

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

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

1. Introduction

The social component of the environment represents a unique aspect among the factors that contribute to differences in fitness. The population-level patterns of social connections that are formed from the interactions among individuals are, thus, of increasing interest. The web of interactions across populations, and where individuals are positioned within this web, is often captured using social network analysis [1,2]. Understanding these social interactions is important on multiple levels. First, most social interactions are often only manifested physically for brief moments, but their consequences can extend well into the future. For example, in primates, rare grooming partners can be important for an individual's survival [3,4], while a vampire bat, *Desmodus rotundus*, donating food to an

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unrelated conspecific can represent a future investment that may be life-saving in case it later goes hungry [5]. Second, the position of individuals within their social environment (i.e. in their social network) can be dependent on both their, and others', social interactions. Indirect, or 'friend of a friend', associations can nevertheless have significant fitness consequences [6,7]. For example, an individual's exposure to disease may not only depend on its own social gregariousness but also on the gregariousness of its associates (see [8]).

Advances in our ability to study and analyse social behaviour [9], especially in the wild, have highlighted the widespread effects of social behaviour on fitness. There is now clear evidence that individuals can exhibit consistent differences in their social network position [10–13], which are resilient to environmental change [14,15] (but see [16]), and that these differences can translate to consequences for fitness [17–21]. For example, being more central in a network has been linked to having access to more information [22], but also being more exposed to disease [23,24]. The overall composition of the social environment can also impact the strength and direction of selection that individuals experience [25,26], with the intensity of interactions among individuals determining the amount of variation in social traits available within versus between populations [27]. Yet, despite over a decade of research on the structure and consequences of animal social networks, little is known about the mechanisms that underlie inter-individual differences in social relationships and network position [28].

Although individuals in a wild population vary extensively in their social behaviour (reviewed in [29]), the ontogenetic sources of that variation remain unclear. A promising area that has recently gained increasing attention is the environmental conditions experienced by individuals during early-life stages. A well-established body of evidence supports the concept that early-life stress exposure increases the probability of social behaviour deficits manifesting later in life across a range of taxa [30–33]. For example, early-life stress increased the probability of psychiatric disorders in humans [30] and had adverse effects on social bonding in prairie voles, *Microtus ochrogaster* [31], and maternal care in rats, *Rattus norvegicus domesticus* [32]. Invertebrates reared in deprived conditions exhibited deficits in social behaviour and cognitive abilities [33], and in the development of behavioural syndromes [34].

Three recent, and complementary, studies on zebra finches [28,35,36] have aimed to comprehensively characterize how the conditions that individuals face during their development can shape different aspects of later social life. All three studies used the same nestlings, from two captive colonies of zebra finches, *Taeniopygia guttata*, that were allocated to two treatments. Approximately half of each brood received physiologically relevant doses of the avian stress hormone corticosterone (stressed juveniles) via pipette feeding, while the other half were handled in the same way, i.e. pipette feeding, but without the active hormone (control juveniles). Once the chicks fledged, the social affiliations among all colony members (including both adults and juveniles) were recorded by detecting the co-membership of individuals fitted with passive integrated transponder (PIT) tags in foraging flocks at feeders using radio frequency identification (RFID) loggers. In the first study, Boogert *et al.* [28] found that stressed juveniles formed less exclusive (or more random) social associations, resulting in a more central network position. Stressed chicks had a higher total number of social associates (higher binary network

degree) and were more often located on the shortest path between two other individuals of the network (higher betweenness) [28]. Betweenness reflects how important an individual is as a point of social connection in the overall network [7] and high betweenness can imply an increased tendency of individuals to switch between different groups [28]. The two following studies investigated how early-life stress influenced social learning strategies [35,36]. Evidence suggested that stressed juveniles switched from acquiring novel foraging behaviours from their parents to acquiring them from unrelated adults [36]. Further, stressed juvenile males were less faithful in copying their father's song, although the mechanism there seemed to be linked to variation in association strengths between father and sons [35]. These studies of the zebra finch in captivity have provided some of the best support to date for the importance of the developmental environment on animal social behaviour. They demonstrate how developmentally mediated differences in social behaviour shape social networks and thus can determine the acquisition of skills relating to fitness (song and foraging behaviour). However, while the amenability of the zebra finch as a focus of behavioural research in the laboratory has permitted insightful studies such as those above, an important challenge remained about the extent to which such studies might reflect natural variation in an appropriate ecological context [28].

