# The influence of early-life conditions on social network position and information transmission

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## Abstract

This study examines the impact of early-life conditions on the social network position of zebra finches (*Taeniopygia guttata*) and investigates whether social network centrality influences information transmission. Using an experimental approach, zebra finches were raised under either harsh or easy early-life conditions, and their social interactions were analyzed using social network analysis (SNA). Key network metrics, including degree, strength, and eigenvector centrality, were assessed to determine whether early-life conditions influence social network centrality. Results show that while early-life conditions did not significantly affect degree and strength, they did influence eigenvector centrality, suggesting that early experiences shape the quality rather than the quantity of social connections. To explore the influence of network centrality and information transmission, learning trends were analyzed in a foodpatch discovery task. No consistent differences were found in learning performance between treatment groups, and birds did not show clear learning improvements over time.

Overall, these findings suggest that early-life conditions have a low, but measurable impact on social network quality but do not strongly determine network positions or enhance information transmission. Social network centrality showed only limited and inconsistent association with resource discovery, highlighting the complexity of factors that influence social behavior and learning in zebra finches.

# 1. Introduction

Interactions between conspecifics occur in all animal species, these interactions can result in communication. The capability for communication is extensively studied in songbirds, which learn their vocalisations early in life, heavily relying on hearing and imitating adult conspecifics (Doupe & Kuhl, 1999). Cross-fostering is a common method to determine whether characteristics are learned from genetic parents or other adults, a concept known as nature versus nurture. In cliff swallows (*Hirundo pyrrhonota*), there are no similarities among the songs of foster siblings, providing no evidence for imitation by chicks from their foster siblings or parents (Medvin et al., 1992), suggesting that song variation is strongly dependent on genetic differences (nature). In addition to cross-fostering, many studies on songbirds related to vocalisation and imitation involve isolating chicks (Janik & Slater, 2000). For example, song sparrows (*Melospiza melodia*) tend to produce original tones even when exposed to songs with altered tones (Nowicki et al., 1999).

Communication, or other social interactions, between individuals within a population constitutes a social network. Social network analysis (SNA) is a valuable concept for examining how patterns of interactions within a social network facilitate the transmission of information and influence. In the SNA framework, individuals (nodes) are interconnected through their interactions (edges), offering a more comprehensive representation than a linear chain (Kim et al., 2011). Originally developed to analyse human societies, SNA has rapidly gained popularity and is now widely employed across various disciplines, including behavioural ecology.

Social interactions rarely occur completely at random, resulting in variations in the strength and number of connections between individuals. Analysing social networks and comparing animal behaviour and characteristics is relatively under examined (Roft, James & Krause, 2008).

Information is more likely to transfer between individuals with stronger interactions, thereby following different paths within the social network. In three wild tit species (family *Paridae*), researchers recorded the order of arrival of individuals at a new food resource. First, they established their social network. If individuals use social information, food resources are discovered in different orders, because not all individuals receive the same information. Results showed that individuals with a more central position in the social network had higher patch-discovery success, indicating that the information flow aligns with the social network structure (Aplin et al., 2012). Additionally, in non-territorial great tits (*Parus major*), a positive relationship has been demonstrated between fast exploration and higher social network centrality (Snijders et al., 2014). Manipulating developmental stress by elevating stress hormone levels can alter learning strategies, thereby demonstrating the plasticity of phenotypically social learning (Farine et al., 2015).

In addition to exploration, courtship behaviour and communication techniques can be transferred more effectively through increased interactions, leading to higher individual success. In wild male house finches (*Haemorhous mexicanus*), centrality in the social network appears to be positively associated with pairing success probability (Kevin & Alexander, 2010). In an island population of the ground-nesting shorebird, the Kentish plover (*Charadrius alexandrinus*), pre-breeding social network organisation impacts breeding success. Stronger social associations between male and female plovers during the pre-breeding period are positively correlated with the probability of these individuals forming a pair in the following breeding season (McDonald et al., 2020).

Increased interactions can also lead to unintended social behaviours. Zebra finches (*Taeniopygia guttata*) learn vocalisations by imitating their parents. A greater number of nest siblings, and thus more interactions, resulted on average in shorter songs with fewer varied notes (Tchernichovski & Nottebohm, 1998). More complex songs are associated with greater reproductive success and, consequently, higher individual fitness. Another example involves hermit crabs (*Coenobita compressus*), which have limited capabilities to locate resources individually. However, as they gather at a resource, their aggregation can be noticed by passing rival foragers (Laidre, 2009).

Moreover, being centrally positioned in a social network can have negative effects. More interactions with different conspecifics increase the probability of disease transmission (Herrera & Nunn, 2019). Determining social network structure and community segregation can help predict disease transmission in populations. Badgers (*Meles meles*) were divided into two main groups: movers and non-movers. Non-movers consistently interacted with each other, facilitating easier transmission of Bovine Tuberculosis among these individuals (Böhm et al., 2008). Conversely, movers may play a key role in interpopulation disease transmission.

Individuals with central positions in the social network are connected to a greater number of other individuals. The number or strength of interactions between individuals, and thus their position in the social network, depends on several factors. Differences in social network positions appear to be related to sex and age in bottlenose dolphins (*Tursiops*) living in Doubtful Sound, New Zealand (Lusseau & Newman, 2004). The tendency to spend more time with other bottlenose dolphins of the same age and sex can be explained by changing association patterns when females become pregnant. Pregnant females spend more time with other pregnant females. After giving birth, this segregation from the population continues (Wells et al., 1987). Consequently, calves are raised alongside others of their own age and interact primarily with each other.

Relatedness also influences interaction patterns and, therefore, the social network position. Bottlenose dolphins (*Tursiops*) appear to interact more frequently with relatives (Lusseau & Newman, 2004). Being near relatives may facilitate nepotism, where individuals favour their kin.

However, spending more time with relatives can also increase the risk of inbreeding (Holmes & Sherman, 1983). Relatives may also be closer due to matching personalities. In many territorial species, personality, defined as consistent individual differences in behaviour, is significant for the social network structure in populations (Pike et al., 2008). For instance, shy sticklebacks (*Gasterosteidae*) prefer staying in small groups and therefore have a less central position in the social network. These shy fish are less likely to explore unknown areas of a tank when already interacting with another individual. In contrast, bold fish have fewer interactions overall and tend to explore regardless of whether they are interacting, resulting in a more central network position. Similarly, in wild great tit (*family Paridae*) populations, individuals that explore more slowly tend to stay with the same foraging flock (Aplin et al., 2013). Personality is largely influenced by genetic factors and nurturing. Early-life manipulations also indicate strong developmental plasticity of personality traits (Groothuis & Carere, 2005). By experimentally manipulating developmental stress, it is shown that social learning targets are phenotypically plastic. While control juveniles learned foraging skills from their parents, their siblings, exposed as nestlings to experimentally elevated stress hormone levels, learned exclusively from unrelated adults (Farine et al., 2015).

Finally, developmental (stress) conditions also appear to influence social network position (Farine et al., 2015; Brandl et al., 2019). In zebra finches (*Taeniopygia guttata*), developmental conditions were manipulated by elevating the levels of the stress hormone corticosterone (CORT). Elevated CORT levels suggest harsh developmental conditions. The total number of interactions was assessed by counting the number of individuals foraging together. Chicks with increased CORT levels foraged with more individuals and exhibited greater independence from their parents. Consequently, they occupied more central positions within the social network compared to their conspecifics (Farine et al., 2015). In wild zebra finch chicks (*Taeniopygia guttata*), stress levels can also be elevated by increasing brood size. Chicks raised in enlarged broods foraged with more conspecifics, exhibited less selectivity, and thus occupied more central positions within the social network (Brandl et al., 2019). These findings suggest that early-life conditions can predict an individual's later-life strategies.

Lamarque (2019) also conducted research on the developmental conditions and social network positions of zebra finches (*Taeniopygia guttata*). Instead of increasing CORT levels or brood size, chicks were raised under either easy or harsh developmental conditions (Koetsier & Verhulst, 2011). Similar to previous studies (Farine et al., 2015; Brandl et al., 2019), foraging interactions were used as an indicator of social interactions. However, in addition to the number of interactions, the total duration of foraging together was measured to exclude incidental interactions. The research found that chicks raised under harsh developmental conditions foraged with fewer conspecifics, resulting in these individuals occupying less central positions within the social network compared to those raised under easy conditions. The findings of Farine et al. (2015) and Brandl et al. (2019) contrast with those of Lamarque (2019), leaving it unclear whether developmental stress in zebra finches leads to more or less central social network positions.

Developmental stress may hinder individuals from investing in or maintaining social interactions due to energy constraints (West-Eberhard, 1987). Chicks raised under harsh conditions may need to prioritise growth over the development of traits essential for evolving social skills and interacting with conspecifics. The silverspoon hypothesis suggests that individuals raised under favourable conditions consistently exhibit higher fitness compared to those raised under harsh conditions (Monaghan, 2008). Research (Song, Zou, and Hu, 2018) on crested ibis (*Nipponia nippon*) regarding hatching order also supports this hypothesis. First-hatched siblings demonstrate several advantages over later-hatched siblings, including higher adult survival rates, earlier reproductive onset, longer breeding lifespans, and consequently, greater individual fitness.

Based on these studies, this research will examine the impact of early-life conditions on the position of zebra finches (*Taeniopygia guttata*) in the social network. Second part is to investigate if social network centrality has an impact on finding new resources and therefore information transmission. The main question is: Do early-life conditions influence the social network position of zebra finches (*Taeniopygia guttata*) and is there an association between information transmission and network centrality?

In this research the early-life conditions of the individuals will be altered by foraging conditions (Koetsier & Verhulst, 2011) and foraging duration is taken as interaction, like in Lamarque's (2019) research. Therefore we expect the same results for social network centrality of individuals. In other words, individuals with harsh early-life conditions will have a less central position in later-life. Studies and theories also support this hypothesis. West-Eberhard (1987), Monaghan (2008), and Song, Zou, and Hu (2018) highlight how harsh developmental conditions negatively influence social interactions and fitness outcomes.

Results of experiments (Aplin et al., 2012) in great tits (*family Paridae*) showed higher social network centrality individuals have higher patch-discovery success. Also is shown a positive relation between fast exploring and high social network centrality (Snijders et al., 2014). Therefore we expect individuals with a high central position to explore the food box with excess to food faster relative to less central individuals.

# 2. Materials and methods

## Test group

The group during the initial testing period consisted of 10 male zebra finches (*Taenopyia guttata*), divided into two aviaries. Each aviary consists of two zebra finches with harsh developmental conditions and three raised under easy developmental conditions. All zebra finches were born from May 2022 till August 2022 in an outside aviary. The second test group consisted of 23 zebra finches (*Taenopyia guttata*), of which 12 were females and 11 were males, divided over two aviaries based on sex. Each aviary housed 6 individuals raised under harsh developmental conditions. All zebra finches used in the second period were born from May 2023 till August 2023 in an outside aviary.

## Developmental manipulations

To alter the developmental conditions of the test groups, the method of Koetsier and Verhulst (2011) was used. A key element in changing developmental conditions is food deprivation. Food deprivation is an often used method, but has disadvantages. Food deprivation corresponds less to free-living animals, because instead of foraging during the whole day, animals are often restricted to the amount of meals and food a day. In free-living animals reduction in food availability does not lead to food deprivation but results in higher foraging costs. Koetsier and Verhulst (2011) developed two foraging treatments. In short, food is offered in a food container which is suspended from the ceiling. At the bottom of the side of a food container are five holes where zebra finches have access to food. The difference between the two treatments is that only in the easy foraging treatment the holes are provided with perches underneath. Therefore individuals in the harsh foraging treatment are forced to fly to the food container, hover to get seeds out the container, fly back to somewhere they can sit and consume the seeds. This method causes a difference in foraging costs and therefore developmental conditions.

