

Growing up with nutritional stress leads to peripheral social network positions, independent of ‘personality’

Yoran H. Gerritsma^{*,1} , François Lamarque¹, Merijn M. G. Driessen ,
Simon Verhulst 

University of Groningen, Groningen, the Netherlands

ARTICLE INFO

Article history:

Received 11 October 2024

Initial acceptance 7 January 2025

Final acceptance 18 February 2025

Available online 8 May 2025

MS. number: 24-00618

Keywords:

assortativity
degree
early life stress
eigenvector centrality
strength
zebra finch

Social integration predicts life span in gregarious species, including humans, but the causes of variation in social integration and its link to behaviour (‘personality’) in other domains are not well known. Early life conditions also shape fitness variation, possibly through effects on personality and social integration. We studied social integration in zebra finches, *Taeniopygia castanotis*, reared with different levels of nutritional stress, which we showed to affect offspring growth and thereby fitness prospects. Growing up with nutritional stress caused individuals to attain more peripheral positions in social networks, as they interacted (1) with fewer individuals, (2) less frequently with their connections and (3) less with well-connected (i.e. ‘popular’) individuals. Thus early-life adversity effects on social integration may mediate effects on fitness. In contrast, behaviour in five standardized tests was independent of early life adversity, and consistent with these findings, behavioural scores were at most weakly predictive of network position. Choice of interaction partner did, however, depend on personality, with individuals interacting assortatively with respect to gregariousness and disassortatively with respect to boldness. Thus, developmental conditions may affect fitness prospects through effects on social integration, independent of ‘personality’, and suggest that some level of (social) challenge is required to reveal carry-over effects of early development.

© 2025 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Social integration, that is, the quality and quantity of social interactions, predicts human wellbeing (Fowler & Christakis, 2009) and mortality risk (reviewed in Cohen, 2004; House et al., 1988). Social bonds also predict mortality (Archie et al., 2014; Silk et al., 2003, 2010; Thompson & Cords, 2018) and reproductive success in animals (Grabowska-Zhang, Wilkin, & Sheldon, 2012; Schülke et al., 2010). Having more social bonds benefits predator avoidance, gives a competitive advantage (Gilby et al., 2013; Goodwin & Podos, 2014; Grabowska-Zhang, Sheldon, & Hinde, 2012) and increases access to information (Aplin et al., 2012). However, engaging in social bonds and maintaining a social position may come at a cost (reviewed in Tamashiro et al., 2005), for example, through increased exposure to disease (Adelman et al., 2015; Deere et al., 2021) and accelerated ageing (Anderson et al., 2021; Verhulst et al., 2014). The optimal balance between costs and benefits is likely to depend on individual state and circumstances and it is not surprising therefore that sociability, that is, the tendency to interact

with conspecifics (Réale et al., 2007), varies strongly within populations. However, the factors causing variation in social integration and its link with sociability and other personality dimensions are not well known. Neither is it well known how the link between social integration and its health consequences arise (Thompson, 2019), which can be difficult to ascertain because social position can reinforce the individual differences that initially caused variation in social position (Fig. 1; Verhulst et al., 2014). For example, high-ranking male baboons, *Papio cynocephalus*, have faster wound healing (Archie et al., 2012), which may arise through a positive effect of being highly ranked on phenotypic state. However, an alternative explanation, not mutually exclusive, is that phenotypic state has direct and independent effects on both social integration and wound healing. Prospective studies of factors that predict social integration are therefore needed to unravel the causes and consequences of variation in social integration.

Early life adversity is known to have long-term effects on phenotypic state and fitness prospects (Krause et al., 2017; Lindström, 1999; Nussey et al., 2007; Spencer, 2017), and developmental conditions are therefore a likely candidate to also shape variation in social success. Indeed, fitness consequences of adverse

* Corresponding author.

E-mail address: yorangerritsma@gmail.com (Y. H. Gerritsma).

¹ These authors contributed equally to this work.

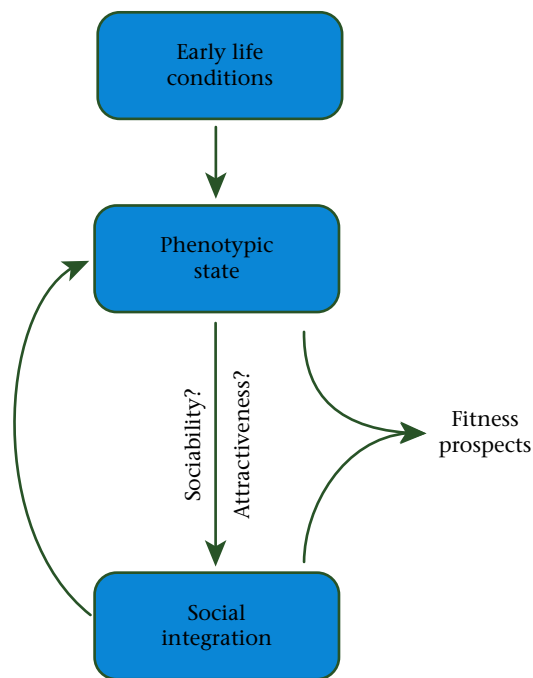


Figure 1. Schematic overview of the hypothesized effect of developmental effects on fitness prospects. This effect will in part be a direct consequence of variation in phenotypic state, affecting physical performance, but in addition phenotypic state may affect social integration, which independently affects fitness prospects. Such effects could arise through effects of early life conditions on sociability (that is, personality aspects), or, not mutually exclusive, through effects on attractiveness as social partner. Moreover, poor (good) social integration may negatively (positively) affect phenotypic state, thereby reinforcing the effect of developmental conditions on social integration. Small differences in phenotypic state may in this way be amplified to large differences in phenotypic state, social integration and consequently fitness prospects.

developmental conditions may in part arise through effects on social integration. For example, female baboons that experienced more early life adversity achieved lower fitness and were more socially isolated from other females (Tung et al., 2016). This study was observational, leaving room for alternative interpretations, but experimental studies in zebra finches, *Taeniopygia castanotis*, also reported the effects of early life adversity on position in social networks (Boogert et al., 2014; Brandl et al., 2019). However, these offspring were studied in family groups during their transition to social independence, which likely affected their social behaviour (Loonen et al., 1999). Whether adverse developmental conditions affect social integration in adulthood therefore remains largely unknown.

Social integration is the outcome of behavioural interactions, in which some individuals may be more attractive than others as interaction partners, constraining individual control on social integration (Fig. 1). At the same time, behavioural interactions are at least in part under the control of individuals as expressed in aspects of their personality, such as sociability (Krause, James, & Croft, 2010; Wolf and Krause, 2014). Personality therefore potentially explains variation in social integration. However, although this seems eminently plausible, evidence supporting this hypothesis is mixed. Multiple studies showed that great tits, *Parus major*, who explored a novel environment faster were more likely to be in central network positions (Aplin et al., 2013; Snijders et al., 2014). Similarly, faster-exploring Caribbean flamingos, *Phoenicopiterus ruber*, were also more likely to hold central positions; however, this association was not found in Chilean flamingos, *Phoenicopiterus chilensis*, in the same study (McCully & Rose, 2023). In other species, there was no direct association between exploration and social

network position (Chock et al., 2017; Schürch et al., 2010) and bolder individuals had either stronger associations (Díaz López, 2020) or weaker associations (Croft et al., 2009; Pike et al., 2008). In zebra finches, fast exploring males, but not females, interacted with fewer individuals (McCowan & Griffith, 2015). Summarizing, there is a complex interplay between early life adversity, personality and social integration, which is currently not well understood.

Experimental manipulation of developmental conditions can be a key step towards unravelling the interactive effects of phenotypic state, behaviour and social integration when these are studied in conjunction, but to our best knowledge, there is no such study in the literature. We manipulated foraging conditions of captive zebra finch parents and previously showed this manipulation to affect growth of their offspring (Gerritsma et al., 2022). Early life adversity hereby reduced phenotypic quality and fitness prospects, as reduced fledging mass is linked to lower survival rates (Birkhead et al., 1999; Briga et al., 2017; De Kogel, 1997). We here report how early life adversity affected position in single-sex social networks in adulthood. We predicted high-quality individuals to attain better social integration, that is, more central positions. Before studying effects of developmental conditions on social integration, we subjected all birds individually to multiple standardized behavioural tests (reported in Gerritsma et al., 2023). In this paper, we showed that our developmental manipulation did not impact the behaviour of zebra finches in these standardized assays. Here, we use these data to investigate the extent to which effects of developmental conditions on social integration may be mediated by personality as assayed in the behavioural tests. Individuals may interact preferentially with individuals that are either similar or dissimilar to themselves. We therefore also tested whether individuals assorted based on developmental conditions or performance in the behavioural tests.

