Article

Multilayer social networks reveal the social complexity of a cooperatively breeding bird

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Highlights

We analyzed the effects of individual and environmental traits on various social networks

We also illustrated individuals' social niches resulting from all six interaction types

Depending on the interaction type, the effect of the traits varied across networks

Only age affected individuals' social niches

Article

Multilayer social networks reveal the social complexity of a cooperatively breeding bird

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SUMMARY

The social environment of individuals affects various evolutionary and ecological processes. Their social environment is affected by individual and environmental traits. We assessed the effects of these traits on nodes and dyads in six layers of networks of Arabian babblers, representing different interaction types. Additionally, we tested how traits affect social niches in the multilayer networks using the t-distributed stochastic neighbor embedding (tSNE) dimensionality reduction algorithm. The effect of group size and season was similar across network layers, but individual traits had different effects on different layers. Additionally, we documented assortativity with respect to individual traits in the dominance display and allopreening networks. The joint analysis of all six layers revealed that most traits did not affect individuals' social niches. However, older individuals occupied fewer social niches than younger ones. Our results suggest that multilayer social networks are an important tool for understanding the complex social systems of cooperative breeders and intragroup interactions.

INTRODUCTION

Animal species live in a variety of asocial or social systems. Social relationships among individuals in a population have been shown to impact a range of ecological and evolutionary processes, via their effects on pathogen transmission, sexual selection, reproductive success, and survival (Cantor et al., 2021; Kurvers et al., 2014). It is thus important to understand the forces and individual traits shaping the structure and dynamics of animal social networks. Traditionally, social relationships were defined using a single interaction type, such as aggression, grooming, or coordinated activity. The primates literature stands out in using multiple interaction types to estimate the strength of social relationships (Kulahci et al., 2017; Pereira et al., 2020; Seyfarth et al., 2012; Smith-Aguilar et al., 2018); however, multiple interaction types were recorded in other taxa as well (Drewe, 2010; Gadagkar, 2001).

Social network analysis is a useful tool that provides researchers with the means to analyze and compare the structure of animal societies across different taxa and social systems. An emerging subfield within network theory is the study of multilayer networks, in which each layer describes a different interaction type (Fisher and Pinter-Wollman, 2021). Multilayer networks move beyond simple networks and provide a more complex but also more realistic framework (Robitaille et al., 2020). For example, including various layers in the analysis allows researchers to account for interdependencies between different traits in those layers, such as different locations or interaction types (Silk et al., 2018). In baboons (*Papio cynocephalus*), association and grooming interactions were often analyzed together, as affiliative interactions. However, analyzing these two interaction types as separate layers showed that individuals' centrality in each layer was significantly different from centrality in the aggregated network (Finn et al., 2019). A recent study on vervet monkeys (*Chlorocebus pygerythrus*) using multilayer social networks provided additional insights into animal social dynamics (Bonnell et al., 2020). Besides the correlation between males' strength of grooming with females and their social rank found in single network analysis (Young et al., 2017), the study by Bonnell and colleagues also found correlations between different layers of the multilayer network. Specifically, male connectedness with females in grooming networks affected aggression received from other males and consequently increased the number of grooming interactions in future time steps (Bonnell et al., 2020). Multilayer social networks could be especially important for studying the social niches of animals. Social niches are defined as a summary of an individual's social relationships in all social networks in which the individual participates (Flack et al., 2006).

Social relationships and the position of individuals within their social networks depend on individuals' traits. For example, older humans and chimpanzees maintain fewer social relationships than younger individuals (Rosati et al., 2020). Sex also strongly affects the social relationships of animals (Jacoby et al., 2010; Spiegel et al., 2018), with the philopatric sex usually found to establish stronger bonds (Podgórski et al., 2014; Seyfarth et al., 2012). Other traits that were found to affect individuals' positions in social networks include personality (Aplin et al., 2013), hormone levels (Boogert et al., 2014), and social rank (Ilany et al., 2015). Besides individual traits, other factors also affect individuals' social relationships such as group size (Pollard and Blumstein, 2011) and food availability (Holekamp et al., 2012). Yet, little is known about the effects of individual and environmental traits on individuals' positions in multilayer social networks. A trait that implies high centrality in one network may cause the opposite effect in another network, highlighting trade-offs and sources of variation in social behavior. Studying multiple traits in the context of a multilayer network should provide a comprehensive account of how traits shape the social structure and may advance the understanding of social niches and the evolution of social behavior.

The Arabian babbler (*Argya squamiceps*) is a cooperatively breeding passerine bird species living in deserts in the Middle East. Group members help to raise the offspring of the dominant breeding pair. Group size varies between 2 and 17 (Keynan and Ridley, 2016). Most of the groups are "simple" family groups, composed of a dominant mating pair and their offspring as helpers. Some groups are "complex," composed of more than two potential breeders. In complex groups, subordinate individuals have a small chance to reproduce (0–5% chance for males and 0.5% for females) (Lundy et al., 1998). Each group occupies the same territory all year round. They have a clear, age-dependent linear hierarchy structure (Dattner et al., 2015; Zahavi, 1991). Their mating season spans from February to July, during which they can have up to four broods with usually four eggs in each clutch (Ostreiher, 1999). Arabian babblers are considered adults when they are one year old (Ostreiher, 1999; Ridley, 2007). They interact with conspecifics in multiple ways, including allooreening, playing, proximal foraging, and agonistic interactions (Kalishov et al., 2005; Zahavi, 1991).

The first aim of our study was to test multiple hypotheses regarding the structure of multilayer social networks in a wild Arabian babbler population (Figure 1). We asked how sex, age, group size, and season affect the position of individuals within networks. We predicted that males will be more central than females in dominance display and proximal foraging networks, while in other networks, the difference will be small or insignificant. Furthermore, younger individuals were expected to be more central than older individuals in scrounging, playing, and proximal foraging networks. Additionally, we expected more interactions during autumn because food is more abundant and the days are longer. We hypothesized that individuals will be selective about the distribution of interactions and hence that group size will have a limited effect on individuals' centrality and that most interactions will be between individuals of the same sex or age class.

Our second goal was to quantify the social niche, that is, the individual's position within the multidimensional social space. We predicted that there should be recurring positions across groups when considering several types of interactions. For example, we predicted that the highly skewed reproduction (Lundy et al., 1998) and stability of family groups (Zahavi, 1991) will result in different social niches for breeding versus non-breeding individuals. Different social interests could cause behavioral differences between parents and their offspring. Furthermore, parents in family groups are residents as long as their partner is present, which could favor their intra-group interactions compared with their offspring. Additionally, as males are more likely to stay in their natal groups (Ridley and Huyvaert, 2007), we expected differences in social connectivity between males and females. Specifically, males were predicted to benefit more than females from establishing stronger social bonds within their groups.

RESULTS

Factors correlated with individuals' strength

Using generalized linear mixed models (GLMMs), we identified the factors correlated with individuals' strength in each interaction layer of the network.