## Network tracking set-up

### Foodbox

The foodboxes are built-up by an aluminium frame, the bottom plate measured 33 x 33 cm and on every edge of the bottom plate an aluminium standard is placed, measuring 3 x 3 x 25 cm in length, width and height. Between the standards five plexiglass plates are placed, each of being 25 x 25 cm and 4 mm thick. One of the five plexiglasses is provided with a circular antenna, of the model “ANTC40” (DorsetID, Aalten, The Netherlands) with a radius of 4 cm, meant as the entrance and exit point of the foodbox. Radio-frequency identification (RFID) is used to identify and track tags attached to individuals. All individuals are tagged with a PIT tag “ID100A Micro Transponder“ (DorsetID, Aalten, The Netherlands). To receive the information, an OEM decoder of the model “LID 650” (DorsetID, Aalten, The Netherlands) was used. Against the wall in the opposite of the wall with the antenna, two food silos are placed with a tropical seed mix (Bogena, Hedel, The Netherlands), to get their food from (*figure 1*).

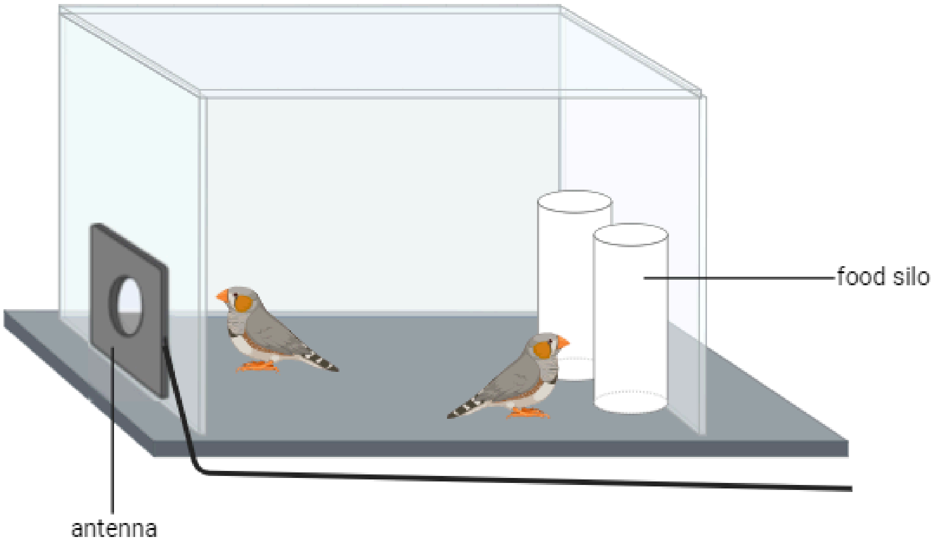


*Figure 1: Foodbox*

## Aviary

The whole experiment took place at the University of Groningen. Both aviaries are similar, measuring 3 x 1,5 x 2,3 meters in length, width and height. The aviaries are outside next to each other and provided with a gutter, meant as drinking water, in which every half an hour freshwater flows for 15 minutes. Furthermore, the aviaries are provided with two sandboxes, a perch and a rope suspended from the ceiling. The food boxes are placed on the floor in a square shape (*figure 2*).

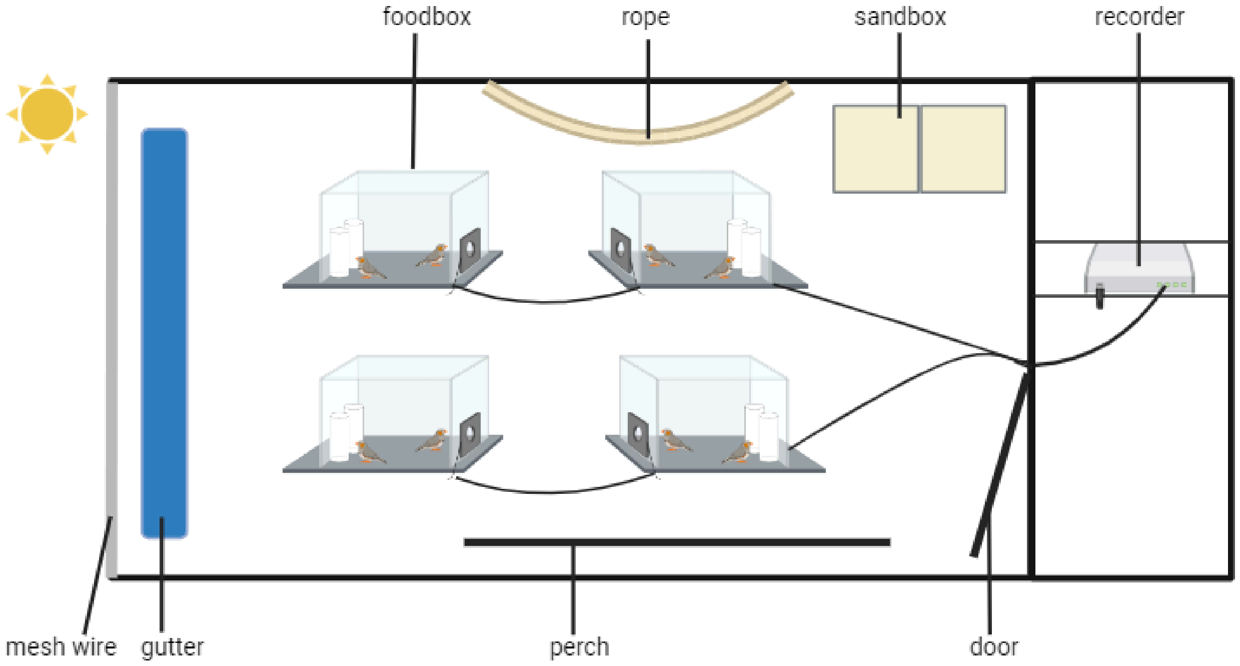


*Figure 2: Aviary network tracking set-up*

## Acclimatisation period

Individuals of the first testing period were transported to the test aviaries on 10 January 2023, the start date of the acclimatisation period. Individuals of the second period were transported to the test aviaries on 15 Februari 2024. At the beginning of the acclimatisation period, four foodbox frames were placed with only one wall with the antenna in both aviaries. The remaining walls will be placed one by one during this period. The first step is to get the zebra finches used to the foodsilos, during this period most of the day another food source was available in the aviary. During the first steps of closing the boxes, special food (‘eggfood’, Bogena, Hedel, The Netherlands) will always be presented around the antenna, to attract the birds. After the zebra finches learned to eat from the foodsilos, the second wall, on the opposite side of the antenna, will be placed. After this step, the upper wall will be placed, following with one of the side walls. After every step will be decided if the zebra finches are still able to get food from the foodsilos. If not, we took a step back. The last wall is not directly placed in the frame, but the wall is slowly lowered in the frame. By minimising an entrance and exit point through the wall, it makes it more attractive to use the antenna as an entrance and exit point. Individuals which were unable to get out of the boxes after having foraged, were set free from the foodbox. The enddate of the acclimatisation period for the first group was 30 January 2023 and therefore the start date of the first test period. The start date of the second test period was on 6 March 2024.

## Social network analysis (SNA)

There are various levels of analysis possible in social networks. The smallest level of analysis, the dyad, is used to present the impact of one individual on another individual. In the highest level of SNA, network-level, the social network is considered as a whole. This level can for example be used for indicating differences between and benefits of several networks (Scott & Carrington, 2011). We are interested in the interactions within the social network and not between, therefore we used the most well known and used level, the node-level. Node-level presents individuals as nodes and these can be connected by interactions between individuals, shown as edges. The purpose is to establish the position of an individual within the network (Snijders et al., 2014). Thereafter, we can investigate whether the position within the social network is related to a characteristic of the individual, in our case, early-life conditions.

Network centrality, the position of an individual within the structure, is calculated with reference to several metrics. The most widely used measurements are: (weighted) degree, betweenness and eigenvector centrality (Farooq et al., 2018). Degree of an individual can be computed by the sum of edges, in other words, the amount of neighbours the individual is directly connected with. By linking additional information to edges, it is called weighted degree, also known as strength. Strength can be computed by the sum of weights of all edges connected to an individual. This is achieved by dividing the sum of interactions per individual by the total number of interactions. Another metric is betweenness. Betweenness is calculated by the amount of steps that are necessary to reach another individual you are not directly connected with. Betweenness will not have an influence on the network centrality in our research. The test group is too small and all birds will (probably) meet each other in the foodboxes. So for all birds in this research the betweenness should be zero. Nevertheless, in bigger test groups, individuals with high betweenness can occupy important roles in the network as they can be the connection between different groups within the whole network. We still want to include this metric. Therefore we have adjusted it slightly. In this experiment, betweenness is calculated daily until one individual in the group is connected to all other individuals. Up to this point, betweenness is measured for all individuals in the group.

The next metric is eigenvector centrality. Eigenvector centrality measures how well an individual is connected to individuals with high (weighted) degree. The rank and power of an individual can be altered by their directly connected neighbours. In this research, eigenvector centrality is computed by the sum of neighbours' strengths of an individual (Tabassum et al., 2018). Finally, we wanted to test whether individuals from easy foraging conditions have more or less random connections by calculating the coefficient of variation (CV). A higher CV suggests that individuals prefer some congers over others, instead of equally spending time with all (Brandl et al, 2019).

The analysis is conducted in R version 4.3.2. To utilise the data, it first had to be cleaned. This involved removing incomplete data entries and duplicated records. After the data cleaning process, columns for "time start" and "time end" were established to track when an individual enters and exits a box. The loop iterates separately for each individual, estimating the entry and exit times for each individual in a given box per day. Following this, daily networks can be created based on the frequency of individuals meeting or the duration of time they spend together in a food box. The frequency or duration is then used to calculate the weight of the interaction using the Simple Ratio Index.

Next, the social network of the individuals needs to be visualised. To achieve this, developmental treatment must be implemented. Interactions (edges) between individuals (nodes) are examined, and the visual properties of both nodes and edges are determined by their weights and strengths. Social networks for individuals were reconstructed for each day. Analysing these individual networks alone does not allow us to determine whether there is a significant difference in centrality between the two developmental conditions. Therefore, networks from all days are merged and categorised into distinct groups based on the two characteristics we use in the statistical analysis: early-life treatment and sex, allowing for comparisons between various groups in the end. Early-life treatment and sex variables and their interaction are set as fixed effects. After completing the data editing process, we can proceed to create plots for parts of the social network analysis (SNA). The following metrics were analysed: degree, strength, coefficient of variation (CV), and eigenvector centrality. Degree and CV were normally distributed and therefore a paired T-test is used. Strength and eigenvector centrality were binomially distributed and thus the Mann-Whitney U-test is employed.

## Information transmission analysis

The second part of this research involves examining the transmission of information regarding food locations. This part of the research was structured as follows: initially, the birds have access to food in all four foodboxes. Subsequently, food is provided in only one of the boxes, followed by a return to food availability in all four boxes after three hours. The tests were not conducted at the same time each day, so it is crucial to use the correct data for each specific day. The data utilised for the information transmission analysis includes the following periods:

- 2 hours before the test, when food is available in all boxes
- 3 hours period, when only in one box food is presented
- 2 hours following the test, when food is again available in all boxes

The tests were carried out over 8 different days in 2 separate aviaries, resulting in a total of 16 datasets.