METHODS

Ethical Note

All methods and experiments in this research were performed with the approval of the Central Committee for Animal Experiments ('Centrale Commissie Dierproeven') of the Netherlands, under licence AVD1050020174344. The main concern for ethical wellbeing during the study was that individuals would not access the boxes to obtain food. To mitigate this risk, we built the boxes to be modular. This meant that all four walls and the ceiling were easily removed. Additionally, we chose Perspex materials; hence, individuals would be able to observe their surroundings at all times. At the start, we ensured there was an additional food source available besides the food, a commercial seed mixture, placed in the food boxes, such as a larger silo (identical commercial seed mixture). The habituation process began with only the bottom plates in place, with two small food silos in each 'box' and sprinkled eggfood over the bottom plates to attract the birds.

After a day and only once individuals were observed eating from food silos on the bottom plates, we removed the primary food source. Next, we introduced the front plate containing the antenna. To encourage the birds to visit the antenna, we placed eggfood in front of, behind and on the inside of the antenna. We observed the birds daily, replenishing eggfood around the antenna as needed. During this phase, we activated the RFID system to collect data to determine whether all birds entered a box.

Following this, we assembled the box step-by-step (maximum of one step per day), starting with the ceiling, then adding the back wall, followed by either the left or right-side wall. Finally, we installed the remaining wall, fully enclosing the box. We took special care during this final step, as it was often intimidating for

the birds. We observed the aviaries multiple times per day after the box was closed to monitor. Additionally, we ensured that box assembly was not completed on Fridays and checked the data to confirm that each bird had entered a box. No injuries or mortality were observed during the testing phase or during the social network measurements. Animals were kept alive for further experiments after this study.

After the boxes were fully assembled, we observed that some birds could enter but had difficulty exiting. To address this, we visited the aviaries multiple times daily. When a bird became trapped, we raised one of the side or back walls slightly (avoiding the front wall) and guided the bird out through the antenna. We continued this process until no birds were trapped in the boxes for at least a full day.

Animals and Developmental Treatment

Subjects were 36 zebra finches (20 males, 16 females, with all birds having similarly coloured plumage) with a mean age $\pm$ SE of 542 ± 15 days that were raised in 26 different broods as described in [Gerritsma et al. \(2022\)](#). In brief, broods were raised in four aviaries ($310 \times 210 \times 150$ cm) that differed in foraging conditions. Each breeding aviary contained a food container filled with seeds, suspended from the ceiling, either equipped with perches (benign foraging) or without perches (harsh foraging; [Koetsier & Verhulst, 2011](#)). In short, a commercial seed mixture was offered in a single container ($120 \times 10 \times 60$ cm), which was suspended from the ceiling. Each side of the container had five holes, giving a total of ten access points for the birds to reach the seeds. In the easy foraging condition, perches were installed below each hole, allowing birds to sit comfortably while feeding, resulting in low foraging costs. In contrast, the harsh foraging conditions had no perches, requiring the birds to fly back and forth between a distant perch and the container for each seed. Offspring growth was reduced in nestlings growing up when their parents were subjected to harsh foraging conditions: individuals were lighter and had smaller wing and head-bill lengths at the age of 15 (± 1) days [details in ([Gerritsma et al., 2022](#))]. Offspring were still lighter at the age of 31 (± 1) days, at which age offspring were moved to different aviaries in which foraging conditions were benign for all individuals (silos with food on the floor). We therefore refer to individuals growing up under harsh foraging conditions as being low quality (LQ), and individuals from benign foraging conditions as being high quality (HQ).

Personality Tests

Prior to social network testing, we performed standardized behavioural tests (mean $\pm$ SE age at first test: 325 ± 3 days). Behavioural tests and results are described in [Gerritsma et al. \(2023\)](#) and we therefore describe only the essence here. (1) Novel environment: an individual was introduced to a novel environment with artificial trees. We measured latency in entering the environment, number of unique locations explored and number of position changes. For the second test, we changed the tree's colour and position. (2) Novel object: an individual was introduced to a novel object in a familiar cage. Novel objects, green clothes peg or black hair clamp were balanced across the first and second test. We measured the latency to first move and the latency to interact with the novel object. (3) Tonic immobility: an individual was fixed on its back for 5 s and time spent immobile was measured. If immobilization was unsuccessful 10 times, a score of 1 s was assigned. (4) Sociality: an individual was placed in a cage with two side cages, each containing two or 10 same-sex, unfamiliar and conspecifics. We observed for 10 min and calculated the proportion of time spent

next to either group (group preference). (5) Dominance: individuals were pooled into teams of six same-sex conspecifics. Within each pool, all dyads competed against each other twice. Thus, each individual in a pool competed against every other individual twice (resulting in 10 matches per individual). Individuals competed over a single perch and time spent on the perch was used to calculate David's Score ([Gammell et al., 2003](#); [Hemelrijk et al., 2005](#); [Verhulst et al., 2014](#)). Matches were not observed by other individuals.

We performed five tests, always in the same order: (1) novel environment, (2) novel object, (3) tonic immobility, (4) sociality and (5) dominance. Each individual was subjected to each test twice before the next behavioural test in the sequence. Repeatability of the behavioural scores ranged from 0.31 to 0.55, and the extrapolated repeatability (that is, repeatability of average over the two scores) ranged from 0.48 to 0.71 (see [Gerritsma et al., 2023](#) for details). As described in detail in [Gerritsma et al. \(2023\)](#), the foraging costs manipulation did not significantly affect behaviour in any of the tests, and correlations between behaviour in the different tests ('behavioural syndromes') were negligible.

Between the personality tests (performed at age 325 ± 3 , mean $\pm$ SE, days) and the social network testing (performed at 542 ± 15 , mean $\pm$ SE, days), birds were housed in single-sex aviaries with a maximum of 24 individuals per aviary, with food available *ad libitum*.

Social Network

Social network position was estimated in single-sex flocks in two outdoor aviaries ($310 \times 210 \times 150$ cm) where the birds were exposed to natural temperature fluctuations but shielded from rain. Each aviary contained four transparent Perspex boxes (cubes with 25 cm aluminium ribs), placed in a row along one of the aviary walls (Fig. S1 and S2). Each box contained two silos with a tropical seed mixture and these were the only food source in the aviary. Each box had one entrance, a round 4 cm (in diameter) hole in one wall, on which a circular antenna was mounted ('ANTC40', DorsetID, Aalten, The Netherlands). All birds carried a leg ring with a PIT tag ('ID100A Micro Transponder', DorsetID), which was read when going through the antennas. Antenna readings were stored in an OEM decoder ('LID650, DorsetID'), located outside the aviary.

Acclimatization and Testing Period

Individuals were trained to use food boxes gradually, starting with the four bottom plates and adding one Perspex plate per day. Individuals were observed daily to see whether they gathered food. First, the front plate with the antenna was mounted and eggfood was provided on both sides of the antenna. Next, we mounted the ceiling and on the subsequent 3 days, on the other walls. After habituation, all individuals were able to enter and exit the food box independently.

In total four groups were used to generate social networks. The first two groups contained 12 males (five HQ, seven LQ) and 10 females (five HQ, five LQ), whereas the second two groups contained eight (four HQ, four LQ) males and six females (three HQ, three LQ). We recorded each of the four groups for 21 days, counting from the end of habituation, resulting in 84 daily social networks (Fig. S3).

Social Network Analysis

We inferred social structures based on foraging associations, that is, birds present together in a box. Using R version 4.0.3 ([R Development Core Team, 2008](#)) and the 'dplyr' package

(Wickham et al., 2021), we inferred the start time and the end time of all box visits.