Playing

Age was strongly correlated with node strength in the playing network, with older individuals having lower strength ($\beta = -1.74$, $p < 0.001$; Table 1). Sex and group size were not associated with node strength. Playing was more common during autumn than during winter ($\beta = -2.16$, $p = 0.005$; Table 1).
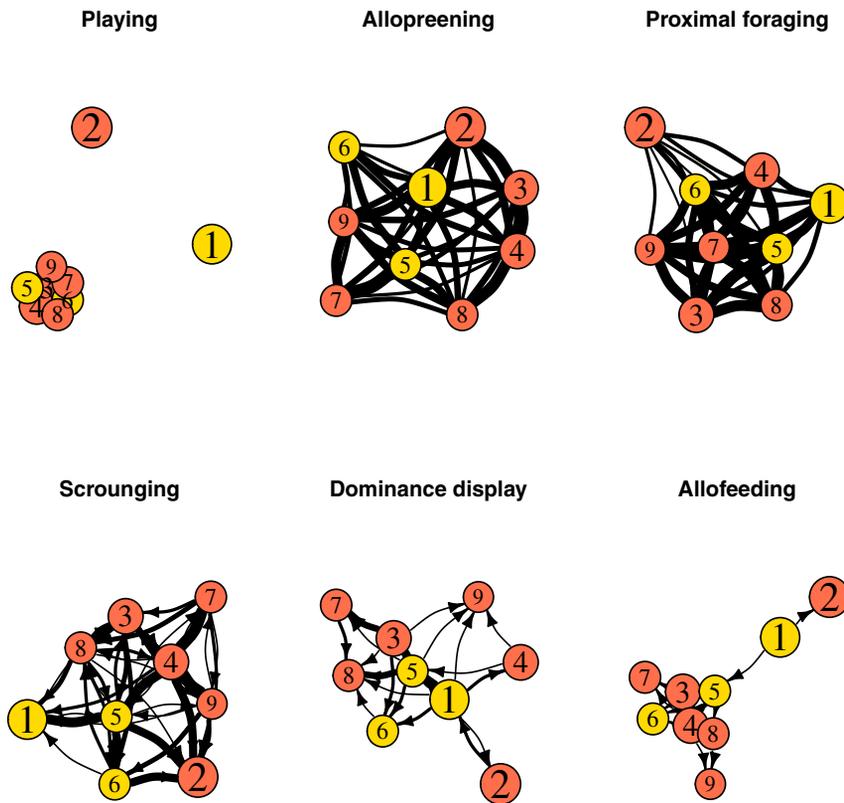
Figure 1. Differences between layers in a multilayer social network

Each layer is constructed based on a single interaction type. The size of nodes represents individuals' age. Males are depicted in yellow, and females in red. The number in nodes shows social rank within the group, with 1 being the highest-ranked babbler.

Allopreening

Age and group size were not correlated with the number of allopreening interactions. Males had interacted more than females ($\beta = 0.11$, $p = 0.021$). Individuals interacted significantly less during winter ($\beta = -0.57$, $p = 0.036$; Table 1).

Proximal foraging

While other interactions were more common during autumn, proximal foraging was significantly more common during winter ($\beta = 0.137$, $p < 0.001$; Table 1). Group size was positively correlated with node strength ($\beta = 0.24$, $p < 0.001$; Table 1). Age was negatively correlated with node strength ($\beta = -0.31$, $p =< 0.001$; Table 1). There was no significant difference between males and females.

Scrounging

Younger individuals were more likely to be scroungers because scrounging out-strength was lower for older individuals ($\beta = -1.33$, $p < 0.001$; Table 1), while older individuals were usually producers (age had a positive effect on scrounging in-strength; $\beta = 0.527$, $p < 0.001$; Table 1). Scrounging in-strength was significantly more common during autumn ($\beta = -1.065$, $p = 0.014$; Table 1).

Dominance display

Sex significantly affected the number of dominance displays, with males being actors more often ($\beta = 0.86$, $p < 0.001$; Table 1) and females being receivers more often ($\beta = 0.379$, $p = 0.013$; Table 1). Age was positively correlated with dominance display out-strength ($\beta = 0.5$, $p = 0.009$; Table 1) and negatively correlated with dominance display in-strength ($\beta = -1.585$, $p < 0.001$; Table 1). Individuals in larger groups were more aggressive, with dominance display out-strength being positively correlated with group size ($\beta = 0.164$, $p < 0.001$; Table 1). As with the other directed interactions, individuals were less active during winter (out-strength $\beta = -0.78$, $p < 0.001$; in-strength $\beta = -0.572$, $p = 0.016$; Table 1).

Table 1. Effects of individual traits on individuals' strength

	Playing strength	Allopreening strength	Proximal foraging strength	Scrounging out-strength	Scrounging in-strength	Dominance display out-strength	Dominance display in-strength	Allofeeding out-strength	Allofeeding in-strength
Intercept	**8.373**	**3.726**	**4.099**	**6.185**	**1.197**	**−1.656**	**4.752**	**−2.202**	**7.389**
Sex (male)	0.024	**0.113**	0.052	0.138	0.021	**0.864**	−0.379	0.014	**−0.559**
Age (log10)	**−1.738**	0.092	**−0.312**	**−1.330**	**0.527**	**0.500**	**−1.585**	**1.038**	**−1.844**
Group size	−0.043	−0.057	**0.240**	−0.037	−0.001	**0.164**	0.126	**0.044**	**−0.178**
Season (winter)	**−2.163**	**−0.573**	**0.137**	**−0.691**	**−1.065**	**−0.783**	**−0.572**	**−1.413**	**−0.963**

Values are coefficients calculated using GLMM (Model 1). Significance was calculated using the null model approach, with random data sets generated through node permutation. Significant values (p < 0.05) are in bold. Standard errors and p values are presented in Tables S1–S9. For categorical factors (sex and season), the reference values are "female" for sex and "autumn" for seasons.

Allofeeding

Females were more likely to be receivers of allofeeding interactions ($\beta = -0.559$, p = 0.004; Table 1). Age had a positive effect on out-strength ($\beta = 1.038$, p < 0.001; Table 1) and negative effect on in-strength ($\beta = -1.844$, p < 0.001; Table 1). Both out-strength and in-strength were lower during winter ($\beta = -1.413$ and $\beta = -0.963$, p = 0.007; Table 1).

Factors correlated with association strength

The summary of Model 2 is presented in Table 2. Sex, age, group size, and season were correlated with dyads strength similarly to node strength for the majority of interaction types. However, in allopreening and dominance display networks individuals showed assortativity in their connectedness based on age and sex.