To estimate whether network position influences information transmission, the first hour following a change in food availability is analysed. Specifically, this involves the hour when food is available in only one food box and the subsequent hour when food is available in all food boxes. The extent of food patch discovery, represented as a measure of information transmission, is determined by calculating the frequency of entries into the food box containing food, divided by the total number of entries into all food boxes during a specific hour. A higher percentage will indicate better information transmission. During the first hour after food availability in all food boxes, the same calculation is performed. However, in this context, a higher percentage will indicate reduced information transmission. We refer to these percentages as the ‘ratio’ from now on.  The outcomes are correlated with the individuals' early-life conditions to compare differences in information transmission between those with easy and harsh early-life conditions.

The information transmission analysis was also conducted using R version 4.3.2. The datasets for this analysis correspond to each day from the box where food was available during the third, fourth, and fifth hours. After importing the data, hours that are not relevant to the analysis were removed. Subsequently, we examined the ratio of entering the correct food box during the third and sixth hours for both groups to determine if there were significant differences. This comparison between the two early-life treatments was conducted using a Two Sample T-test.

Following this, the ratios from the third and sixth hours were linked to the key metrics, namely strength, degree, eigenvector centrality and the coefficient of variation. For each metric, a linear regression model was applied. This regression model was used to estimate the relationship between the dependent variable and the independent variable. The goal was to understand if the metric, as the independent variable, influences the difference in ratio, as the dependent variables.

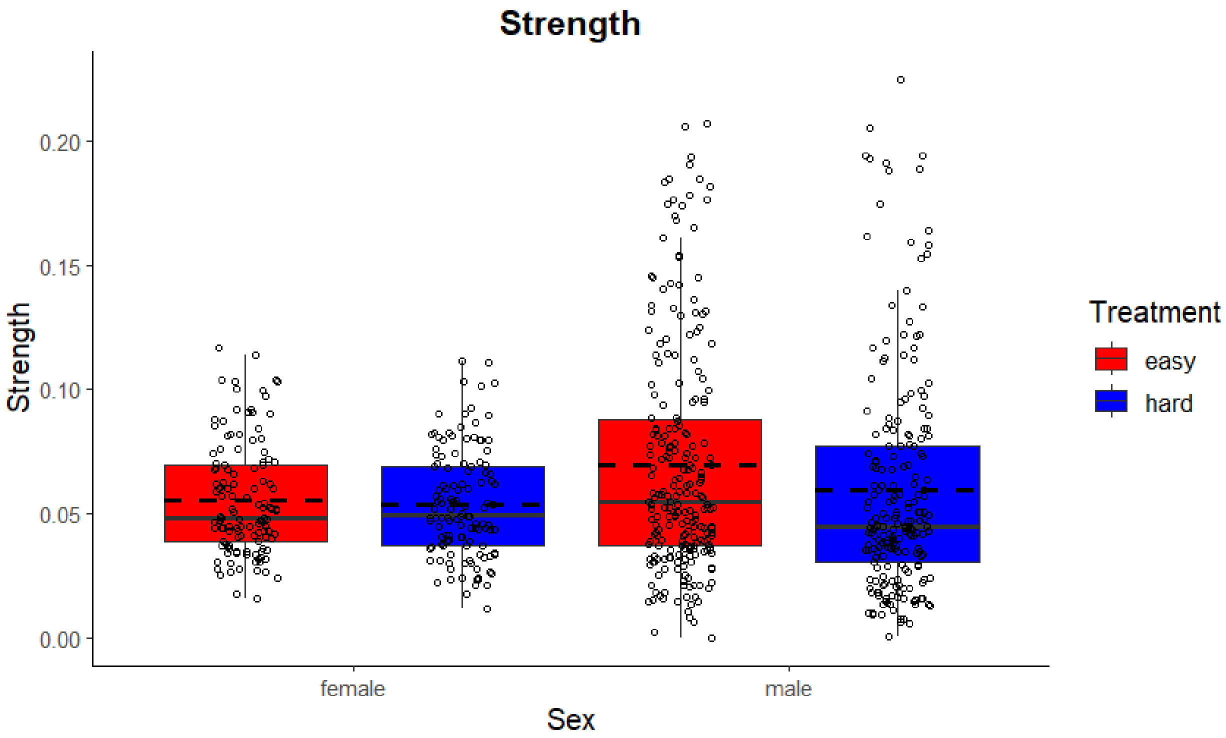
## Additional Analyses

To understand whether there were patterns in how the birds visited the correct food boxes, we actually had to conduct an analysis of visitation behaviors first. This was necessary to ensure that any observed behaviors were not random or coincidental. After completing this analysis, we returned to the beginning of the process to confirm that clear patterns existed or not before proceeding with further investigations.

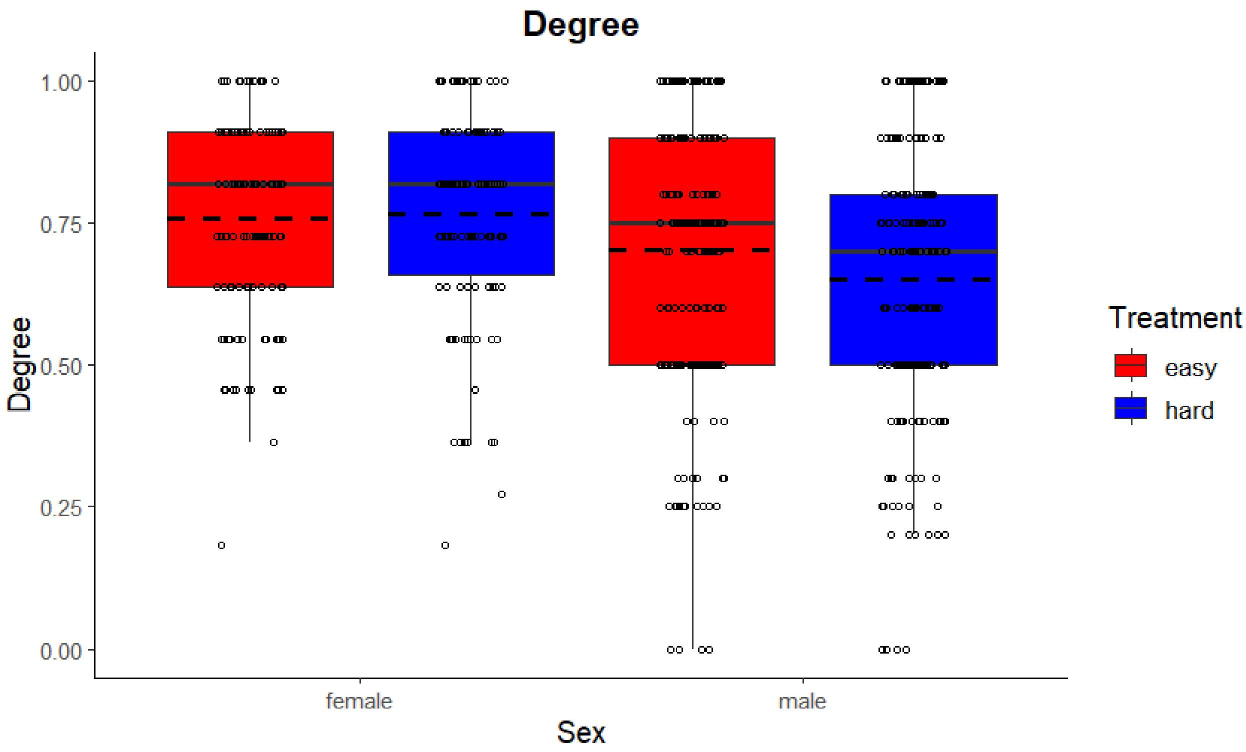
The frequency of visits to the correct food box, the one containing food during the restricted 3 hour period, was compared across different time periods. First, we examined the initial two hours when food was available in all boxes. Next, we analyzed the first hour when food was restricted to one box. This analysis was then extended to the second and third hours of the restricted period to see if the birds focused more on the correct box over time. To investigate potential learning patterns, we created graphs that plotted the ratio of visits to the correct box compared to total visits for each individual and each day. These graphs included data from both treatment groups to observe any differences in behavior. Additionally, we analyzed individual learning trends by comparing visitation proportions between the first two hours (food in all boxes available) and the restricted period. The results were plotted to examine whether behavior changed over time with repeated testing, as indicated by differences in behavior across days, with each day represented as a separate point. A metric was developed to measure progressive learning trends. This metric focused on the first hour of the restricted food period across all days and calculated the proportion of visits to the correct box compared to total visits. The average learning trend for each individual was then compared to their centrality measures, such as strength, to explore potential links between social network position and learning efficiency. This analysis is based on a Network-Based Diffusion Analysis (NBDA) framework to examine information transmission (Aplin et al., 2012). This method identifies social learning processes by analyzing whether the spread of behavior follows the patterns of connections in a social network. NBDA assumes that social transmission occurs along association routes, with stronger associations leading to faster or more reliable transmission. By adding these analyses, we aimed to provide a clearer understanding of how social network position and early-life conditions change learning and information transmission behaviors in zebra finches.

