Social niche construction in captive Gouldian Finch (*Erythrura gouldiae*) Flocks

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Abstract

The organization of animal groups is both a cause of, and consequence of, patterns of interactions among individuals. The stability of animal social organization reflects how individuals construct and maintain resilient patterns of interactions across changes in group size and membership. In this study we describe patterns of social interactions in captive flocks of Gouldian Finches (*Erythrura gouldiae*) that were exposed to changing social conditions. A flock of adult Gouldian Finches was exposed to two changing conditions, an introduction condition where juveniles were introduced to the flock, and a fission-fusion condition where the flock was split into two smaller flocks and a new group of juveniles introduced to each. We show that the social organization of captive Gouldian finch flocks is characterized by stable homophilic communities of adult females and juveniles. Females showed higher rates of approaches to other adult females, while juveniles maintined higher rates of approaches towards other juveniles. These findings highlight how the stable interactive decisions made by individuals contribute to higher-order patterns of organization in bird flocks. Furthermore, this study is one of the few to demonstrate self-assortment of juveniles in passerine flocks and suggests that peer and sibling interactions are an unexplored area in avian social development.

INTRODUCTION

Describing the factors that shape social connections, and how those connections create enduring patterns of organization at the group level is core feature of research on animal social systems (Lott 1991). Most social species inhabit dynamic and loosely cohesive fission-fusion societies where group size and composition fluctuate over short timescales. The stability and organization of groups reflects the ability of individuals to reconstruct patterns of connections across fission-fusion changes (Kohn 2019, Mason 1978). If changing conditions force individuals to "rewire" their connections, the social organization will change, but if individuals respond by reconstructing similar social connections than the social organization will remain resilient. Thus, an important aspect of understanding animal social systems is describing how behavioral responses to period of social change allow the social organization to be continually reconstructed across changing contexts. This study aims to describes the processes maintaining patterns of social organization in an passerine, the Gouldian Finch (*Erythrura gouldiae*).

Homophily reflects preferential associations with like individuals and is a core feature of social systems from economies to small group dynamics (McPherson, Smith-Lovin, & Cook 2001). In animals, variation in sex, age, familiarity, morphology and personality play a large role in shaping who associates with whom (Ebenau, 2019; Kohn, King, Scherschel, & West, 2011). In some species, homophily is caused by morphological and physiological differences resulting in divergent patterns of activity synchronization between individuals (Conradt, Ruckstuhl, & Neuhaus, 2005). During parts of the year, this can result complete segregation, with individuals of different sex and ages classes inhabiting separate groups (Ruckstuhl & Neuhaus, P. 2000). More frequently, incomplete social assortment is observed in groups. While a diverse range of individuals inhabit the same group, distinct subgroups and communities emerge as individuals have stronger social connections with like conspecifics and other group members. While such subgroups are prevalent throughout the vertebrates, little is known about the behavioral processes underlying the emergence and stability of these subgroups across group changes.

Assortment by sex has been documented extensively in social mammals and increasingly in birds and invertebrates. Across taxa there has been a tendency for females to form strong connections with other females, whereas males disperse to neighboring groups (Ward & Webster, 2016). In mammals (Stanley, Liddiard Williams, & Preziosi, 2018), birds (Kohn, King, Scherschel, & West, 2011), and insects (Stanley, Williams, Preziosi 2017) females have been observed to form cohesive female subgroups within the larger group. Strong connections among familiar females often have beneficial consequences for females such as reduced risk from male harassment (Cameron, Setsaas & Linklater,. 2009), higher offspring survival (Silk et al. 2009), lowering stress responses, and facilitating access to social information (Gros-Louis, White, King & West 2003). In horses (*Equus ferus*) and yellow baboons (*Papio cynocephalus*), strong and stable connections between females are associated with higher offspring survival and lower mortality (Carter, Lee, Marshall, Ticó, & Cowlishaw, 2015; Silk et al. 2010, 2009). In Brown-headed Cowbirds (*Molothrus ater*) females form stable subgroups with familiar females across group changes, and females with the strongest preference for familiar females during the fall have higher rates of reproductive output during the spring (Kohn, 2017).