In the current study, we examine the same question as in the Boogert *et al.* [28] study (described above) in a wild population of zebra finches using a natural source of developmental stress—brood size. We then collected data on foraging associations among individuals (both adults and juveniles, each fitted with a PIT tag) at RFID-equipped feeders located in the surroundings of six breeding colonies. Finally, we conducted the same statistical tests as the original study, thereby producing an almost exact experimental replication, but importantly in a very different context, i.e. using a natural stressor, and in a wild population. Boogert *et al.* [28] called for replication in the wild using brood size as a natural stressor, thus we experimentally increased and decreased the size of broods within the natural range of variation. We predicted that nestlings from enlarged broods would experience higher sibling competition (as shown in the wild by Mariette & Griffith [37]). If the early-life effects on social network position [28] are transferrable to the wild, we expect the juveniles in our study to respond in a similar way to juveniles that were exposed to the corticosterone stress hormones as nestlings in the original study. Thus, we predicted that juveniles from enlarged broods would also be less choosy in their associations, forage with more conspecifics and be more central in the overall social network.

2. Material and methods

(a) Study site

The study was conducted at Gap Hills, located at Fowlers Gap, UNSW Arid Zone Research Station (31°05'13.1" S 141°42'17.4" E), New South Wales, Australia, between September and December 2017. The roughly rectangular area of about 4 km² holds a dam with a mostly permanent water body in the centre. We provided 180 wooden nest-boxes arranged in six colonies (mean distance to nearest neighbouring colony \pm s.e. = 413.62 \pm 63.62 m) of 30 boxes each (mean distance to nearest neighbouring nest-box within clusters \pm s.e. = 10.36 \pm 1.98 m; [38]) and an additional 64 boxes scattered in the periphery of the colonies.

(b) Brood size manipulations

Brood manipulations were conducted when nestlings were 3 days old (hatching date = day 0). Nestlings were measured (tarsus length, measured to an accuracy of 0.01 mm), weighed (to an accuracy of 0.2 g) and then swapped between pairs of nests (triplets, if necessary), bi-directionally, i.e. all nests received at least one chick from another brood. In each nest pair, we created a reduced brood with two nestlings ($n = 15$ nests; i.e. low stress) and an enlarged brood with five to eight nestlings (mean number chicks: 6.00 ± 0.18 s.e.; $n = 16$ nests; i.e. high stress). Mean brood size across the study population on day 3 after hatching, before the manipulation, was 3.69 ± 0.13 s.e. chicks. The change in brood size through the manipulation was on average plus 2.13 ± 0.13 s.e. chicks in the enlarged broods and an average decrease of minus 1.95 ± 0.24 s.e. chicks in the reduced broods. The broods in all nests were manipulated, except for five nests where no other nest with nestlings at the same age was available for swapping (juveniles from these nests were included when generating the social networks but not used in the analyses comparing juveniles across treatments). Chicks from these unmanipulated nests were not used because they were naturally mismatched in age compared to others, represented too small a sample size to use as a 'control' group, and because the aim of our study was to replicate the previous results as precisely as possible. A number of studies have previously shown that brood size manipulations can lead to differences in growth rates and body size [37], increased levels of plasma corticosterone [39] and negatively affect the immunocompetence [40] and survival [41] of the offspring raised in enlarged broods in birds. It is also well established that birds optimize their clutch and brood size [42–45], thus, an increase through external manipulation can be expected to cause stress and increase sibling competition. Similar stress responses can be observed, for example, in mammals with large litters [46,47], suggesting that this is a universal mechanism.