# 3. Results

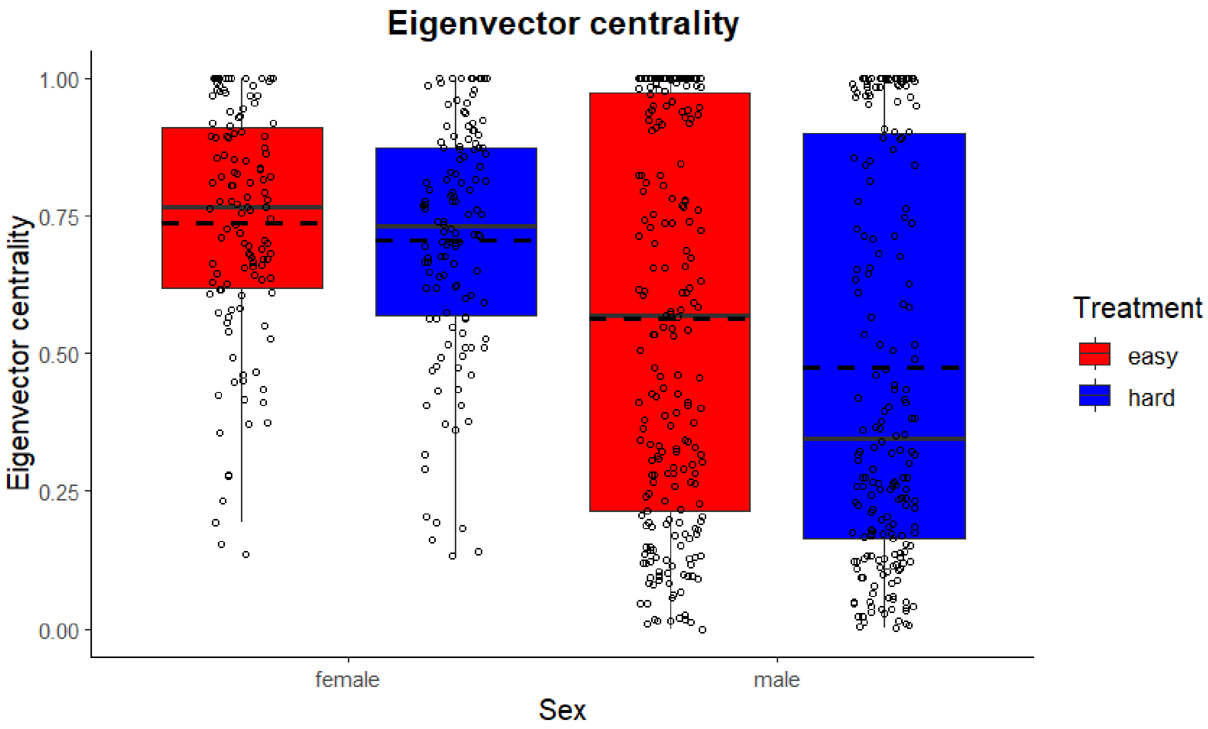
To eliminate the possibility of incidental interactions, the duration of time individuals spend together in a food box is utilised. Strength *(graph 1)* is the first metric examined to determine if there are significant differences between early-life conditions. The analysis reveals no significant difference in strength (p = 0.59). Individuals raised under easy conditions exhibit a slightly higher strength (easy: 0.0645±0.0401, harsh: 0.0574±0.0381). Similarly, degree *(graph 2)* does not show a significant difference (p = 0.072), with individuals raised under easy conditions again exhibiting a slightly higher degree (easy: 0.722±0.224, harsh: 0.693±0.224). The eigenvector centrality *(graph 3)*, which is significant between the two treatments (p = 0.0095), indicates a difference in how well individuals are connected to others with high network centrality depending on the treatment conditions. Lastly, the coefficient of variation (graph 4), calculated by considering only the effect of early-life treatment as with the previous metrics, also indicates no significant difference (p = 0.38). Analyzing the influence of sex reveals a strong significant effect of sex (p = 1.69e-06), indicating that sex has a substantial influence on the dependent variable, regardless of early-life treatment. The positive estimate (0.601) suggests that individuals of one sex have consistently higher average values than the other. However, no significant interaction between sex and early-life treatment was found (p = 0.95), meaning that early-life treatment affects both sexes similarly rather than causing different effects in males and females. The strong effect of sex could be due to an inherent biological or social difference between males and females in their social network position or behavior. This result is expected, as males and females conducted the test separately. For all results from the significant tests, we refer to tables 1 and 2 on the last pages.



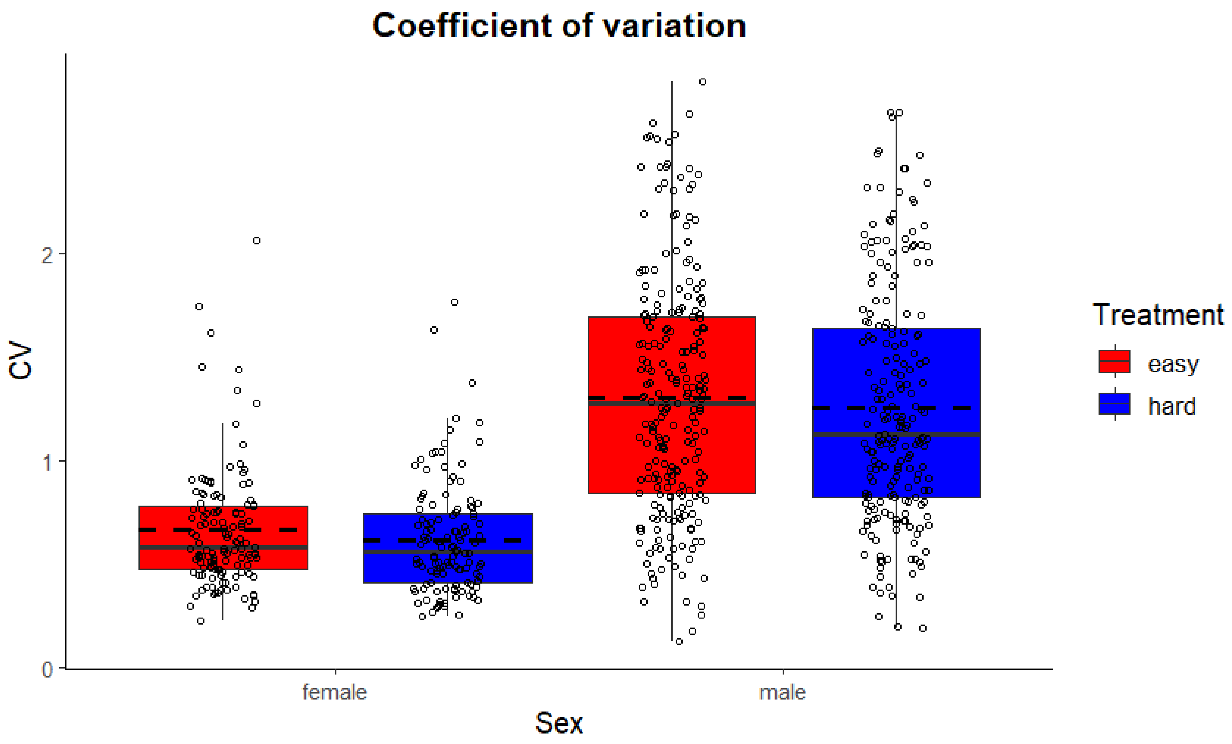
*Graph 1 shows the average strength (weighted degree) of individuals, grouped by sex and treatment (easy = red; blue=hard). While individuals raised under easy conditions exhibit slightly higher strength compared to those raised under harsh conditions, the difference is not statistically significant (p = 0.57).*



*Graph 2 presents the degree (number of direct connections) for individuals, grouped by sex and treatment (easy = red; blue=hard). Individuals raised under easy conditions show a slightly higher degree compared to those raised under harsh conditions, but the difference is not statistically significant (p = 0.072).*



*Graph 3 presents eigenvector centrality scores, grouped by sex and treatment (easy = red; blue=hard). The results reveal a significant difference between early-life conditions (p = 0.0095), indicating that early-life treatment influences how well individuals are connected to others with high network centrality.*



*Graph 4 presents the coefficient of variation, grouped by sex and treatment (easy = red; blue=hard). No significant difference is observed between early-life conditions alone (p = 0.45), suggesting there is not a preference for specific social partners.*

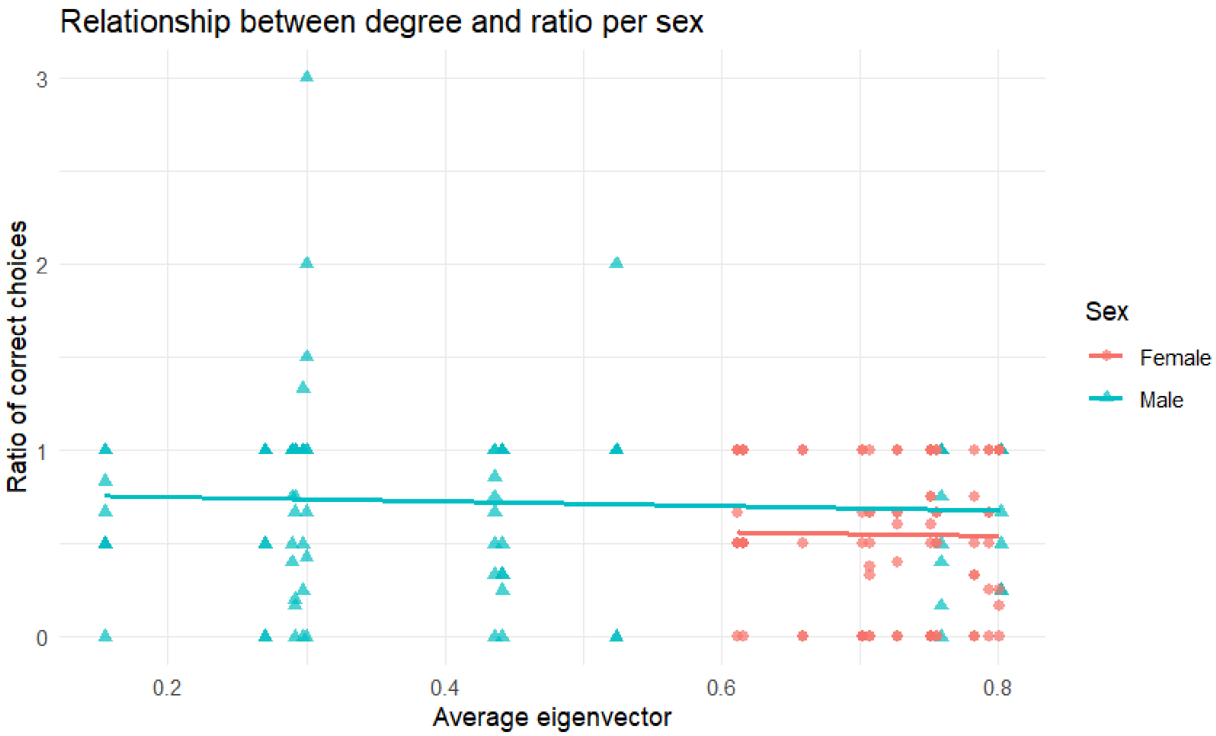
For the next part of the research, early-life conditions and metrics of the social network analysis (SNA) will be linked to information transmission after a change in food availability in the food boxes. The extent of food patch discovery, represented as a measure of information transmission, is determined by calculating the frequency of entries into the food box containing food, divided by the total number of entries into all food boxes during a specific hour (ratio). Observing the first hour of food availability in only one box, which is the third hour of the entire test, a higher ratio of entries into this box indicates more effective information transmission. During the first hour after food is made available in all boxes, which is the sixth hour of the whole experiment, a higher ratio may indicate less information transmission.

In the first group, the male zebra finches, there is no significant difference based on treatment in the ratio during the third (p = 0.70) and sixth hour (p = 0.82). The mean ratio for individuals subjected to harsh treatment is slightly higher in the third hour (easy = 0.624; harsh = 0.635) and slightly lower in the sixth hour (easy = 0.739; harsh = 0.715). Based on these observations, males raised under harsh conditions appear to be better informed about food availability and thus exhibit better information transmission. For the second test group, the female zebra finches, the ratios in the third and sixth hours relative to their early-life conditions also do not show significant differences. For the third hour, it is not even possible to calculate the p-value, as the mean and standard deviation for the easy treatment are too close to each other. In the sixth hour (p = 0.30), the mean ratio for individuals with harsh treatment is slightly higher (easy = 0.505; harsh = 0.591). This suggests that individuals from the easy treatment group received information about food availability in all boxes slightly faster than those from the harsh treatment group. Lastly, both groups were combined. Once again, it was not possible to calculate the p-value for the third hour. At the sixth hour, no significant difference was found between the two treatment groups (p = 0.59). The mean value for the easy treatment group was slightly higher (easy = 0.616; harsh = 0.653), suggesting that individuals from the easy treatment condition may exhibit greater information transmission.

