Beyond the dyad: uncovering higher-order structure within cohesive animal groups

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ABSTRACT

Revealing the consequences of social structure in animal societies is largely determined by our ability to accurately estimate functionally relevant patterns of social contact among individuals. To date, studies have predominantly built up social structure from dyadic connections. However, many associations or interactions can involve more than two individuals participating together, which current approaches cannot distinguish from independent sets of dyadic connections. Here we demonstrate the application of higher-order networks to detect the central roles of dominance and sex in structuring social groups of vulturine guineafowl (*Acryllium vulturinum*). Specifically, we find that while females and low-ranking group members engage in more dyadic interactions, males and more dominant group members are substantially more likely to be observed forming hyperlinks—edges that contain more than two individuals (e.g. a triad). These results demonstrate how higher-order networks can provide a deeper understanding of the multidimensionality in the difference of centrality among group members.

INTRODUCTION

It is well-established that the repeated patterns of social contact among individuals can have far reaching consequences (Cantor *et al.* 2021). For example, how distributed social contacts are and how frequently they are formed shapes the spread of information (Voelkl & Noë 2008; Aplin *et al.* 2012) and disease dynamics (Silk *et al.* 2019; Ashby & Farine 2022). Further, the quality of relationships that individuals maintain can have consequences on their survival and that of their offspring (Alberts 2019; Gerber *et al.* 2022), while who they interact with can impact their ability to reproduce (Farine & Sheldon 2015; Fisher *et al.* 2016). Even though the consequences of the structure that arises from social contacts are evident, little progress has been made over the past decades on how this structure can be inferred. This step is critical because the associations or interactions that we are able to observe among individual animals represent, at best, an approximation of any real underlying network (Krause *et al.* 2013; Farine & Whitehead 2015). Thus, our ability to generate insights on the ecological or evolutionary implications of social contacts will largely depend on how we define those contacts. Drawing from network science and statistical physics, we demonstrate the potential for higher-order networks as a tool for extracting key social components from high-resolution tracking data.

Social networks—where nodes represent individuals and edges reflect the inferred relationship between the individuals—are widely used to describe the emergent properties of social groups or broader populations (Farine & Whitehead 2015; Sosa *et al.* 2021). In general, constructing networks starts with observations of dyadic associations (two individuals present together) or dyadic interactions (either affiliative or agonistic). For example, individual giraffes have been defined as belonging to the same observed group when they forage or move together, but not when they move past each other in opposite directions, with groups defined as clusters of Masai giraffes (*Giraffa camelopardalis*) that are more than 500 m from other giraffes (Bond *et al.* 2021). In other examples, great tits (*Parus major*) (Psorakis *et al.* 2012; Aplin *et al.* 2015) and juvenile hihis (*Notiomystis cincta*) (Franks *et al.* 2020) are assumed to belong to the same group if observed visiting feeders together within the same feeding 'wave', and when constructing association networks, members of olive baboon (*Papio anubis*) troops are assumed to be interacting when they groom each other (Tung *et al.* 2015). While each of these methods differ in their biological definition, they generally all then follow the same principle of summarising observations of individual associations or interactions into rates (Whitehead 2008; Hoppitt & Farine 2018) forming the basis for generating social networks.

Beyond the attention required when defining what constitutes a biologically relevant social contact, social network analysis encompasses several more challenges. Empirically driven simulation studies suggest that networks are data intensive, requiring many observations per dyad (Davis *et al.* 2018; Sunga *et al.* 2021). Recent technological advances, such as miniaturised GPS tags with upload and automated reverse GPS-systems (Nathan *et al.* 2022) are now revolutionising the ability to collect data from the wild, and are particularly promising for the study of cohesive social groups (He *et al.* 2022). For example, data from a group of baboons where the majority of members were fitted with GPS collars was used to infer how groups make movement decisions (Strandburg-Peshkin *et al.* 2015) and how social relationships impact where individuals move next (Farine *et al.* 2016). In captivity, a high resolution tracking system applied to zebra finch (*Taeniopygia castanotis*) colonies was used to infer the establishment of breeding pairs over time (Maldonado-Chaparro *et al.* 2021) and how the developmental environment

affects the emergent structure of populations (Wang *et al.* 2022). However, at the same time, such high-resolution data can amplify the noise present in the system, potentially masking true social relationships (Farine 2018; Gilbertson *et al.* 2021). For example, in species living in stable groups that move cohesively, group members spend their lives in very close proximity to each other. Within these groups, stronger social preferences might be present among subsets of individuals, but these preferences can be challenging to extract when individuals come into frequent contact with all members of their group—both preferred and not. For example, there are increasing numbers of multilevel societies—where social units aggregate into two or more levels of organisation (Grueter *et al.* 2020; Papageorgiou & Farine 2021; Camerlenghi *et al.* 2022)—being discovered among animals, and individuals in such societies are likely to have stronger and distinct preferences for members of their core social unit than with individuals from other social units. As more studies engage with methods allowing group-level higher resolution data on movement and associations to be collected and apply this to more stratified types of animal societies, we also need to explore new techniques for extracting the social signal from these data.

