Double Dish</i>
G	I	00 53	01 00	7	R	AM	<i>Double Dish</i>
G	K	00 53	01 00	7	R	AM	<i>Double Dish</i>
B	N	00 46	00 47	1	L	AM	<i>Double Dish</i>
I	K	00 00	00 08	8	R	AM	<i>Double Dish</i>
G	I	00 00	00 11	11	R	AM	<i>Double Dish</i>
G	K	00 00	00 08	8	R	AM	<i>Double Dish</i>
D	I	00 14	01 00	46	R	AM	<i>Double Dish</i>
D	I	00 00	01 00	60	R	AM	<i>Double Dish</i>
G	K	00 00	00 21	21	L	AM	<i>Double Dish</i>
K	O	00 21	00 22	1	L	AM	<i>Double Dish</i>

L	N	00 47	00 49	2	L	AM	<i>Double Dish</i>
E	F	00 30	00 37	7	R	AM	<i>Double Dish</i>
F	G	00 22	00 23	1	R	AM	<i>Double Dish</i>
G	L	00 31	00 32	1	R	AM	<i>Double Dish</i>
A	E	00 00	00 12	12	R	AM	<i>Double Dish</i>
E	F	00 20	00 21	1	R	AM	<i>Double Dish</i>
A	E	00 30	00 34	4	R	AM	<i>Double Dish</i>
K	N	00 59	01 00	1	R	AM	<i>Double Dish</i>
A	E	00 00	00 12	12	R	AM	<i>Double Dish</i>
E	F	00 12	00 16	4	R	AM	<i>Double Dish</i>
F	G	00 20	00 28	8	R	AM	<i>Double Dish</i>
F	M	00 00	00 44	44	L	AM	<i>Double Dish</i>
B	C	23 35	23 56	21	L	AM	<i>Double Dish</i>
B	C	23 58	24 35	37	L	AM	<i>Double Dish</i>
A	N	08 31	08 32	1	L	AM	<i>Double Dish</i>
K	N	05 54	05 55	1	L	AM	<i>Double Dish</i>
K	P	06 40	06 50	10	L	AM	<i>Double Dish</i>
K	P	06 57	07 28	31	L	AM	<i>Double Dish</i>
O	P	07 29	07 45	16	L	AM	<i>Double Dish</i>
E	P	08 29	08 37	8	L	AM	<i>Double Dish</i>
B	E	10 04	10 09	5	L	AM	<i>Double Dish</i>
O	P	24 41	24 56	15	R	AM	<i>Double Dish</i>
G	P	24 55	24 56	1	R	AM	<i>Double Dish</i>
G	O	24 55	25 26	31	R	AM	<i>Double Dish</i>
B	C	04 38	05 39	71	L	AM	<i>Double Dish</i>
B	C	06 05	06 09	4	L	AM	<i>Double Dish</i>
O	P	10 38	10 54	16	R	AM	<i>Double Dish</i>
J	N	10 07	10 22	15	n/a	AM	<i>Single Dish</i>
J	N	10 23	10 25	2	n/a	AM	<i>Single Dish</i>
A	J	02 48	03 05	17	n/a	AM	<i>Single Dish</i>
A	P	03 05	03 29	24	n/a	AM	<i>Single Dish</i>
A	E	03 20	03 29	9	n/a	AM	<i>Single Dish</i>

