Here, we present a protocol for collecting data on multiple interaction types in small, stable groups of Arabian babblers (*Argya squamiceps*). We describe the procedure of habituation, the recording of social interactions, and how to classify the interaction types. Additionally, we provide code for testing, comparing, and visualizing data. The high-resolution data collection is time demanding and requires several data tests before forming the final protocol. The collected data can then be used for multiplex social network analysis.

Publisher’s note: Undertaking any experimental protocol requires adherence to local institutional guidelines for laboratory safety and ethics.
Protocol

Protocol to record multiple interaction types in small social groups of birds

Nikola Dragić,1,3,* Oded Keynan,2 and Amiyaal Ilany1,4,*

1Faculty of Life Sciences, Bar Ilan University, Ramat Gan 5290002, Israel
2Dead Sea and Arava Science Center, Central Arava Branch, Hatzeva 86815, Israel
3Technical contact
4Lead contact
*Correspondence: gidra90@gmail.com (N.D.), amiyaal@gmail.com (A.I.)
https://doi.org/10.1016/j.xpro.2022.101814

SUMMARY

Here, we present a protocol for collecting data on multiple interaction types in small, stable groups of Arabian babblers (Argya squamiceps). We describe the procedure of habituation, the recording of social interactions, and how to classify the interaction types. Additionally, we provide code for testing, comparing, and visualizing data. The high-resolution data collection is time demanding and requires several data tests before forming the final protocol. The collected data can then be used for multiplex social network analysis.

For complete details on the use and execution of this protocol, please refer to Dragić et al. (2021).

BEFORE YOU BEGIN

Animal

Arabian babblers (Argya squamiceps) are cooperatively breeding birds that live in groups of up to 17 individuals (Keynan and Ridley, 2016). They live in compact groups and are highly territorial. We observed a habituated population of Arabian babblers in central Arava, Israel (Ostreiher, 1999; Zahavi, 1991). Arava is a highly arid area with sparse vegetation, mostly in dry riverbeds. All individuals were color-banded, hence we were able to quickly differentiate between individuals (Ridley and Huyvaert, 2007) (Figure 1). Their territoriality, habituation, and sparse habitat allowed us to observe their behavior with great resolution.

Analysis of multiple interaction types in small groups of animals

Social network analysis is a useful tool that provides researchers with the means to quantify the effects of sociality on various evolutionary and ecological processes (Farine and Whitehead, 2015; Finn et al., 2019). Networks are composed of nodes and edges. Nodes usually represent individuals, while edges usually represent interactions and relationships between individuals. An emerging subfield within network theory is the study of multilayer networks which provide a more detailed and nuanced framework for studying animal sociality. Multiplex social networks are a class of multilayer social networks that are used for analyzing multi-relational systems (Pereira et al., 2020). As in single-layer networks, each layer in a multiplex network is composed of nodes and edges. However, in a multiplex network, each layer contains the same set of nodes, while edges in each layer represent a different interaction type (Silk et al., 2018). Multiplex networks found their use in analyzing social niches (Flack et al., 2006), relationships between different interaction types (Barrett et al., 2012), detecting social status (Sharma et al., 2022), and other (Finn et al., 2019). Considering the potential that multilayer network analysis has for animal behavior studies, it is important to adopt standardized protocols which will allow their implementation when studying different animal species. That will
allow us more streamlined comparisons between different social systems and a better understanding of the effects of sociality on ecological and evolutionary processes.

In this protocol, we focus on the procedures of data collection on multiple interaction types in small groups of *Argya squamiceps*. This protocol also includes the code for data testing, comparison, and visualization. While the subsequent multilayer social network analyses are beyond the scope of this protocol, users can refer to several tools specialized for multilayer social networks analysis, such as multiple regression quadratic assignment procedures (MRQAP) (Dekker et al., 2007), exponential random graph model (ERGM) (Chen, 2018), and the R package “muxViz” (De Domenico et al., 2015).

Institutional permissions

© Timing: 3–6 weeks

Before habituation and marking animals, it is necessary to acquire a permit to work with wild animals. Permits to study wild animals usually require two parts. The first is a permit from a university committee to conduct the research, and the second is a permit from a governmental authority. Researchers should contact the university’s ethical committee to learn more details.

Note: This study has been approved by The Israel Nature and Parks Authority (NPA) (permit number 2023/43151).