Allopreening

Although sex did not significantly affect individuals' strength, it affected their assortativity. Male-male dyads were significantly stronger than female-female dyads ($\beta = 0.251$, p < 0.001; Table 2). In Model 1, there was also no correlation between node strength and age. However, analysis of dyads showed a difference

Table 2. Effects of traits on dyads' strength

	Playing	Allopreening	Proximal foraging	Scrounging	Dominance display	Allofeeding
Intercept	**1.568**	**3.176**	**2.100**	**2.528**	**−0.744**	**1.631**
Sex (male-female)	−0.003	0.051	−0.005	**−0.196**	**0.517**	−0.017
Sex (male-male)	0.001	**0.251**	0.048	0.035	**0.751**	**−0.598**
Age class (adult-yearling)	**1.465**	−0.113	**0.131**	−0.044	**−0.578**	−0.218
Age class (adult-early clutches)	**1.823**	**−0.341**	0.097	**0.399**	**−0.602**	0.172
Age class (adult-late clutches)	**1.464**	**−0.427**	**0.215**	**0.446**	**−0.567**	−0.467
Age class (yearling-yearling)	**3.824**	0.005	**0.535**	**0.493**	**−0.413**	−0.075
Age class (yearling-early clutches)	**4.084**	−0.166	**0.488**	**0.725**	**−0.617**	**0.894**
Age class (yearling-late clutches)	**3.658**	**−0.478**	**0.370**	**0.729**	−0.054	**1.222**
Age class (early clutches-early clutches)	**4.177**	−0.271	**0.496**	**0.641**	0.429	−0.252
Age class (early clutches-late clutches)	**3.973**	**−0.472**	**0.545**	**0.436**	−0.034	**0.689**
Age class (late clutches-late clutches)	**3.877**	−0.206	**0.793**	**0.667**	**0.554**	0.448
Group size	**−0.351**	**−0.170**	**0.107**	**−0.191**	0.081	**−0.279**
Season (Winter)	**−2.717**	**−0.606**	**0.142**	**−0.906**	**−0.756**	**−1.175**

Presented values are coefficients calculated using GLMMs (Model 2). Significance was calculated using a null model approach, with random data sets generated by node permutation. Significant values (p < 0.05) are in bold. Standard errors and P values are presented in Tables S10–S15. For sex, the reference value was "female-female" dyads, "adult-adult" for age class, and "autumn" for season.
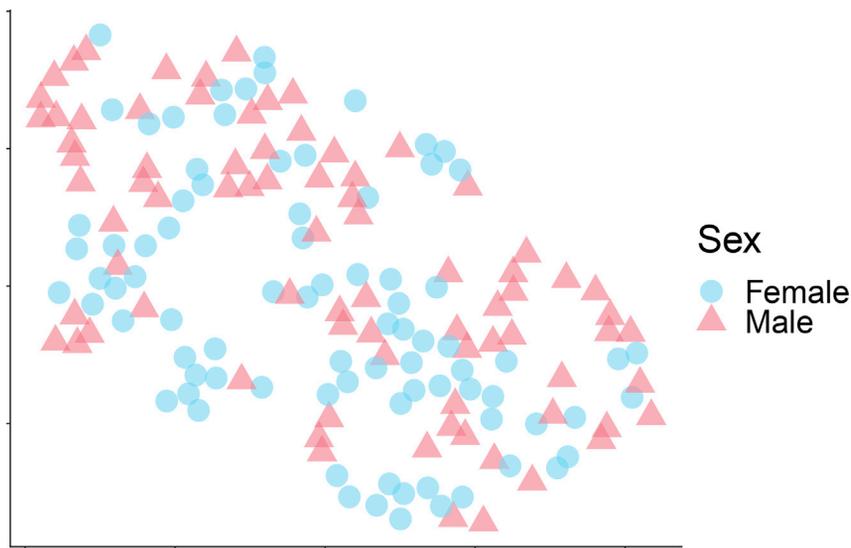
Figure 2. Males and females occupied similar social niches
The t-SNE analysis of all six layers of the network showed almost no differences between males and females.

between dyads within age classes (adult-adult, yearling-yearling, and early clutches-early clutches) and between different age classes (Table 2). Adult-yearling dyads were not different from adult-adult dyads. Furthermore, late clutches-late clutches dyads were significantly different from adult-adult dyads ($\beta = -0.2016$, $p = 0.02$; Table 2). Although group size was associated with individuals' strength, it was not significantly associated with the strength of dyads.

Dominance display

Males were more involved in dominance display because both male-female dyads ($\beta = 0.517$, $p < 0.001$; Table 2) and male-male dyads ($\beta = 0.751$, $p < 0.001$; Table 2) were significantly stronger than female-female dyads. Adults were mostly producing dominance display toward other adults, whereas dyads with other age classes were significantly weaker (Table 2). Table 1 shows that age was negatively correlated with dominance display. Additionally, Table 2 shows that younger individuals were less selective about their dominance display than adults. The only outlier was dyads between yearlings and early clutches ($\beta = -0.616$, $p = 0.011$; Table 2). Group size did not affect dyads, but there were fewer dominance displays during winter ($\beta = -0.756$, $p = 0.046$; Table 2).

Multilayer network analysis and t-SNE

We used both node and dyad strength for the visualization of social niches. For Figures 2, 3, and 4, we applied t-SNE on a multidimensional matrix with nine axes, where each axis was individuals' strength in a different layer of the network. For directed interactions, we used both in-strength and out-strength. All axes were normalized. Sex did not affect the distribution of points across the graph (Figure 2). In contrast, age and breeding status affected the distribution. Older individuals occupied fewer social niches (Figure 3), especially parents, with almost all breeding individuals having similar interaction patterns (Figure 4).

For Figure 5, we applied t-SNE on a multidimensional matrix with six axes: dyads strength in each social network layer. The breeding status of individuals affected their social niches, with a clear difference between dyads including parents and dyads between siblings (Figure 5). Other traits did not affect the social niche.

DISCUSSION

We provide a detailed multifaceted description of sociality in a cooperative breeder, the Arabian babbler. Our analysis applies a multilayer network approach, emphasizing that social relationships and the structure of animal societies may vary substantially when observed via different lenses, such as different interaction types. In general, we find that the position of individuals within their social networks varies but can be explained by individual traits such as sex and age (Figure 6). Individual traits also affected with whom individuals will interact, focusing
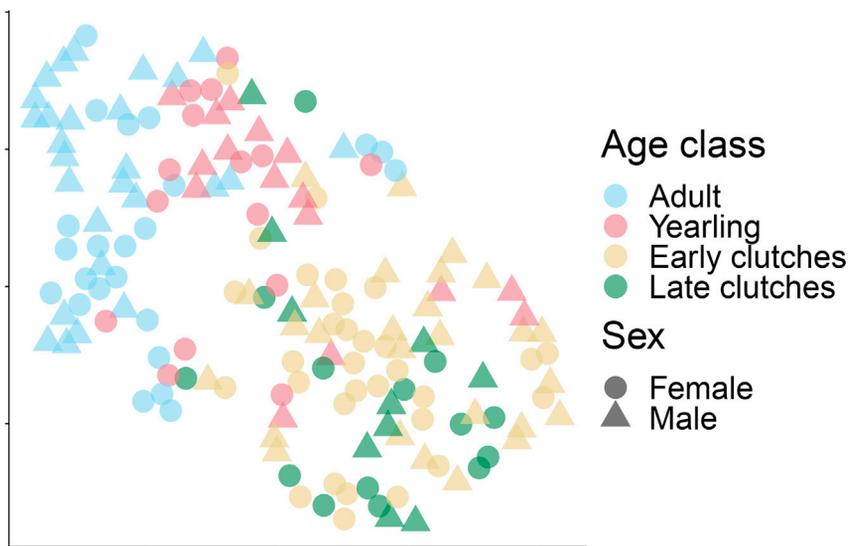
Figure 3. Social position stabilized when individuals reached their second year