Age is a significant determinant of social connections in many animal societies. While extensively documented in primates, the existence of juvenile groups and subgroups has been observed in animals ranging from fish to equids to invertebrates. Many factors can facilitate the emergence of juvenile assortment independent of mutual attraction between juveniles. Juveniles often show distinct morphological and physiological differences from adults, and this can cause juveniles to cluster based on shared physiological needs and habitat preferences. Some studies have shown that juvenile form "gangs" around contested resources to better compete with more experienced adults (Dall & Wright, 2009; Franks et al. 2020) Adults may also corral their offspring into all-juvenile groups for protection from predation and preferentially avoid interacting with the more active and disruptive juveniles (Munro, & Bédard,1977; Wanker, Bernate & Franck,1996). In summary, while juvenile groups are commonly observed across taxa the behavioral processes underlying their formation and stability is largely unknown.

Juveniles can self-assort by preferring to interact with similar-aged peers who are more behaviorally compatible than adults (Lindgren & Shapiro, 1990). Goat kids (*Capra aegagrus hircus*) will form subgroups with peers two weeks after birth by preferring interactions with peers over parents (Lickliter, 1987). This pattern is observed across many equids (Boyd, 1988) and other social mammals. In birds little is known about the social relationships, experiences, and interaction preferences of juveniles upon becoming independent. While some have suggested that birds associate with siblings and peers for an extended time after independence (Hötker, 1982; Loretto, Fraser, & Bugnyar, 2012; Nicolai, 1956), it's unknown if juvenile subgroups exist in many species, and if mutual interaction preferences play a role in their formation. One aim of the current study is to describe patterns of age-based assortment in a Gouldian finch flocks and investigate if shared interaction preferences among juveniles lead to the formation of juvenile subgroups.

Peer interactions among juveniles are often necessary for the development of species-typical behaviors and competencies. When isolated from peers, juveniles often develop distinct behavioral repertoires and have long-lasting behavioral deficiencies when compared to typically reared individuals (Suomi & Harlow, 1972). Juveniles are much more active, playful, and social than adults, and juvenile subgroups may allow for young individuals to explore their behavioral potentials and refine their behavioral abilities. Ultimately behaviors acquired through peer interactions can allow juveniles to become socialized into the wider group (Pellis & Pellis, 2007; Poirier & Smith, 1974). For example, in Brown-headed cowbirds, interactions within juvenile subgroups predicts the development of later courtship competence used to secure pair bonds as adults (Kohn, King, Dohme, Meredith & West, 2013), and rhesus macaques (*Macaca mulatta)* infants raised in social isolation were able to acquire species-normative social behavior after an extensive period of social interaction with peers (Suomi & Harlow, 1972).

This study aims to describe the social organization in flocks of captive Gouldian finches. Gouldian finches are an endangered estrildid finch that inhabits the subtropical grasslands of northern Australia. While little is known about the social organization or behavior of Gouldian finches, in the wild, large fission-fusion flocks composed of hundreds of individuals of mixed age and sex composition are commonly observed. The fluidity and diversity of estrildid flocks has led some to speculate that they lack significant patterns of within-group structure (Bolton, et al. 2016; Dostine, Johnson, Franklin, Zhang, Hempel, 2001).

Gouldian finches also exhibit a startling color polymorphism. Adults show discrete differences in head coloration with some having either red, black, or yellow heads, while juveniles have grey plumage with olive backs. Differences in head coloration correspond with differences in behavior and personality. Red headed individuals are more aggressive, with fights between red-headed individuals being more intense than others, and red-headed females displacing black-headed females more often (Pryke, 2007). In the wild, black-headed individuals are the first to descend to waterholes (O'Reilly, Hofmann & Mettke-Hofmann, 2019). In captivity, some studies have shown that black-headed individuals were more likely to approach and interact with a novel object faster and return to a food bowl sooner after the presentation of a simulated predator (Williams, King, & Hoffman 2012, Mettke-Hofmann 2012), while others have found that red-headed individuals are more neophilic in other contexts (Fragueira & Beaulieu, 2019).

It is currently unknown how the different color morphs, sexes, and age classes associate with each other in a semi-naturalistic context. Due to the behavioral differences across individuals of various sex, age, and head-color status, it is hypothesized that Gouldian finch flocks will show significant assortment by both age, sex, and color morph status. Research on animal social networks often focuses on associations, where social connections are measured when two or more individuals inhabit the same place in close proximity. While associations can be powerful measures of social organization, the social choices that build connections can be difficult to measure without observing directed interactions between known individuals. By recording interaction preferences, we can discover how these social choices construct higher-order patterns of organization (Hinde, 1976). Who individuals prefer and avoid engaging will often directly contribute to the communities, subgroups, hierarchies at the group and population level. By describing the stable social preferences creating patterns of assortment in changing Gouldian Finch flocks this study will highlight the behavioral mechanisms generating the social network organization by discovering *stable* social preferences consistently expressed across different contexts which correspond to higher order structural attributes of group organization.