We constructed animal social networks using both frequency-based and duration-based methods. The frequency-based method counts each interaction equally and hereby does not differentiate between short or long encounters. The duration-based method, however, considers interaction duration and provides a more nuanced understanding of social connections.

We calculated either the frequency or duration of interactions of each unique pair of birds. The weights of the edges were calculated using the simple ratio index with the 'assocInd' package (Hoppit & Farine, 2017). This index corresponds to the amount of time (either in frequency or duration) two individuals spent foraging together, divided by the amount of time they spent foraging apart. We built networks for each day using the 'Igraph' package (Csardi & Nepusz, 2006) and calculated various node-level metrics. Following Boogert et al. (2014) and Brandl et al. (2019), we determined degree, strength, eigenvector centrality and betweenness centrality for each individual per day.

Degree is the number of direct connections (Boogert et al., 2014; Wey et al., 2008). Strength is the combined weight of the interactions of an individual (Wey et al., 2008) and reflects how often it interacts with other individuals. Eigenvector centrality reflects connectedness to individuals with high degrees, and betweenness centrality indicates the number of shortest paths between every pair of individuals on which an individual lies (Wey et al., 2008). Individuals with high betweenness tend to connect different sub-communities of the networks together and thus play a crucial role in the cohesion of the group (Brent, 2015; Wey et al., 2008). We further calculated the coefficient of variation (CV) of edge weights for each individual, where a higher CV indicates that a bird interacts preferentially, whereas a lower CV indicates indistinctive associations (Boogert et al., 2014).

We scaled social network metrics based on group size to allow for comparison between groups. Degree, strength and betweenness centrality were scaled according to the formulas proposed by Freeman (1978), and eigenvector centrality was scaled using the scale argument of the eigen-centrality function of the Igraph package (Csardi & Nepusz, 2006).

All individuals interacted with every other member of their group on most days, resulting in maximum degree and minimum betweenness, we created networks based on interactions up until the time it took for one individual to reach maximum degree. With these networks, we calculated degree and betweenness, but only degree was used in the further analysis as betweenness was highly zero-inflated. Strength, eigenvector centrality and CV were based on full daily social networks.

Statistical Analyses

All analyses were performed in R v 4.0.3 (R Development Core Team, 2008) in the RStudio IDE (v1.3.1073; Rstudio Team, 2020) using the degree, strength, eigenvector centrality and betweenness centrality for each individual per day as data points.

Effect of Early Life Adversity on Social Networks

We used (generalized) linear mixed models to investigate the effect of developmental conditions on social network metrics. Models were constructed using the lme4 and lmerTest packages (Bates et al., 2015; Kuznetsova et al., 2017), and each social network metric was the response variable in a model. We used linear models with either a Gaussian, for strength and the log10-transformed CV, or a binomial family for degree and EC. As fixed effects, we included developmental treatment, sex and brood size, and interactions

between (1) treatment and sex, and (2) treatment and brood size. Developmental treatment, sex and broodsize were mean-centred (mean = 0) to allow for informative main effects despite the presence of the interaction term. Random effects were the identity of the genetic father, genetic mother and 'groupday', a combined variable indicating the test day of each sex-specific group. If a random effect explained less than 2% of the variance, it was excluded from the model. Identical models were built for the frequency-based and duration-based social networks; we report results based on duration-based estimates, after which we briefly report the results of a comparison with results based on frequency-based estimates. In the binomial models, we included an observation-level random effect to prevent overdispersion, following Harrison (2014).

Repeatability of Social Network Metrics

We used the rptR (v0.9.22) package (Nakagawa & Schielzeth, 2010) to calculate repeatability estimates of standardized social network metrics. Individual identity was included as a random effect and day as a fixed effect. Degree and eigenvector centrality were arcsine transformed to meet assumptions of normality (Sokal & Rohlf, 1995). We also tested sex-specific repeatability estimates and calculated extrapolated repeatability using equation 37 from Nakagawa and Schielzeth (2010) to estimate the effect of averaging multiple metrics.

Predictive Power of Personality

As we have multiple measures of each social network metric, one per bird per day, we used multivariate response models, which allow us to estimate individual-level pairwise residual correlations between the different social network metrics. To this end, we constructed Bayesian multivariate mixed models using the brms package (v2.14.4, Bürkner, 2017), interfaced with the MCMC sampler of RStan (v2.19.2, Stan Development Team, 2020). We used standardized social network metrics as response variables to facilitate the comparison of residual correlations and effect sizes and increase the efficiency of the MCMC sampler. Strength and the arcsine transformed values for degree and EC, and the log10-transformed CV were standardized (mean = 0, SD = 1) to facilitate multivariate analyses. We used weakly informative Gaussian priors (mean = 0, SD = 1, Lemoine, 2019) for the fixed effects and default brms priors for random effects, a Student's *t* density with three degrees of freedom for SDs and an LKJ density (Lewandowski et al., 2009) for correlations.

Multivariate models were run on three chains, first warming up with 1000 iterations and followed by 3333 iterations per chain. To prevent divergent transitions, we set adapt_delta to 0.99. To check for proper convergence and mixing of chains, we used trace plots and checked whether Rhat values were 1. The function pp_check() from the brms package was used to evaluate model fits.

We calculated the probability of direction (Pd) to test hypotheses (Makowski, Ben-Shachar, Chen & Lüdtke, 2019). The Pd is the proportion of the posterior that is in the same direction as the mean and is often considered to be the 'Bayesian *P* value'. Pd values above 0.95 are interpreted as a trend, corresponding to a frequentist *P* value between 0.05 and 0.10, and values above 0.975 are interpreted as evidence for the tested hypothesis, corresponding to frequentist *P* values below 0.05. Effect sizes are calculated as the posterior mean, with the 95% CI calculated with the hdi function from the 'bayestestR' package (v0.8.2., Makowski, Ben-Shachar & Lüdtke, 2019).

As fixed effects, we included sex, each of the five personality traits, and the interaction between sex and each personality trait.

For the personality traits, we used the values as calculated in Gerritsma et al. (2023). In brief, we used a principal components analysis on the novel environment and novel object tests to reduce the number of variables into a single component variable. The scores for sociality and tonic immobility were, respectively, square-root and log10-transformed to meet assumptions of normality. David's score (dominance) was normally distributed. To calculate whether personality was predictive of individual functioning in social networks, we took the average value of the two tests of each personality trait. We subsequently standardized (mean = 0, SD = 1) all personality traits. Furthermore, as we found interactions between the standardized measure of sociality and sex on the social network metrics, we ran additional sex-specific multivariate models.

Assortativity

To test whether individuals interacted (dis)assortatively we calculated assortativity coefficients following Newman (2002, 2003). We estimated assortativity coefficients, described in the Supplementary Material, with respect to developmental background (discrete) and (separately) each of the five personality traits (continuous).

We used the 'assortment.discrete' or 'assortment.continuous' functions from the assortnet package (v0.12), which implemented weighted versions of the formulas (Farine, 2014). We used the average of all daily networks within a group as a single weighted matrix.

We tested whether assortment was significant using a randomization test, by assigning the traits of the group (e.g. developmental manipulation; 'benign' or 'harsh') randomly within their group and calculated the assortativity coefficient for each randomized group. This process was repeated for 5000 iterations per group. Significance was calculated as the proportion of the randomized distribution that was equal to or more extreme than the observed value. The *P* value over all groups combined was calculated using Fisher's method for combining *P* values (Fisher, 1925).

RESULTS

Food Box Usage

Food box usage was not affected by early life adversity (box visits per day, mean $\pm$ SD, LQ: 25.62 $\pm$ 14.33; HQ: 24.27 $\pm$ 9.45, box visit duration, seconds, LQ: 210 $\pm$ 369; HQ: 228 $\pm$ 379, time in box per day, seconds, LQ: 5370 $\pm$ 2261; HQ: 5537 $\pm$ 2355, all *P* > 0.05). Social interactions, defined as two or more birds being simultaneously in a food box, occurred on average 256 times per day per flock (SD = 153.89), and these interactions lasted 122 seconds on average (SD = 209.16).