(c) Social network data

We collected data on social associations in almost exactly the same way as the Boogert *et al.* [28] study. We caught adults with mist-nets, with walk-in feeder traps and at the nest-boxes when nestlings were between 6 and 11 days old, whereupon we fitted each individual with a uniquely numbered ABBBS metal ring and subcutaneously injected each with a uniquely coded PIT tag (Minichip; Micro Products Australia, Perth, Australia). Nestlings were weighed, measured (tarsus length) and tagged on day 11. For practical reasons, we did not tag all nestlings, but a number proportional to the manipulated brood size (mean proportion of tagged nestlings in small broods: 0.9 ± 0.1 s.e., and in large broods: 0.7 ± 0.1 s.e.). This amounted to a total of 64 nestlings from enlarged broods, 27 from reduced broods and 14 from unmanipulated broods.

We provided 16 feeders (a wire cage of $70 \times 40 \times 50$ cm, see [48]), each fitted with an RFID antenna (*ca* 20 cm diameter) at its entrance, connected to an RFID decoder (RFIDLOG; Priority 1 Design, Melbourne, Australia). These allowed us to detect the presence of individuals as they entered and exited the food source (a very similar design to the original study). Feeders were located in a minimum distance of 200 m from the dam and from each other, minimum 100 m away from the nest-box colonies and within a maximum of 800 m from the relatively central water (dam). The feeders were all refilled daily with commercial finch seed mix from 22 September until 1 October. From 2 October to 6 December, eight of the feeders were kept always filled with food (stable feeders), while the remaining eight feeders were provisioned as an ephemeral food source, as part of another experiment (only half of them filled for 10 h every other day with egg and biscuit formula mixed in with the seeds; all eight feeders were empty every third day). From 7 to 17 December, eight of

the feeders were removed and the other eight were filled daily. We used the social association data from all feeders from the entire period, as any co-visitations still represent social associations while foraging, even if no food was present. In terms of breeding, the establishment of the first broods (first egg laid) was on 15 September, and reproduction continued through to the end of the final brood (last egg laid on 20 November).

(d) Statistical analyses

We used the same Gaussian mixture model approach as Boogert *et al.* [28] to infer co-feeding events. This algorithm identifies temporally clustered detections of PIT tags in non-uniform data streams at a given feeder on a given day [49,50]. We combined the data from the feeding events detected across all of the feeders on all days to construct one population-level social network. As with the previous study, associations between individuals, or 'edges', in this social network were calculated using the simple ratio index [51], which represents the probability of observing two individuals in the same event given that at least one was observed. Unlike the original study by Boogert *et al.* [28], we did not create daily networks, as the wild population had a much lower density of social associations given the greater freedom of movement and higher number of potential food sources (see [52] for more details on why replicated, or daily, networks are often required in captive populations). Further, because birds regularly visited multiple feeders spanning different local colonies, we did not create a separate network for each colony as the population-level network was overall well connected (figure 1). The Gaussian mixture model and network construction were done using the *asnipe* package [53,54] in R [55].