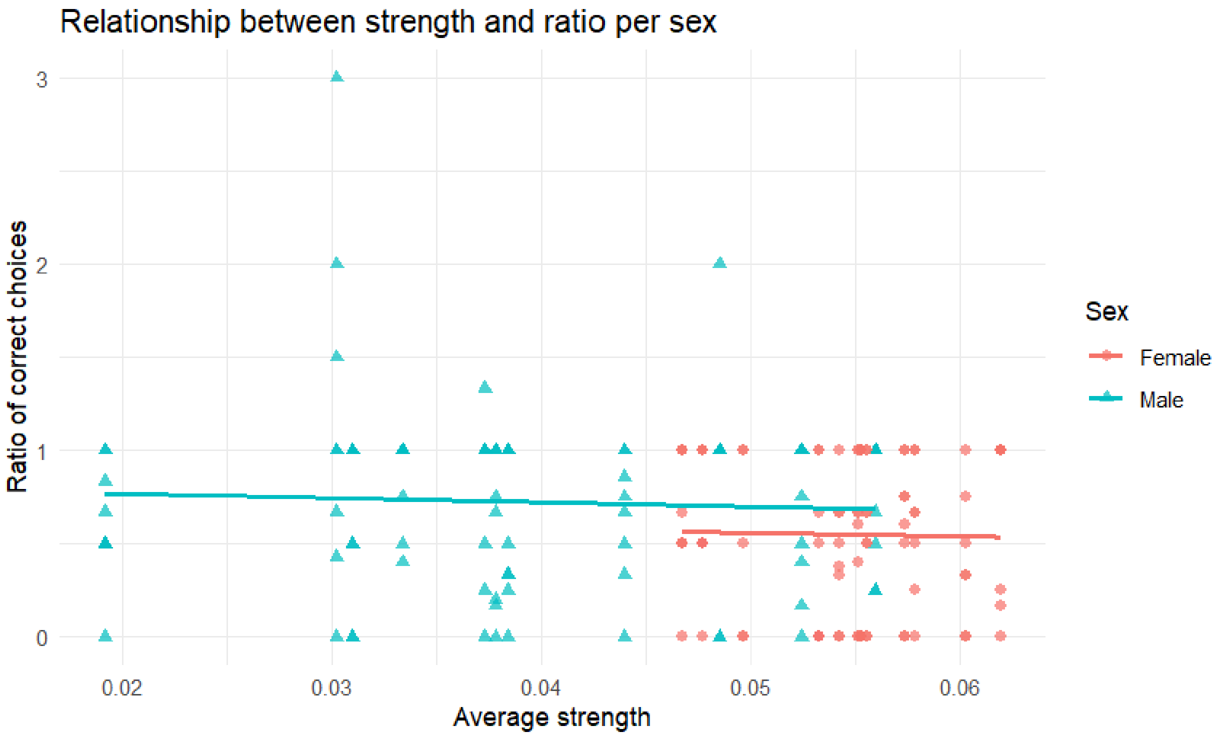
Next, we aimed to link the ratio of entering the box to the SNA metrics. The ratios for the third and sixth hours of the test are compared with all metrics calculated in the first part of the research. For the first group, the male zebra finches, none of the metrics show a significant difference in the ratio when compared to the ratios of the third and sixth hours. In the second group, the females, two of the metrics show a significant difference in the ratio during the third hour, specifically strength (p = 0.018) and eigenvector centrality (p = 0.021). Unfortunately, for the sixth hour, none of the metrics have a significant effect on the ratio.

Next, we pooled the two groups to create a larger test sample, which may increase the likelihood of detecting a significant difference. Linear regression analysis revealed a significant positive relationship between strength and the ratio of correct choices during the third hour where food was available only in the correct box (β = 6.043, p = 0.029). This suggests that individuals with higher strength adapted more quickly, as they showed a higher ratio, meaning they exhibit greater information transmission. When food was once again available in all locations during the sixth hour, significant negative relationships were found between both eigenvector centrality (β = -0.357, p = 0.026) and strength (β = -6.67, p = 0.028) with the ratio. This could indicate that individuals with higher eigenvector centrality or strength adjusted more effectively to the new condition, as they reduced their preference for the correct box, leading to a lower ratio. A lower ratio during this hour suggests better information transmission, as individuals stopped favoring the location with food and explored other food sources. For all results from the linear regression analysis, we refer to tables 3 and 4 on the last pages.

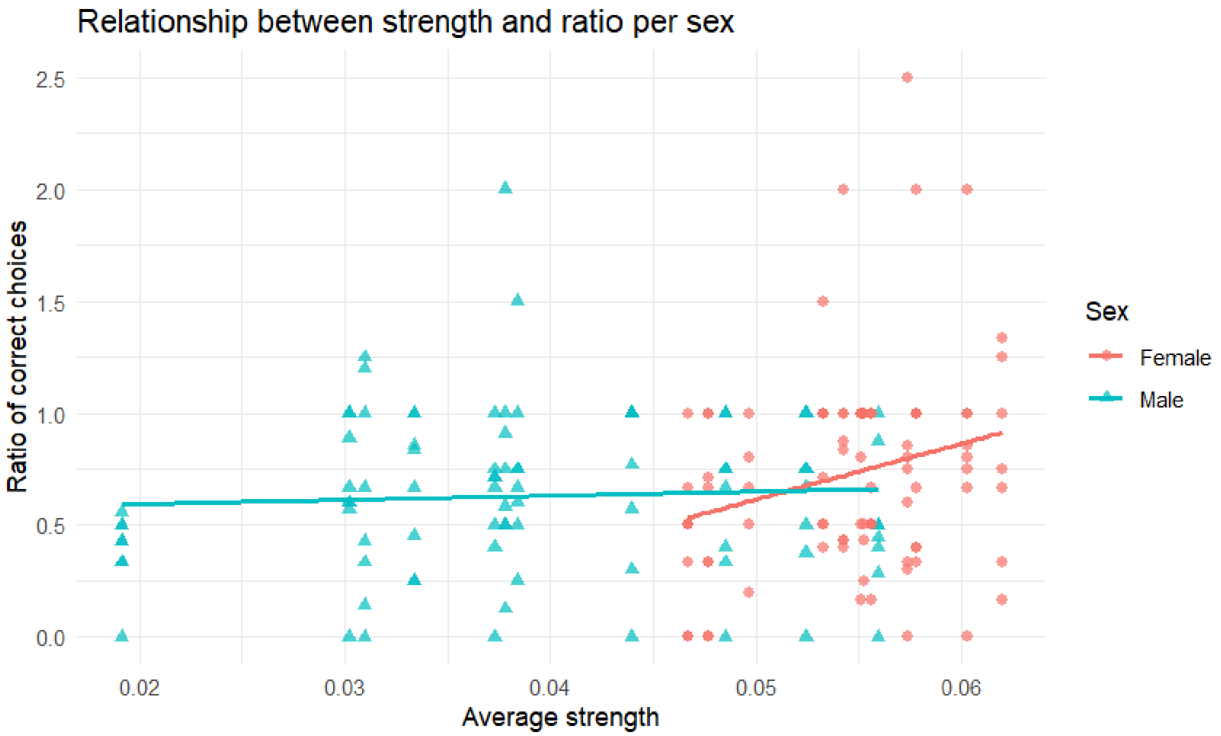
However, when sex and the interaction between sex and eigenvector centrality were included in the model, this effect was no longer significant (*graph 5*), suggesting that the initial relationship may have been influenced by underlying group differences. This suggests that, during this hour, eigenvector centrality did not predict how quickly individuals adjusted to the new condition. Therefore, information transmission as measured by changes in box preference appears unrelated to eigenvector centrality at this point in time. A similar pattern was found for strength (*graph 6*), where the inclusion of sex and its interaction with strength made the previously significant effect non-significant. Linear regression analysis during the third hour revealed a significant interaction between strength and sex (β = -23.088, p = 0.028), with a strong positive relationship between strength and correct choices for females, but not for males (*graph 7*). This suggests that females with stronger social connections were better able to adapt early on, showing more efficient information transmission.



*Graph 5: Relationship between eigenvector centrality and the ratio of correct choices during the sixth hour (interval 5), split by sex. No significant relationship was found for either sex.*



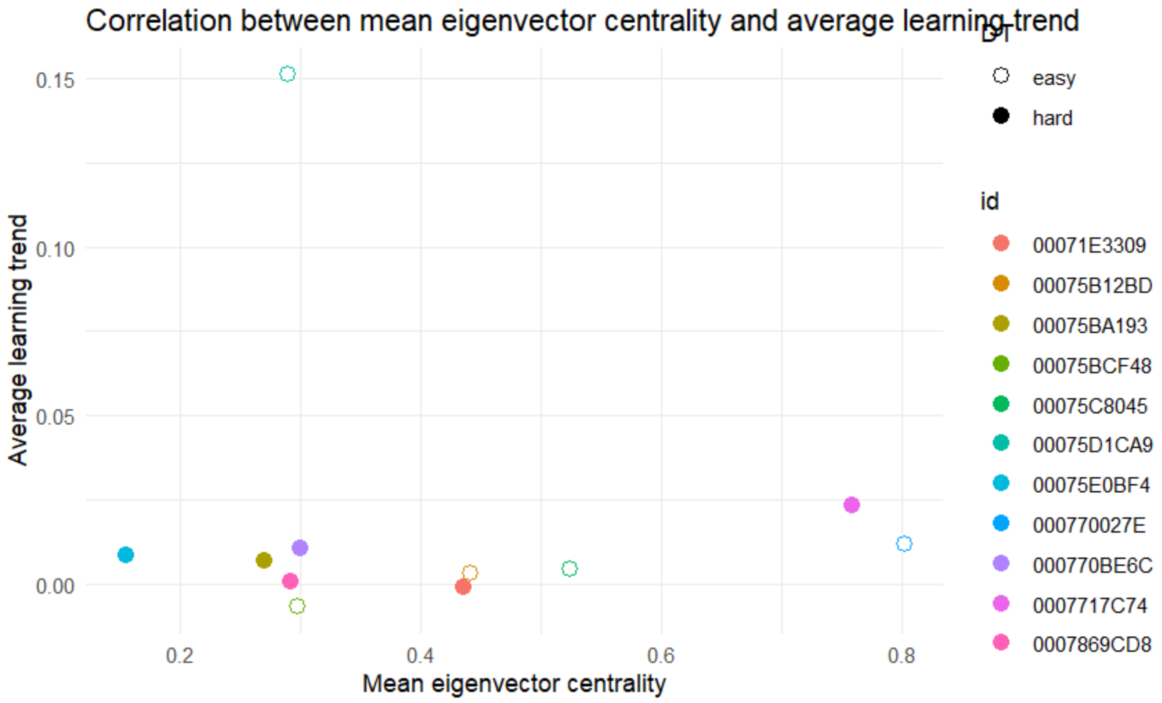
*Graph 6: Relationship between strength and the ratio of correct choices during the sixth hour (interval 5), split by sex. No significant relationship was found for either sex.*