E	P	03 20	03 54	34	n/a	AM	<i>Single Dish</i>
E	P	03 57	04 48	51	n/a	AM	<i>Single Dish</i>
A	E	04 29	04 30	1	n/a	AM	<i>Single Dish</i>
A	P	04 29	04 30	1	n/a	AM	<i>Single Dish</i>
A	E	04 39	04 48	9	n/a	AM	<i>Single Dish</i>
A	P	04 39	04 57	18	n/a	AM	<i>Single Dish</i>
K	P	10 32	11 34	62	n/a	AM	<i>Single Dish</i>
F	K	11 20	11 34	14	n/a	AM	<i>Single Dish</i>
F	P	11 20	14 31	131	n/a	AM	<i>Single Dish</i>
F	O	11 52	14 31	39	n/a	AM	<i>Single Dish</i>
O	P	11 52	15 23	91	n/a	AM	<i>Single Dish</i>
G	P	35 48	36 04	16	n/a	AM	<i>Single Dish</i>
C	G	01 59	02 00	1	n/a	AM	<i>Single Dish</i>
C	G	02 01	02 35	34	n/a	AM	<i>Single Dish</i>
C	F	02 37	02 44	7	n/a	AM	<i>Single Dish</i>
C	P	03 48	03 50	2	n/a	AM	<i>Single Dish</i>
C	P	04 36	05 09	33	n/a	AM	<i>Single Dish</i>
G	K	17 37	17 40	3	n/a	AM	<i>Single Dish</i>
B	I	25 03	25 17	14	n/a	AM	<i>Single Dish</i>
B	D	25 19	25 20	1	n/a	AM	<i>Single Dish</i>
I	J	18 20	18 23	3	n/a	AM	<i>Single Dish</i>
I	J	19 29	19 34	5	n/a	AM	<i>Single Dish</i>
I	L	19 37	19 38	1	n/a	AM	<i>Single Dish</i>
L	P	24 58	24 59	1	n/a	AM	<i>Single Dish</i>
L	P	25 06	25 07	1	n/a	AM	<i>Single Dish</i>
L	P	25 55	25 59	4	n/a	AM	<i>Single Dish</i>
F	P	26 08	25 30	22	n/a	AM	<i>Single Dish</i>
L	P	28 16	28 20	4	n/a	AM	<i>Single Dish</i>
F	H	00 01	00 06	5	n/a	AM	<i>Single Dish</i>
F	G	00 11	00 12	1	n/a	AM	<i>Single Dish</i>
C	G	00 28	00 30	2	n/a	AM	<i>Single Dish</i>
A	P	03 04	03 05	1	n/a	AM	<i>Single Dish</i>

E	O	09 30	09 31	1	n/a	AM	<i>Single Dish</i>
E	K	11 26	12 47	79	n/a	AM	<i>Single Dish</i>
G	P	16 57	17 12	15	n/a	AM	<i>Single Dish</i>
G	K	17 02	17 05	3	n/a	AM	<i>Single Dish</i>
K	P	17 02	17 05	3	n/a	AM	<i>Single Dish</i>
G	K	17 11	17 12	1	n/a	AM	<i>Single Dish</i>
K	P	17 11	17 12	1	n/a	AM	<i>Single Dish</i>
O	P	17 36	17 55	19	n/a	AM	<i>Single Dish</i>
E	P	26 35	26 36	1	n/a	AM	<i>Single Dish</i>
C	H	29 51	29 52	1	n/a	AM	<i>Single Dish</i>
A	M	06 50	08 29	99	n/a	AM	<i>Single Dish</i>
A	M	08 30	08 56	26	n/a	AM	<i>Single Dish</i>
F	H	14 01	14 25	24	n/a	AM	<i>Single Dish</i>
A	F	14 28	14 29	1	n/a	AM	<i>Single Dish</i>
J	L	08 23	08 29	6	L	AM	<i>Double Dish</i>
I	J	08 34	08 42	8	L	AM	<i>Double Dish</i>
D	E	08 45	08 46	1	R	AM	<i>Double Dish</i>
E	L	08 45	08 46	1	R	AM	<i>Double Dish</i>
D	L	08 45	08 46	1	R	AM	<i>Double Dish</i>
H	I	08 54	09 12	16	L	AM	<i>Double Dish</i>
H	J	09 06	09 07	1	L	AM	<i>Double Dish</i>
I	J	09 06	09 07	1	L	AM	<i>Double Dish</i>
E	L	09 07	09 14	7	R	AM	<i>Double Dish</i>
D	I	09 13	09 37	24	L	AM	<i>Double Dish</i>
D	F	09 29	09 33	4	L	AM	<i>Double Dish</i>
F	I	09 29	09 33	4	L	AM	<i>Double Dish</i>
D	F	09 35	09 37	2	L	AM	<i>Double Dish</i>
F	I	09 35	09 44	9	L	AM	<i>Double Dish</i>
F	L	09 43	09 44	1	L	AM	<i>Double Dish</i>
I	L	09 43	09 44	1	L	AM	<i>Double Dish</i>
E	L	09 18	09 20	2	R	AM	<i>Double Dish</i>
E	L	09 28	09 29	1	R	AM	<i>Double Dish</i>