Each point represents a value calculated by applying the t-SNE algorithm on individuals' strengths in six different network layers. Adult individuals (blue) had similar positions in the multilayer social network. In contrast, the strength of young individuals (red, yellow, and green) varied across different groups.

their social time on individuals of the same sex or age class (Table 2). In addition, individuals' social output varies seasonally and depending on group size, demonstrating flexibility in social decision-making in this group-living bird. Different social niches, describing the multidimensional aspects of centrality in interaction networks, were occupied by parents versus helpers, and another stratification corresponds to age. In contrast, the two sexes did not occupy different social niches. Finally, parent-offspring relationships were different in the multilayer network from those of siblings but cannot be distinguished from parent-parent relationships.

The social environment imposes selective forces on individuals. Both quantitative geneticists and behavioral ecologists have reached the same conclusion: social interactions with conspecifics can influence
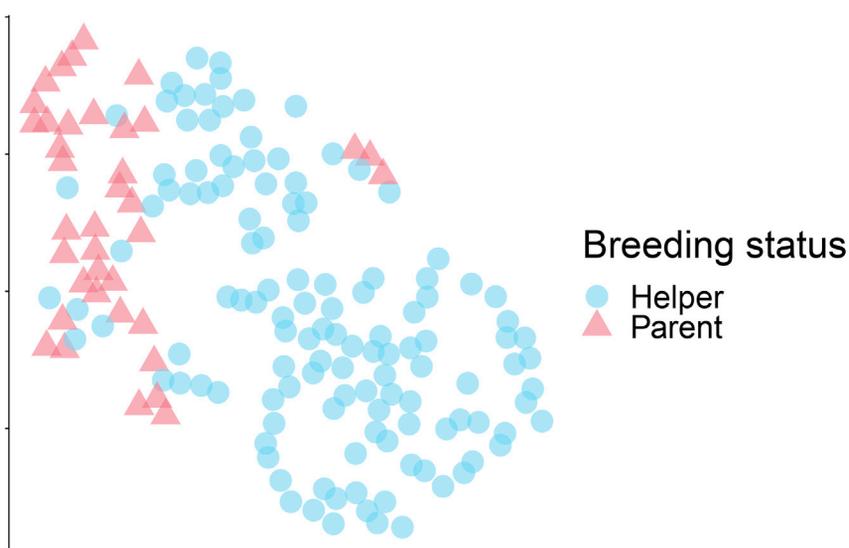
Figure 4. Parents occupied fewer social niches than helpers

Each point represents a value calculated by applying the t-SNE algorithm on individuals' strength in six different network layers. Parents (red) from almost all groups had similar social positions within the multilayer network. Helpers' positions (blue) varied; even individuals from the same group and social status can occupy different social niches.
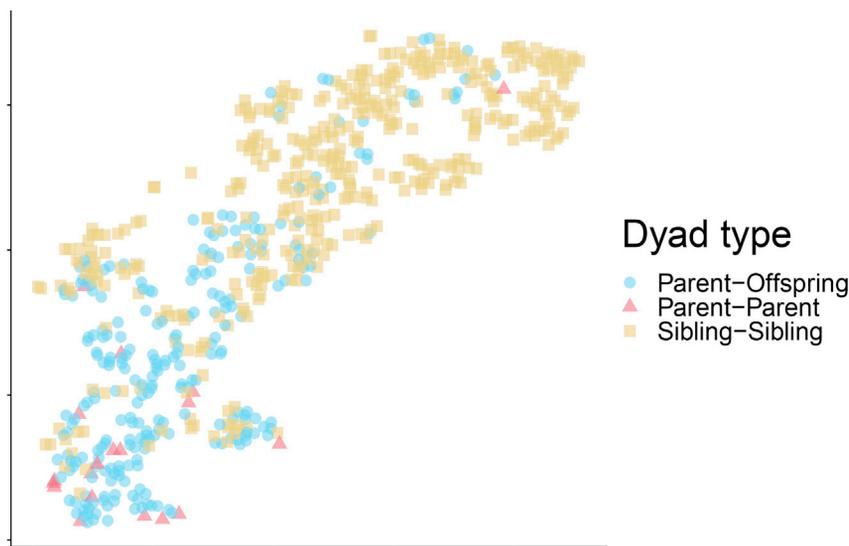
Figure 5. Breeding status affected relationships of Arabian babblers
Each point represents a value calculated by applying the t-SNE algorithm on individuals' strength in six different layers of the networks. Non-breeding individuals formed different relationships with their parents (blue) and their siblings (yellow). There was no difference between parent-parent (red) and parent-offspring (blue) dyads.

both an individual's phenotype and its fitness (reviewed in the study by Fisher and McAdam, 2017). For example, social relationships have been found to affect survival (Barocas et al., 2011; Silk et al., 2010), reproductive success (Barrett et al., 2012), and sexual selection (McDonald, 2007), as well as pathogen and information transmission (Stroeymeyt et al., 2018; VanderWaal et al., 2014). Thus, the position of individuals in their social networks is not expected to be random and may be affected by their traits. Network position has been suggested to be a key component in the characterization of social personality types (Wilson et al., 2013). However, in an ever-changing social network, individuals are expected to be exposed to temporal dynamics even if they are socially passive, and thus, the relationship between a trait such as sex or weight and social position is not straightforward. Several previous studies have demonstrated how traits of individuals affect their position within social networks. These traits include personality, sex, and social rank, among others (Aplin et al., 2013; Ilany et al., 2015; Spiegel et al., 2018). Our findings suggest that traits that affect the social position in one context, for example, in proximal foraging, do not necessarily affect the social position in other contexts. Researchers in this field should carefully consider whether they should aggregate different interaction types into general "affiliative" social networks, as has been conducted before, or, alternatively, construct multilayer networks that will provide a more nuanced description of the social environment. This decision should depend on two main factors. First, there might not be enough data on each layer of the network to allow separation. Second, a preliminary analysis can reveal if the different layers are correlated. No or negative correlation will mean that aggregating multiple layers into a single network may bias inference of the structure of the social network, as contrasting effects may balance each other to show average social relationships that do not actually represent any of their constituents.