One recently developed method that has the potential to increase the power to infer social relationships among individuals that associate frequently is higher-order networks (Battiston *et al.* 2020; Battiston & Petri 2022). One current drawback of traditional network approaches is that they cannot distinguish genuine group associations from the accumulation of dyadic ties. For example, consider an observed network consisting of a simple triangle connecting individuals i, j and k. From such a network, it is not clear if i, j and k all participated together in a single association, or if they associated in different pairs, i and j, j and k, i and k, at different times. The reason for this is that the inferred relationships are encoded in links that, by definition, can only properly describe relationships taking place between two individuals at a time. While some types of associations can only be dyadic, there is also greater awareness of important multi-actor associations and associations within animal groups. For example, a dominance association between two individuals can be influenced by third-party support (Strauss & Holekamp 2019; Dehnen *et al.* 2022a). Higher-order representation of networked data, such as hypergraphs, can overcome the fundamental limitation of regular networks. In such networks, so-called hyperlinks can explicitly encode associations or interactions

among an arbitrary number of individuals. In the case discussed above, if the system displays only pairwise association we will have three hyperlinks of size 2, [i,j],[j,k],[i,k], while if they participated in a group association this will be stored as a single hyperlink of size 3 [i,j,k].

Higher-order network representations have been demonstrated to generate important insights into real-world networked systems. Adopting a higher-order approach allows to effectively represent interactions and or associations that occur in groups of different sizes, helping in better understanding the structural differences between interacting agents that belong to different domains. For example, higher-order motif analysis (Lugo-Martinez *et al.* 2021; Lotito *et al.* 2022) revealed that clustered pairwise collaborations among scientific authors are predictive of future 3-way interactions (Benson *et al.* 2018), and that protein or chemical compounds that interact in groups typically cannot do so in single pairs with other agents. In general, the decomposition of large hyperlinks (e.g. triads, etc.) into the many dyads that they comprise leads to the formation of densely connected cliques that can bias traditional algorithms aimed at identifying characteristics of network structure. For this reason, recent work has proposed new algorithms to extract centrality rankings (Tudisco & Higham 2021), communities (Eriksson *et al.* 2021) and statistically validated groups (Musciotto *et al.* 2021) in the presence of non-dyadic ties. It is important to note that higher-order networks are not only an important tool to characterise the structure of real-world systems, but they also allow to better model the emergent dynamics (Battiston *et al.* 2021), from spreading processes in the presence of group dynamics (Iacopini *et al.* 2019) as well as evolutionary dynamics (Alvarez-Rodriguez *et al.* 2021). Higher-order network analytical approaches can also shed more light on ecological processes where multiple species can interact simultaneously (Bairey *et al.* 2016; Grilli *et al.* 2017; Xiao *et al.* 2020), providing new explanations for coexistence in complex communities (Levine *et al.* 2017).

In this paper, we demonstrate the use of higher-order networks to extract information on the social structure within a group of wild vulturine guineafowl (*Acryllium vulturinum*). Vulturine guineafowl are large and predominantly terrestrial birds that are endemic to East Africa. They are also highly social, living in groups of 11 to 65 individuals that move cohesively together (Papageorgiou *et al.* 2019). GPS-based tracking has revealed that

these groups associate preferentially with specific other groups to form a multilevel society (Papageorgiou *et al.* 2019). However, while the population-level structure—the stability of group membership over time and the association among groups that form the upper two levels of this three-level society—is clearly evident, capturing what happens within groups has been proven to be more challenging. To date, we know that groups contain multiple reproductive males and females (Papageorgiou et al. 2019), and that the society is male-structured, with all males being on the top of the dominance hierarchy (Papageorgiou & Farine 2020; Dehnen *et al.* 2022b) and females being the dispersing sex (Klarevas-Irby *et al.* 2021). However, the high degree of cohesion within groups makes it challenging to uncover how social preferences are directed among members of the same group, and whether the tendency to form higher-order hyperlink is greater among more dominant individuals. To address this, we fit high-resolution solar-powered GPS tags to all individuals in one group, allowing us to collect continuous data on the movements and relative position of individuals over 6 days. We then use a higher-order network approach to extract the details of the interaction patterns of individuals in subgroups (hyperlinks) of different sizes. Given our recent insights on dispersal patterns, we expect to observe a distinct male-bias in higher-order hyperlinks (i.e. sets of individuals consistently observed together), which we use as our *a priori* knowledge (Ferreira *et al.* 2020) to evaluate the performance of the higher-order network method.

METHODS

GPS data collection

We fitted high-resolution solar-powered GPS tags (15 g Bird Solar, e-obs Digital Telemetry, Grünwald, Germany) to all 25 adult members of one social group of vulturine guineafowl. GPS tags, together with the harnesses and the platform, which is used to elevate the tag and prevents the solar panel from being covered by feathers, weighed less than 2% of a small bird's weight, which aligns with biologging ethical guidelines (Portugal & White 2018). GPS tags collected data every fourth day, allowing the battery to charge over the three days that the tags were not operating. The tags were programmed to work from dawn (06:00) to dusk (19:00), collecting high resolution (1Hz) data throughout most of this period. For more details on trapping the birds, tag deployment, programming, and data storage, see Papageorgiou *et al.* (2019) and for the vulturine guineafowl study system's design see He *et al.* (2022). For the present study, we used data

collected on six different days between 06/03/2018 and 30/03/2018, representing a transition period between a dry and a wet season during which groups maintained a fixed home range and stable group membership.