D	I	09 58	10 29	31	L	AM	<i>Double Dish</i>
D	O	10 24	10 35	11	L	AM	<i>Double Dish</i>
I	O	10 24	10 29	5	L	AM	<i>Double Dish</i>
J	P	12 10	12 13	3	R	AM	<i>Double Dish</i>
G	K	16 50	17 19	29	R	AM	<i>Double Dish</i>
D	P	19 18	19 19	1	L	AM	<i>Double Dish</i>
K	M	19 34	19 38	4	R	AM	<i>Double Dish</i>
D	G	19 43	19 52	9	L	AM	<i>Double Dish</i>
C	P	21 44	21 45	1	L	AM	<i>Double Dish</i>
A	B	24 11	24 38	27	R	AM	<i>Double Dish</i>
D	H	17 12	17 13	1	R	AM	<i>Double Dish</i>
H	I	17 22	18 06	44	R	AM	<i>Double Dish</i>
H	I	18 50	19 08	18	R	AM	<i>Double Dish</i>
D	H	19 06	19 08	2	R	AM	<i>Double Dish</i>
D	I	19 06	19 08	2	R	AM	<i>Double Dish</i>
J	K	11 37	11 43	6	R	AM	<i>Double Dish</i>
F	O	21 16	21 27	11	R	AM	<i>Double Dish</i>
M	O	23 12	23 24	12	L	AM	<i>Double Dish</i>
A	G	06 26	06 28	2	R	AM	<i>Double Dish</i>
B	C	00 55	01 00	5	n/a	PM	<i>Single Dish</i>
B	N	00 00	00 10	10	n/a	PM	<i>Single Dish</i>
D	N	00 00	00 10	10	n/a	PM	<i>Single Dish</i>
B	D	00 00	00 56	56	n/a	PM	<i>Single Dish</i>
G	O	00 57	01 00	3	n/a	PM	<i>Single Dish</i>
G	I	00 30	01 00	30	n/a	PM	<i>Single Dish</i>
D	I	00 05	00 43	38	n/a	PM	<i>Single Dish</i>
D	I	00 47	00 58	11	n/a	PM	<i>Single Dish</i>
I	O	09 07	09 34	27	n/a	PM	<i>Single Dish</i>
K	O	09 31	09 34	3	n/a	PM	<i>Single Dish</i>
I	K	09 31	10 59	88	n/a	PM	<i>Single Dish</i>
G	P	27 51	28 38	47	n/a	PM	<i>Single Dish</i>
A	P	29 37	31 26	109	n/a	PM	<i>Single Dish</i>

B	P	32 58	33 00	2	n/a	PM	<i>Single Dish</i>
D	G	24 34	25 07	31	n/a	PM	<i>Single Dish</i>
D	G	25 09	25 51	42	n/a	PM	<i>Single Dish</i>
B	E	28 36	28 41	5	n/a	PM	<i>Single Dish</i>
F	P	31 38	31 47	9	L	PM	<i>Double Dish</i>
F	O	31 46	32 31	35	L	PM	<i>Double Dish</i>
O	P	31 46	31 47	1	L	PM	<i>Double Dish</i>
E	I	02 58	03 51	53	L	PM	<i>Double Dish</i>
O	P	07 27	07 55	28	L	PM	<i>Double Dish</i>
J	O	16 11	16 38	27	R	PM	<i>Double Dish</i>
K	O	24 04	24 09	5	L	PM	<i>Double Dish</i>
L	P	01 57	01 58	1	L	PM	<i>Double Dish</i>
L	P	02 36	02 38	2	L	PM	<i>Double Dish</i>
K	P	03 58	03 59	1	L	PM	<i>Double Dish</i>
G	P	04 28	05 27	59	L	PM	<i>Double Dish</i>
E	P	07 02	07 03	1	L	PM	<i>Double Dish</i>
E	P	07 28	08 15	47	L	PM	<i>Double Dish</i>
L	P	08 35	08 36	1	L	PM	<i>Double Dish</i>
C	E	10 06	10 08	2	n/a	PM	<i>Single Dish</i>
D	I	11 22	13 22	120	n/a	PM	<i>Single Dish</i>
D	F	13 21	13 22	1	n/a	PM	<i>Single Dish</i>
F	I	13 21	13 22	1	n/a	PM	<i>Single Dish</i>
D	F	15 13	15 21	8	n/a	PM	<i>Single Dish</i>
E	K	04 29	04 52	23	n/a	PM	<i>Single Dish</i>
E	O	13 28	13 30	2	n/a	PM	<i>Single Dish</i>
F	P	12 01	14 40	159	n/a	PM	<i>Single Dish</i>
G	M	27 23	27 38	15	n/a	PM	<i>Single Dish</i>
G	M	28 33	28 44	11	n/a	PM	<i>Single Dish</i>
G	O	07 54	07 55	1	n/a	PM	<i>Single Dish</i>
A	G	09 03	09 10	7	n/a	PM	<i>Single Dish</i>
B	O	04 23	04 24	1	n/a	PM	<i>Single Dish</i>
B	C	04 27	04 51	24	n/a	PM	<i>Single Dish</i>