The different layers of the network varied in their dependency on the traits of the interacting individuals. Proximal foraging and allopreening, and to a lesser extent scrounging, were more similar across different dyad types (Figure 1). In contrast, playing, allofeeding, and dominance displays were more variable depending on dyad types. We observe that some layers, such as allopreening, may be more "sensitive" to the dyad types. For example, we did not find age to affect allopreening (Table 1). However, when taking the traits of both individuals into account (Table 2), we find that adult-adult dyads are different from dyads between different age classes (Table 2). Despite having the highest average dyad strength, late clutches-late clutches dyads are not significantly different from other dyads which include the youngest individuals, indicating that in early age Arabian babblers are not selective about their allopreening partners. We observed a similar effect in dominance display networks, in which adult-adult dyads were significantly stronger than other dyads involving adults, while other age classes seemed to be less selective about their
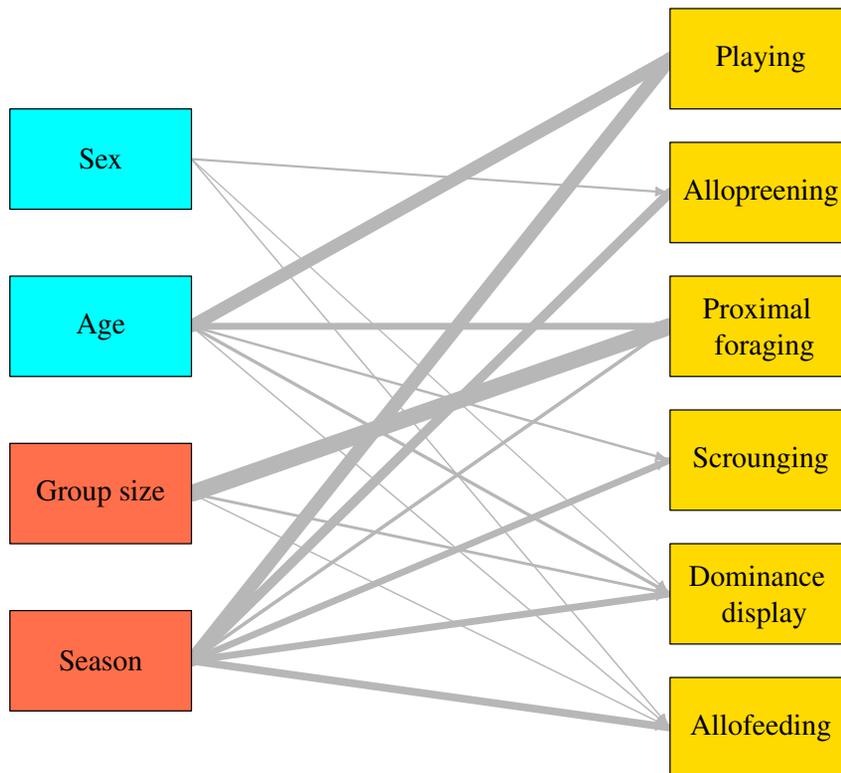
Figure 6. A summary of the individual and environmental effects on Arabian babbler social networks
Line width is proportional to the magnitude of the effect (Z values of Model 1). Only significant effects are presented.
Environmental and individual traits are depicted in red and cyan, respectively.

dominance display (Table 2). Individuals' capacity for social interactions is limited (Byrne and Bates, 2007); hence, they need to prioritize their relationships. That may explain why young individuals invest in playing and dominance display, which is important for their development and social rank in early stages (Ostreiher, 1999), whereas adults invest in allopreening which is linked to reduced aggression and the possible formation of coalitions (Radford, 2008; Ridley, 2012).

When analyzing the composite node strength of individuals in multiple layers of the network, we find that babblers of different ages, and in different breeding states, occupy different social niches, that is, older and breeding individuals can be clustered in terms of their social interactions to feature similar behaviors. It is remarkable that individuals belonging to different groups, varying in geographical location, group size, and group composition, occupy similar social niches. Although this finding can be partially attributed to the effect of traits on strength in network layers, we also show that the composite sociality description can be predicted by some traits, but not by others. For example, although sex affected individuals' strength in the allofeeding, dominance display, and scrounging layers, it did not play a major role in the overall social niche (Figure 2). Thus, males and females had similar social niches when considering their strength within the multilayer network. In contrast, the two traits that did distinguish between babblers in the multilayer network were temporally variable. Our findings suggest that when babblers age, they change their social niches, for example, by spending less time playing and scrounging while spending more time allofeeding, alloopreening, and in dominance displays. This is in line with behavioral patterns across several mammalian species, including humans (Murphy et al., 2020; Rosati et al., 2020).

This was the first study to record multiple interaction types of Arabian babblers simultaneously, and one of the first to use a multilayer network approach in any species. Although most of the interactions were previously described (Dattner et al., 2015; Pozis-Francois et al., 2004; Zahavi, 1991), the knowledge about their abundance and seasonal character was limited. We limited our analysis to only three individual traits, age, sex, and breeding status, to maintain individuals' habituation throughout the observation period. However,

future studies should aim to describe the effects of other factors as well (e.g., personality, hormone levels, social rank), as well as the effects of sociality on different interaction types. We expect that multilayer network analysis can add insight into the social behavior of many species, especially those with multiple types of interactions.

Limitations of the study

Two main limitations of our study were variation in group size and the properties of animal multilayer networks. In the first two seasons, only three groups had more than six individuals. Hence, there was a significant difference between the smallest (6) and the largest group (15). We controlled for group size in each statistical model, but a more uniform group size would rule out a potential bias. In addition, we focused only on family groups because during all three seasons there were no complex groups with more than four individuals.

Determining the "value" of interactions will probably remain one of the biggest challenges of animal multi-layer social networks. In our t-distributed stochastic neighbor embedding (tSNE) analysis, node and dyad strength from different layers contributed equally to individuals' position in the multiaxis matrix. For example, while aggression is significantly rarer than proximal foraging, the intensity of interaction may impose a similar effect on individuals' social environment. However, different social systems or data collection methods could choose to analyze node strength as non-normalized. For example, if allopreening is more abundant than playing then it should have a stronger effect on nodes' position in the multiaxis matrix. Future studies analyzing relationships between different interaction types could provide a better answer to this question.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

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AUTHOR CONTRIBUTIONS

Conceptualization, All authors; Funding Acquisition, O.K. and A.I.; Data Collection, N.D; Analysis, N.D.; Visualization, N.D.; Writing – Original Draft, N.D. and A.I.; Writing – Review & Editing, All authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour *49*, 227–267.

Aplin, L.M., and Morand-Ferron, J. (2017). Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour. Proc. R. Soc. B Biol. Sci. *284*, 20162872.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A., and Sheldon, B.C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). Ecol. Lett. *16*, 1365–1372.

Barocas, A., Ilany, A., Koren, L., Kam, M., and Geffen, E. (2011). Variance in centrality within rock hyrax social networks predicts adult longevity. PLoS ONE *6*, 1–8.

Barrett, L., Henzi, S.P., and Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. Philos. Trans. R. Soc. B *367*, 2108–2118.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., and White, J.S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. *24*, 127–135.