When individuals entered a food box, it could either be empty or occupied by one or more flock members. When LQ individuals entered a food box, this was significantly more likely to be unoccupied compared with HQ individuals entering a food box (sexes pooled: $z = -2.77$, *P* < 0.01). However, more detailed analysis showed this effect to be sex-dependent (HQ males: proportion visits to empty boxes $\pm$ SE: 0.67 $\pm$ 0.01; LQ male, 0.61 $\pm$ 0.01; HQ female, 0.56 $\pm$ 0.01; LQ female, 0.58 $\pm$ 0.01; interaction sex:treatment: $z = -5.14$, *P* < 0.01). Consequently, LQ individuals spent a larger proportion of their time alone in food boxes (sexes pooled: $z = 4.45$, *P* < 0.01), and this effect was also sex-dependent (interaction: $z = 2.57$, *P* = 0.01; HQ male, proportion $\pm$ SE: 0.27 $\pm$ 0.01; LQ male, 0.36 $\pm$ 0.01; HQ female, 0.36 $\pm$ 0.01; LQ female, 0.38 $\pm$ 0.01).

Repeatability

Individual network positions can only be meaningfully estimated when they are repeatable. Repeatability estimates of network metrics ranged from 0.09 to 0.43 (sexes combined) and repeatability estimates were higher in males for CV and EC (Table S1). However, when there are data for multiple days, the extrapolated repeatability is more relevant, which can be thought of as the repeatability of the network metric averaged over the entire measurement period. Extrapolated repeatability estimates were high, ranging from 0.67 to 0.92 (Table S1). As expected, the different social network metrics were significantly correlated (Table S2).

Social Network Position

LQ birds scored lower on all social network metrics and this difference was statistically significant for strength, degree and eigenvector centrality, but not for CV (Table 1, Figs. 2 and 3). There was a trend for the effect of developmental conditions on degree to be stronger in females (HQ male, mean $\pm$ SE: 0.70 $\pm$ 0.02; LQ male, 0.68 $\pm$ 0.01; HQ female, 0.75 $\pm$ 0.02; LQ female, 0.70 $\pm$ 0.01). In contrast, the effect of developmental conditions on eigenvector centrality tended to be stronger in males (HQ male, mean $\pm$ SE: 0.73 $\pm$ 0.02; LQ male, 0.57 $\pm$ 0.02; HQ female, 0.74 $\pm$ 0.02; LQ female, 0.69 $\pm$ 0.02). The effect of developmental conditions on strength (HQ, mean $\pm$ SE: 0.09 $\pm$ 0.0; LQ, 0.08 $\pm$ 0.0) was similar in the sexes.

As both the developmental manipulation and brood size independently affected nestling growth (Gerritsma et al., 2022), we tested whether brood size also affected social network position. Growing up in larger broods did not affect an individual's interaction strength ($t = 0.62$, *P* = 0.54), CV ($t = -0.90$, *P* = 0.38) or eigenvector centrality ($z = 1.60$, *P* = 0.11) but did affect degree, with individuals reared in larger broods interacting with more individuals ($z = 3.16$, *P* < 0.01). Note, however, that the direction of this effect was opposite to the expectation based on the developmental treatment effect.

Table 1
Network metrics in relation to developmental conditions and sex

	DT		Sex		Broodsize		DT:Sex		DT:Broodsize	
	t/z	<i>P</i>	t/z	<i>P</i>	t/z	<i>P</i>	t/z	<i>P</i>	t/z	<i>P</i>
Strength (<i>t</i>)	-2.33	0.03	-1.47	0.15	0.62	0.54	-1.25	0.22	0.05	0.96
Degree (<i>z</i>)	-2.24	0.03	0.85	0.39	3.16	<0.01	1.90	0.06	1.76	0.08
Coefficient of variation (<i>t</i>)	-1.59	0.12	0.08	0.94	-1.15	0.26	-0.35	0.73	-0.89	0.38
Eigenvector centrality (<i>z</i>)	-2.92	<0.01	-1.52	0.13	1.60	0.11	-2.13	0.03	-0.20	0.84

DT = developmental treatment. Variables separated by ':' indicate an interaction. Values provided are *t* or *z*-scores and the corresponding *P* value. Network metrics were included in models as dependent variable, including a random intercept for individual identity, the combined group-day variable, genetic mother and an observation-level random effect. Significant effects are in bold and italics.

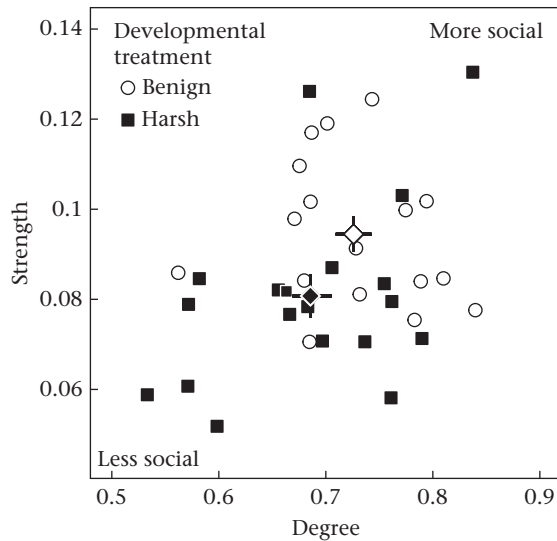


Figure 2. Individuals from a harsh development interacted with fewer individuals (degree) and did so less often (strength). Each point is the average value per individual over 21 days. Colour of the points indicates developmental treatment, with white for those from benign conditions and black for those from harsh conditions. The diamonds and whiskers indicate the mean and SE per group.

Personality and Social Network Position

Behaviour in personality tests did not generally predict social network metrics (Fig. 4), with credible intervals overlapping zero (Table S3 and S4). The exceptions are group preference and tonic immobility. Individuals that stayed immobile for longer in the tonic immobility test interacted more frequently within their networks (Strength, $P_d = 0.98$, mean [95% CI] = 0.16 [0.01, 0.32]). Group preference behaviour in the individual sociality test predicted behaviour in the social networks in a sex-specific manner (Fig. S4). To better understand this relationship, we ran additional multivariate models per sex (Table 2). Males displaying more social behaviour in the standardized sociality test showed similar behaviour when in networks, interacting with more individuals (degree). However, they were less likely to be central individuals

(that is, with high eigenvector centrality). More social males were also less selective in their interactions (CV). More social females interacted more often within their network and also attained more central positions (that is, higher eigenvector centrality). However, more social females did not interact with more individuals than their less social counterparts nor were they more or less indistinct in their connections. Summarizing, the predictive value of 'personality' with respect to network position was limited; more gregarious females had stronger and more stable relationships with fewer individuals, whereas more gregarious males had weaker and more casual interactions with a larger group of individuals.

Assortativity

Individuals did not assort based on their developmental background ($P = 0.27$, Fig. S5). However, they did assort significantly positively with respect to behaviour in the sociality test ($P = 0.03$), which means that gregarious individuals interacted more with other gregarious individuals than expected by chance. With respect to boldness, as determined by the novel object test, birds showed significant negative assorting ($P = 0.02$), indicating that relatively bold individuals interacted more than expected by chance with individuals that were timid relative to their group members. There was no significant assorting based on the results of the other standardized tests (Fig. 5): exploration ($P = 0.38$), tonic immobility ($P = 0.28$) and dominance ($P = 0.62$). To allow a general conclusion, given the multiple tests with mixed outcomes, we calculated a combined P value over the five tests for assortment with respect to performance in the behavioural tests using Fisher's method to combine P values. We find that over the five tests pooled the observed assortment deviated significantly from chance expectation ($\chi^2_{10} = 20.25$, $P = 0.03$).