Calculating dominance ranks

To estimate the dominance hierarchy in the study group, we first recorded all the winners and losers of agonistic associations that we observed, while following the study group on foot for one year [724 agonistic associations collected from January to December 2018, for more details on the association types see Table S3 in Papageorgiou & Farine (2020)]. To estimate a robust dominance rank for each individual (Dehnen *et al.* 2022b), we calculate Elo scores (Neumann *et al.* 2011) by randomising 1000 times the ordering of associations. After creating the 1000 replicated datasets, we calculate the mean and 95% confidence intervals of ranks of individuals. For this process we use the R Package "aniDom" (Sánchez-Tójar *et al.* 2018; Farine & Sanchez-Tojar 2021).

Defining associations and Higher-order network inference

We define associations between birds based on GPS proximity. Specifically, we use GPS coordinates to extract Euclidean distances between all pairwise combinations (dyads) of group members, obtaining a completely connected network. We then filter the adjacency matrix by dropping all connections whose distance is above a threshold t=1m, and extract all connected components from the resulting network. Each connected component represents a hyperlink of birds that were deemed to be associating with each other at that given time point [equivalent to the gambit of the group (Franks *et al.* 2010)]. Finally, we track the persistence of each hyperlink over time.

The above procedure produces a weighted higher-order network, where hyperlinks are connected components in the filtered proximity graphs and their weight is the number of seconds in which that hyperlink was observed. This approach allows us to distinguish among associations of birds in hyperlinks (i.e. subgroups) of different size, in order to uncover whether this dimension carries additional insights on the behaviour of our study group of vulturine guineafowl.

Data analysis

What is the role of sex in structuring the lower level the multilevel society?

We start by testing whether individuals of different sex have a distinct social position within the group, i.e. the lowest level of the multilevel society of vulturine guineafowl. For each individual, we quantify the extent of their higher-order associations. This is done by counting the number of hyperlinks in which the individual appears at different sizes. We then use the Kruskal Wallis statistics to assess the difference between the distributions of the number of associations across hyperlinks of different sizes between the two sexes. We also use the number of hyperlinks to which any individual participates at different sizes as a 1-D variable for a k-means algorithm that splits the individuals into two clusters, and use the Adjusted Rand Index [ARI (Hubert & Arabie 1985)] to quantify how well our data-driven partition agrees with the one induced by sex, with values closer to 1 suggesting that the network data would accurately partition individuals into the different sex categories.

Does dominance determine individuals' position within their higher order network?

We next repeat the above procedure to assess the role of dominance in the pattern of associations between birds. Specifically, we compute the Spearman correlations between the Elo-based ranking and the number of hyperlinks at different sizes to which each individual participates. Unlike extracting the degree in a pairwise network, which is related to quantifying the neighbours of each bird discarding any information about size of associations, counting the hyperlinks of a bird corresponds to quantifying in how many associations of a specific size that bird was appearing. In this way, we can determine if a specific bird tends to associate more in smaller or larger subgroups. To disentangle dominance and sex, we use three linear regression models. In the first we predict the number of hyperlinks of a given size to which a bird participates from its dominance ranking. Since all males are ranked above all females, in the second model we add sex as a control variable. In the third model we add an interaction term between dominance and sex (Papageorgiou & Farine 2020; Dehnen *et al.* 2022b).

Do individuals form stronger social connections with associates from the same or different sex?

Finally, we ask whether the sex composition of a dyad predicts its propensity to emerge within higher- or lower-order hyperlinks. We compare the amount of time spent together by within-male, within-female, and between-sex dyads by terms of a non-parametric Kruskal test.

RESULTS

Males appear significantly more in larger hyperlinks than females

We observe that males tend to have significantly more associations than females at larger hyperlink sizes (Fig. 1). Females appear more rarely in larger hyperlinks, whereas the difference is less pronounced for dyadic and triadic associations, with Kruskal Wallis tests rejecting the null hypothesis of equal distribution for sizes larger than 3 (Table 1). Moreover, after size 4, the ARI between the k-means outcome and the natural partition into 2 groups induced by sex jumps to 0.7. In other words, sex clearly explains differences in the distributions of hyperlink sizes among individuals. However, the ARI never reaches 1 at larger sizes, showing that the two sexes are not perfectly separated by their higher-order behaviour. In fact, we observe that there is a male that behaves as females and a female that behaves as males at large hyperlink sizes, as shown by the outliers in Fig. 1. To understand better which additional factor might be driving this anomalous behaviour, we next included dominance ranking into our analysis.

Hyperlink size	score	P
3	0.2	0.66
4	8.4	0.004
5	13.9	<0.001
6	14.3	<0.001
7	14.3	<0.001
8	16	<0.001
9	16.4	<0.001
10	16.4	<0.001

Table 1. Summary of the differences in hyperlinks between males and females. Score and p-value of Kruskal-Wallis test between distributions of the number of

hyperlinks of males and females. Low p-value rejects the null hypothesis of identical distributions.

