Factors Impacting Sociality Among Asiatic wild ass (*Equus hemionus*) Females

Networks in biology and ecology course, 2024

Background

״Fission-fusion is a social structure characterized by frequent group formation and separation (Archie et al., 2006; Papastamatiou et al., 2020). Among equid species, such as the Asiatic wild ass (*Equus hemionus*) in Israel (Renan et al., 2018), the structure is adapted to arid environments (Boyd et al., 2016). Lactating females rely heavily on water during the mating season, moving between water and food sources with other females (Tesfai et al., 2021), suggesting that their social interactions are crucial for resource utilization and overall fitness. Yet, the factors impacting these associations are unknown. Patterns that have been suggested to influence social associations are genetic relatedness and homophily. Genetic relatedness may play a role due to the benefits of inclusive fitness (Hamilton, 1964), and advantages that had been linked with this pattern include food intake, longevity, and reproductive success (Archie et al., 2006; Silk et al., 2010). Homophily, the tendency to interact with similar individuals in age, sex, or reproductive status (Bouskila et al., 2016; Nicolás-Carlock et al., 2024), helps meet shared physiological needs (Tesfai et al., 2021). In resource-scarce environments, females may be less selective about social partners. Understanding the mechanisms shaping social associations in such habitats can reveal how sociality promotes fitness and if kin selection occurs in extreme environments.

Research question

What factors impact social associations among Asiatic wild ass females?

Methods

I used data based on direct observations and non-invasive fecal sampling (genetic data) collected from directly observed female groups (up to 15 individuals per group). Sampling was performed in the Negev Highlands, Israel from 2020-2023, outside main activity points (water sources and vegetation patches), in order to avoid cases of encounters that are not necessarily by choice. DNA was extracted from all fecal samples and then sequenced using 625 SNPs to generate genetic profiles of individuals. Based on the produced genetic profiles, the relationships between sociality and relatedness, age, reproductive status, and reproductive success, were examined using two network-based methods:

1. *Exponential Random Graph Model (ERGM):* ERGM tests the probability of covariates predicting overall network structure and edge formation (Robins, 2011). It models potential edges between individuals as stochastic variables within the adjacency matrix, with the response variable being the probability of matching the observed network to the explanatory variables representing structural features (Silk & Fisher, 2017). The advantages of the model are that it considers the dependency of individuals and their links of the network and allows testing both edge and node attributes in a single model (Robins, 2011). I used the R package 'ergm' for the analysis (Krivitsky et al., 2023), and a Goodness-of-fit model was also performed to ensure the ERGM captures the key structural features of the observed networks.
2. *Similarity of community clustering using the Normalized Mutual Information (NMI) measure:* The NMI measure, ranging from 0 (no similarity) to 1 (perfect similarity), quantifies the similarity between two clustering results (McDaid et al., 2011). Community clustering was performed using the R package 'Infomap' (Farage et al., 2021), and NMI values were calculated with 'aricode' (Albouy et al., 2021). Significance of NMI was determined by: 1) Constructing 1,000 random networks with fixed shuffling for genetic relatedness, reproductive status, and age; 2) Running Infomap for cluster detection; 3) Testing NMI for each network against the observed NMI.

The social network (used as the observed network in both analyses), was designed as a weighted, undirected network, with nodes representing different individuals and edges representing the number of encounters between females in social groups. This method, based on the locations of fecal samples, differs from traditional social network construction methods that are usually based on video and photo recordings (Rubenstein et al., 2015). To avoid bias generated from coincidental encounters, only females with at least two social edges were eventually included in the analysis. The explanatory variables (for the first analysis) or networks (for the second analysis) were designed as follows:

1. *Genetic relatedness:* pairwise genetic relatedness was calculated using the Coancestry 1.0.1.2 program (Wang, 2011), with values ranging from 0 to 1. A minimum threshold of 0.125 (first cousins) was used to indicate the presence of an edge. For the ERGM analysis it was set as an edge attribute (matrix). For the community clustering test it was designed as a weighted, undirected network.
2. *Age:* The age of individuals as determined by dung size. Females sampled as juveniles in their first year were classified as "young," while those sampled as adults throughout the period were classified as "adult." For the ERGM model it was tested as a Node

attribute. For the community clustering test it was designed as a binary, unweighted network, where "1" indicates similar age category and "0" indicates different age category.

3. *Reproductive status:* The number of times two females had a foal at the same year divided by the total number of shared years they were recaptured. For the ERGM model it was tested as an Edge attribute (matrix). For the community clustering test it was designed a weighted, undirected network.
4. *Reproductive success:* The number of offspring produced by a female throughout the sampling period (2020-2023). For the ERGM model it was tested as node attribute. This parameter was not tested for the community clustering similarity test as it was too similar to the reproductive statues variable when set as an edge.

Results

A total of 2,014 samples were collected, of which 100 unique female genotypes were identified after a careful filtering procedure. Of these, 87 genotypes were sampled more than once (ranging between 1-5 times). The eventual social network comprised 57 unique genotypes that had at least 2 edges.