Habituation

© Timing: Months – Years

The habituation of individuals depends on species behavior and ecology (Brent et al., 2013; Clutton-Brock et al., 1998; Raihani et al., 2010). The habituation of animals is done by constant exposure to observers, during which animals become less vigilant. This allows researchers to observe animals from a close distance without disturbing their natural behavior. Feeding individuals or placement of food stations can make the habituation faster and easier. However, in some cases feeding animals can be dangerous for observers or significantly alter animals’ behavior.

Note: All individuals in our study population were habituated to human presence since they fledged.
1. Visit groups for recording census and habituation at least once a week.

   *Note:* Habituation could vary between groups and individuals, but observers should have a standardized routine during the work with groups.

2. Follow the standardized routine.
   a. Use whistling as a contact call to announce your presence to the group and sit on the ground.

      *Note:* Most animals are less vigilant if observers sit.

   b. Initially use low-reward food to attract group members, such as breadcrumbs.

      *Note:* Low-reward food is food that individuals are interested in, but not willing to fight for.

   c. Once all group members are present give them 1–2 mealworms.

      *Note:* Giving too much high-reward food, such as mealworms, can disturb their natural foraging habits.

   d. After that, the observer can stand up and follow the group.

      *Note:* If an individual is lower ranked and less habituated, observers should spend more time following that individual and, if needed, use additional food once the rest of the group is not in proximity.

### Marking individuals

© Timing: Years

*Note:* Marking individuals at an early age reduces the time needed for the habituation of these individuals (Clutton-Brock et al., 1998; Raihani et al., 2010).

3. Ring nestlings when they were ten days old (Ostreicher, 1999).

   *Note:* The best time for ringing nestlings is 2–3 days before fledgling and it can vary between species and populations.

4. If there are unringed adults in the population capture them using walk-in traps. Use both bread and mealworms as bait.

   *Note:* The trap should be activated manually, by the trapper who sits ~5 meters from the trap (Keynan, 2015).

5. Use a unique combination of color rings for each individual (Figure 1).
   a. Using four rings gives enough color combinations for a population of 200–300 individuals.

      *Note:* Having a diverse set of colors can speed up the identification of individuals and allow for identification even when individuals disperse from the group or lose some of the rings.

   b. One ring should be a metal ring, which is less likely to get lost and can contain an individual’s ID number.
Creating an ethogram and choosing interactions

Timing: 4–10 weeks

Arabian babblers have a diverse set of behaviors and social interactions that have been studied for the last fifty years (Zahavi, 1991). We recorded almost all known interactions, and classify them into six interaction types: allopreening, aggression, allofeeding, playing, proximal foraging and scrounging. These interaction types included more than 99% percent of all recorded interactions. More information about the interaction types is in our corresponding paper (Dragić et al., 2021). During the creation of the protocol, we used previous studies and tried several options before forming the final ethogram. Here are a few universal steps for deciding which interactions to collect:

1. Define interactions as directed or undirected.

   Note: Directed interactions have an actor and a receiver in each interaction. For example, in aggression, there is an actor (the “attacker”) and a receiver (the “victim”).

   Note: Directed networks are more informative than undirected ones and can always be transformed into undirected networks.

   a. We used the gambit of the group method to record associations in groups as undirected edges (Franks et al., 2010).

2. Define interactions precisely to avoid sampling errors.
3. Test for correlations between different networks.

Note: See the script “Testing correlation between matrices using QAP” in Data S1 for more information.

Note: If networks are correlated, the interactions probably have a similar biological function, or one of them is directly caused by the other. The correlation and interchangeability between networks can be tested using matrix correlation tests (Farine, 2017) or permutations (Farine and Whitehead, 2015; van der Marel et al., 2021).

Note: Testing the correlation of matrices can sometimes give inconclusive results, especially if the study species’ animals live in small groups. For example, in our study allofeeding and dominance display had a strong correlation in some groups (Table 1). However, the two interactions had a different biological functions which we could see in changes in interaction patterns (Figure 3). In addition, the two interactions were clearly defined in previous studies (Zahavi, 1991) and easy to distinguish in the field. The similarities probably came from the uni-directional nature of both interactions, where the actor is always a higher-ranked individual.

4. Omit rare interactions from the analysis. Sparse graphs can be noisy and produce inaccurate results (Farine and Whitehead, 2015).

Note: While recording as many interactions as possible could be beneficial, animal social networks give the best results with clearly defined and abundant interaction types. For example, an interaction called morning dance (Zahavi, 1991) occurred only in some groups. Since it could not be joined to any other interaction type, morning dance was excluded from the analysis.