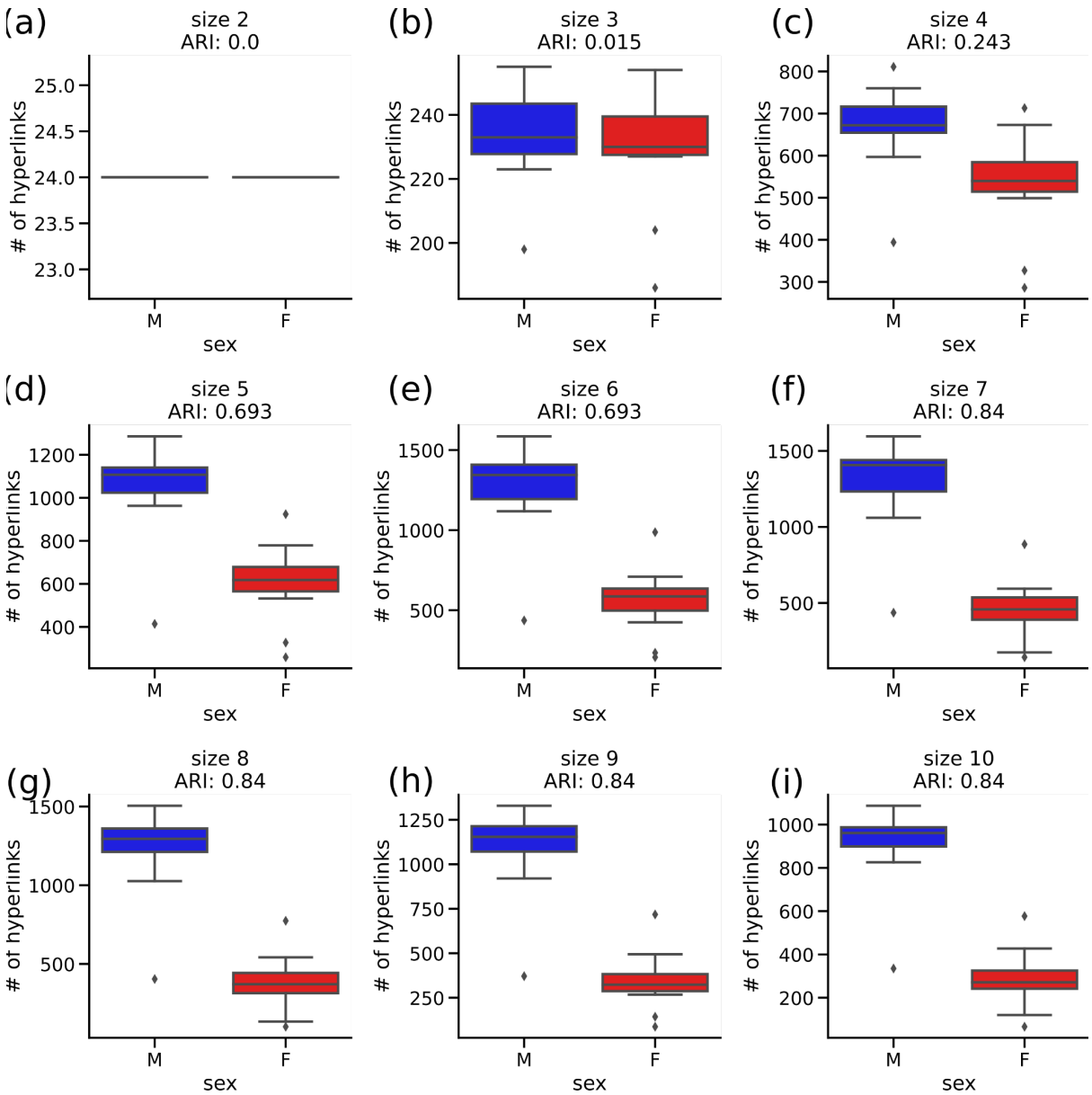

Fig. 1 Sex differences in hyperlink formation. (a-i) Distribution of the number of hyperlinks of different sizes in which males (blue box) and females (red box) are detected. Each panel also reports the Adjusted Rand Index (ARI) between sex partition and clustering induced by the number of interactions and extracted using the k-means algorithm.

Dominant males and females appear significantly more in larger hyperlinks

We compute the Spearman correlation between dominance ranking and the number of distinct associations of each bird across each hyperlink size. At hyperlink size 2, no pattern is observed between dominance ranking and the number of associations, as each bird appears in all the possible dyads with any other individual (Fig. 2). As the size of hyperlinks increases, a significant positive correlation emerges, suggesting that the most dominant individuals appear in more associations (Table S1). Combining the information on sex and dominance ranking allows us to identify the two birds that behave as birds of the opposite sex. The male guineafowl behaving as a female is the least dominant male, while the female bird behaving as a male is the second-most dominant female. This pattern is reflected more generally, with higher-ranked individuals within each sex expressing greater presence in larger hyperlinks (Table 2), which appears to be consistent across the sexes (i.e. the interaction between sex and dominance is not significant, Table S2). Thus, both sex and dominance appear to have an effect on higher-order within-group social structure in vulturine guineafowl.

Hyperlink size	β_{Dom}	P_{Dom}	β_{Sex}	P_{Sex}	R^2
3	1.28	0.16	-12.3	0.35	0.03
4	11.92	0.04	-21.08	0.80	0.37
5	22.06	0.03	157.31	0.30	0.64
6	28.23	0.03	334.44	0.08	0.73
7	29.73	0.02	448.25	0.03	0.78
8	26.03	0.03	503.74	0.008	0.8
9	25.13	0.02	422.15	0.01	0.81
10	19.37	0.02	367.58	0.005	0.83

Table 2. Summary of the effects of dominance rank on the number of hyperlinks at different sizes after adding sex as a control variable. Regression coefficients, p-values and R-squared of the linear model $y = a + bx + cz$ where y is the number of hyperlinks, x is dominance ranking and z is sex. Effect of dominance ranking is reduced after adding sex, remaining significant at $p<0.05$ for sizes larger than 3.