METHODS

Subjects: All individuals in this study were Gouldian finches. All finches were acquired from professional breeders in Arizona and Florida U.S.A. Each bird was provided with a uniquely colored leg band for individual recognition. Males, females, and juveniles were distinguished from each other based on plumage and behavior differences, with adult females being much more subdued in their chest coloration in contrast to males.

All juveniles were hatched and raised in separate cages prior to being introduced to experimental flocks. At around 40 days after fledging juveniles become independent of their parents and can feed and drink on their own without any sign of parental provisioning. Juveniles were distinguished from adults based on their grey head's olive back and lack of typical adult plumate. In this study all juveniles were under one year of age since fledging the nest and adults were older than a year and exhibited adult plumage. Head color was easily observed in adults and assessed in juveniles at the time of their first molt after the end of the data collection period. We used a total of 5 adult males and 6 females and 10 juveniles for this study.

All birds were provided with a daily diet consisting of finch seed mix (Kaytee) and soaked Perle Morbide pellets, with eggshell, boiled eggs, and dandelion greens provided twice a week. Fresh water was continually available.

Aviaries: We used a series of two aviaries in this study. Each aviary consisted of identical dimensions (23 x 72 x 41 in) and similar environmental conditions. The aviaries were located inside next to a large window allowing for sunlight and ventilation. Each aviary contained both natural eucalyptus and plastic privacy perches, small shrubs, a feeding station, and a bowl for water baths.

Data Collection: We used focal sampling during data collection. During observation periods all individuals in the flock were observed for a 5-minute focal block. We recorded all approaches, occurred within a 2-inch radius around the focal individual being observed. All observations were done using voice recognition technology allowing the observer to maintain continual visual contact with the focal bird throughout the sampling block. An approach was scored when another individual approached another within a radius of 2 inch. Before data collection, video of marked perches was made to establish that 2 inches was the typical social distance observed between two resting adult finches. All focal samples were collected by GMK.

Procedure

Baseline Session: From 8/7/2020 to 8/17/2020 focal samples were taken measuring approach behavior. A total of 352 focal samples were taken. Each individual was observed 32 blocks for a total of 160 minutes each.

Fusion session: On 10/5/2020 to four novel juveniles (40 days post fledging) were introduced into the aviary. From 10/06/2020 to 12/22/2020 an additional 503 focal samples were taken. All individuals observed 34 blocks for a total of 170 minutes except one individual who was removed from the flock temporarily for health reasons and was observed for 26 blocks.

Fission-Fusion Session: On 2/10/2021 the fusion flock was split up into two separate flocks. Three males, two females, and two juveniles were moved into flock 1, and four females, two males, and one juvenile were moved to flock 2. In each flock, three new juveniles (40 days post fledging) were randomly introduced to both flocks. From 2/11/2021 to 4/20/2021 a total of 84 blocks were recorded in each aviary. Each individual was observed for 8 blocks for a total of 40 minutes each.

ANALYSIS

Due to the small non-independent sample sizes, permutation statistics was used. Permutation tests are designed to deal with the unique challenges of small non-independent and sample sizes while maintaining an appropriate type I error rate.

Modeling social network structure: Generative network modeling and clustering algorithms were used to model social network structure. We used exponential random graph models (hereafter ERGMs) for valued and directed networks (R package ergm.count in the statnet suite). ERGMs

are like generalized linear models, except the dependent variable is the distribution of connections in the social network (the network topology) and the explanatory variables are statistical terms that assess the influence social processes on the distribution of connections in the network (Silk, M. J., & Fisher, D. N. 2017). We conducted an ERGM for each seperate flock in each condition, and for all models the terms included as explanatory factors were the influence of age, sex, and head-color based homophily.

When a model identified any significant homophilous terms a post hoc clustering algorithm was used to look at the subgroup structure of the network. A subgroup is a set of individuals who share more ties within the community then they do outside the community. A spinglass cluster algorithm was used to identify subgroups. This algorithm is suited to smaller networks with weighted and directed connections between individuals and seeks to rewards ties between community members while minimizing edges for within community members and places an emphasis on missing edges between individuals (Pasta & Zaidi, 2017).