### Semi-focal observations

© Timing: 6–12 months

| Group round | Scrounging - aggression | Scrounging - allofeeding | Aggression - allofeeding |
|-------------|-------------------------|--------------------------|--------------------------|
| ARU_01      | 0.471                   | 0.066                    | 0.06                     |
| ARU_02      | 0.310                   | 0.437                    | 0.013                    |
| BER_01      | 0.229                   | 0.455                    | 0.024                    |
| BER_02      | 0.03                    | 0.269                    | 0.457                    |
| BOR_01      | 0.085                   | 0.22                     | 0.235                    |
| BOR_02      | 0.372                   | 0.317                    | 0.02                     |
| BOR_03      | 0.004                   | 0.213                    | 0.215                    |
| HIL_01      | 0.219                   | 0.576                    | 0.852                    |
| HVR_01      | <0.001                  | 0.516                    | 0.405                    |
| KOT_01      | 0.061                   | 0.55                     | 0.007                    |
| KOT_02      | 0.53                    | 0.329                    | 0.616                    |
| NIS_02      | 0.412                   | 0.225                    | 0.057                    |
| NIS_04      | 0.142                   | 0.158                    | 0.033                    |
| NIS_05      | 0.003                   | 0.218                    | 0.303                    |
| THG_01      | 0.454                   | 0.443                    | 0.008                    |
| THG_02      | 0.004                   | NA                       | NA                       |
| THG_03      | 0.101                   | 0.313                    | <0.001                   |
| THG_04      | 0.436                   | 0.425                    | 0.019                    |
| ZEV_01      | 0.024                   | 0.336                    | 0.007                    |

Values in the table present P values calculated using Quadratic Assignment Problem (QAP). If one of the adjacency matrices is empty (no interactions) or almost empty (< 90%) the correlation was not calculated (NA).
Traditionally, behavioral observations follow two types of data collection: focal observations and all occurrences of behavior in the group (Altmann, 1974). However, groups of Arabian babblers are mostly compact, and it is possible to observe and record the interactions of 4–8 individuals at any moment. If we recorded only interactions of only one individual we would “lose” the majority of observed behavior. Altmann (1974) suggested that predetermined subgroups of individuals can be observed, but babbler movement was hard to predict and hence it was difficult to define a predetermined group. Our solution was semi-focal observations, where the subgroup was determined by the distance to the focal individual. During the semi-focal observations, we recorded all interactions involving the focal individual as well as interactions involving all individuals in a ~10 meters radius.

5. Determine duration of sampling time.

*Note:* Depending on the species, focal observations can last from a few minutes (Coleman and Wilson, 1998; Manson, 1999; Stahl et al., 2001) up to 14 h for focal observation of groups (Ruckstuhl, 1998).

*Note:* Our sampling time was ten minutes. There was no exact reasoning for ten minutes focal observations, but it allowed us to observe each individual in an average group once before the temperatures become too high and babblers reduced their activity.

*Note:* We would pause the observations if we would lose the focal individual from sight or if any of the individuals would interact with the observer. The observation would be continued once we find the individual or all individuals go back to their natural behavior.

6. Determine the number of focal observations.

*Note:* The number of focal observations depends on the abundance of interactions and their distribution. There are several methods to test the quality of sample size, including...
bootstrapping and jackknifing, which can be used once the data are collected (Farine and Whitehead, 2015; Lusseau et al., 2008; Wey et al., 2008).

Note: It is important to note that there is still no consensus about the right sample size and testing method.

a. We used a technique as in jackknifing, where we measured the difference between normalized strengths of individuals (Figure 4). Since we observed all individuals equally, in our study strength was defined as the total number of interactions an individual had during the observation period.

Note: See the “Testing semi-focal observations” script in Data S2 for more details.

b. For each number of focal rounds, calculate the mean strength for each individual and normalized it.

c. Compare the normalized values between focal rounds.

Note: For example, we compared individuals’ normalized strength after just one round to normalized strength after two rounds and so on.

d. The preferred number of focal rounds is the one after which changes in normalized mean strength approach zero.

Note: In our study, changes in mean strength approached zero after ten focal rounds for all interaction types (Figure 4).