Frequency Versus Duration-Based Social Networks

We analysed social network data using the duration of interactions, but repeated the analyses using the frequency of interactions. The results were broadly consistent between the two methods (section 2 of Supplementary Material). An exception was that eigenvector centrality was positively associated with broodsize

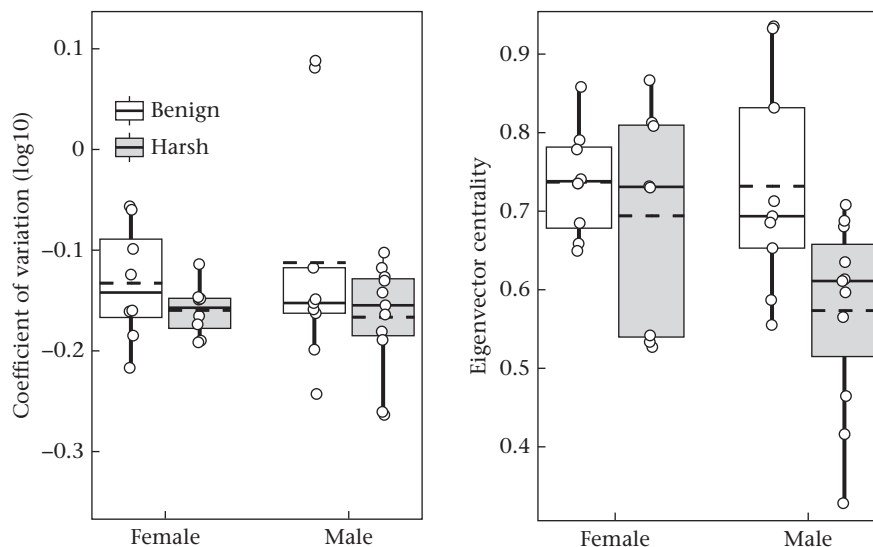


Figure 3. The developmental manipulation did not affect the coefficient of variation, but affected eigenvector centrality. Box plots of coefficient of variation (log-10 transformed) and eigenvector centrality, as obtained from the duration-based method. The box plots show the median (solid line), mean (dashed line), IQR (box) and the average value per individual over the 21 days (point). Whiskers indicate those values that are within 1.5 times the IQR.

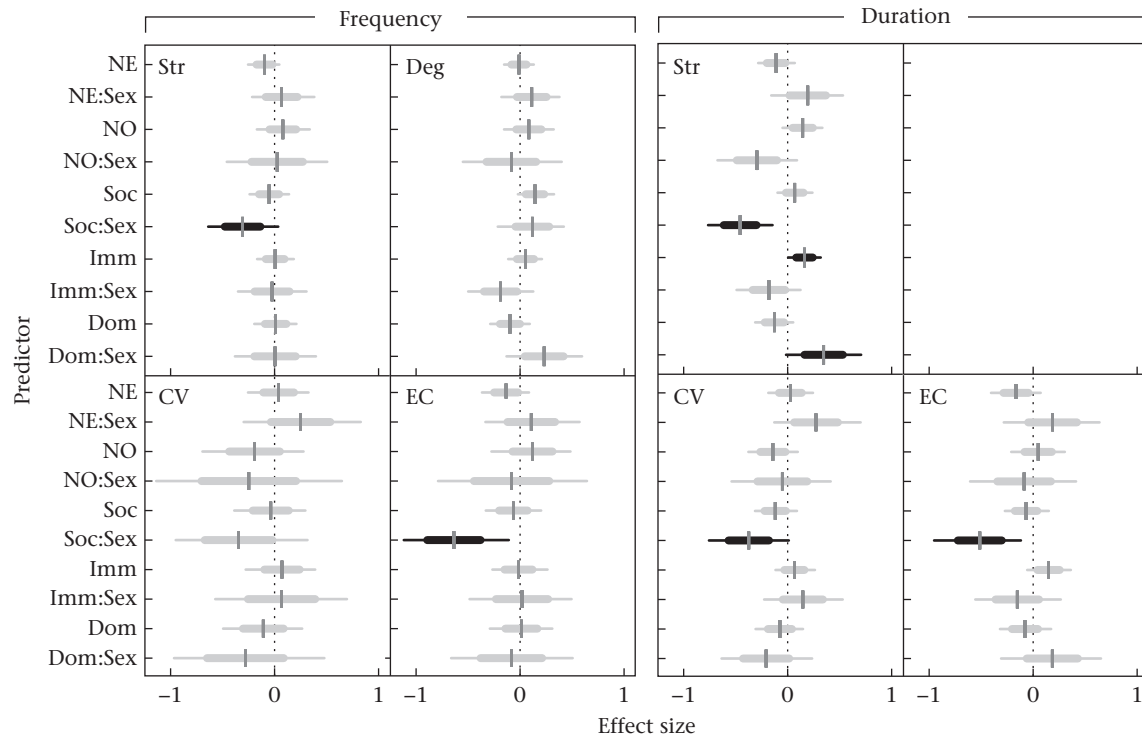


Figure 4. Standardized effects of personality traits on social network metrics calculated using either frequency or duration of interactions. Standardized effect sizes are denoted as a vertical line (estimate), with the SE (thick whisker) and 95% CI (thin whisker). Black and grey correspond to Pd values above and below 0.95 respectively. Degree is identical between the two methods, and was therefore omitted from the duration-based method. NE = novel environment, NO = novel object, Soc = sociality, Imm = tonic immobility, Dom = dominance.

Table 2
The relation between the standardized gregariousness with metrics from the social network

	Males		Females	
	Pd	Posterior mean [95% CI]	Pd	Posterior mean [95% CI]
Strength	0.92	−0.15 [−0.38, 0.06]	1	0.28 [0.08, 0.48]
Degree	0.98	0.20 [0.01, 0.39]	0.70	0.09 [−0.30, 0.47]
Coefficient of variation	0.99	−0.31 [−0.57, −0.03]	0.76	0.10 [−0.21, 0.39]
Eigenvector centrality	0.98	−0.32 [−0.62, −0.03]	0.98	0.20 [0.01, 0.40]

Marginal effects of standardized gregariousness on social network metrics in males and females. Significant effects (Pd > 0.975) are in bold and italics.

in the frequency-based method ($z = 2.54$, $P = 0.01$, Table S3–S5), but not in the duration-based method. In the frequency-based method, we also found that males displaying more gregariousness in the standardized sociality test were not more or less selective in their interactions (CV, Table S6). Among females, there was no relation between group preference behaviour and behaviour in the social networks, and neither was there a relation between time spent immobile in the tonic immobility test and the strength of interactions (Pd = 0.52, mean [95% CI] = 0 [−0.17, 0.18]).

DISCUSSION

Social integration predicts fitness prospects, driving interest in understanding causes of individual variation in social integration (see Introduction for references). Developmental adversity depresses fitness prospects, possibly mediated at least in part through lower levels of social integration. We therefore tested experimentally whether developmental adversity affected social integration. Developmental adversity, which suppressed growth, caused individuals to interact with fewer conspecifics (that is, lower degree) and less often (that is, lower strength), and they were less connected to ‘popular’ individuals (that is, lower eigenvector

centrality). Summarizing, in accordance with our expectations (Fig. 1), zebra finches subjected to early life adversity attained more peripheral positions in their social network, suggesting that early life adversity effects on fitness are at least in part mediated by effects on social integration.

Multiple processes, not mutually exclusive, may explain the more peripheral social network positions of individuals of lower phenotypic quality due to developmental adversity. First, lower-quality individuals may be less attractive to interact with compared with higher-quality individuals. In a social learning context, manipulated phenotypic quality affected whose behaviour was copied (Riebel et al., 2012), indicating that social attention to other individuals is modulated by their phenotypic quality. However, whether a similar process contributed to the more peripheral social positions of lower-quality individuals remains to be tested. Second, lower-quality individuals may be less proficient at social interactions. Little is known about social proficiency in zebra finches, but social dominance was not affected by developmental adversity (Gerritsma et al., 2023). Evidence from other species nevertheless indicates that this is a plausible mechanism. For example, interaction style was modulated by early life adversity in baboons (Patterson et al., 2022), and reducing nutritional stress and