Permutation tests for social structure: After conducting ERGMs and cluster analysis, permutation tests were used to assess the significance and direction of social preferences. A null distribution was computed for each flock by doing row-wise permutations. For each permutation, the number and distribution of approaches directed towards others was preserved but the individual they were directed towards was randomized. A total of 100,000,000 permuted networks were generated. For each permuted network, the approach rate per-individual toward the different age, sex, and head color categories was calculated by taking the total number of approaches directed towards those categories and dividing it by the number of group members in those categories. The null distributions reflected the approach rates across all permutations. Observed interaction rates were then compared to the null distribution and empirical p-values were calculated to assess if specific approach rates occurred above or below expected values. These p-values were calculated by taking the number of observations either above or below the observed value and dividing them by the total number of permutations. All permutation tests used a two-tailed significance with an alpha of 0.05 (above or below 0.025 in each tail)

Pairwise differences in approach rates were used to see if individuals maintained higher rates of approaches toward like individuals in contrast to other group members. For each individual we subtracted the approach rate directed toward homophilous conspecifics from approaches directed towards other conspecifics and compared the mean of those differences to a permuted null distribution. For example, to see if females preferred females over males we subtracted the approaches to males from the approaches to females. This observed mean difference was compared to null distributions of mean differences across the permuted networks. Empirical p-values were calculated to show if approach rates toward homophilous conspecifics were significantly higher than expected with an alpha of 0.05. All permutation tests were also conducted using data stream permutations with equivalent results (Farine, 2017), and multiple comparisons were corrected using the False Discovery Rate (FDR) correction.

Repeatability of adult network structure: To assess if social networks remained resilient to group changes, we specifically looked at the adult network from baseline to the introduction period. To see if the adult network was significantly robust to the introduction of juveniles a uniform graph correlation (gscor in statnet) was performed with a conditioned uniform graph test (cugtest in statnet) being used to calculate empirical-p values.

Results:

Basic: During the baseline period a total of 5,655 approaches were recorded. After the baseline period a group of four juveniles were added to the group and a total number of 8840 approaches were recorded. After the this a fission-fusion was performed where the flock was split up into two separate flocks and three juveniles added to each one, here a total of 2184 approaches were observed in flock 1 and 2345 approaches were observed in flock two.

Social network structure: Our Gouldian finch flock was organized around sex and age-based preferences. During both the baseline and introduction period the models found significant patterns of social assortment. During the baseline, fusion, and fission-fusion periods the ERGM model found significant assortment by both sex, age, and head color, with assortment by sex showing the strongest positive coefficient in all conditions (Table 1).

Community Structure: During the baseline period the clustering algorithm identified two communities, one consisting of the six females and the other consisting of the five males (Fig 1). During the fusion condition, three different communities were identified, one community containing the six females, another contained all five males, and the other contained all four juveniles. During the fission-fusion period, distinct communities were observed in both flocks. In the first flock, three communities were observed, one containing three adult individuals including both adult females and their paired male, another community contained the three juveniles that were introduced to the flock during this period, and the final community contained two of the juveniles introduced during the fusion period and two adult males. The second flock during the fission-fusion condition showed two distinct communities, one containing only adults including four adult females and two adult males, and another community containing all four juveniles.

Permutation tests for social preferences: In all conditions, social preferences differed significantly from the null expectations. Females had significantly higher rates of approaches towards other females, and juveniles had significantly higher rates of approaches towards other juveniles in all flocks. Adult males showed significant preference to interact with females in all conditions (Table 2). In all conditions, juveniles showed a tendency to avoid interacting with other adult males, but no preference towards approaching or avoiding adult females.

In both the baseline and fusion conditions, females were significantly more likely to interact with females over males and juveniles (Fig 1, Table 3). During the fission-fusion period, the sex ratio became skewed towards females (Flock 2) or males (Flock1) and females showed a tendency to prefer females over male interactions when the ratio was skewed towards males in flock 1. Males showed no consistent pairwise social preferences except with preferring to interact with females over males in flock 1 during the fission-fusion condition. Across all conditions juveniles showed a significant preference to interact with juveniles over adults (Table 3, Figure 1). Across all condition we found no consistent patterns in the social preferences for head colors (Sup Materials 1).

Repeatability of network structure: Adults were able to maintain the connections they had with others between the baseline and introduction period. Structural graph correlation showed high

positive correlations between the baseline and introduction adult networks (gscor = 0.79, CUG test: p = 0.00001).