Bonnell, T.R., Vilette, C., Young, C., Henzi, S.P., and Barrett, L. (2020). Formidable females redux: male social integration into female networks and the value of dynamic multilayer networks. Curr. Zool. 1–17.

Boogert, N.J., Farine, D.R., and Spencer, K.A. (2014). Developmental stress predicts social network position. Biol. Lett. *10*, 1–5.

Byrne, R.W., and Bates, L.A. (2007). Sociality, evolution and cognition. Curr. Biol. *17*, 714–723.

Cantor, M., Maldonado-Chaparro, A.A., Beck, K.B., Brandl, H.B., Carter, G.G., He, P., Hillemann, F., Klarevas-Irby, J.A., Ogino, M., Papageorgiou, D., et al. (2021). The importance of individual-to-society feedbacks in animal ecology and evolution. J. Anim. Ecol. *90* (1), 27–44.

Carlisle, T.R., and Zahavi, A. (1986). Helping at the nest, allofeeding and social status in immature Arabian babblers. Behav. Ecol. Sociobiol. *18*, 339–351.

Croft, D.P., Richard, J., and Krause, J. (2008). Exploring Animal Social Networks (Princeton University Press).

Dattner, A., Zahavi, A., and Zahavi, A. (2015). Competition over guarding in the Arabian babbler (*Turdoides squamiceps*), a cooperative breeder. F1000Research *618*, 1–13.

Drewe, J.A. (2010). Who infects whom? Social networks and tuberculosis transmission in wild meerkats. Proc. R. Soc. B Biol. Sci. *277*, 633–642.

Farine, D.R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. *84*, 1144–1163.

Finn, K.R., Silk, M.J., Porter, M.A., and Pinter-Wollman, N. (2019). The use of multilayer network analysis across social scales in animal behaviour. Anim. Behav. *149*, 7–22.

Fisher, D.N., and McAdam, A.G. (2017). Social traits, social networks and evolutionary biology. Journal of Evolutionary Biology *30*, 2088–2013.

Fisher, D.N., and Pinter-Wollman, N. (2021). Using multilayer network analysis to explore the temporal dynamics of collective behavior. Curr. Zool. *67*, 71–80.

Flack, J.C., Girvan, M., De Waal, F.B.M., and Krakauer, D.C. (2006). Policing stabilizes construction of social niches in primates. Nature *439*, 426–429.

Gadagkar, R. (2001). The Social Biology of *Ropalidia marginata* - toward Understanding the Evolution of Eusociality (Harvard University Press).

Godfrey, S.S., Bull, C.M., James, R., and Murray, K. (2009). Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. Behav. Ecol. Sociobiol. *63*, 1045–1056.

Holekamp, K.E., Smith, J.E., Strelioff, C.C., Van Horn, R.C., and Watts, H.E. (2012). Society, demography and genetic structure in the spotted hyena. Mol. Ecol. *21*, 613–632.

Ilany, A., and Akçay, E. (2016). Social inheritance can explain the structure of animal social networks. Nat. Commun. *7*, 12084.

Ilany, A., Booms, A.S., and Holekamp, K.E. (2015). Topological effects of network structure on long-term social network dynamics in a wild mammal. Ecol. Lett. *18*, 687–695.

Jacoby, D.M.P., Busawon, D.S., and Sims, D.W. (2010). Sex and social networking: the influence of male presence on social structure of female shark groups. Behav. Ecol. *21*, 808–818.

Kalishov, A., Zahavi, A., and Zahavi, A. (2005). Allofeeding in Arabian babblers (*Turdoides squamiceps*). J. Ornithol. *146*, 141–150.

Kam, M., Anava, A., Shkolnik, A., and Degen, A.A. (2003). Energy expenditure and its components in free-living Arabian babblers (*Turdoides squamiceps*). Isr. J. Zool. *49*, 195–202.

Keynan, O., and Ridley, A.R. (2016). Component, group and demographic Allee effects in a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*). Oecologia *182*, 153–161.

Keynan, O., Ridley, A.R., and Lotem, A. (2015). Social foraging strategies and acquisition of novel foraging skills in cooperatively breeding Arabian babblers. Behav. Ecol. *26*, 207–214.

Krause, J., James, R., Franks, D.W., and Croft, D.P. (2014). Animal Social Networks (Oxford University Press).

Krijthe, J.H. https://cran.r-project.org/web/packages/Rtsne/citation.html.

Kulahci, I.G., Ghazanfar, A.A., and Rubenstein, D.I. (2017). Consistent individual variation across interaction networks indicates social personalities in lemurs. Anim. Behav. 1–10.

Kurvers, R.H.J.M., Krause, J., Croft, D.P., Wilson, A.D.M., and Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: emerging issues. Trends Ecol. Evol. *29*, 326–335.

Lundy, K.J., Parker, P.G., and Zahavi, A. (1998). Reproduction by subordinates in cooperatively breeding Arabian babblers is uncommon but predictable. Behav. Ecol. Sociobiol. *43*, 173–180.

van der Maaten, L., and Hinton, G. (2008). Visualizing Data using t-SNE. J. Mach. Learn. Res. *9*, 2579–2605.

McDonald, D.B. (2007). Predicting fate from early connectivity in a social network. Proc. Natl. Acad. Sci. *104*, 10910–10914.

Morand-Ferron, J., Sol, D., and Lefebvre, L. (2007). Food stealing in birds: brain or brawn? Anim. Behav. *74*, 1725–1734.

Murphy, D., Mumby, H.S., and Henley, M.D. (2020). Age differences in the temporal stability of a male African elephant (*Loxodonta africana*) social network. Behav. Ecol. *31*, 21–31.

Newman, M.E.J. (2002). Assortative mixing in networks. Phys. Rev. Lett. *89*, 1–4.

Ostreiher, R. (1999). Nestling feeding-space strategy in Arabian babblers. The Auk *116*, 651–657.

Pereira, A.S., Rebelo, I.D., Casanova, C., Lee, P.C., and Louca, V. (2020). The multidimensionality of female mandrill sociality-a dynamic multiplex network approach. PLoS ONE *15*, 1–14.

Podgórski, T., Lusseau, D., Scandura, M., Sönnichsen, L., and Jędrzejewska, B. (2014). Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. PLoS ONE *9*, e99875.

Pollard, K.A., and Blumstein, D.T. (2011). Social group size predicts the evolution of individuality. Curr. Biol. *21*, 413–417.

Pozis-Francois, O., Zahavi, A., and Zahavi, A. (2004). Social play in Arabian babblers. Behaviour *141*, 425–450.

R Core Team (2020). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing).

Radford, A.N. (2008). Duration and outcome of intergroup conflict influences intragroup affiliative behaviour. Proc. R. Soc. B Biol. Sci. *275*, 2787–2791.

Ridley, A.R. (2007). Factors affecting offspring survival and development in a cooperative bird: social, maternal and environmental effects. J. Anim. Ecol. *76*, 750–760.