B	P	06 28	06 29	1	n/a	PM	<i>Single Dish</i>
I	P	10 20	10 37	17	n/a	PM	<i>Single Dish</i>
H	E	07 26	07 41	15	L	PM	<i>Double Dish</i>
C	H	07 46	08 21	35	L	PM	<i>Double Dish</i>
H	I	09 12	09 15	3	L	PM	<i>Double Dish</i>
D	H	09 14	09 15	1	L	PM	<i>Double Dish</i>
D	I	09 14	09 15	1	L	PM	<i>Double Dish</i>
B	E	08 44	08 47	3	R	PM	<i>Double Dish</i>
C	E	09 35	09 38	3	R	PM	<i>Double Dish</i>
D	I	10 01	10 27	26	L	PM	<i>Double Dish</i>
E	P	11 10	11 19	9	R	PM	<i>Double Dish</i>
E	P	12 07	12 10	3	R	PM	<i>Double Dish</i>
M	O	33 10	33 45	35	L	PM	<i>Double Dish</i>
M	O	37 38	37 40	2	R	PM	<i>Double Dish</i>
G	K	39 30	39 49	19	L	PM	<i>Double Dish</i>
C	P	04 14	04 15	1	L	PM	<i>Double Dish</i>
G	O	26 23	26 24	1	L	PM	<i>Double Dish</i>
G	O	26 24	25 35	11	L	PM	<i>Double Dish</i>
M	O	28 39	28 49	10	L	PM	<i>Double Dish</i>

Table A3. The Association Indices (calculated using the Simple Ratio Index) for every pair of birds under the *Single Dish* and *Double Dish* treatment.

Pair ID	Association Index in <i>Single Dish</i>	Association Index in <i>Double Dish</i>
AB	0	0.118942731
AC	0	0
AD	0	0
AE	0.035250464	0.148148148
AF	0.001360544	0
AG	0.011965812	0.007092199
AH	0	0
AI	0	0
AJ	0.046703297	0
AK	0	0
AL	0	0
AM	0.264270613	0
AN	0	0.012658228
AO	0	0
AP	0.128571429	0
BC	0.082386364	0.366391185
BD	0.131034483	0
BE	0.01497006	0.026666667
BF	0	0
BG	0	0
BH	0	0
BI	0.029661017	0
BJ	0	0
BK	0	0
BL	0	0
BM	0	0
BN	0.064935065	0.005263158
BO	0.005154639	0
BP	0.001015228	0
CD	0	0

CE	0.004424779	0.009230769
CF	0.010802469	0
CG	0.074297189	0
CH	0.003773585	0.106060606
CI	0	0
CJ	0	0.076923077
CK	0	0
CL	0	0
CM	0	0
CN	0	0
CO	0	0
CP	0.031731641	0.005
DE	0	0.002915452
DF	0.012311902	0.015345269
DG	0.125645439	0.020642202
DH	0	0.011494253
DI	0.251114413	0.281481481
DJ	0	0
DK	0	0
DL	0	0.0041841
DM	0	0
DN	0.028169014	0.042918455
DO	0	0
DP	0	0.002392344
EF	0	0.038709677
EG	0	0
EH	0	0.056179775
EI	0	0.089225589
EJ	0	0
EK	0.205231388	0
EL	0	0.069620253
EM	0	0
EN	0	0
EO	0.010204082	0