DISCUSSION

This study described the fine-scale structure of social approaches across changing Gouldian finch flocks. Our results showed that the social organization of Gouldian finch flocks is characterized by sex and age-based assortment patterns. These patterns were robust to changes in group size and composition, with higher levels of female and juvenile homophily occurring in almost every flock we observed. While social assortment can be influenced by a wide range of social and non-social factors, our results suggests that these patterns are driven by the social decisions of juveniles and females. Females maintained higher levels of female-to-female approaches than expected, and significantly preferred to approach females over others in most flocks. Across all conditions, juvenile-to-juvenile approach rates were higher in comparison null expectations, and juveniles preferred to approach other juveniles over adults.

The ability to navigate the risks and benefits of interactions is essential for success in the group (Farine, et al. 2015). There can be significant risks when interacting with novel or aggressive conspecifics, and individuals may buffer against these interactions by becoming selective in whom they approach. Some interactions can have significant benefits, such as access to beneficial social information or experiences necessary for the development of competent behavioral abilities (West & King, 2002). In such cases, individuals may be selective by preferentially interacting with individuals due to the beneficial consequences of those interactions (Hausberger, 1997; Mann & Slater, 1995). To understand the potential risks and benefits of interactions, we must first have a detailed description of how group members allocate their social decisions in the group to see which individuals are preferred or avoided.

Our study found that Gouldian finch females preferentially formed subgroups with other females. In many mammals, females form stable groups with other females whereas males disperse to new groups or all male groups (Ruckstuhl, 2007). Increasingly similar patterns are also being discovered in birds. In red junglefowl, pheasants, brown-headed cowbirds, and others female birds often form cohesive groups and subgroups while males do not (Kohn, King, Scherschel & West, 2011; McDonald, Spurgin, Fairfield, Richardson & Pizzari, 2019; Whiteside, van Horik, Langley, Beardsworth, Capstick & Madden, 2019).

Sex assortment can occur through various behavioral mechanisms. Some have suggested that females prefer to interact with other females to buffer against destabilizing interactions with males. Studies in baboons, horses, and others have shown that the presence of strong stable female relationships are associated with increased survival and fitness (Cameron, Setsaas & Linklater, 2009; Carter, Lee, Marshall, Ticó & Cowlishaw, 2015; Silk, et al. 2009, 2010) and studies in the cockroach *Diploptera punctata* and guppies have suggested that female aggregations limit intrusions by males (Stanley, Liddiard Williams & Preziosi, 2018). If male interactions have a destabilizing effect, we should also observe that they are preferentially avoided. However, in this study we found that while females interacted more often with other females than expected, male interactions did not consistently occur less likely than expected, suggesting that female preferences may carry other motivations for avoiding males.

Females will also preferentially associate with other females to access valuable social information. Cues displayed by females can communicate mate and song preferences and exposure to these cues can shape reproductive, competitive, and social decisions in females (Freed-Brown & White, 2009; West, King, White, Gros-Louis & Freed-Brown, 2006). In brown-headed cowbirds, females acquire mate preferences through interactions with other females, and females who were more familiar with each other during the fall are more competitive with each other during the breeding season (Kohn, in prep). Cowbird flocks also segregate according to age and sex in response to specific stimuli, such as playback of specific songs (Gros-Louis, White, King & West, 2003). While little is known about the mate preferences of Gouldian finches, relationships between females may allow females to monitor the preferences of others. In our flock two of the strongest connected females (FYER and FB2G) were both paired with the same male (MBNB). While further research should investigate the broader consequences of female-to-female interactions, our findings suggests that female interactions may be preferred beyond simply avoiding males.

Our study documented a consistent pattern of age assortment in Gouldian finch flocks, with juveniles preferring interactions with other juveniles across flock changes. Most studies of avian development focus on adult-juvenile interactions to understand the horizontal transmission of social information from adults to juveniles. Nonetheless, it is increasingly recognized that peer and sibling interactions are essential for species-typical development, and isolation from peers causes behavioral deficiencies that negatively impact performance in a wide range of social contexts, from integration into groups to reproductive success (Garnetzke-Stollmann & Franck, D. 1991; Hudson, Bautista, Reyes-Meza, Montor & Rödel, 2011; Liévin-Bazin, Pineaux, Le Covec, Gahr, Bovet & von Bayern 2019). While studies of peer interactions have been largely restricted to social mammals, especially primates, this study suggests that peer interactions are an unexplored area in avian social development. Little is known about sibling and peer interactions in juvenile birds, especially after individuals become independent of their parents. Nonetheless, when followed beyond independence, studies have shown that birds often sustain connections with siblings and peers until sexual maturity .