Figure 3. Seasonal variation in aggression and allofeeding
Dominance display and allofeeding social networks of the same group. The thickness of edges represents the number of interactions between individuals. Arrows represent direction of interactions. While in some cases these two interaction types can have similar interaction patterns, they have different functions, and therefore their frequency can vary between seasons.
7. Prepare the group for the focal observations by following them every day, 3–7 days before the beginning of observations.
   a. The goals of the preparation period are to learn individuals’ names, test the habituation of individuals, and for animals to get used to everyday human presence.
   b. The habituation is considered sufficient if you can approach them to a minimal observation distance (3–6 meters) without disturbing them.

   Note: The minimal observation distance depends on the species.

   c. Once all individuals are habituated start implementing the standardized feeding protocol, 1–2 days before observations begin.

8. Feeding protocol.
   a. Feed animals in the morning, before they begin foraging.
   b. Randomly distribute small pieces of food.

   Note: We fed Arabian babblers with 2–3 mealworms (Tenebrio molitor) and ~5 grams of bread.

   c. Start observations once individuals finish the feeding.

   △ CRITICAL: We fed individuals only before the observations.

   Note: This combination of food as a reward in the morning and consistent following before observations gave us the best results. The level of habituations stayed steady over a long period and animals did not interact with observers after the feeding period.

   Note: Other feeding protocols, as well as observations without supplemented food, did not provide consistent behavior during observations.

9. Prepare the order of focal observations a day before.
   a. Observe each individual once before moving to the next focal round.
Note: For example, if all individuals in the group were observed six times and individual A was observed five times, we would observe individual A.

b. Equally distribute observations of an individual during different periods of the observation time.

Note: For example, in our study individuals had a similar number of observations in the first, the second, and the third hour of observation time.

c. If individuals had the same number and distribution of observations the focal individual was selected randomly.

Data collection tools
For recording multiple interaction types it is preferable to customize an application which will allow fast and accurate documentation.

10. The application should contain the list of individuals and the list of interactions.

   Note: We used the customizable application Cybertracker (https://www.cybertracker.org/) (Figure 2).

11. If the application does not have a built-in time measuring option, use a timer on a watch or mobile phone.

   Note: In case you record the time using a watch, the first window should contain commands for starting, pausing, and ending the focal observation (Figure 2).

12. For directed interactions create two identical windows containing the list of individuals: one for the actor and one for the receiver of interaction.

EXPECTED OUTCOMES
The outcome of observations should be adjacency matrices of chosen interaction types. Adjacency matrices of our study can be found in the key resources table. Adjacency matrices can also be presented as weighted graphs (Figure 3).

QUANTIFICATION AND STATISTICAL ANALYSIS
We used R 4.1 for all analyses. All data and R scripts used in this study are listed in the key resources table.

Testing focal observations
We provided a data stream of our semi-focal observation and the script we used to measure differences between focal series. The links can be found in the key resources table. The provided script uses allofeeding interactions as an example, but all six interaction types had similar results. The numbers in the graph can vary between different runs since random focal rounds were selected for each series.

Testing correlation between matrices
Correlation between matrices can be tested using quadratic assignment procedures (QAP) (Hubert and Schultz, 1976). We used the “qaptest” function from the “sna” package in R (Butts, 2008).

Visualizing social niches using t-SNE
The social niche is a relatively new term in behavioral ecology and the definitions can vary between papers (Saltz et al., 2016). We defined social niches as a summary of all networks in which the
individual participates. Since our six interaction types had almost no correlation and included more than 99% of recorded interactions, we treated them as the different axes which define individuals’ positions in a social group. We then used t-distributed stochastic neighbor embedding (t-SNE) to visualize animal social niches. We used “Rtsne” package (Krijthe, 2015). t-SNE is a dimension reduction algorithm, which transforms high-dimensional data (six dimensions in our example) to low-dimensional data (two dimensions) which is easier to analyze (Figure 5). This algorithm is an unsupervised dimension reduction algorithm, hence the two axes on the final graph have no units.

Note: See the “Plotting t-SNE” script in Data S3 for more details.

LIMITATIONS
The limitations of this method are related to the limitations of similar field observation methods. These methods are usually time demanding, require trained field technicians and can be easily affected by environmental changes. However, to efficiently distinguish between interaction types our method requires additional steps to reach the required level of resolution. Hence, the preparation period requires more time for habituation and more training of observers. Interaction types can also vary in frequency, hence more observation time is needed to record enough data for all interaction types.

TROUBLESHOOTING
Problem 1
Before you begin 3 and Semi-focal observations 6: Individuals become too habituated.