Ridley, A.R. (2012). Invading together: the benefits of coalition dispersal in a cooperative bird. Behav. Ecol. Sociobiol. *66*, 77–83.

Ridley, A.R., and Huyvaert, K.P. (2007). Sex-biased preferential care in the cooperatively breeding Arabian babbler. J. Evol. Biol. *20*, 1271–1276.

Robitaille, A.L., Webber, Q.M.R., Turner, J.W., and Wal Eric, V. (2020). The problem and promise of scale in multilayer animal social networks. Curr. Zool. *00*, 1–11.

Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Thompson, M.E., Muller, M.N., Wrangham, R.W., and Machanda, Z.P. (2020). Social selectivity in aging wild chimpanzees. Science *370*, 473–476.

Seyfarth, R.M., Silk, J.B., and Cheney, D.L. (2012). Variation in personality and fitness in wild female baboons. Proc. Natl. Acad. Sci. *109*, 16980–16985.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. Curr. Biol. *20*, 1359–1361.

Silk, M.J., Finn, K.R., and Porter, M.A. (2018). Can multilayer networks advance animal behavior research? Trends Ecol. Evol. *33*, 376–378.

Smith-Aguilar, S.E., Aureli, F., Busia, L., Schaffner, C., and Ramos-Fernández, G. (2018). Using Multiplex Networks to Capture the Multidimensional Nature of Social Structure (Primates).

Sosa, S., Puga-Gonzalez, I., Hu Feng, H., Zhang, P., Xiaohua, X., and Sueur, C. (2018). A multilevel statistical toolkit to study animal social networks: animal Network Toolkit (ANT) R package. BioRxiv, 347005.

Sosa, S., Sueur, C., and Puga-Gonzalez, I. (2021). Network measures in animal social network analysis: their strengths, limits, interpretations and uses. Methods Ecol. Evol. *12*, 10–21.

Spiegel, O., Sih, A., Leu, S.T., and Bull, C.M. (2018). Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure. Anim. Behav. *136*, 207–215.

Stroeymeyt, N., Grasse, A.V., Crespi, A., Mersch, D.P., Cremer, S., and Keller, L. (2018). Social network plasticity decreases disease transmission in a eusocial insect. Science *362*, 941–945.

VanderWaal, K.L., Atwill, E.R., Isbell, L.A., and McCowan, B. (2014). Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). J. Anim. Ecol. *83*, 406–414.

Venables, W.N., and Ripley, B.D. (2002). Modern Applied Statistics with S (Springer).

Wedderburn, R.W.M. (1974). Quasi-likelihood functions, generalized linear models, and the Gauss—Newton method. Biometrika *61*, 439–447.

Weiss, M.N., Franks, D.W., Brent, L.J.N., Ellis, S., Silk, M.J., and Croft, D.P. (2021). Common datastream permutations of animal social network data are not appropriate for hypothesis testing using regression models. Methods Ecol. Evol. *12*, 255–265.

Whitehead, H. (2008). Analyzing Animal Societies (The Universty of Chicago Press).

Wilson, A.D.M., Krause, S., Dingemanse, N.J., and Krause, J. (2013). Network position: a key component in the characterization of social personality types. Behav. Ecol. Sociobiol. *67*, 163–173.

Young, C., McFarland, R., Barrett, L., and Henzi, S.P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. Anim. Behav. *125*, 61–67.

Zahavi, A. (1991). Arabian babblers: the quest for social status in a cooperative breeder. In Cooperative Breeding in Birds (Cambridge University Press), pp. 105–130.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Adjacency matrices	This paper	Zenodo: https://zenodo.org/record/5065274
Experimental models: Organisms/strains		
Arabian babblers (*Argya squamiceps*)		
Software and algorithms		
R 4.0	R Core Team	https://www.r-project.org/
MASS package	(Venables and Ripley, 2002)	http://www.stats.ox.ac.uk/pub/MASS4/
ANTs package	(Sosa et al., 2018)	http://www.s-sosa.com/ants
Rtsne package	(Krijthe, 2015)	https://www.rdocumentation.org/packages/Rtsne/versions/0.15
Cybertracker		https://www.cybertracker.org/

RESOURCE AVAILABILITY

Lead contact

Requests for further information or materials should be directed to the lead contact Dr. Amiyaal Ilany (amiyaal@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All original adjacency matrices have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.

- All R codes used for this paper are available from the lead contact upon request.

- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The study was conducted in the Sheizaf Nature Reserve in the Central Arava, southern Israel. Observations were conducted during three non-breeding seasons, 2017–2020. The non-breeding season of Arabian babblers lasts from September until February. All observed individuals were over four months old and independent foragers (Ridley, 2007). We observed most groups during autumn and winter (two group rounds per season) to control for seasonal effects. We observed nine groups, for a total of 19 group rounds (Table S16). Group size varied between 6 and 15. We observed a total of 94 individuals. After constructing networks, four individuals with unknown sex were omitted from further analysis, hence the total number of analyzed individuals was 90 (47 females and 43 males). Three groups from the first two seasons disintegrated after only one group round, resulting in an unequal number of observations per individual. The majority of individuals, 57, were observed at least two times. The number of analyzed dyads was 415, with more than half of them (230) being analyzed at least two times. Detailed information about observed groups and individuals can be found in the supplemental information. All study groups were simple groups with one breeding pair and their offspring as helpers. We focused on simple groups since during the observation period complex groups were rare (<10 % of the population) and small (<5 individuals). Simple groups are compact; groups move together and collectively defend their territories. We conducted focal observations of Arabian babblers, in which we observed interactions of the focal individual and individuals in its nearby surroundings (Altmann, 1974). The focal individual was randomly selected and followed during a

ten-minute focal session. Each individual was marked with colored rings and observed ten times in each group round (Figure S1). Observations were conducted for 3–4 hours after sunrise when babblers are most active (Ridley, 2007). For recording observations, we used the customizable phone application Cyber-tracker (https://www.cybertracker.org).

METHOD DETAILS

Data collection

We recorded all known interactions of Arabian babblers. Based on previous studies by Zahavi and colleagues we classified them into six interaction types (Carlisle and Zahavi, 1986; Kalishov et al., 2005; Keynan et al., 2015; Pozis-Francois et al., 2004; Ridley and Huyvaert, 2007; Zahavi, 1991). Rare interactions, e.g., morning dance and unsuccessful allofeeding were not included in the analysis. The recorded interactions were stored as adjacency matrices (see supplemental information). Three interaction types were directed interactions - allofeeding, dominance display, and scrounging. Directed interactions had an actor (initiator) and a receiver of the interaction. The other three interaction types - playing, allopreening, and proximal foraging - were undirected, and may include two or more individuals (Farine and Whitehead, 2015; Godfrey et al., 2009). We constructed six networks for each group round, summarizing all ten focal observations of each of the group members. Preliminary analysis showed that the interaction types were correlated (Tables S17–S18). Individuals were set as nodes and the six interaction types as links (Figure 1). Links between nodes were weighted and they represent the frequency of interactions between individuals (Krause et al., 2014). The total number of an individual's interactions represents the strength (weighted degree) of the node.