We then implemented the same set of 10 analytical tests as performed by Boogert *et al.* [28]. We (1) tested whether mated adults had stronger associations than non-paired adults, and (2) tested whether the association strengths among families were stronger than among non-families (assortativity). The assortativity coefficient is used to describe to which extent individuals are connected with other individuals of a similar phenotype [9,56] (for general definitions of all used social network measures, see [1,7,9]). We also tested whether birds from enlarged broods differed to birds from reduced broods in terms of (3) the size of their foraging groups or (4) the number of foraging groups joined. Having completed these baseline tests, we then investigated the relationship between brood size and social network position. Specifically, we tested whether juveniles from enlarged broods had (5) any difference in weighted degree, (6) a higher unweighted degree, (7) a higher (weighted) betweenness (see definition in Introduction) and (8) any difference in (weighted) eigenvector centrality compared to those juveniles from reduced broods. Unweighted degree is simply the count of the number of connections to distinct individuals, while a weighted degree is the sum of the association strengths (edge weights) that an individual has. Eigenvector centrality captures how well-connected individuals are to individuals with a high degree (here weighted degree as we used a weighted measure of eigenvector centrality). Betweenness and eigenvector centrality both represent measurements of indirect connectedness [8]. We also (9) tested whether juveniles from larger broods had less differentiated relationships (associated more randomly) by calculating the coefficient of variation (CV) of edge weights for each individual. A higher CV suggests that individuals have a mix of both strong and weak connections, whereas a lower CV suggests that individuals associate more equally with all conspecifics. Finally, we (10) tested whether juveniles from larger broods had a weaker association with their parents.

We used the weighted assortment coefficient from the *assortnet* [56,57] package in R to test predictions 1 and 2. We then used linear mixed models to test predictions 3 to 10, fitting the response variable (number of groups, mean size of groups, unweighted degree,