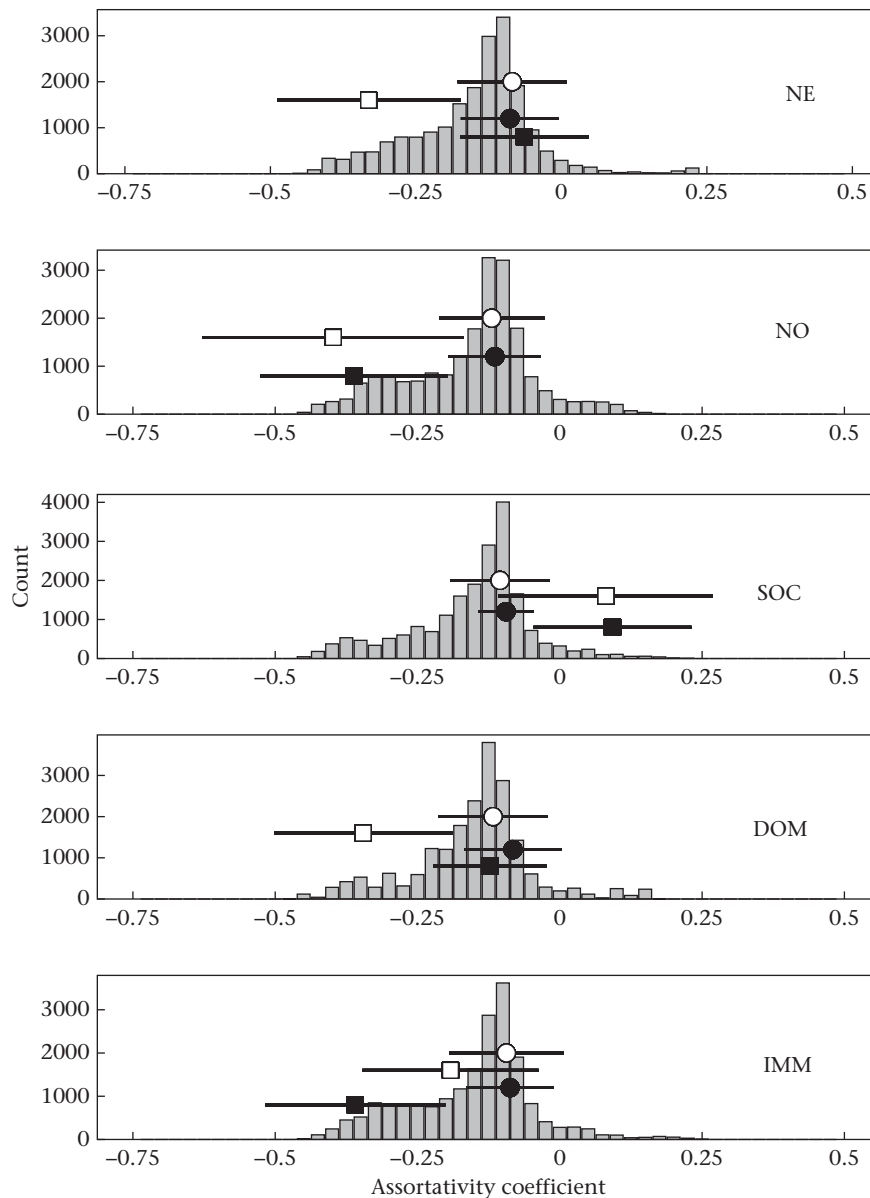


Figure 5. Interacting individuals assorted positively on their behaviour in the sociality test, and negatively with respect to their behaviour in the novel object test. There was no significant assortment for the other behaviours. Interacting individuals did not assort positively or negatively with respect to their developmental background. NE = novel environment, NO = novel object, SOC = sociality, DOM = dominance, IMM = tonic immobility. Points denote the observed assortment ($\pm$ SE) of each of the four groups (σ = black, φ = white, circles = group 1, squares = group 2). Histogram shows the distribution of expected assortment values obtained from 20 000 randomizations (5000 per group). The assortativity coefficient ranges from -1 (fully disassorted) to 1 (perfectly assorted).

sibling rivalry during development induced juvenile ravens to be more attentive to conspecific calls (Gallego-Abenza et al., 2022). Third, phenotypic quality may affect how much time and energy individuals invest in social relations. The observation that lower-quality individuals were more likely than high-quality individuals to spend time in food boxes devoid of other individuals suggests that lower investment may indeed have contributed to attaining more peripheral social positions. However, this behaviour may also reflect negative social experiences in the past, and as such be an indirect effect of being less attractive as a social partner, making it less appealing for low-quality individuals to initiate interactions with group members. Attractiveness as a social partner, investment in social relationships and social proficiency are likely to act in concert to affect social success, for example, because low social proficiency and low social investment are likely to further reduce the attractiveness as social partners. Detailed observations and

experiments focusing on the interplay between phenotypic state and the ontogeny of social relations and proficiency are required to establish how these processes together culminate in the effects of early life adversity on social integration.

Maintaining one's position in a social network requires an ongoing investment in social relations, like having to keep swimming in a stream to stay in the same place. From this perspective, the position of individuals in social networks can be seen as the outcome of an optimisation process, where the fitness benefits of a social position need to be outweighed by the costs of attaining and maintaining a position. Both costs and benefits are likely to vary between individuals, depending on aspects of phenotypic state (which is multidimensional) such as social proficiency and attractiveness. Costs and benefits are also likely to change within individuals, for example, with age, size and (social) experience, as evidenced by reported systematic changes in social status with age

(e.g. Verhulst et al., 2014). It seems likely that the fitness costs of attaining and/or maintaining a central social position are higher for individuals that are less attractive as social partners. Seen from this perspective, the more peripheral positions of birds that experienced adverse developmental conditions may well be the optimal position; given their phenotypic state relative to the phenotypic state of their group members, they are simply making the best of a bad job.

Behavioural interactions are at least in part under the control of the participating individuals, suggesting that individual behavioural variation, that is, personality, will impact position in social networks. However, evidence on associations between personality and social network position is mixed (see Introduction). In our study, such associations were weak, despite using multiple behavioural tests, and in part dependent on the method used to generate the social networks (that is, time versus frequency-based). Nevertheless, there was some evidence indicating that more social females (as assessed in the sociality test) had stronger and more stable relationships with fewer individuals, whereas more social males had weaker and more casual interactions with a larger group of individuals. This pattern may reflect a difference in social strategy between males and females, with social males prioritizing more dispersed social connections and social females prioritizing connections to central individuals.

The attractiveness of a conspecific as social partner with respect to their personality or phenotypic quality may depend on the phenotype of the focal individual, which could lead to assortative or disassortative associations within networks (Pike et al., 2008). Although human studies have documented such effects (Ilmarinen et al., 2017; Youyou et al., 2017), there is little evidence for such assortment in the animal literature (but see: Briard et al., 2015; Keiser et al., 2016; Welch et al., 2020). Assortment did not deviate from chance level with respect to developmental background (benign/harsh). However, over the five behavioural tests combined, there was significant evidence for nonrandom assortment between individuals. This was due to individuals that were more gregarious in the sociality test interacting more with each other than expected by chance, and individuals that were relatively bold in the novel object test interacting less with each other than expected by chance. There was little evidence for assortment with respect to behaviour in the tests for exploration, social dominance and the tonic immobility test. Assortment by gregariousness is likely to arise through a shared higher propensity to initiate interactions, but negative assortment with respect to boldness is more difficult to explain as it is not obvious how it would affect social behaviour in permanent social groups.

Although this study provides valuable insights into the relationship between early life adversity and individual functioning in social networks, some limitations need to be acknowledged. First, the measurements on which the social networks are built are based around feeding interactions. It is not known what interactions individuals have when feeding together, and whether these are agonistic or antagonistic. Second, with the single-sex design of this study, we were able to prevent any effect of mating behaviour, but we must note that zebra finch flocks are usually comprised of males and females. Addressing these limitations in future research could enhance the robustness and generalizability of the findings.

In conclusion, harsh developmental conditions caused individuals to attain more peripheral positions in social networks. Given that social integration is a predictor of fitness components (Schülke et al., 2010; Silk et al., 2003), this indicates that social network position may contribute to the long-term consequences of developmental conditions for health and fitness. The finding that developmental conditions affected network position contrasts with our earlier finding in the same individuals that developmental

conditions did not affect behaviour in an array of behavioural tests, despite substantial repeatabilities of performance in these tests (Gerritsma et al., 2023). This is, however, consistent with the observation that behaviour in these tests did not predict social network position. Our interpretation of the contrasting results is that behaviour of individuals was unconstrained in the behavioural tests (with the exception of the dominance test), whereas attaining a social network position can be seen as a more competitive challenge. Apparently, some level of challenge is required for individual differences in phenotypic quality to emerge. In our study, the challenge was social, in that network position emerges from interactions with conspecifics. It seems likely, however that ecological challenges (e.g. food availability, Briga et al., 2017) would also amplify the effects of developmental conditions on social success, given that phenotypic quality (by definition) modulates the fitness consequences of environmental challenges.