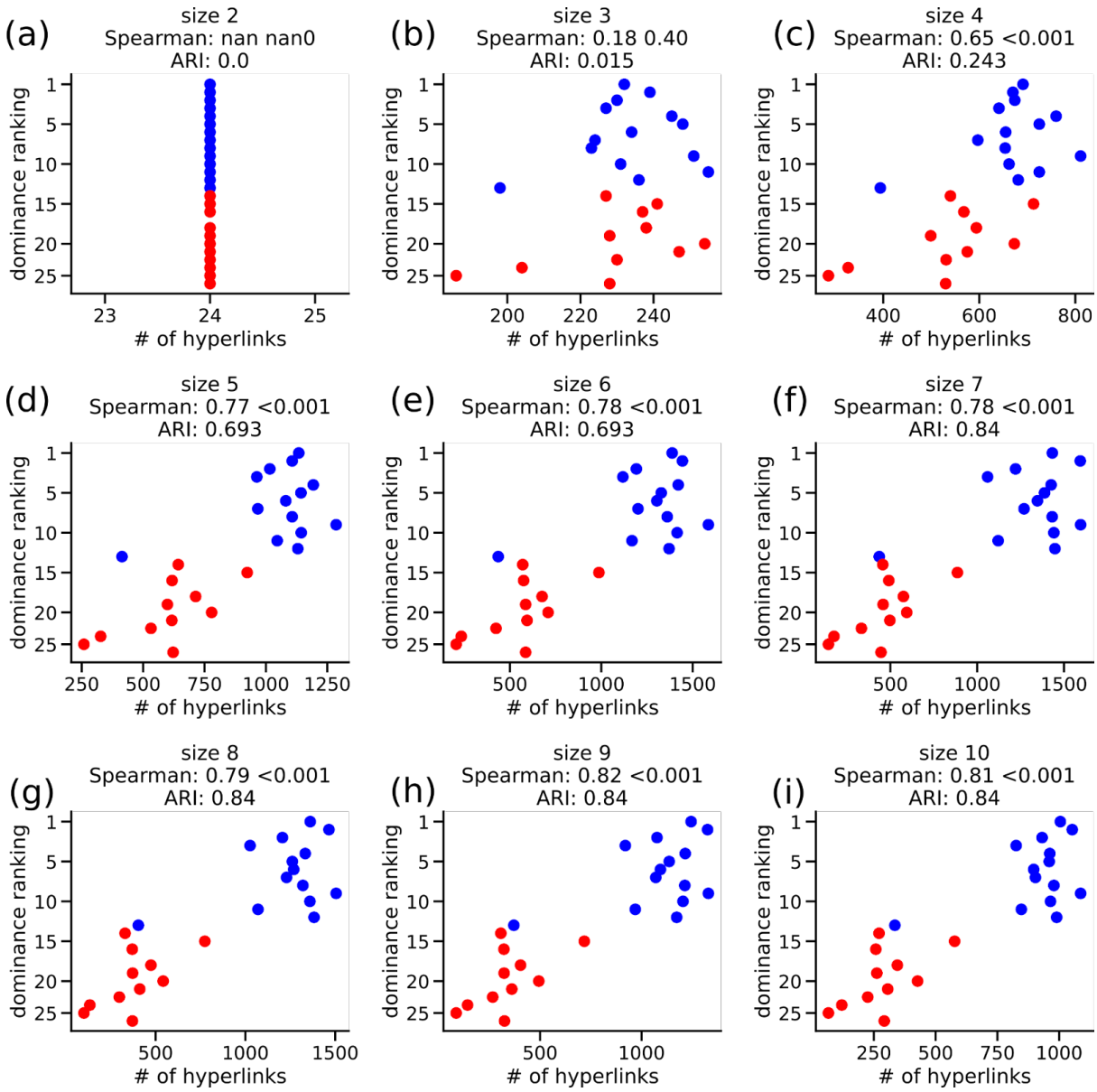

Fig. 2. The effects of dominance rank and sex on hyperlink formation. (a-i) Scatter plot showing the number of hyperlinks in which each bird appears (x-axis) and dominance rank (y-axis, 1 is most dominant) for hypergraphs of different sizes. Spearman values show the correlation and corresponding p-value. Blue points (upper) represent males and red points (lower) represent females.

Male-male dyads co-occur in large hyperlinks, female-female dyads in smaller ones

We consider all possible dyads of birds in the social group and count how many seconds they spent together in hyperlinks of different sizes (Fig. S1). We that behaviour is heterogeneous, with some dyads being more active together in smaller hyperlinks, others showing the opposite trend, and some others being more consistent across hyperlinks of

different sizes. When taking into account sex, we find that these three distinct classes of behaviours are consistently associated with dyads of different sex composition (Fig. 3). Specifically, male-male dyads tend to spend more time in larger hyperlinks than they do in smaller ones, while female-female dyads exhibit the opposite behaviour. Mixed dyads show a more homogeneous distribution of time spent in hyperlinks of different sizes. Moreover, our analysis reveals that female-female dyads spend slightly more time than males in hyperlinks of size 2 (top panel of Fig. 3 and Table S3), while spending dramatically less time together in larger hyperlinks than males (right panel of Fig. 3 and Table S3).