EP	0.079262673	0.201780415
FG	0.00147929	0.039702233
FH	0.065462754	0
FI	0.001302083	0.020249221
FJ	0	0.007751938
FK	0.02020202	0
FL	0	0.004854369
FM	0	0.229299363
FN	0	0.055
FO	0.079591837	0.102678571
FP	0.243559719	0.023376623
GH	0	0
GI	0.048543689	0.062590975
GJ	0	0
GK	0.012891344	0.224669604
GL	0	0.003984064
GM	0.062801932	0
GN	0	0
GO	0.011764706	0.101419878
GP	0.068965517	0.002325581
HI	0	0.135225376
HJ	0	0.004651163
HK	0	0
HL	0	0
HM	0	0
HN	0	0
HO	0	0
HP	0	0
IJ	0.020151134	0.016605166
IK	0.138582677	0.098124098
IL	0.00273224	0.002040816
IM	0	0
IN	0	0
IO	0.0625	0.006830601

IP	0.013900245	0
JK	0	0.019417476
JL	0	0.056603774
JM	0	0
JN	0.215189873	0.04
JO	0	0.077586207
JP	0	0.010526316
KL	0	0
KM	0	0.010958904
KN	0	0.007968127
KO	0.008403361	0.012024048
KP	0.057491289	0.096330275
LM	0	0
LN	0	0.041666667
LO	0	0
LP	0.011376564	0.017167382
MN	0	0
MO	0	0.146039604
MP	0	0
OP	0.116402116	0.16

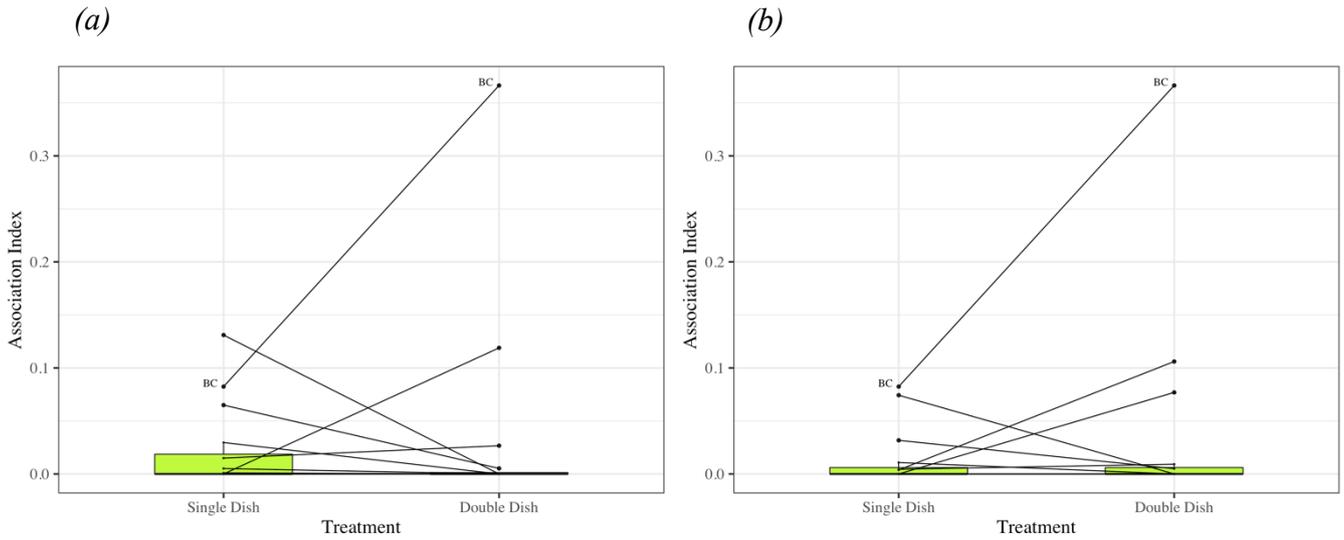


Figure A1. Paired association indices for pairs between the *Single Dish* and *Double Dish* treatments for individuals (a) B and (b) C, with the pair BC labelled in both cases. This indicates the potential presence of a pair bond.