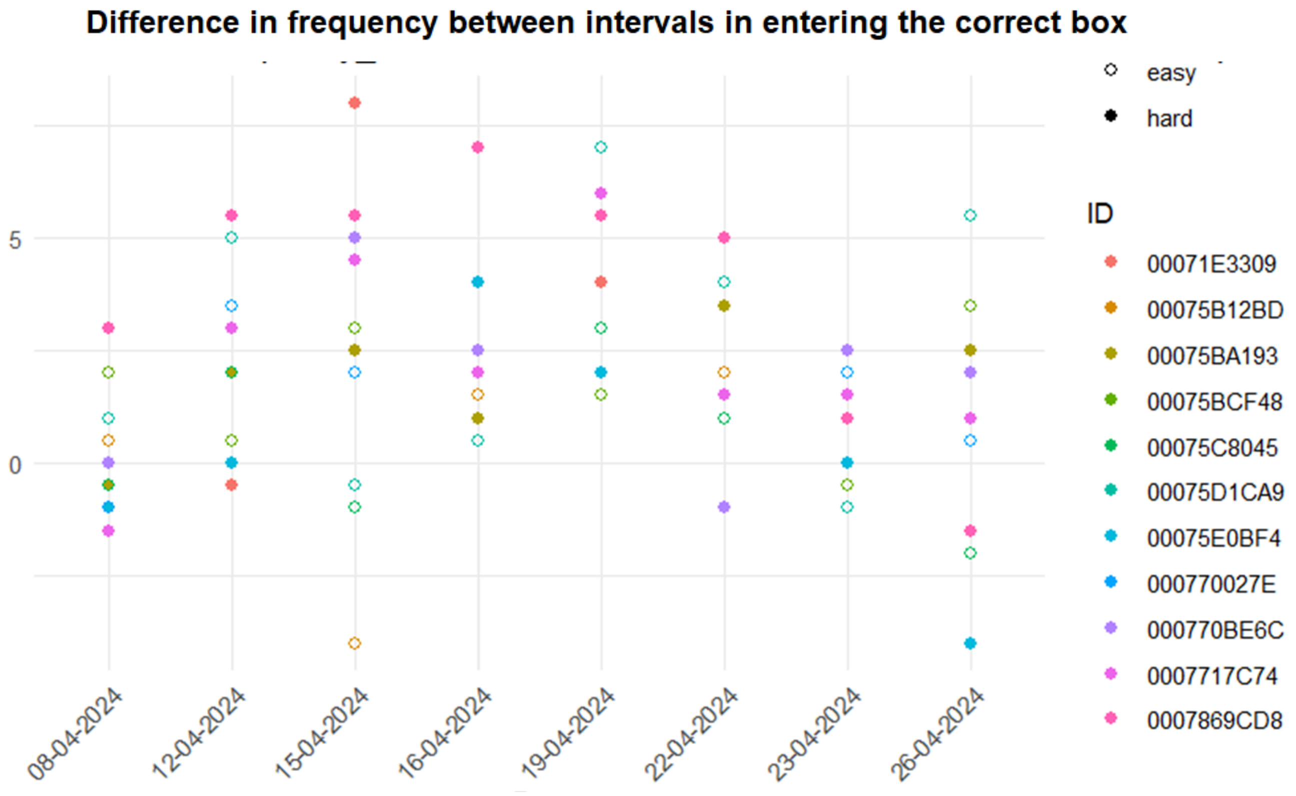


*Graph 7: Relationship between average strength and the ratio of correct choices during interval 2, separated by sex. A positive relationship is visible for females, while no clear trend is observed for males.*

To understand whether there were patterns in how the birds visited the correct food boxes, we actually had to conduct an analysis of visitation behaviors first. This was necessary to ensure that any observed behaviors were not random or coincidental.

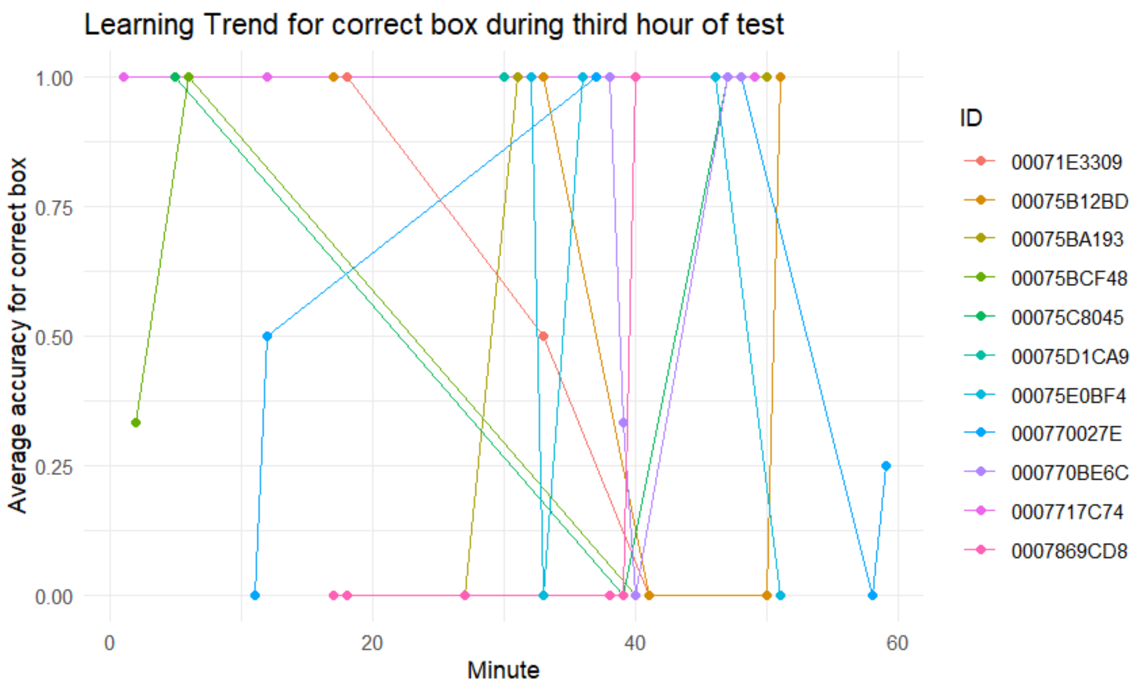
The results from the first set of graphs suggest that zebra finches appeared to visit the correct food box more frequently during the first hour after food was removed from the other boxes as they became more familiar with the setup. This indicates that during the early days of testing, the birds were proportionally less present in the correct box compared to the later days of the test period. To explore this further, a second set of graphs was created. These graphs plotted the difference in visitation ratios between the first two hours (when food was available in all boxes) and the subsequent three hours (when food was restricted to one box) against the test days. Individuals were represented as separate points in the graphs, and this analysis was performed for each of the three restricted hours separately. From these graphs (see *graph 8* as example: the ratios between the first two hours (food in all boxes) and the subsequent hour entering the correct box), no clear pattern of learning was observed. There was no consistent evidence that the birds improved their focus on the correct box over days. Additionally, there were no differences in behavior between birds raised under harsh and easy early-life conditions.





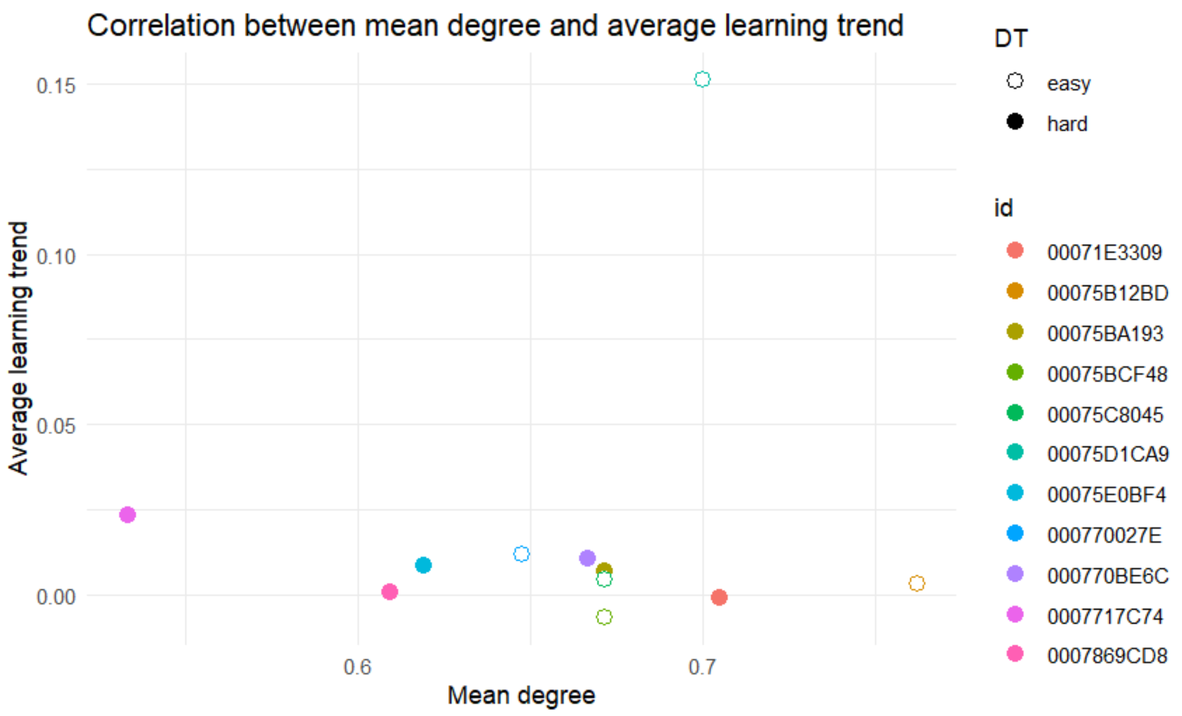
*Graph 8: Difference in frequency of entering the “correct” box between the average of the first two hours and the hour after food was restricted to one box, plotted across days (first group, males). Each individual is represented as a dot, with colored dots indicating harsh early-life conditions.*

To investigate whether individuals with different positions in the social network responded differently to the test, we estimated their response to the restriction of food to one box using a single metric. This metric, referred to as the learning trend, was calculated as the ratio of visits to the correct box to the total number of box visits during the first hour when food was restricted to one box, so during the third hour of the whole experiment. The learning trend was calculated per day for each individual (*see graph 9*) , and the average learning trend over the eight days of testing was determined for each bird. These average learning trends were then plotted against the individuals’ average network centrality values to explore potential relationships between social network position and learning behavior.



*Graph 9: This graph illustrates the learning trends of individual males on the seventh test day. Each line represents an individual's accuracy in selecting the correct box over time, when food access was restricted to a single box.*

The results (*graphs 10, 11 and 12 males, 13, 14, 15 females*) showed no clear pattern linking learning trends to social network centrality. However, a few extreme values in the learning trends were observed, particularly in two females and one male. To investigate whether these outliers were due to a lower frequency of box visits, we analyzed the total number of box visits for these individuals. Only one female appeared to visit the boxes less frequently, but even in her case, the difference was not exceptionally low.