The ERGM model results showed that the only significant predicting factor of the social network was genetic relatedness, with a strong positive effect (Table 1).

Table 1. ERGM results.

Model term	Estimate	Std. Error	Z value	P
Edges	-2.979	0.2171	-13.723	< 1e-04***
Genetic relatedness	**4.045**	**0.904**	**4.623**	**0.000164*** **
Age	-0.267	0.204	-1.076	0.251
Reproductive status	0.387	1.071	-0.792	0.688
Reproductive success	-0.06	0.127	0.738	0.872
Model Fit Statistics				
AIC		625.8		
BIC		647.1		

The Goodness-of-fit model showed that the ERGM model adequately fits the data well (the p-value for all variables ranged between 0.96-1.00), indicating that the estimated parameters were generally meaningful.

The social network was clustered into 10 modules, the genetic network was clustered into 8, reproductive status was clustered into 3 communities, and the age network was clustered into two communities (Figure 1). The similarity testing of networks by their community clustering showed that genetic relatedness had a strong and positive relationship (NMI= 0.38, p<0.01) and the age network had a weak bet significant relationship (NMI=0.066, p<0.0001). Reproductive status was not found to be a significant predicting factor (NMI = 0.198, p = 0.335).

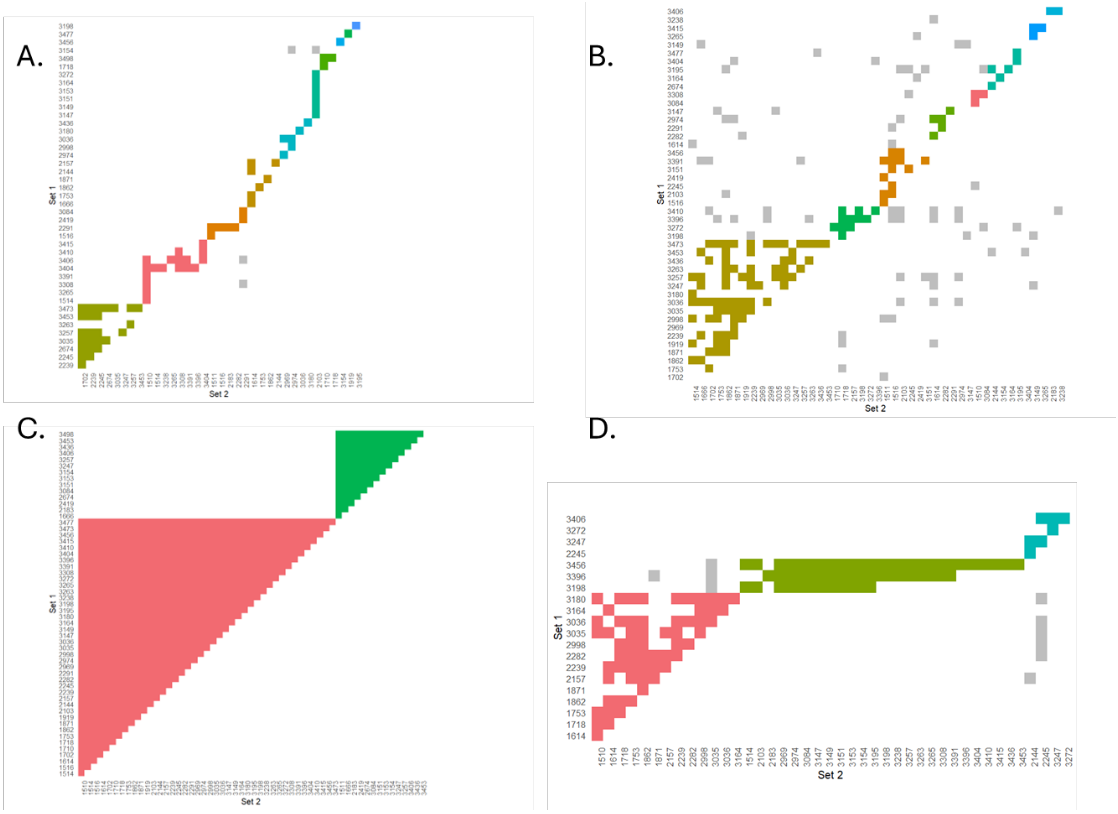

Figure 1. Community clustering visualization of the Social (A), Genetic (B), Age (C) and reproductive status (D) networks.

Discussion

This paperwork examined genetic relatedness, age, reproductive status, and reproductive success as factors explaining the social network of Asiatic wild ass females in the Negev Highlands, Israel, in a time frame of four year (2020-2023). Contrary to expectations in an arid environment, where shared physiological needs are more likely to predict sociality for better resource use, genetic relatedness alone significantly predicted the social network structure and community clustering. This might be due to increased water source availability in the Negev Highlands following a water source management performed by the Israel Nature and Parks Authorities in collaboration with our lab in 2020. It might be that the reduced resource-utility stress allowed females to form a more kin-based social bonds that are linked with various fitness benefits (Archie et al., 2006; Silk et al., 2010; Tong et al., 2015), whereas other factors such as age and reproductive status become less meaningful.