A diverse range of factors may cause the formation of sibling and peer groups in juvenile birds. Some have suggested that competition around patchy food resources may drive juvenile subgroups, in which juveniles form “gangs” with other juveniles that allow them to compete with others for access to limited food sites. Studies have found that in juvenile hihi (*Notiomystis cincta*) and ravens (*Corvus corax*), individuals preferentially associate with juveniles around contested spaces (Franks, Ewen, McCready, Rowcliffe, Smith, D & Thorogood, 2020; Marzluff, Heinrich & Marzluff, 1996). Others have suggested that social groups formed to protect individuals from predation. In some birds such as spectacled parottlets, parents bring their offspring to areas with unrelated juveniles that serve as crèches, suggesting adults play the causal role in the formation of subgroups (Garnetzke-Stollmann & Franck, 1991, Velando, 2001, Wanker, Bernate, & Franck, 1996). In other cases, adults avoid or are aggressive towards juveniles, forcing juveniles to preferentially associate with peers.

Our results suggest that juvenile Gouldian finches self-assort by preferentially choosing to interact with siblings and peers after becoming independent of their parents. This is among the

few examples of self-assortment of juveniles within passerine flocks (Hötker, 1982; Kohn, King, Scherschel, & West, 2011; Nicolai, 1956; Templeton, Reed, Campbell & Beecher, 2012). While adults did tend to avoid interactions with juveniles, juveniles significantly preferred to interact with each other over adults. Both male and female juveniles spend considerable time engaging in peering displays and exchanging courtship-like hopping and head shaking displays with other juvenile siblings in a play-like manner (Kohn, personal observation). Play behavior is expressed preferentially in juveniles and allows individuals to acquire the skills to dynamically adjust behavior to ambiguous social cues (Pellis, Pellis & Bell, 2010). Thus, juvenile subgroups may facilitate the horizontal co-construction of social skills necessary to navigate interactions during later periods (Kohn, 2019). While play has been documented in birds (Diamond & Bond, 2003; Pellis, 1981) its extent and influence in juvenile passerines is not fully known. Current studies are looking at the specific details of juvenile-to-juvenile interactions and comparing it to the interactions between juveniles and adults.

Head color did not seem to be an important factor in shaping the social organization of Gouldian finch flocks. While significant in the ERGM model, further analysis in each condition showed no clear pattern in either approach or avoidance between individual of differing head colors. This result held both when juveniles were included with their eventual adult plumage, and when juveniles were removed form the analysis. However, in this study, head colors were biased according to the sex of the individual, with black being more prominent in females and red being more prominent in males. Further studies will likely be needed to conclusively determine the extent that head color shapes social networks in this species.

From guiding the ontogeny of species-typical abilities to constraining patterns of cultural evolution across populations, the social organization of groups is the pivot upon which many social phenomenon orbit. Describing the social decisions individuals make in fluid naturalistic conditions is essential to understanding the factors underlying the emergence of group organization. This study is among the first to show that the behavioral decisions made across age-sex classes reconstruct patterns of social organization in fission-fusion Gouldian finch groups. As birds are heavily dependent on socially transmitted information this study suggests that the emergence of an organized network of social connections provides the structured environment necessary the development of avian behavioral competencies.

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Table 1: Results from the Exponential Random Graph Models

Condition	Homophilly	Coefficient	s-Error	z-value
Baseline	Sex	3.58345	0.035	102.38*
	Age	0.62427	0.03701	16.87*
	Head Color	0.44437	0.03884	11.44*
Fusion	Sex	3.26371	0.02299	141.99*
	Age	0.71065	0.02992	23.75*
	Head Color	0.87981	0.03046	28.89*
Fission-Fusion Flock 1	Sex	2.18036	0.05905	36.92*
	Age	1.42661	0.05497	25.95*
	Head Color	0.9629	0.05097	18.89*
Fission-Fusion Flock 2	Sex	2.17984	0.06002	36.32*
	Age	1.42576	0.05448	26.17*
	Head Color	0.96428	0.05127	18.81*

Results from the ERGM model for the baseline, fusion and fission-fusion flocks. The * symbol indicates a significant effect below 0.0001.