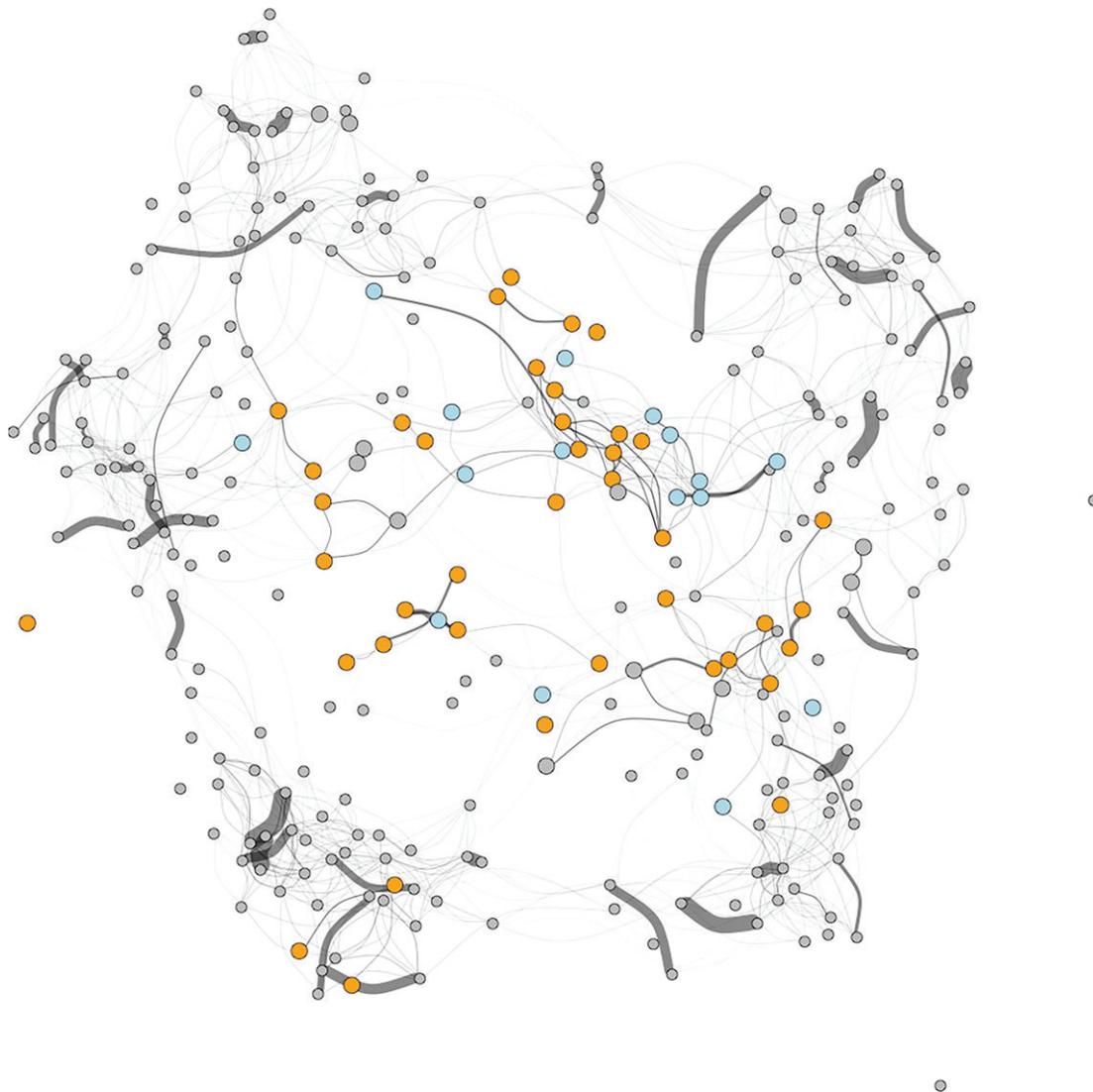


Figure 1. Social network from data collected from a population of wild zebra finches between September and December 2017 at feeders in the Australian desert. Small nodes represent adults, with the many wide edges showing the high association strength between pair-bonded individuals. Large nodes represent juveniles, with juveniles from enlarged broods shown in orange and juveniles from reduced broods shown in blue. Large grey nodes are juveniles not part of the experimental treatment groups. Network is plotted based on each individual's six strongest edges only, although all edges were used in the analyses. The unweighted network plot is provided as the electronic supplementary material, figure S1.

etc.) with treatment being the only predictor, and family and colony fitted as random effects. Because we did not have replicated networks, we did not need to fit time as a fixed effect or individual identity as a random effect. However, because network data are inherently non-independent [58], the significance of each coefficient in each model (herein p_{rand}) was calculated by comparing the observed data to 10 000 coefficients calculated by fitting the same model to permuted versions of our data [59]. As per Boogert *et al.* [28], we used a standard pre-network permutation procedure (originally described by [60], see also [2]), in which pairs of observations of two individuals observed at the same feeder on the same day were swapped between groups. After each swap, we recalculated the network, thus producing 10 000 random networks. Significance was calculated by comparing the observed coefficient value to the distribution of coefficient values from the randomized networks (following [59], see also [61]). For effects that were significant in Boogert *et al.* [28], we used a one-tailed significance test, whereas we used a two-tailed test for effects that were not significant in Boogert *et al.* [28].

Given that birds entered and left the population during the course of the study, our permutation test specifically controlled for any differences in the locations, number of foraging events joined and temporal patterns of presence across individuals in the population. That is, if a chick fledged early in the season, it

would have had more opportunity to forage with others. When generating the distribution for the null hypothesis (using pre-network permutations of the data), the observation of that juvenile on a given day could only be swapped with observations of other juveniles on the same day and at the same location. This means that any patterns arising because an individual had more opportunity to forage with more conspecifics (it was present on more days) were maintained in the randomized data (meaning it had an equal opportunity to forage with many conspecifics in the distribution for the null hypothesis). For this reason, the standard errors of the coefficients from the linear models can sometimes be large despite the permutation test generating a significant p -value (i.e. because variation among individuals pertaining to their general differences in when and where they were detected are maintained in the permutation test, but contribute towards calculating standard errors).