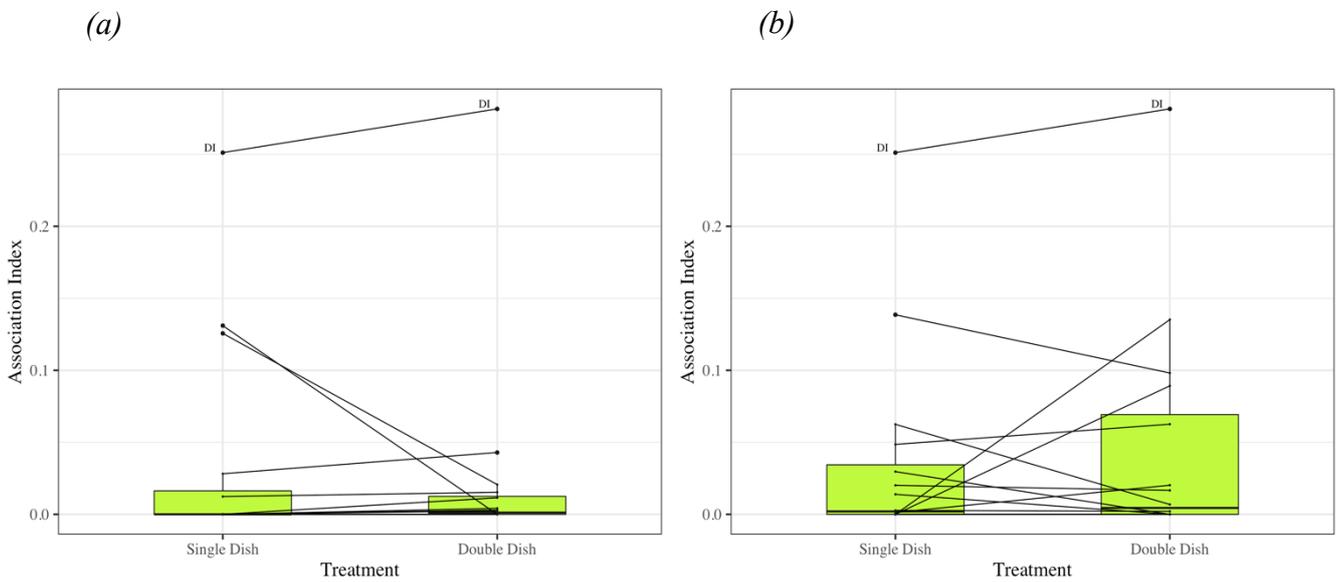


Figure A2. Paired association indices of pairs between the *Single Dish* and *Double Dish* treatments for individuals (a) D and (b) I, with the pair DI labelled in both cases. Similarly, this also indicates the potential presence of a pair bond.