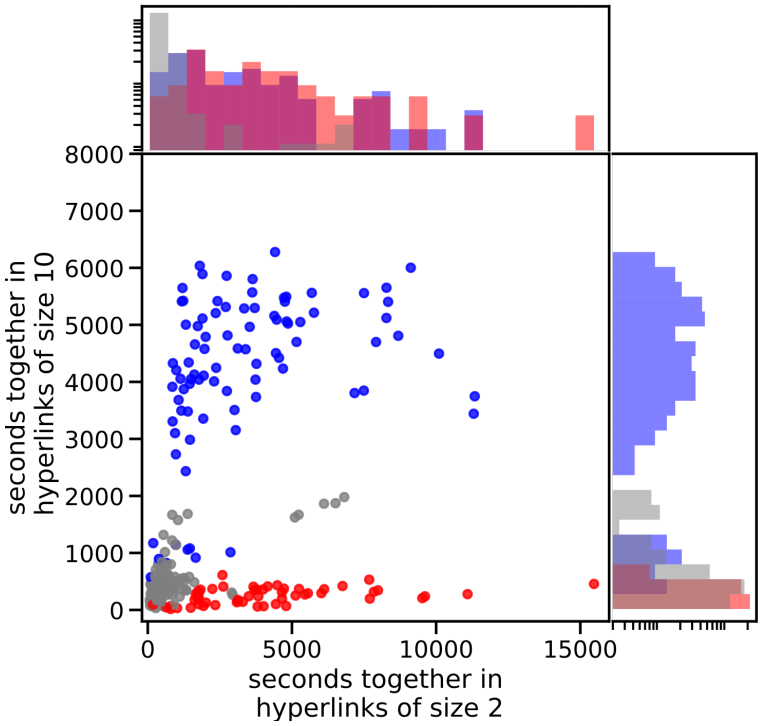

Fig. 3. Heterogeneity of behaviour at different sizes. Scatter plots showing the seconds two individuals spent together in a dyad (x-axis) and in a hyperlink of size 10 (y-axis). Marginal plot on the right shows the probability density function (pdf) of the points on the y axis and plot on the top shows the pdf of the points on the x axis. Blue points represent male-male dyads, red points represent female-female dyads, and grey points represent mixed-sex dyads.

DISCUSSION

Uncovering the fine-scale structure of animal groups can be challenging. Here, we have illustrated how a higher-order network approach can help us better understand the lowest level of the multilevel society of vulturine guineafowl, which concerns intra-group association patterns. Our method has revealed a striking pattern: groups (the intermediate level) are predominately structured around males, with male-male dyads being significantly over-represented in larger hyperlinks. In other words, male-male associations are consistently found together in larger, consistent subgroups, whereas male-female and female-female associations are typically more pairwise, and rarely expressed in larger subgroups. Thus, males have substantially more associations than females. Dominance also plays a major role in determining the lower level of vulturine guineafowl societies. As we might expect given the extremely steep dominance hierarchies within social groups, more dominant males and females are consistently found to form larger hyperlinks. While standard analyses could have identified differences in centrality among sexes, higher-order analysis adds a deeper understanding of the multidimensionality in the difference of centrality among group members, showing that the trend is more pronounced for hyperlinks of larger size (e.g. dyadic relationships differ little between sexes, whereas larger sized hyperlinks are distinctly biased towards males, Fig. 4).

In social systems where males are philopatric and rarely disperse from their natal group, such as in hamadryas baboons (*Papio hamadryas*) (Jolly 2020) and guinea baboons (*Papio papio*) (Kopp *et al.* 2015), there should be high genetic relatedness among male group members (Städele *et al.* 2015). Genetic relatedness, in turn, has long been linked to the strength of social bonds (Hamilton 1964) with kin bonds often setting the core of social systems and enabling cooperation (Städele *et al.* 2015). In social systems where males are philopatric and set the core of their social group, such as in superb fairy-wrens (*Malurus cyaneus*), males can promote cooperation not only between members of their group but also between groups that used to be united and split after they increased in size (Camerlenghi *et al.* 2022). In guinea baboons, males that share strong social bonds also support each other when conflicts emerge (Dal Pesco *et al.* 2022). We found that in groups of vulturine guineafowl, in which males are likely to be highly related to each other, males also form the core of their social group. In addition, we found an independent

effect of dominance, which is demonstrated by the second-most dominant female in the group behaving more like a male by being often found as part of large hyperlinks. A plausible explanation here could be that this female had dispersed in the group years ago and therefore many of the adult males were her sons or grandchildren, given also that the most dominant females are the most successful breeders in their group and from one breeding season to the next, they consistently pair up with the most dominant males (Nyaguthii 2021). Therefore, the kin bonds that more dominant females build over time may allow them to form stronger social relationships with other group members, similarly to what males do. We also found that the least dominant male that was behaving more like a female, as higher-order network analysis revealed, could have been avoiding other males to escape from male-male aggression, as all males were able to challenge and win a contest against him (Dehnen *et al.* 2022b). A missing element of our study, which could better explain intra-group association patterns in vulturine guineafowl, is the quantification of genetic relatedness between group members and the enhanced social relationships it may be generating (e.g. mother-offspring).