3. Results

Brood size manipulations had a strong effect on nestling weight. We detected no difference in weight (day 3, weight \sim numerical brood size after swapping: $\beta \pm \text{s.e.} = 0.038 \pm 0.042$,

Table 1. Summary of the statistical results, including the predictions based on results from Boogert *et al.* [28]. (Coefficients from linear models (β) are given for juveniles from enlarged broods relative to individuals from reduced broods for the results from the current data. p_{rand} values are calculated by comparing the observed coefficients to a distribution drawn from 10 000 permutations of the data. We used one-tailed tests when the prediction involved a directional effect, and two-tailed tests when no difference was predicted. Complete results tables, including random effects, are provided as tables in the electronic supplementary material (the number is given in the electronic supplementary material, table column).)

test		prediction	observed (coef \pm s.e.)	signif.	match	electronic supplementary material, table
1	pair bonds	positive assortment	$r = 0.163 \pm 0.015$	$p_{\text{rand}} < 0.001$	yes	—
2	family structure	positive assortment	$r = 0.211 \pm 0.033$	$p_{\text{rand}} < 0.001$	yes	—
3	size of foraging groups	no difference	$\beta = -0.160 \pm 0.443$	$p = 0.708$	yes	S5
4	number of foraging groups	no difference	$\beta = 44.36 \pm 61.74$	$p = 0.513$	yes	S6
5	weighted degree	no difference	$\beta = 0.143 \pm 0.411$	$p_{\text{rand}} = 0.196$	yes	S7
6	unweighted degree ^a	stressed chicks higher	$\beta = 9.514 \pm 20.301$	$p_{\text{rand}} = 0.014$	yes	S8
7	betweenness	stressed chicks higher	$\beta = 218.1 \pm 202.3$	$p_{\text{rand}} = 0.049$	yes	S9
8	eigenvector centrality	no difference	$\beta = 0.018 \pm 0.090$	$p_{\text{rand}} = 0.280$	yes	S10
9	coefficient of variation of edge weights	stressed chicks lower	$\beta = -0.007 \pm 0.064$	$p_{\text{rand}} = 0.001$	yes	S11
10	strength of bonds to parents	stressed chicks weaker	$\beta = 0.000 \pm 0.007$	$p_{\text{rand}} = 0.257$	no	S12

^aSee the electronic supplementary material, table S8a for results without connections to family members, which are qualitatively identical.

$t = 0.902$, $p = 0.366$, see the electronic supplementary material, table S1 for full results) or tarsus length (day 3, tarsus length \sim numerical brood size after swapping: $\beta \pm$ s.e. = 0.064 ± 0.054 , $t = 1.181$, $p = 0.246$, see the electronic supplementary material, table S2 for full results) among chicks according to their end brood size on the day of manipulation. However, by day 11, every additional nestling in a nest reduced a nestling's weight by 1.6%, or approximately 10% between the smallest and largest manipulated broods (numerical brood size: $\beta \pm$ s.e. = -0.153 ± 0.057 , $t = -2.660$, $p = 0.009$, see the electronic supplementary material, table S3 for full results). Nonetheless, we found no effect of brood size manipulations on body size on day 11 (tarsus: $\beta \pm$ s.e. = -0.018 ± 0.037 , $t = -0.485$, $p = 0.614$, see the electronic supplementary material, table S4 for full results).

We detected a total of 200 adults, 69 juveniles and 14 individuals of unknown age at the RFID-equipped feeders, from which we constructed the social network ($n = 283$ in total). Of the juveniles, 40 were from experimentally enlarged broods (0.63 of those tagged), 16 were from reduced broods (0.59 of those tagged), eight were from unmanipulated broods (0.57 of those tagged) and five were caught as juveniles from unknown sources (the last two categories were not used in the analyses).