Correlation between mean degree and average learning trend
Average learning trend
0.15
0.10
0.05
0.00
0.6
0.7
Mean degree
DT
easy
hard
id
00071E3309
00075B12BD
00075BA193
00075BCF48
00075C8045
00075D1CA9
00075E0BF4
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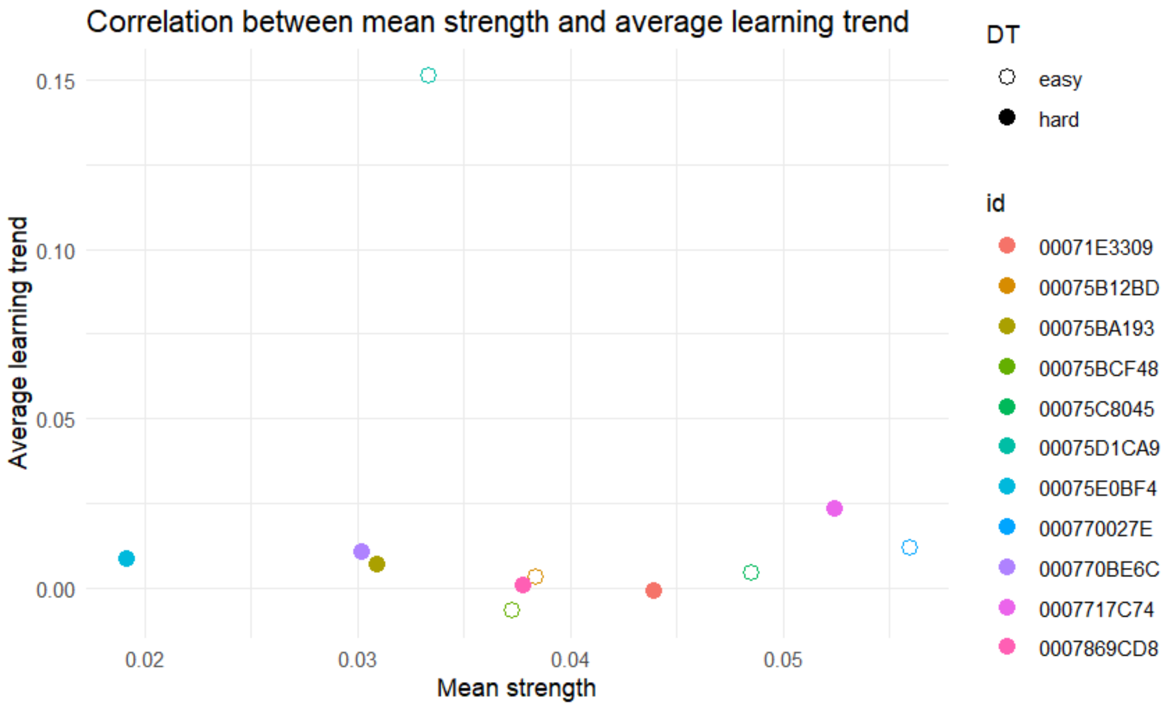
Correlation between mean strength and average learning trend
Average learning trend
0.15
0.10
0.05
0.00
0.02
0.03
0.04
0.05
Mean strength
DT
easy
hard
id
00071E3309
00075B12BD
00075BA193
00075BCF48
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00075D1CA9
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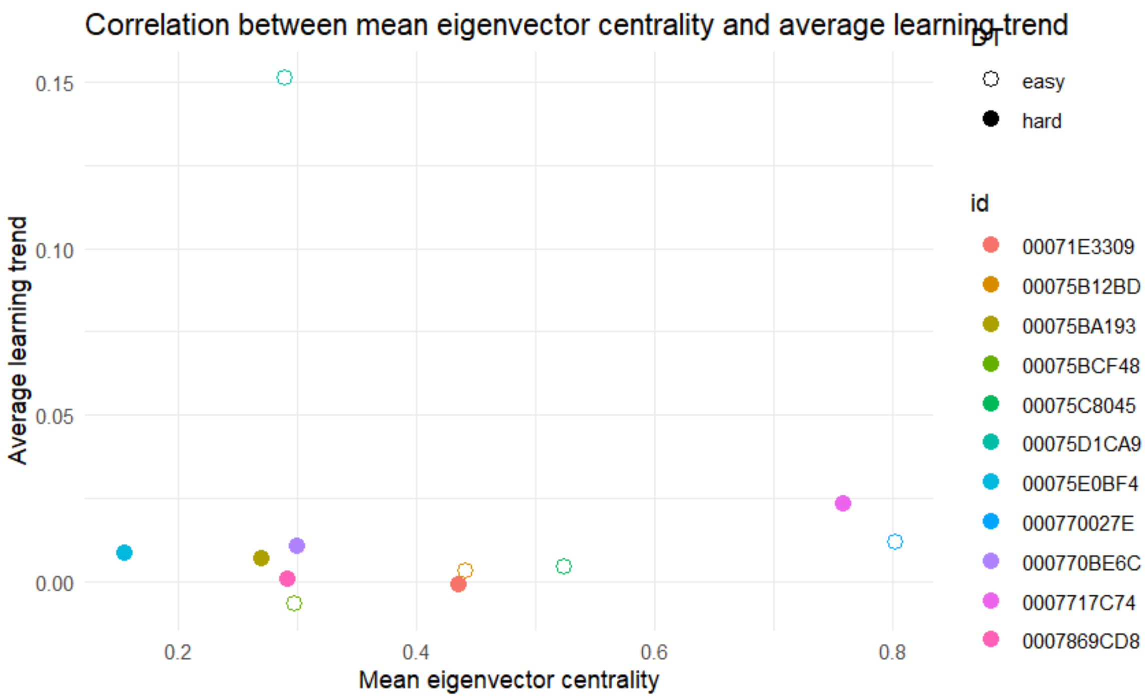
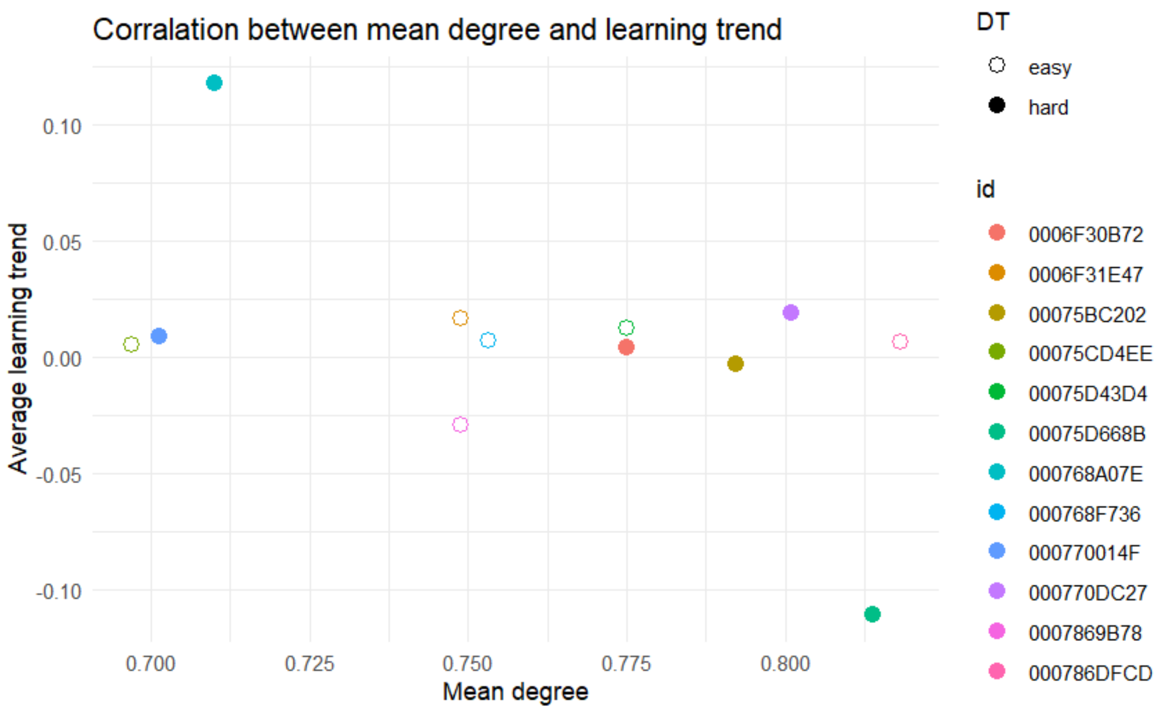


*Graph 10/11/12 (first group, males): Average learning trend (proportion of visits to the "correct" box during the first restricted hour) over eight days plotted against individuals' average centrality values (degree, strength and eigenvector centrality). Each dot represents an individual, with colored dots indicating harsh early-life conditions.*


Corralation between mean degree and learning trend
Average learning trend
0.10
0.05
0.00
-0.05
-0.10
0.700
0.725
0.750
0.775
0.800
Mean degree
DT
easy
hard
id
0006F30B72
0006F31E47
00075BC202
00075CD4EE
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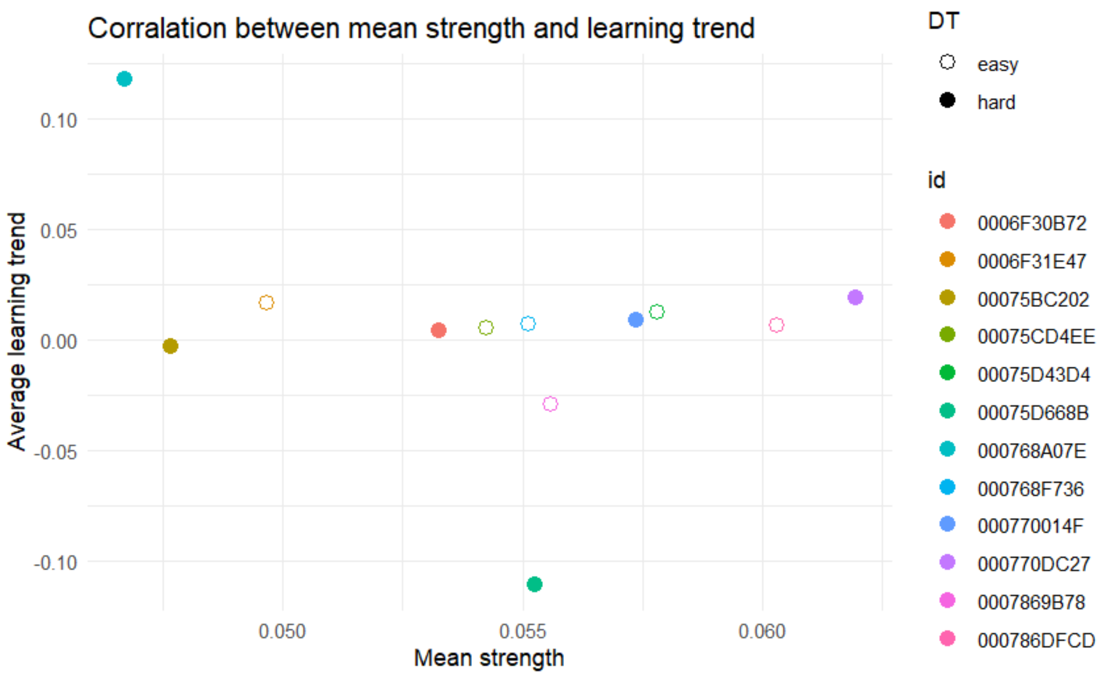
Corralation between mean strength and learning trend
Average learning trend
0.10
0.05
0.00
-0.05
-0.10
0.050
0.055
0.060
Mean strength
DT
easy
hard
id
0006F30B72
0006F31E47
00075BC202
00075CD4EE
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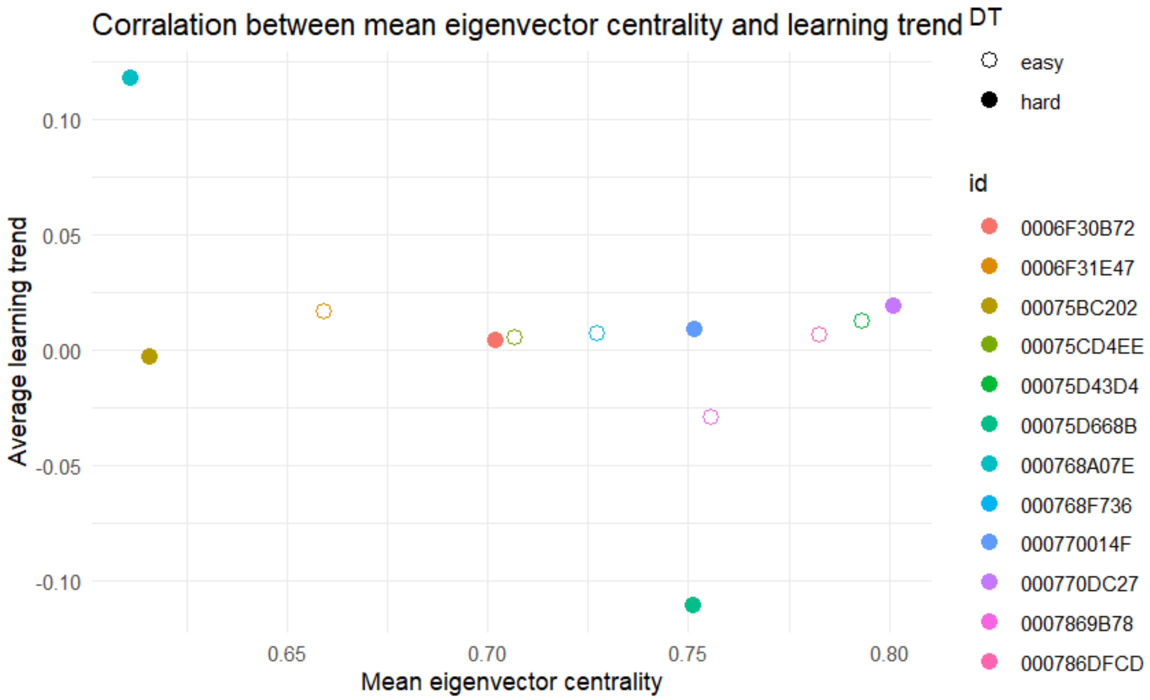