Author Contributions

Merijn M.G. Driessen: Writing – review & editing, Project administration, Investigation. **Yoran H. Gerritsma:** Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **François Lamarque:** Writing – review & editing, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Simon Verhulst:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Data Availability

Data are available at <https://doi.org/10.5281/zenodo.11246797>.

Declaration of Interest

The authors declare that there are no conflicts of interest.

Acknowledgments

We thank Thomas Brüggén for his help in maintaining the social networks. Y. H. G. and M. M. G. D. were supported by Adaptive Life grants awarded by the University of Groningen. Y. H. G. was also supported by the Dr J. L. Dobberke Foundation for comparative psychology.

Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123199>.

References

- Adelman, J. S., Moyers, S. C., Farine, D. R., & Hawley, D. M. (2015). Feeder use predicts both acquisition and transmission of a contagious pathogen in a north american songbird. *Proceedings of the Royal Society B: Biological Sciences*, 282(1815), Article 20151429. <https://doi.org/10.1098/rspb.2015.1429>
- Anderson, J. A., Johnston, R. A., Lea, A. J., Campos, F. A., Voyles, T. N., Akinyi, M. Y., ... Tung, J. (2021). The costs of competition: High social status males experience accelerated epigenetic aging in wild baboons. *Elife*, 10, Article e66128. <https://doi.org/10.7554/eLife.66128>
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, 16(11), 1365–1372. <https://doi.org/10.1111/ele.12181>
- 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>

- Archie, E. A., Altmann, J., & Alberts, S. C. (2012). Social status predicts wound healing in wild baboons. *Proceedings of the National Academy of Sciences*, 109(23), 9017–9022. <https://doi.org/10.1073/pnas.1206391109>
- Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 281(1793), Article 20141261. <https://doi.org/10.1098/rspb.2014.1261>
- Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), v2–v14.4. <https://doi.org/10.18637/jss.v080.i01>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–21. <https://doi.org/10.18637/jss.v067.i01>
- Birkhead, T. R., Fletcher, F., & Pellatt, E. J. (1999). Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 266(1417), 385–390. <https://doi.org/10.1098/rspb.1999.0649>
- Boogert, N. J., Farine, D. R., & Spencer, K. A. (2014). Developmental stress predicts social network position. *Biology Letters*, 10(10), Article 20140561. <https://doi.org/10.1098/rsbl.2014.0561>
- Brandl, H. B., Farine, D. R., Funghi, C., Schuett, W., & Griffith, S. C. (2019). Early-life social environment predicts social network position in wild zebra finches. *Proceedings of the Royal Society B: Biological Sciences*, 286(1897), Article 20182579. <https://doi.org/10.1098/rspb.2018.2579>
- Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Animal Behaviour*, 103, 211–222. <https://doi.org/10.1016/j.anbehav.2015.01.020>
- Briard, L., Dorn, C., & Petit, O. (2015). Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses. *Ethology*, 121(9), 888–902. <https://doi.org/10.1111/eth.12402>
- Briga, M., Koetsier, E., Boonekamp, J. J., Jimeno, B., & Verhulst, S. (2017). Food availability affects adult survival trajectories depending on early developmental conditions. *Proceedings of the Royal Society B: Biological Sciences*, 284(1846), Article 20162287. <https://doi.org/10.1098/rspb.2016.2287>
- Chock, R. Y., Wey, T. W., Ebensperger, L. A., & Hayes, L. D. (2017). Evidence for a behavioural syndrome and negative social assortment by exploratory personality in the communally nesting rodent, *Octodon degus*. *Behaviour*, 154(5), 541–562. <https://doi.org/10.1163/1568539X-00003433>
- Cohen, S. (2004). Social relationships and health. *American Psychologist*, 59(8), 676–684. <https://doi.org/10.1037/0003-066X.59.8.676>
- Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology*, 63(10), 1495–1503. <https://doi.org/10.1007/s00265-009-0802-x>
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal*, 1695. Retrieved from <https://igraph.org>
- Díaz López, B. (2020). When personality matters: Personality and social structure in wild bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, 163, 73–84. <https://doi.org/10.1016/j.anbehav.2020.03.001>
- De Kogel, C. H. (1997). Long-term effects of brood size manipulation on morphological development and sex-specific mortality of offspring. *Journal of Animal Ecology*, 66(2), 167. <https://doi.org/10.2307/6019>
- Deere, J. R., Schaber, K. L., Foerster, S., Gilby, I. C., Feldblum, J. T., VanderWaal, K., ... Gillespie, T. R. (2021). Gregariousness is associated with parasite species richness in a community of wild chimpanzees. *Behavioral Ecology and Sociobiology*, 75(5), 87. <https://doi.org/10.1007/s00265-021-03030-3>
- Farine, D. R. (2014). Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. *Animal Behaviour*, 89, 141–153. <https://doi.org/10.1016/j.anbehav.2014.01.001>
- Fisher, R. A. (1925). *Statistical methods for research workers*. Oliver & Boyd.
- Fowler, J. H., & Christakis, N. A. (2009). Dynamic spread of happiness in a large social network: Longitudinal analysis over 20 years in the Framingham Heart Study. *British Medical Journal*, 338(7685), 23–26. <https://doi.org/10.1136/bmj.a2338>
- Freeman, L. C. (1978). Centrality in social networks conceptual clarification. *Social Networks*, 1(3), 215–239. [https://doi.org/10.1016/0378-8733\(78\)90021-7](https://doi.org/10.1016/0378-8733(78)90021-7)
- Gallego-Abenza, M., Boucherie, P. H., & Bugnyar, T. (2022). Early social environment affects attention to social cues in juvenile common ravens, *Corvus corax*. *Royal Society Open Science*, 9(6), Article 220132. <https://doi.org/10.1098/rsos.220132>
- Gammell, M. P., De Vries, H., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003). David's score: A more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour*, 66(3), 601–605. <https://doi.org/10.1006/anbe.2003.2226>
- Gerritsma, Y. H., Driessen, M. M. G., Tangili, M., de Boer, S. F., & Verhulst, S. (2022). Experimentally manipulated food availability affects offspring quality but not quantity in zebra finch meso-populations. *Oecologia*, (199), 769–783. <https://doi.org/10.1007/s00442-022-05183-y>
- Gerritsma, Y. H., Driessen, M. M. G., & Verhulst, S. (2023). Zebra finch behaviour differs consistently between individuals but is not affected by early life adversity. *Animal Behaviour*, 199, 79–94. <https://doi.org/10.1016/j.anbehav.2023.02.014>
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitional aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, 67(3), 373–381. <https://doi.org/10.1007/s00265-012-1457-6>
- Goodwin, S. E., & Podos, J. (2014). Team of rivals: Alliance formation in territorial songbirds is predicted by vocal signal structure. *Biology Letters*, 10(2), Article 20131083. <https://doi.org/10.1098/rsbl.2013.1083>
- Grabowska-Zhang, A. M., Sheldon, B. C., & Hinde, C. A. (2012). Long-term familiarity promotes joining in neighbour nest defence. *Biology Letters*, 8(4), 544–546. <https://doi.org/10.1098/rsbl.2012.0183>
- Grabowska-Zhang, A. M., Wilkin, T. A., & Sheldon, B. C. (2012). Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). *Behavioral Ecology*, 23(2), 322–333. <https://doi.org/10.1093/beheco/arr189>
- Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, 2014(1), Article e616. <https://doi.org/10.7717/peerj.616>
- Hemelrijk, C. K., Wantia, J., & Gygas, L. (2005). The construction of dominance order: Comparing performance of five methods using an individual-based model. *Behaviour*, 142(8), 1043–1064.
- Hopit, W., & Farine, D. R. (2017). *assocInd: Implements New and Existing Association Indices for Constructing Animal Social Networks*. Retrieved from <https://cran.r-project.org/package=assocInd>
- House, J. S., Landis, K. R., & Umberson, D. (1988). Social relationships and health. *Science*, 241(4865), 540–545.
- Ilmarinen, V. J., Vainikainen, M. P., Verkasalo, M. J., & Lönnqvist, J. E. (2017). Homophilous friendship assortment based on personality traits and cognitive ability in middle childhood: The moderating effect of peer network size. *European Journal of Personality*, 31(3), 208–219. <https://doi.org/10.1002/per.2095>
- Keiser, C. N., Pinter-Wollman, N., Augustine, D. A., Ziemba, M. J., Hao, L., Lawrence, J. G., & Pruitt, J. N. (2016). Individual differences in boldness influence patterns of social interactions and the transmission of cuticular bacteria among group-mates. *Proceedings of the Royal Society B: Biological Sciences*, 283(1829), Article 20160457. <https://doi.org/10.1098/rspb.2016.0457>
- Koetsier, E., & Verhulst, S. (2011). A simple technique to manipulate foraging costs in seed-eating birds. *Journal of Experimental Biology*, 214(Pt 8), 1225–1229. <https://doi.org/10.1242/jeb.050336>
- Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B*, 365(1560), 4099–4106. <https://doi.org/10.1098/rstb.2010.0216>
- Krause, E. T., Krüger, O., & Pogány, A. (2017). Zebra finch nestlings, rather than parents, suffer from raising broods under low nutritional conditions. *Behavioral Ecology and Sociobiology*, 71(10). <https://doi.org/10.1007/s00265-017-2382-5>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), v3.1. <https://doi.org/10.18637/jss.v082.i13>, 0.
- Lemoine, N. P. (2019). Moving beyond noninformative priors: Why and how to choose weakly informative priors in Bayesian analyses. *Oikos*, 128(7), 912–928. <https://doi.org/10.1111/oik.05985>
- Lewandowski, D., Kurowicka, D., & Joe, H. (2009). Generating random correlation matrices based on vines and extended onion method. *Journal of Multivariate Analysis*, 100(9), 1989–2001. <https://doi.org/10.1016/j.jmva.2009.04.008>
- Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, 14(9), 343–348.
- Loonen, M. J. J. E., Bruinzeel, L. W., Black, J. M., & Drent, R. H. (1999). The benefit of large broods in barnacle geese: A study using natural and experimental manipulations. *Journal of Animal Ecology*, 68(4), 753–768. <https://doi.org/10.1046/j.1365-2656.1999.00325.x>
- Makowski, D., Ben-Shachar, M. S., Chen, S. H. A., & Lüdtke, D. (2019a). Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology*, 10, 1–14. <https://doi.org/10.3389/fpsyg.2019.02767>
- Makowski, D., Ben-Shachar, M. S., & Lüdtke, D. (2019b). bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software*, 4(40), 1541. <https://doi.org/10.21105/joss.01541>
- McCowan, L. S. C., & Griffith, S. C. (2015). Active but asocial: Exploration and activity is linked to social behaviour in a colonial breeding finch. *Behaviour*, 152(9), 1145–1167. <https://doi.org/10.1163/1568539X-00003272>
- McCully, F. R., & Rose, P. E. (2023). Individual personality predicts social network assemblages in a colonial bird. *Scientific Reports*, 13(1), 1–11. <https://doi.org/10.1038/s41598-023-29315-3>
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), 935–956. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>
- Newman, M. E. J. (2002). Assortative mixing in networks. *Physical Review Letters*, 89(20), 1–4. <https://doi.org/10.1103/PhysRevLett.89.208701>
- Newman, M. E. J. (2003). Mixing patterns in networks. *Physical Review E - Statistical Physics, Plasmas, Fluids, and Related Interdisciplinary Topics*, 67(2), 13. <https://doi.org/10.1103/PhysRevE.67.026126>
- Nussey, D. H., Kruuk, L. E. B., Morris, A., & Clutton-Brock, T. H. (2007). Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biology*, 17(23), 1000–1001. <https://doi.org/10.1016/j.cub.2007.10.005>
- Patterson, S. K., Strum, S. C., & Silk, J. B. (2022). Early life adversity has long-term effects on sociality and interaction style in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 289, Article 20212244. <https://doi.org/10.1098/rspb.2021.2244>, 1968.
- Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society*