Our data on juveniles from enlarged and reduced broods supported 9 of the 10 predictions made based on Boogert *et al.* [28] (see table 1 for summary results and electronic supplementary material, tables S1–S12 for full results). More specifically, we found our network captured the strong familial structure in the population. The strong connections between

paired birds resulted in significant assortment in the social network by pair, while strong within-family links produced significant assortment by family. In both tests of assortment, we found that the network of wild zebra finches was much more strongly assorted than the networks of captive zebra finches (pair bond: $r_{\text{captive}} = 0.111$ versus $r_{\text{wild}} = 0.163$; family: $r_{\text{captive}} = 0.091$ versus $r_{\text{wild}} = 0.211$). We found no evidence that birds from enlarged broods differed to birds from reduced broods in the size or number of foraging groups they joined, or in their weighted degree. However, birds from enlarged broods had a significantly higher unweighted degree, meaning that they had foraged with a greater number of conspecifics than birds from smaller broods. Although this might be the effect of living in larger families, the effect size was also significant if we removed each juvenile's connections to its family members. They also had a significantly higher betweenness, suggesting that they were potentially more important in the global connections of individuals across the whole population. We found no significant difference in eigenvector centrality, but birds from enlarged broods had a higher CV, meaning that they had more differentiated relationships. Finally, we found no evidence for a difference in the strength of relationships that juveniles from enlarged broods had with their parents when compared to juveniles from reduced broods. This was the only test where our results did not support the results of Boogert *et al.* [28]. However, we found that the direction (birds from enlarged broods had lower connection strength to their parents) and size ($\beta_{\text{captive}} = -0.008$ versus $\beta_{\text{wild}} = -0.007$) of the coefficients were very similar to the original study.

4. Discussion

Our data strongly support the prediction that developmental conditions can underlie consistent differences in social network position. The social network of wild zebra finches captured several aspects of social structure that we expected from birds that form lifelong breeding pairs where both parents contribute to the raising of the offspring, and forage together in a coordinated way [37,62]. Associations in the network were significantly assorted by breeding pair, meaning that the density of connections (sum of edges divided by the number of possible edges) between pairs of individuals that bred together was disproportionately higher than expected by chance and also reflected a high degree of assortment by family. In fact, nearly 20% of the total sum of edge weights was between individuals from the same family, despite these representing only 6% of the total possible edges in the network. However, not all families were created equal, and by manipulating the early-life social environment of chicks, through brood size manipulations, we found that being raised in a nest containing more ‘siblings’ resulted in marked differences in social network position later in life. In particular, juveniles who grew up in experimentally enlarged groups foraged with a greater number of conspecifics, were less ‘choosy’ and were more central in the overall social network.

The adaptive significance and life-history implications of the position individuals occupy in their social network has received increased attention over the last years. Several studies were able to demonstrate fitness consequences in the wild population linked to network positions. For example, being more central in a social network can lead to improved survival for adults [63] and their offspring [64,65]. Network centrality can also lead to more stable interactions with known individuals, which could facilitate decision-making [13]. The association between network position and its fitness effect is becoming increasingly evident, particularly when it is related to sexual selection, as in the case of the coordinated and cooperative lek display behaviour of male wire-tailed manakins, *Pipra filicauda* [19,66]. A number of studies have found important effects of betweenness, particularly during the juvenile period on fitness. For example, being less ‘choosy’ and moving more often between social groups (having a higher betweenness score) was shown to increase male reproductive success in wild house finches, *Carpodacus mexicanus* [67], and has been linked to the greater acquisition of social information in flocks of wild songbirds [22]. On the other hand, gregariousness might promote the spread of pathogens [68], with wild house finches that were more central being more likely to acquire a bacterial pathogen, *Mycoplasma gallisepticum* [23]. Generally, social network positions might be viewed as an extended phenotype [18,69,70] which is underlying plasticity and can be closely linked to fitness.