However, this study has several limitations, mainly related to the construction manner of the networks. First, the social network does not account for variance in recaptures per female, which could affect encounter counts (that represent the edges of the social network). Second, the edges of the genetic network were filtered by a threshold 0.125+ (first cousins), therefore excluding edges between unrelated individuals, potentially skewing the results. Therefore, it might be that analyzing network structure by edge *values* rather than *presence* might be more accurate for this analysis. Third, the age network, which is based on age categories ("young" or "adult"), does not account for overlapping ages across years. For this purpose, I plan to re-analyze this variable using data of specific years separately to better reflect each individual's age category.

To summarize, network analysis has shown good potential as a reliable method to estimate relationships between sociality and other predictive factors. Genetic relatedness and the other tested variables should be further examined in comparison with the social network as discussed above. Using this method more precisely in the future should provide a clearer understanding of the research question addressed in this study.

References

Albouy, J., Guegan, M., & Arbel, J. (2021). *aricode: Efficient Computations of Clustering Comparison Measures.* R package version 1.0.0. https://CRAN.R-project.org/package=aricode

Archie, E. A., Moss, C. J., & Alberts, S. C. (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B. Biological Sciences, 273*(1586), 513-522.

Bouskila, A., Lourie, E., Sommer, S., De Vries, H., Hermans, Z. M., & Van Dierendonck, M. (2015). Similarity in sex and reproductive state, but not relatedness, influence the strength of association in the social network of feral horses in the Blauwe Kamer Nature Reserve. Israel Journal of Ecology and Evolution, 61(2), 106-113.

Boyd, L., Scorolli, A., Nowzari, H., & Bouskila, A. (2016). Social organization of wild equids. In J. I. Ransom & P. Kaczensky, *Wild equids: Ecology, Management, and Conservation* (pp. 7-22). JHU Press.

Connor, T., Frank, K., Qiao, M., Scribner, K., Hou, J., Zhang, J., ... & Liu, J. (2023). Social network analysis uncovers hidden social complexity in giant pandas. *Ursus, 2023*(34e9), 1-13.

Farage, C., Edler, D., Eklöf, A., Rosvall, M., & Pilosof, S. (2021). Identifying flow modules in ecological networks using Infomap. *Methods in Ecology and Evolution, 12*(5), 778-786.

Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology, 7*, 1–52.

Krivitsky, P. N., Hunter, D. R., Morris, M., & Klumb, C. (2023). ergm 4: New Features for Analyzing Exponential-Family Random Graph Models. *Journal of Statistical Software*, *105*(6), 1–44. https://doi.org/10.18637/jss.v105.i06

Nicolás-Carlock, J. R., Boyer, D., Smith-Aguilar, S. E., & Ramos-Fernández, G. (2024). Strength of minority ties: the role of homophily and group composition in a weighted social network. *Journal of Physics: Complexity*, *5*(1), 015009.

McDaid, A. F., Greene, D., & Hurley, N. (2011). Normalized mutual information to evaluate overlapping community finding algorithms. *arXiv preprint arXiv:1110.2515*.

Papastamatiou, Y. P., Bodey, T. W., Caselle, J. E., Bradley, D., Freeman, R., Friedlander, A. M., & Jacoby, D. M. (2020). Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. *Proceedings of the Royal Society B*, *287*(1932), 20201063.

Renan, S., Speyer, E., Ben-Nun, T., Ziv, A., Greenbaum, G., Templeton, A., Bar-David, S., & Bouskila, A. (2018). Fission-fusion social structure of a reintroduced ungulate: Implications for conservation. *Biological Conservation, 222*, 261-267.

Robins, G. (2011). Exponential random graph models for social networks. In P. J. Carrington, & J. Scott (eds.) *The Sage handbook of social network analysis* (pp. 484-500). Sage Publications.

Rubenstein, D. I., Sundaresan, S. R., Fischhoff, I. R., Tantipathananandh, C., Berger-Wolf, T. Y. (2015). Similar but Different: Dynamic Social Network Analysis Highlights Fundamental Differences between the Fission-Fusion Societies of Two Equid Species, the Onager and Grevy's Zebra. *PLoS ONE, 10*(10), e0138645.

Silk, M. J., & Fisher, D. N. (2017). Understanding animal social structure: exponential random graph models in animal behaviour research. *Animal Behaviour*, *132*, 137-146.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), 1359-1361.

Tesfai, R. T., Parrini, F., Owen-Smith, N., & Moehlman, P. D. (2021). African wild ass drinking behaviour on the Messir Plateau, Danakil Desert, Eritrea. *Journal of Arid Environments, 185*, 104327.

Tong, W., Shapiro, B., & Rubenstein, D. I. (2015). Genetic relatedness in two-tiered plains zebra societies suggests that females choose to associate with kin. *Behaviour*, *152*(15), 2059-2078.

Wang J. (2011). COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources*, *11*(1), 141–145. https://doi.org/10.1111/j.1755-0998.2010.02885.x