Taken together, higher-order network analysis reveals that the social structure of vulturine guineafowl is predominantly driven by groups formed by sets of males, and not built-up from dyadic relationships, neither pairs of males nor females. Across a broad range of social animals, groups are likely to be composed of more than pairs of individuals that aggregate together, but rather of sets of individuals that form non-random units. Evidence for this comes from a range of systems, even some in which social associations have long been thought to be expressed relatively randomly. For example, the social network in winter flocks predicts breeding neighbourhoods during the subsequent spring in both great tits (Firth & Sheldon 2016) and blue tits (*Cyanistes caeruleus*) (Beck *et al.* 2020). In wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) that form multi-level alliances, second-order alliances consist of up to 14 individuals including multiple duos and trios of dolphins (first-order alliances) that move and consort females collectively. Second-order alliances can also have preferential associations with specific other second-order alliances, forming third-order alliances that can compete against dolphins from rival third-order alliances (King *et al.* 2021). Finally, bell miners (*Manorina melanophrys*) are socially organised into colonies that are formed from several cooperative-breeding units that also associate preferentially with each other to form

coteries (Painter *et al.* 2000). Such patterns suggest that membership to a group (or a subgroup) represents distinct social units that are not reducible down to dyads, even if the dyads within might still vary in the strength of their social bonds. When combined with novel analytical tools, higher-order networks represent a powerful and potentially profoundly new way of analysing and interpreting animal social networks.

In broad terms, the use of higher-order networks promises to unveil several new dimensions on animal sociality that are inaccessible to traditional network analyses. Firstly, they allow clearer delineation of different types of social connections. The decomposition of large hyperlinks (e.g. triads, etc.) by traditional network analyses into the many dyads that they comprise leads to the formation of densely connected cliques that can bias traditional algorithms aimed at identifying characteristics of network structure. For instance, a topic of wide interest in animal social networks is to identify more central individuals, or even just the relevance of a given individual in their population, which is typically measured using a range of network centrality measures. Unsurprisingly, when the system only has dyads (or when working with dyads obtained as projections of larger group interactions), high centrality is associated with a high number of contacts. In systems where higher-order interactions are predominant, however, high centrality may be achieved with diverse strategies, namely a high number of (possibly small, i.e. pairwise) interactions, or by participating in (possibly a limited number) of diverse large groups. Such distinct dimensions of sociality cannot be distinguished when higher-order relational data are projected as a combination of small dyads. Secondly, higher-order networks provide greater social context to observed associations or interactions. For example, it might be of interest to distinguish if an individual participating in group interactions also forms connections with those individuals in smaller, pairwise, contexts, an insight which can be obtained through higher-order motif analysis (Lotito *et al.* 2022). Similar reasoning applies to the mesoscale properties of a networked society. For instance, communities (i.e. closely connected groups of individuals who interact more among them than with other members of the population) should be obtained by considering the joint effect of having network subgraphs which are dense not only because of a high number of interactions, but also because of large hyperlinks where relevant population members interact collectively. Finally, the same two dimensions are relevant when considering the core of

a social network—the set of central and tightly connected individuals typically able to highly influence and affect the whole population's behaviour. Specifically, it may be worth testing whether higher-order hypergraphs are more or less influential in the core of social networks than individuals connected in more pairwise manners.

The last decades' technological advances in biologging have facilitated the collection of high-resolution and high-precision data, enabling thus the 'reality mining' of social relationships in tracked animal groups (Krause *et al.* 2013; He *et al.* 2022). However, the high density of data that these methods produce can also generate overly dense networks, and continuing efforts are needed to develop methods to analyse animal social networks to follow these advancements (Webber & Vander Wal 2019). Here, we applied a higher-order network approach, recently developed by statistical physicists, to successfully uncover the within-group social structure in a group of highly cohesive GPS-tagged vulturine guineafowl. These methods allowed us to gain insights that would not have been revealed by traditional social network analysis techniques. We therefore recommend the use of the higher-order methodological approach to shed new light on beyond-the-dyad building blocks of social groups or communities. In the future, adding a time- , seasonal- and potentially a context-perspective to such studies will facilitate the understanding of how environmental conditions shape the formation and persistence of higher-order associations within animal groups.

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STATEMENT OF AUTHORSHIP

DP and DRF designed the data collection and collected data in the field. FM and FB performed higher-order network analyses and DP calculated dominance ranks. All authors wrote the first draft of the manuscript and contributed substantially to revisions.

REFERENCES

Alberts, S.C. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *J. Anim. Ecol.*, 88, 47–66.

Alvarez-Rodriguez, U., Battiston, F., de Arruda, G.F., Moreno, Y., Perc, M. & Latora, V. (2021). Evolutionary dynamics of higher-order interactions in social networks. *Nat. Hum. Behav.*, 5, 586–595.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B.C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518, 538–541.

Aplin, L.M., Farine, D.R., Morand-Ferron, J. & Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B Biol. Sci.*, 279, 4199–4205.

Ashby, B. & Farine, D.R. (2022). Social information use shapes the coevolution of sociality and virulence. *Evolution*. In press.

Bairey, E., Kelsic, E.D. & Kishony, R. (2016). High-order species interactions shape ecosystem diversity. *Nat. Commun.*, 7, 12285.

Battiston, F., Amico, E., Barrat, A., Bianconi, G., Ferraz de Arruda, G., Franceschiello, B., *et al.* (2021). The physics of higher-order interactions in complex systems. *Nat. Phys.*,

17, 1093–1098.