Recorded interactions

Social play (Video S1) is not frequently observed among birds, but was recorded in several independent lineages (Pozis-Francois et al., 2004). Both juveniles and adult Arabian babblers play. It resembles mammalian social play and includes play-fights, tug-of-war, and displacements. It also includes several play signals: crouching, rolling over, the elevation of sticks, play bow, establishing eye contact, and freezing briefly in the middle of play. Sometimes it can resemble aggressive dominance displays, but it is easy to distinguish those interactions by duration and two-way involvement of the participants (Pozis-Francois et al., 2004).

Allopreening (Video S2) refers to an individual cleaning and grooming other members of the group (Radford, 2008; Zahavi, 1991). Although this interaction has an actor and a receiver, the receiver usually reciprocates immediately. In addition, Arabian babblers often preen in groups. We thus recorded allopreening as an undirected interaction.

Proximal foraging (Video S3) is non-contact interaction similar to proximity interactions recorded in primates (Flack et al., 2006; Smith-Aguilar et al., 2018). Arabian babblers mainly feed on arthropods, as well as fruits, seeds, and flowers (Kam et al., 2003; Keynan et al., 2015). They forage for food in the ground or under the bark of trees. They also occasionally hunt small vertebrates such as lizards, snakes, and even birds. We used the following rule to record proximal foraging: individuals that are foraging next to each other within a 1 m distance for more than 10 seconds. Of note, a group can be split into multiple subgroups of individuals foraging together. Thus, proximal foraging does not necessarily reflect group size.

Scrounging (Video S4) has several definitions in the literature: direct theft (i.e. kleptoparasitism (Morand-Ferron et al., 2007), joining food patches discovered by others (Aplin and Morand-Ferron, 2017), or taking over food patches discovered by others (Keynan et al., 2015). We used all three definitions and recorded scrounging as any interaction where an individual obtains food found by others.

Dominance displays (Video S4) are brief aggressive and ritualized chases, usually towards a lower-ranked individual. An individual can also display dominance by replacing a lower-ranked individual in a sentinel position. Aggressive dominance displays are not harmful. There is no resistance, fight, injuries or casualties. Real fights between group members are rare and usually result in the expulsion of the subordinate individual from the group (Zahavi, 1991).

Allofeeding (Video S5) is the act of an individual feeding another individual within the group. Besides the act of feeding, allofeeding usually contains a specific body posture and calls by the actor and the receiver.

Allofeeding can be an act of parental care or a dominance display, but it is almost always unidirectional in that the donor is a higher-ranked individual (Carlisle and Zahavi, 1986; Kalishov et al., 2005; Zahavi, 1991).

QUANTIFICATION AND STATISTICAL ANALYSIS

Single network analysis

To test whether individuals' traits were associated with strength centrality across different networks we used generalized linear mixed models (GLMM) (Bolker et al., 2009). The analyses were performed in R 4.0 (R Core Team, 2020) and we used the MASS package (Venables and Ripley, 2002). We used the function glmmPQL and quasi-Poisson distribution for over-dispersed data (Wedderburn, 1974). We constructed two models:

Model 1: the response variable was node strength (total number of interactions for each individual). For directed interactions, we analyzed out-strength (sum of links when the individual is the actor) and in-strength (sum of links where the individual is the receiver) separately in the models.

Model 2: we analyzed assortativity and the response variable was the weight of links. Assortativity is the preference of individuals to bond with similar individuals with respect to some trait (Ilany and Akçay, 2016). We assigned the traits of both individuals to dyads. For example, sex had three levels: female-female, male-female, and male-male. The analysis of dyads did not consider directionality (Newman, 2002; Sosa et al., 2021).

The independent variables in both models were sex, age, group size, and season. Group ID was set as a random factor. The ID of individuals (Model 1) and ID of dyads (Model 2) was set as nested random effects within each group. We know the exact date of birth for 86 out of 90 individuals, hence the age of individuals was measured in days. The four individuals without an exact date were ringed as adults, so we know that they were at least one year old when ringed. None of these four individuals were excluded since they were breeding individuals, and thus important group members. Instead, we ran the models with three different age corrections (one, three, and five years) for those four individuals ringed as adults. The results were similar for all three age corrections. The presented numbers are with the age addition of three years. The range of ages was between 4 months (136 days) and 10 years (3500+ days), hence we used a logarithmic transformation of age. In Model 2 using age as continuous or discrete variables provided similar results, however, interpreting the results with age classes was easier. Individuals were separated into four age classes:

1. Late clutches - The youngest individuals in the group, hatched 4–6 months before observations. Individuals at that age are mostly independent (Ostreiher, 1999; Ridley, 2007).

2. Early clutches - Completely independent individuals, 6–12 months old. Arabian babblers rarely disperse from a group in their first year (Ridley, 2007).

3. Yearlings - individuals in their second year (Pozis-Francois et al., 2004).

4. Adults - Individuals over two years old (Ostreiher, 1999; Ridley, 2007).

We used a null model approach to test whether traits were associated with position in social networks more than expected by chance (Farine and Whitehead, 2015; Sosa et al., 2018). Z values from 1000 random datasets were compared to the Z values from our GLMM models. Random datasets were created by node-level permutation of the observed dataset (Croft et al., 2008; Weiss et al., 2021; Whitehead, 2008). We used the "perm.net.nl" function from the "ANTs" package for node permutation (Sosa et al., 2018). The strength of each node was assigned to a random node within the same network. This way we tested if individual traits were linked to individuals' strength while preserving the network structure (Sosa et al., 2018). We applied the same permutation method for Model 2.

Multilayer network analysis

To analyze all networks as multidimensional objects we used strength from the single-interaction networks. We used the dimension reduction algorithm t-SNE to represent the multi-axis matrix as a two-dimensional plot (van der Maaten and Hinton, 2008). This algorithm finds similarities between the different axes and returns two axes. The main advantage of the t-SNE algorithm over the most commonly used dimension

reduction algorithm PCA (Principal Component Analysis) is that it also accounts for non-linear correlations between axes (van der Maaten and Hinton, 2008). We treated individual's strength in each network as a different axis. In the case of node strength, we had nine axes: playing, allopreening, and proximal foraging strength, as well as scrounging, dominance display, and allofeeding in-strength and out-strength. The t-SNE algorithm returns two axis which individually cannot be interpreted, however, points that are close to each other in the t-SNE plot represent similarity in the multi-axis matrix. For dimension reduction we used the R package "Rtsne" (Krijthe, 2015). All interaction types were treated as equal, therefore they were normalized using the "normalize_input" function from the "Rtsne" package, which sets the mean strength of each network to zero and equally scales individuals' strength in different networks. Values were normalized for each group round separately. Perplexity was set to 15 and the maximum number of iterations was limited to 2000. Beside using individuals as points, we also analyzed dyads. In the case of dyads, there were six axes representing dyadic weights in each network.