Our replication study found support for 9 of the 10 predictions for the role of developmental conditions on individual network position from the original study conducted on captive zebra finches. The stronger assortment by pair and family we found in the wild zebra finches (compared to captivity) is, in large, expected because the wild birds can spread over a much larger area and had access to a larger number of feeders. These data extend the evidence for the importance of foraging in family groups by zebra finches. In the one test where our results did not support the predictions of Boogert *et al.* [28], i.e. no difference in the relationship of juveniles to parents

between enlarged and reduced broods, direction and size of the effects were nevertheless very similar in both studies, which raises the possibility that future studies may find support for this particular prediction. While we could directly compare the coefficients from these three tests (assortment by pair, assortment by family and the relationship of juveniles to their parents), this was unfortunately not possible for the other network metrics. Most network metrics are strongly influenced by the size of the networks, which were different between the captive and wild studies. Thus, the different scale makes a direct comparison of effect sizes challenging [1,6]. However, our results all point towards a tendency for more competition during development to increase gregariousness, which might enable offspring to more quickly reach independence. As already proposed in [28], growing up in adverse conditions may promote a phenotype which might better enable juveniles to disperse quickly from the poor natal nest site.

While there is an inherent preference for novel results in the peer-reviewed publication process [71–73], an increasing number of papers have highlighted the importance of replication in behavioural sciences [74–78]. The value of good replication is perhaps particularly important for those studies that have used a controlled laboratory environment, and less natural manipulation (e.g. directly administering stress hormones), to examine behavioural outcomes. For example, a recent meta-analysis of 23 publications focused on the red-green colour band paradigm in laboratory studies of the zebra finch, concluded that effects were largely irreproducible and that this very well-used experimental paradigm is false [79]. Over the last four decades, numerous studies had suggested that coloured leg bands affected the behaviour, attractiveness, physiology and fitness of zebra finches, with the most pronounced differences being reported between birds wearing either red or green bands (reviewed in [79]). One key hypothesis, that zebra finch males wearing red leg bands are preferred by females over males with green leg bands (presumably because it amplifies the signal of the beak ornamentation) was supported by many studies from different laboratories [80–82], but was rejected by the large-scale meta-analysis [79].

Our current study is a relatively unique example of direct replication of a captive study in the wild (see also studies on personality in zebra finches in the wild and captivity [83,84], and a recent study of sexual coloration in wild guppies [85]). The value of our replicate experiment is enhanced by having used a naturally occurring stressor, here variation in the brood size that juveniles have experienced. This means that we can realistically expect our findings to translate directly to natural situations. Further, although the original study by Boogert *et al.* [28] suggested that the close confines of captivity made it potentially difficult to detect individual differences in some network metrics, such as eigenvector centrality, our data generated almost exactly the same results. This support for the original study suggests that well-designed captive experiments can produce meaningful insights into the natural, free-ranging, social behaviour of zebra finches. Whether this is more broadly applicable or mostly true for zebra finches only (which naturally live and reproduce in small colonies) remains to be determined. Further, the similarity in the design of the data collection (using PIT tag readers that produce large numbers of observations) and analysis between the current and original study, with slight adjustments to the analysis

method fitting the respective circumstances (i.e. using daily networks to avoid being swamped by noise for the captive bird data), may have also played a role in producing results that could be so closely replicated (across a number of tests and in effect sizes) in the wild.

There is a clear body of evidence linking differences in early-life developmental conditions to the social behaviour, and resulting social structure [21,28,86,87]. Developmental history could be a key factor underpinning consistent differences in individual behaviour [88–93]. For example, differences in brood size during early life can generate effects that are carried over into the following generations [94]. However, we still know relatively little about why stress appears to programme individuals to be more socially gregarious and less choosy. Captive experiments in which finer details about the directionality of inter-individual interactions can be captured, facilitated by recent innovations in long-term high-resolution tracking individuals [95], could provide new insights into the mechanisms—how do stressed individuals end up being more central and well-connected? A combination of new technology and methods, and additional targeted field studies, will hopefully allow us to determine whether the differences that have been

observed are caused by the decisions of the stressed individuals themselves or the behaviour of others towards them.

Ethics. The work was approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2015/017) and the Australian Bird and Bat Banding Scheme.

Authors' contributions. All authors contributed to the ideas of this study; H.B.B. and C.F. collected the data; D.F. and H.B. conducted analyses and wrote the initial draft of the manuscript; all other authors provided substantial feedback. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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