Table 2: Permutation tests for Interaction Types

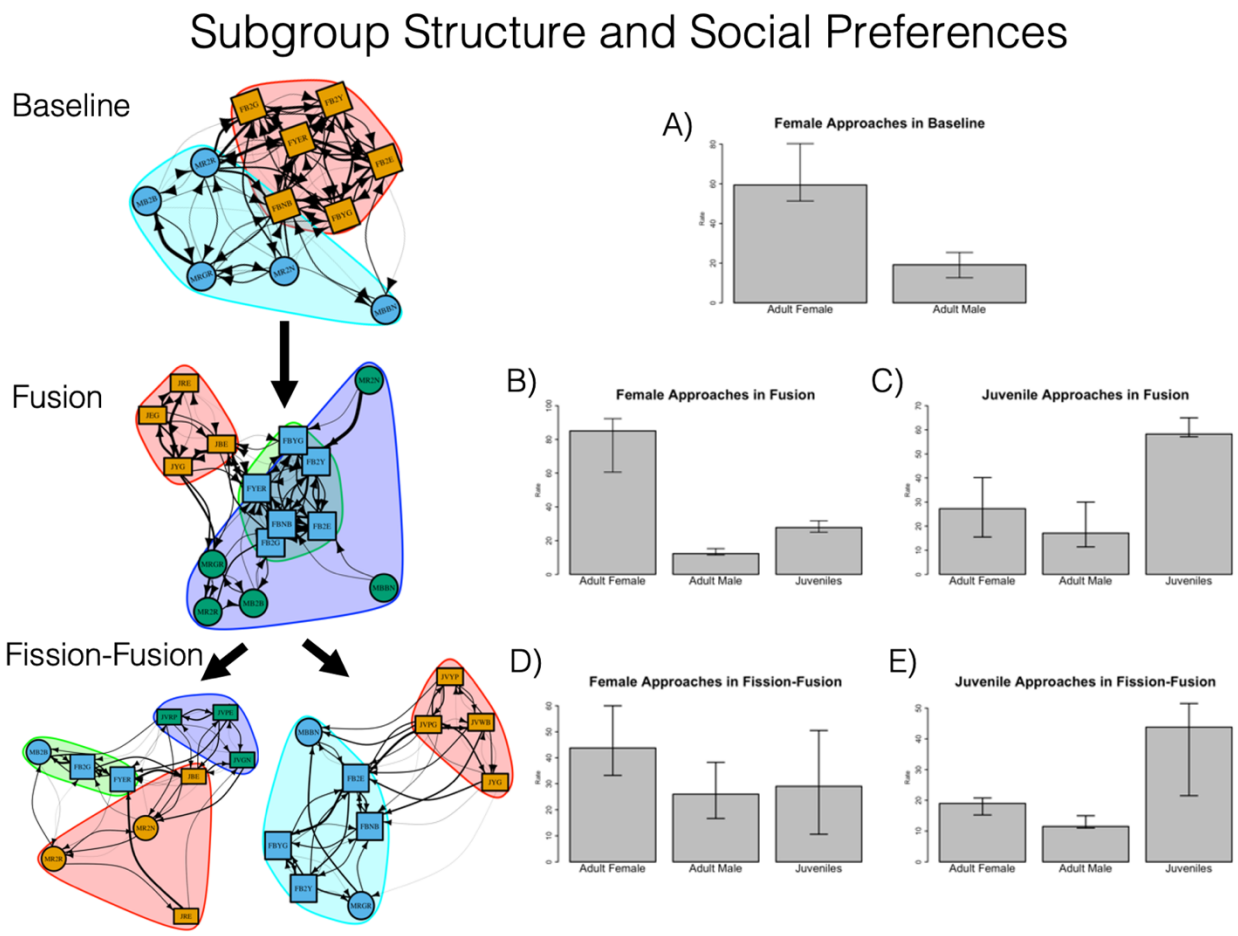
Condition	Interaction	Mean	97.5 Int	p-value Up	p-value Down
Baseline	F-F	66	39 -53	< 0.0001*	0.99
	F-M	18	34-55	0.65	0.35
	M-F	58	37-61	0.06	0.95
	M-M	38	35 - 63	0.92	0.07
Introduction	F-F	80.97	33-57	< 0.0001*	1.00
	F-M	13.46	30-59	1.00	< 0.0001*
	F-J	28.62	29-61	0.97	0.02*
	M-F	57.36	25-51	< 0.0001*	0.99
	M-M	28.24	24-54	0.89	0.11
	M-J	21.15	23-58	0.01*	0.99
	J-F	27.54	24-43	0.86	0.13
	J-M	18.65	22-44	0.99	< 0.0001*
	J-J	59.37	20-47	< 0.0001*	0.99
Flock 1	F-F	60	4-63.75	0.04	0.96
	F-M	15.5	5.83-49	0.55	0.45
	F-J	10.3	8.2-35.4	0.91	0.10
	M-F	47.33	5.33-39.33	< 0.0001*	1.00
	M-M	12	6.67-32.11	0.70	0.30
	M-J	8.07	8.6-25.6	0.99	0.01
	J-F	18	12.1-39.3	0.81	0.20
	J-M	15.01	14.67-35.53	0.97	0.03
	J-J	32.96	17.8-31.52	0.01*	0.99
Flock 2	F-F	37.7	13-30	< 0.0001*	1.00
	F-M	33.12	9.25-36.4	0.06	0.94
	F-J	10.375	14-30	0.99	< 0.0001*
	M-F	31.5	6.75-29.5	0.01*	0.99
	M-M	11.75	4.5-38.25	0.70	0.30
	M-J	7	6.75-29.625	0.97	0.03
	J-F	18.65	17.65-38.875	0.96	0.04
	J-M	11	12.375- 46.50	0.99	0.01*
	J-J	46	17.625-38.9375	< 0.0001*	0.99