*Graph 13/14/15 (second group, females): Average learning trend (proportion of visits to the “correct” box during the first restricted hour) over eight days plotted against individuals’ average centrality values (degree, strength and eigenvector centrality). Each dot represents an individual, with colored dots indicating harsh early-life conditions.*

# 4. Conclusion

This research investigated the impact of early-life conditions on the social network positions of zebra finches and explored whether social network centrality influences information transmission. The results show that early-life conditions, manipulated through foraging treatments, do not significantly alter social network metrics such as strength and degree. However, although not statistically significant, individuals from easy developmental conditions tend to score higher on every metric (*see table 2)*, and therefore take a more central position in the network. Eigenvector centrality, which measures connections to well-connected individuals, revealed a significant difference between the treatment groups. This suggests that early-life conditions may influence the quality rather than the quantity of social connections.

In terms of information transmission, no significant differences were found in the ability of male or female zebra finches to locate the correct food box based on their early-life conditions. Although males from harsh conditions showed slightly higher ratios during the third hour of testing, and females from easy conditions showed a trend toward faster information learning, these differences were not statistically significant. Furthermore, an analysis of visitation behavior over multiple days revealed no consistent learning patterns, indicating that the birds did not improve their ability to focus on the correct food box over time.

To find out whether social network metrics were related to information transmission (or learning behaviour) the learning trend, a metric reflecting the proportion of visits to the correct food box during the first restricted hour, was compared to individuals' centrality measures (degree, strength and eigenvector centrality). A few individuals with extreme learning trend values were examined further, but their behavior did not appear to be linked to unusually low box visitation frequencies. While no consistent patterns emerged, and therefore further analysis was not realistically possible, results show that female zebra finches exhibited significant correlations between certain metrics (strength and eigenvector centrality) and their ability to locate the correct food box during the first hour after removing food in other boxes. However, these correlations were absent in the hour after replacing the food in all boxes and during both hours for male zebra finches.

After pooling both groups, additional patterns emerged that provided further insight into the role of social network metrics in learning behavior. A significant positive relationship was initially found between strength and the ratio of choosing the correct box during the third hour, when food was restricted to one location. This suggested that individuals with higher strength adapted more quickly and demonstrated greater information transmission. However, further analysis revealed that this relationship was primarily driven by females, as the interaction between strength and sex was significant, and the positive effect of strength was only present in females.

In the sixth hour, when food was once again available in all boxes, initial analyses showed significant negative relationships between both strength and eigenvector centrality with the ratio of correct choices. This seemed to indicate that individuals with higher centrality adjusted more effectively to the restored situation by reducing their preference for the previously rewarded location. However, after including sex and its interaction with these metrics, the effects were no longer significant. This suggests that the previously observed relationships may have been influenced by underlying group differences rather than the centrality measures themselves.

Taken together, these results indicate that while social network metrics such as strength appear to play a role in how quickly individuals adjust to changing conditions, these effects are not consistent across sexes. Moreover, the overall effect sizes remained small, suggesting that although social connections may influence information transmission to some extent, they explain only a limited portion of the variation in learning behavior.

In conclusion, while early-life conditions may influence specific aspects of social network quality, they do not strongly determine broader network positions or significantly enhance information transmission. Social network centrality showed limited and inconsistent relationships with learning and resource discovery, with some evidence of influence in the female and pooled group under certain network centrality metrics, but these findings are not reliable, as overall no consistent patterns emerged, making this analysis not realistically possible. These findings highlight the complexity of social and environmental factors in altering learning and information transmission behaviors in zebra finches.

# 5. Discussion

Comparing the results of this study with previous findings highlights both similarities and differences in how early-life conditions influence social network metrics in zebra finches. While this research found no significant effect of early-life conditions on degree and strength, Lamarque reported a significant decrease in degree for individuals raised under harsh conditions compared to those raised in easy environments. Although our effects were not statistically significant, a similar pattern emerged: individuals from easy developmental conditions tended to score higher on all social network metrics (*see table 2*).

Both studies, however, identified significant differences in eigenvector centrality. Our findings and those of Lamarque show that zebra finches raised under harsh conditions have lower eigenvector centrality, indicating weaker connections to well-connected individuals. This aligns with the silverspoon hypothesis (McInerney et al., 2016), which suggests that birds raised in less favorable conditions may struggle to form or maintain strong social ties, possibly due to limited resources available for social interaction. We also suggest that differences in eigenvector centrality may reflect the quality rather than the quantity of social connections. The significant effect of sex on eigenvector centrality observed in Lamarque's study, where males exhibited lower values than females, was also reflected in our research, where sex was found to significantly influence social preferences. The coefficient of variation (CV) did not show significant differences based on early-life conditions in either study, suggesting that early-life conditions may not strongly influence how selective individuals are in their social interactions.

Interestingly, Lamarque discussed the environmental matching hypothesis (McInerney et al., 2016), which proposes that early-life stress might prepare zebra finches for harsh adult environments. However, our results from the information transmission test provide mixed support for this theory. While males raised under harsh conditions appeared to be better informed about food availability, suggesting enhanced information transmission and preparation for later life, females from the easy treatment group received this information slightly faster than females with the harsh early-life treatment. Additionally, when both groups were combined, no significant difference was found between treatments in the sixth hour, though the slightly higher mean value for the easy treatment group suggests they may exhibit greater information transmission.

Future research should consider multi-generational networks that include both sexes to better replicate natural social environments, as also suggested by Lamarque. Increasing group sizes could also help reduce limitations related to the betweenness metric, as larger networks would likely present more complex social structures.

In summary, while both studies acknowledge that early-life conditions impact social network structure, our findings indicate that these effects are more nuanced and primarily influence the quality of social connections rather than their quantity. The relationship between social centrality and resource discovery remains inconsistent, suggesting that early-life stress does not determine social network roles or enhance information transmission in zebra finches.

### Table 1: Summary of statistical tests for treatment effects

| **Metric** | **Effect** | **Test type** | **Estimate** | **Std. error** | **df** | **t/W-value** | **p-value** |
|---|---|---|---|---|---|---|---|
| **Strength** | intercept | t-test | 0.0655 | 0.00466 | 74.2 | 14.1 | <2e-16 |
| | DT | t-test | -0.00371 | 0.00679 | 25.3 | -0.546 | 0.59 |
| | sex | t-test | 0.0171 | 0.00995 | 79.8 | 1.72 | 0.83 |
| | DT : sex | t-test | -0.00308 | 0.0139 | 25.2 | -0.221 | 0.83 |
| **Degree** | DT | Wilcoxon | - | - | - | 64701 | 0.072 |
| **Eigenvector centrality** | DT | Wilcoxon | - | - | - | 66800 | 0.0095 * |
| **Coefficient of variation** | intercept | t-test | -0.143 | 0.0528 | 45.9 | -2.708 | 0.0095 |
| | DT | t-test | -0.0821 | 0.0912 | 26.5 | -0.901 | 0.38 |
| | sex | t-test | 0.601 | 0.110 | 48.8 | 5.44 | 1.7e-06 * |
| | DT : sex | t-test | -0.0117 | 0.187 | 26.5 | -0.063 | 0.95 |

### Table 2: Summary average of metrics for treatment

| **Metric** | **Easy treatment** | **Harsh treatment** |
|---|---|---|
| **Strength** | 0.0645 ± 0.0401 | 0.0574 ± 0.0381 |
| **Degree** | 0.722 ± 0.224 | 0.693 ± 0.224 |
| **Eigenvector centrality** | 0.625 ± 0.323 | 0.562 ± 0.334 |
| **Coefficient of variation** | 1.076 ± 0.584 | 1.015 ± 0.570 |

### Table 3: Effect of network centrality metrics on ratio

### (for choosing the correct box, third hour)

| Metric | Group | Estimate | Std. error | t-value | p-value |
|---|---|---|---|---|---|
| **Strength** | Males | 1.89 | 3.78 | -0.501 | 0.62 |
| | Females | 25.0 | 10.4 | 2.41 | 0.018 * |
| | Both | 6.04 | 2.75 | 2.20 | 0.029 * |
| **Degree** | Males | 0.574 | 0.686 | 0.836 | 0.41 |
| | Females | 0.537 | 1.179 | 0.456 | 0.65 |
| | Both | 0.788 | 0.438 | 1.80 | 0.074 |
| **Eigenvector centrality** | Males | -0.0172 | 0.120 | -0.088 | 0.93 |
| | Females | 1.75 | 0.750 | 2.34 | 0.021 * |
| | Both | 0.242 | 0.146 | 1.66 | 0.098 |
| **Coefficient of variation** | Males | 0.0121 | 0.100 | 0.121 | 0.90 |
| | Females | 0.322 | 0.663 | 0.486 | 0.63 |
| | Both | -0.0755 | 0.0597 | -1.27 | 0.21 |

### Table 4: Effect of network centrality metrics on ratio

### (for choosing the correct box, sixth hour)

| Metric | Group | Estimate | Std. error | t-value | p-value |
|---|---|---|---|---|---|
| **Strength** | Males | -2.31 | 5.17 | -0.446 | 0.66 |
| | Females | -1.79 | 9.23 | -0.194 | 0.85 |
| | Both | -6.67 | 3.02 | -2.21 | 0.028 * |
| **Degree** | Males | 0.367 | 0.942 | 0.390 | 0.70 |
| | Females | 0.209 | 1.01 | 0.207 | 0.84 |
| | Both | -0.739 | 0.479 | -1.54 | 0.12 |
| **Eigenvector centrality** | Males | 0.119 | 0.270 | -0.441 | 0.66 |
| | Females | -0.0977 | 0.670 | -0.146 | 0.88 |
| | Both | -0.357 | 0.159 | -2.24 | 0.026 * |
| **Coefficient of variation** | Males | -0.152 | 0.136 | -1.12 | 0.27 |
| | Females | 0.147 | 0.576 | 0.256 | 0.80 |
| | Both | 0.102 | 0.0654 | 1.56 | 0.12 |

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