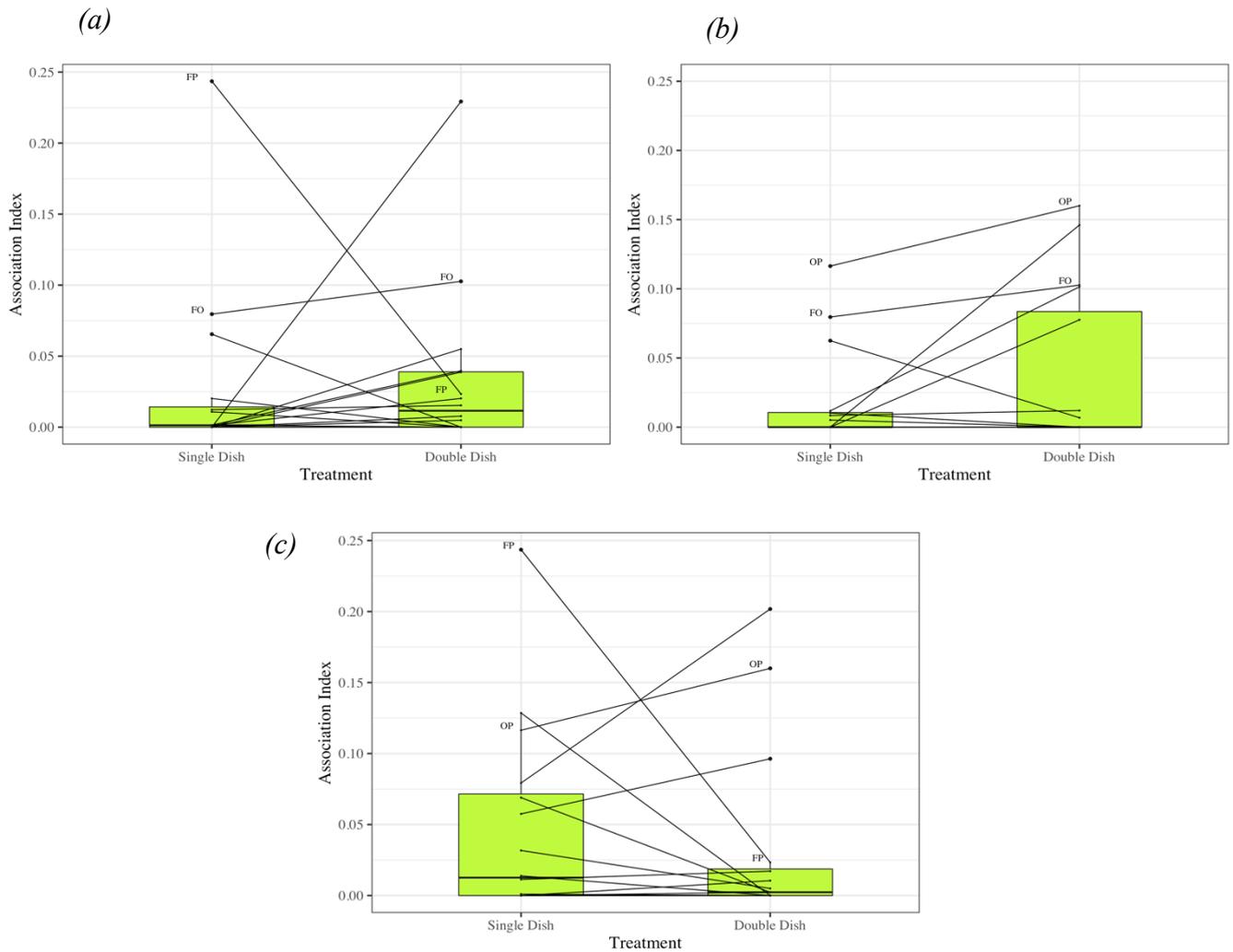


Figure A3. Paired association indices of pairs between the *Single Dish* and *Double Dish* treatments for individuals (a) F, (b) O and (c) P. The labelled pair *FO* indicates the potential presence of a pair bond, and the pairs *FP* and *OP* indicate likely association between parents and offspring.