Potential solution
If individuals become too habituated and interact with observers during observations, a possible solution is to clearly separate cues for feeding from observations. For example, we were sitting while feeding individuals and standing while observing them. In addition, we were whistling while feeding them and feeding them only at the beginning of the morning. That resulted in individuals interacting with observers rarely and short, usually under a minute on 1,000 min of observations. On those rare occasions, we paused the focal observation, moved a few steps back and wait for individuals to return to their normal behavior.

Problem 2
Data collection tools: Issues with Cybertracker. Cybertracker is an old application and it is not user-friendly. It can be hard to set up the application and time-consuming if you work with several groups.
Potential solution
Fulcrum (https://www.fulcrumapp.com/) gives the same level of customization, but it is more intuitive and has better customer support. The only downside is that, unlike Cybertracker, Fulcrum is a paid app.

Problem 3
Quantification and statistical analysis: Effects of extrinsic factors and changes in groups.

Potential solution
In our GLMM models, we used groups as random effects to control for potential differences in habitat. In addition, we used individuals as nested random effects, since some of the individuals disappeared between focal observation sessions.

Problem 4
Creating an ethogram and choosing interactions: Deciding whether to pull or separate interactions.

Potential solution
This mainly depends on study questions. We recorded all interactions separately and pulled them during analysis if it was necessary. For example, we recorded theft (stealing food directly from the receiver) and taking over the food patch as two interactions. In our analysis of social niches, we analyzed them as one interaction type, since these two interactions were relatively similar and correlated. If, for example, we analyzed scrounging behavior of Arabian babblers, we would analyze them separately.

There is a proposed framework regarding this question by van der Marel and her colleagues (van der Marel et al., 2021).

Problem 5
Quantification and statistical analysis: Analyzing both directed and undirected interactions pose a challenge. Depending on the research questions and interactions’ properties, some statistical methods are applicable only if all interactions are of the same type.

Potential solution
A potential solution is to focus on ERGM or similar dyadic models. Studies sometimes record directed interactions as undirected, since it is easier to analyze different layers if they have similar properties (Smith-Aguilar et al., 2018).

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Amiyaal Ilany (amiyaal@gmail.com).

Materials availability
This study did not generate new unique reagents.

Data and code availability
All original adjacency matrices and individuals’ traits have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.

R scripts are available through Zenodo and listed in the key resources table.

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

Supplemental information can be found online at https://doi.org/10.1016/j.xpro.2022.101814.

ACKNOWLEDGMENTS

This study was supported by grants 244/19 and 245/19 from the Israel Science Foundation and grant 2019156 from the U.S.-Israel Binational Science Foundation. We are thankful to Djordje Markovic and Yael Alon for their help in collecting data, as well as Dorit Narinsa and the Haze Field School for their hospitality during fieldwork.

AUTHOR CONTRIBUTIONS

All three authors worked on conceiving the protocol and defining the ethogram; N.D. wrote the code and the manuscript. All authors discussed and commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour 49, 227–267. https://doi.org/10.1163/156853974X00533.

Barrett, L., Henzi, S.P., and Lusseau, D. (2012). Taking sociability seriously: the structure of multidimensional social networks as a source of information for individuals. Philos. Trans. R. Soc. B 367, 2108–2118. https://doi.org/10.1098/rstb.2012.0113.

Brent, L.J.N., Heilbronner, S.R., Horvath, J.E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A.G., Skene, J.H.P., and Platt, M.L. (2013). Genetic origins of social networks in rhesus macaques. Sci. Rep. 3, 1042–1048. https://doi.org/10.1038/srep01042.

Butts, C.T. (2008). Social network analysis with sna. J. Stat. Softw. 24. https://doi.org/10.18637/jss.v024.i06.

Chen, T.H.Y. (2018). Statistical Inference for Multilayer Networks in Political Science (Social Science Research Network).

Clutton-Brock, T.H., Brotherton, P.N., Smith, R., Mclrath, G.M., Kansky, R., Gaynor, D., O’Riain, M.J., and Skinner, J.D. (1998). Infanticide and group and demographic Allee effects in a group. J. Evol. Biol. 11, 1018–1028. https://doi.org/10.1111/j.1420-9101.1998.10521.x.

Farine, D.R. (2017). A guide to null models for animal social network analysis. Methods Ecol. Evol. 8, 1309–1320. https://doi.org/10.1111/2041-210X.12772.

Farine, D.R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. 84, 1146–1163. https://doi.org/10.1111/1365-2656.12418.