- B: *Biological Sciences*, 275(1650), 2515–2520. <https://doi.org/10.1098/rspb.2008.0744>
- R Development Core Team. (2008). R: A language and environment for statistical computing. <http://www.r-project.org>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Riebel, K., Spierings, M. J., Holveck, M. J., & Verhulst, S. (2012). Phenotypic plasticity of avian social-learning strategies. *Animal Behaviour*, 84(6), 1533–1539. <https://doi.org/10.1016/j.anbehav.2012.09.029>
- Rstudio Team. (2020). *Rstudio: Integrated Development for R*. Retrieved from Rstudio. Boston, MA: PBC. www.rstudio.com.
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Schürch, R., Rothenberger, S., & Heg, D. (2010). The building-up of social relationships: Behavioural types, social networks and cooperative breeding in a cichlid. *Philosophical Transactions of the Royal Society B*, 365(1560), 4089–4098. <https://doi.org/10.1098/rstb.2010.0177>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302(5648), 1231–1234. <https://doi.org/10.1126/science.1088580>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20(15), 1359–1361. <https://doi.org/10.1016/j.cub.2010.05.067>
- Snijders, L., van Rooij, E. P., Burt, J. M., Hinde, C. A., van Oers, K., & Naguib, M. (2014). Social networking in territorial great tits: Slow explorers have the least central social network positions. *Animal Behaviour*, 98, 95–102. <https://doi.org/10.1016/j.anbehav.2014.09.029>
- Sokal, R. R., & Rohlf, F. J. (1995). Biometry: The principles and practice of statistics in biological research. *Journal of the Royal Statistical Society: Series A*, 133, 102. <https://doi.org/10.2307/2343822>
- Spencer, K. A. (2017). Developmental stress and social phenotypes: Integrating neuroendocrine, behavioural and evolutionary perspectives. *Philosophical Transactions of the Royal Society B*, 372(1727), Article 20160242. <https://doi.org/10.1098/rstb.2016.0242>
- Stan Development Team. (2020). *RStan: The R interface to Stan*. Retrieved from <http://mc-stan.org/>.
- Tamashiro, K. L. K., Nguyen, M. M. N., & Sakai, R. R. (2005). Social stress: From rodents to primates. *Frontiers in Neuroendocrinology*, 26(1), 27–40. <https://doi.org/10.1016/j.yfrne.2005.03.001>
- Thompson, N. A. (2019). Understanding the links between social ties and fitness over the life cycle in primates. *Behaviour*, 156(9), 859–908. <https://doi.org/10.1163/1568539X-00003552>
- Thompson, N. A., & Cords, M. (2018). Stronger social bonds do not always predict greater longevity in a gregarious primate. *Ecology and Evolution*, 8(3), 1604–1614. <https://doi.org/10.1002/ece3.3781>
- Tung, J., Archie, E. A., Altmann, J., & Alberts, S. C. (2016). Cumulative early life adversity predicts longevity in wild baboons. *Nature Communications*, 7, Article 11181. <https://doi.org/10.1038/ncomms11181>
- Verhulst, S., Geerdink, M., Salomons, H. M., & Boonekamp, J. J. (2014). Social life histories: Jackdaw dominance increases with age, terminally declines and shortens lifespan. *Proceedings of the Royal Society B: Biological Sciences*, 281(1791). <https://doi.org/10.1098/rspb.2014.1045>
- Welch, M. J., Smith, T., Hosie, C., Wormell, D., Price, E., & Stanley, C. R. (2020). Social experience of captive livingstone's fruit bats (*Pteropus livingstonii*). *Animals*, 10(8), 1–25. <https://doi.org/10.3390/ani10081321>
- 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>
- Wickham, H., François, R., Henry, R., & Müller, K. (2021). *dplyr: A grammar of data manipulation*. Retrieved from <https://cran.r-project.org/package=dplyr>.
- Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology & Evolution*, 29(6), 306–308. <https://doi.org/10.1016/j.tree.2014.03.008>
- Youyou, W., Stillwell, D., Schwartz, H. A., & Kosinski, M. (2017). Birds of a feather do flock together: Behavior-based personality-assessment method reveals personality similarity among couples and friends. *Psychological Science*, 28(3), 276–284. <https://doi.org/10.1177/0956797616678187>