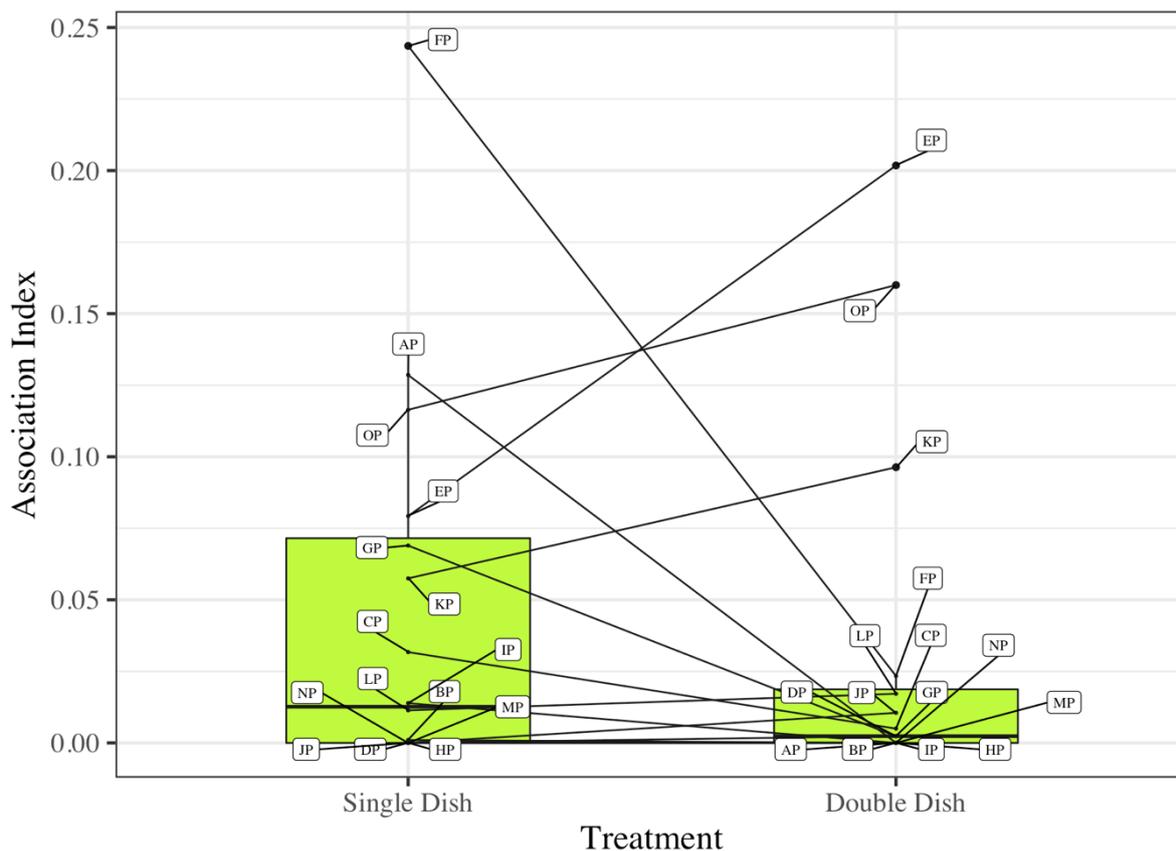


Figure A4. Paired association indices of pairs between the *Single Dish* and *Double Dish* treatments for individual *P*. The rank of association indices for given pairs is highly variable, indicating a lack of preferential feeding.

MANAGEMENT REPORT

I initially contacted Dr. Ada Grabowska-Zhang in October 2018 to express my interest in working with her on a project based on avian behaviour and ecology, and we agreed to meet in early November. Before the Christmas vacation, I formulated an initial plan of a project that might investigate the flexibility of social structures or hierarchies in groups of birds, with help from Ada. In late November, Prof. Graham Taylor presented me with the opportunity to use the captive zebra finches in his lab as an experimental study system in this project, which was agreed on in December. For the duration of Hilary term, the project proposal was formalised more precisely between Ada and myself via email, and I started some initial reading around the topic of avian social structures to help with the development of my proposed experimental study.

On my return to Oxford in Trinity term, I had my second-year finals exams, which led to a brief hiatus in my project development. However, following this period, by early June, I signed and submitted my Animal Welfare and FHS Safety Registration form, and upon completion I visited the John Krebs Field Station to meet Lucy Larkman and Helen Sanders, the animal care technicians in the Taylor Lab. I took details of the captive flock that were relevant to my study, and within the week I met with Ada to finalise my experimental design. I underwent a pilot test in late June, using a motion sensor camera to film, in order to find out how often the birds fed during the day, and I also observed the flock from outside the aviary over the following week. This helped me to decide how long the experimental period would have to be in terms of collecting sufficient data within the flock. Following this, I decided I would need five days of data collection, filming for four hours each day. Ada retrieved a camera for my experiment from Prof. Andy Gosler, and I began data collection on July 1st and finished on July 5th, visiting and remaining in the Field Station each day.

Over the summer vacation, I undertook my data processing by going through the footage and logging all relevant information. I kept in contact with Ada via email, and also exchanged emails with Dr. Josh Firth with advice regarding analysis of my data, I also taught myself relevant techniques in RStudio that I would use in the analysis. I returned to Oxford in September, undertaking my data analysis and starting my write-up over Michaelmas term. I completed my first draft over the Christmas vacation, and received feedback from Ada and my college tutor Dr. Ailsa McLean. I continued to work on the project write-up, completing my final draft on Friday of 1st week, leaving me the weekend to make final adjustments and format the project ready for submission.