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.

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. https://doi.org/10.1038/nature04326.

Flaks, D.W., Ruxton, G.D., and James, R. (2010). Sampling animal association networks with the gambit of the group. Behav. Ecol. Sociobiol. 64, 493–503. https://doi.org/10.1007/s00265-009-0865-8.

Hubsport, L., and Schultz, J. (1976). Quadratic assignment as a general data analysis strategy. Br. J. Math. Stat. Psychol. 29, 190–241. https://doi.org/10.1111/j.2044-8317.1976.tb00716.x.

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. https://doi.org/10.1007/s00442-016-3656-8.

Krieg, J.H. (2015). Rtsne: T-Distributed Stochastic Neighbor Embedding Using Barnes-Hut Implementation. https://github.com/jkrijthe/rttsne.

Lusseau, D., Whitehead, H., and Gero, S. (2008). Incorporating uncertainty into the study of animal social networks. Anim. Behav. 75, 1809–1815. https://doi.org/10.1016/j.anbehav.2007.10.029.

Manson, J.H. (1999). Infant handling in wild Cebus capucinus: testing bonds between females? Anim. Behav. 57, 911–921. https://doi.org/10.1016/j.anibe.1998.1052.

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

Pereira, A.S., Rebello, 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, 0230942. https://doi.org/10.1371/journal.pone.0230942.

Raikhani, N.J., Nelson-Flower, M.J., Golabek, K.A., and Ridley, A.R. (2010). Routes to breeding in cooperatively breeding pied babblers Turdoides bicolor. J. Avian Biol. 41, 681–686. https://doi.org/10.1111/j.1600-046x.2010.05211.x.

Ridley, A.R., and Huyvaert, K.P. (2007). Sex-biased preferential care in the cooperatively breeding Arabian babbler: J. Evol. Biol. 20, 1271–1276. https://doi.org/10.1111/j.1420-9101.2007.01316.x.

Ruckstuhl, K.E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. Anim. Behav. 56, 99–106. https://doi.org/10.1006/anbe.1998.0745.

Saltz, J.B., Geiger, A.P., Anderson, R., Johnson, B., and Marren, R. (2016). What, if anything, is a social niche? Evol. Ecol. 30, 349–364. https://doi.org/10.1007/s10682-015-9792-3.

Sharma, N., Gadagkar, R., and Pinter-Wollman, N. (2022). A reproductive heir has a central position in multilayer social networks of paper wasps. Anim. Behav. 165, 21–36. https://doi.org/10.1016/j.anbehav.2021.12.011.
Silk, M.J., Finn, K.R., Porter, M.A., and Pinter-Wollman, N. (2018). Can multilayer networks advance animal behavior research? Trends Ecol. Evol. 33, 376–378. https://doi.org/10.1016/j.tree.2018.03.008.

Smith-Aguilar, S.E., Aureli, F., Busia, L., Schaffner, C., and Ramos-Ferna´ndez, G. (2018). Using multiplex networks to capture the multidimensional nature of social structure. Primates. https://doi.org/10.1007/s10329-018-0686-3.

Sosa, S., Puga-Gonzalez, I., Hu, F., Pansanel, J., Xie, X., and Sueur, C. (2020). A multilevel statistical toolkit to study animal social networks: the Animal Network Toolkit Software (ANTS) R package. Sci Rep 10, 12507. https://doi.org/10.1038/s41598-020-69265-8.

Stahl, J., Tolsma, P.H., Loonen, M.J.J.E., and Drent, R.H. (2001). Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim. Behav. 61, 257–264. https://doi.org/10.1006/anbe.2000.1564.

van der Marel, A., Prasher, S., Carminito, C., O’Connell, C.L., Phillips, A., Kluever, B.M., and Hobson, E.A. (2021). A framework to evaluate whether to pool or separate behaviors in a multilayer network. Curr. Zool. 67, 101–111. https://doi.org/10.1093/cz/zoaa077.

Venables, W.N., and Ripley, B.D. (2002). Modern applied statistics with S (Springer). https://www.stats.ox.ac.uk/pub/MASS4/.

Wey, T., Blumstein, D.T., Shen, W., and Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. 75, 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020.

Zahavi, A. (1991). Arabian babblers: the quest for social status in a cooperative breeder. In Cooperative Breeding in Birds, P.B. Stacey and W.D. Koenig, eds. (Cambridge University Press), pp. 105–130.