This table shows if specific interaction types occurred above and below null expectations. A significant p-value are indicated by the * symbol. Mean represents the observed mean approach rate and the 97.5 column represent the 95.6 is the confidence interval for the permuted mean approach rate. P-value up above represents mean approach rates that occurred above null expectations, whereas the p-value down below represent mean approach rates that occurred below null expectations.

Table 3 Permutation tests for Interaction Preferences

Condition	Comparison	Mean Difference	97.5 Int	p-value
Baseline	FF-FM	23.1	-37.52	0.007*
	MM-MF	-20.14	-24.7-25.03	0.94
Introduction	FF-FM	67.51	-2.37-2.31	< 0.00001*
	FF-FJ	52.35	-2.55-2.43	< 0.00001*
	MM-MF	-29.12	-24.1-25.8	0.99
	MM-MJ	7.09	29.02-27.1	0.34
	JJ-JF	31.83	-19.42-20.44	< 0.00001*
	JJ-JM	40.72	-20.3-21.0	< 0.00001*
Flock 1	FF-FM	44.5	-40-52.4	0.04
	FF-FJ	49.7	-40-52.4	0.03
	MM-MF	-35.33	-28.6-23.6	1.00
	MM-MJ	3.933333	-17.6-22.13	0.36
	JJ-JF	14.46	-19.08-13.6	0.01*
	JJ-JM	17.89333	-16.21-15.4	0.001*
Flock 2	FF-FM	4.5625	-19.7-17.8	0.33
	FF-FJ	27.3125	-15.2-15.2	< 0.00001*
	MM-MF	-19.75	-22.12-27.1	0.95
	MM-MJ	4.75	-22-27.25	0.35
	JJ-JF	35	-19.7-17.8	< 0.00001*
	JJ-JM	27.375	-19.7-17.8	< 0.00001*

This table shows significant pairwise interaction preferences. The letter F stands for adult females, M for adult males and J for juveniles. The type of interaction is indicated by two letters such that the direction of approach is indicated by the first letter ad initiator and the second letter as the receiver. For example, FF is female-to-female and MJ is male-to-juvenile approaches. Comparison column represents which differences between mean approach rates are investigated. For example, FF-FJ represents the mean difference in approach rates from female-to-female approaches subtracted by female-to-juvenile approach rates. Significant p-values are indicated by the * symbol. Mean difference represents the observed mean difference.The 97.5 column represent the 95.6 is the confidence interval for the permuted mean differences.



Changes in social network subgroup structure across the baseline, fusion, and fission-fusion conditions. Shapes represent individuals and arrows represent the approaches between individuals. Communities identified via the spinglass algorithm are outlined in each social network as a cluster of individuals. Rectangles represent juveniles, circles represent adult males and squares represent adult females. Bar graphs represent the mean approach rates of adult females and juveniles in the three conditions. Error bars represent 95% confidence intervals.

Picture of juvenile subgroup. Associations between juveniles often resulted in visually clustered associations within the larger flock.