Battiston, F., Cencetti, G., Iacopini, I., Latora, V., Lucas, M., Patania, A., *et al.* (2020). Networks beyond pairwise interactions: Structure and dynamics. *Phys. Rep.*, 874, 1–92.

Battiston, F. & Petri, G. (Eds.). (2022). *Higher-Order Systems*. Understanding Complex Systems. Springer International Publishing, Cham.

Beck, K.B., Farine, D.R. & Kempenaers, B. (2020). Winter associations predict social and extra-pair mating patterns in a wild songbird. *Proc. R. Soc. B Biol. Sci.*, 287, 20192606.

Benson, A.R., Abebe, R., Schaub, M.T., Jadbabaie, A. & Kleinberg, J. (2018). Simplicial closure and higher-order link prediction. *Proc. Natl. Acad. Sci.*, 115, E11221–E11230.

Bond, M.L., König, B., Lee, D.E., Ozgul, A. & Farine, D.R. (2021). Proximity to humans affects local social structure in a giraffe metapopulation. *J. Anim. Ecol.*, 90, 212–221.

Camerlenghi, E., McQueen, A., Delhey, K., Cook, C.N., Kingma, S.A., Farine, D.R., *et al.* (2022). Cooperative breeding and the emergence of multilevel societies in birds. *Ecol. Lett.*, 25, 766–777.

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

Dal Pesco, F., Trede, F., Zinner, D. & Fischer, J. (2022). Male–male social bonding, coalitionary support and reproductive success in wild Guinea baboons. *Proc. R. Soc. B Biol. Sci.*, 289.

Davis, G.H., Crofoot, M.C. & Farine, D.R. (2018). Estimating the robustness and uncertainty of animal social networks using different observational methods. *Anim. Behav.*, 141, 29–44.

Dehnen, T., Arbon, J.J., Farine, D.R. & Boogert, N.J. (2022a). How feedback and feed-forward mechanisms link determinants of social dominance. *Biol. Rev.*, 97, 1210–1230.

Dehnen, T., Papageorgiou, D., Nyaguthii, B., Cherono, W., Penndorf, J., Boogert, N.J., *et al.* (2022b). Costs dictate strategic investment in dominance interactions. *Philos. Trans. R. Soc. B Biol. Sci.*, 377.

Eriksson, A., Edler, D., Rojas, A., de Domenico, M. & Rosvall, M. (2021). How choosing

random-walk model and network representation matters for flow-based community detection in hypergraphs. *Commun. Phys.*, 4, 133.

Farine, D.R. (2018). When to choose dynamic vs. static social network analysis. *J. Anim. Ecol.*, 87, 128–138.

Farine, D.R. & Sanchez-Tojar, A. (2021). Package 'aniDom': Inferring Dominance Hierarchies and Estimating Uncertainty. version 0.1.5. https://cran.r-project.org/package=aniDom

Farine, D.R. & Sheldon, B.C. (2015). Selection for territory acquisition is modulated by social network structure in a wild songbird. *J. Evol. Biol.*, 28, 547–556.

Farine, D.R., Strandburg-Peshkin, A., Berger-Wolf, T., Ziebart, B., Brugere, I., Li, J., *et al.* (2016). Both Nearest Neighbours and Long-term Affiliates Predict Individual Locations During Collective Movement in Wild Baboons. *Sci. Rep.*, 6, 27704.

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

Ferreira, A.C., Covas, R., Silva, L.R., Esteves, S.C., Duarte, I.F., Fortuna, R., *et al.* (2020). How to make methodological decisions when inferring social networks. *Ecol. Evol.*, 10, 9132–9143.

Firth, J.A. & Sheldon, B.C. (2016). Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. *Ecol. Lett.*, 19, 1324–1332.

Fisher, D.N., Rodríguez-Muñoz, R. & Tregenza, T. (2016). Comparing pre- and post-copulatory mate competition using social network analysis in wild crickets. *Behav. Ecol.*, 27, 912–919.

Franks, D.W., Ruxton, G.D. & James, R. (2010). Sampling animal association networks with the gambit of the group. *Behav. Ecol. Sociobiol.*, 64, 493–503.

Franks, V.R., Ewen, J.G., McCready, M., Rowcliffe, J.M., Smith, D. & Thorogood, R. (2020). Analysing age structure, residency and relatedness uncovers social network structure in aggregations of young birds. *Anim. Behav.*, 166, 73–84.

Gerber, L., Connor, R.C., Allen, S.J., Horlacher, K., King, S.L., Sherwin, W.B., *et al.* (2022). Social integration influences fitness in allied male dolphins. *Curr. Biol.*, 32, 1664-1669.e3.

Gilbertson, M.L.J., White, L.A. & Craft, M.E. (2021). Trade-offs with telemetry-derived contact networks for infectious disease studies in wildlife. *Methods Ecol. Evol.*, 12, 76–87.

Grilli, J., Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2017). Higher-order interactions stabilize dynamics in competitive network models. *Nature*, 548, 210–213.

Grueter, C.C., Qi, X., Zinner, D., Bergman, T., Li, M., Xiang, Z., *et al.* (2020). Multilevel Organisation of Animal Sociality. *Trends Ecol. Evol.*, 35, 834–847.

Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *J. Theor. Biol.*, 7, 1–16.

He, P., Klarevas-irby, J.A., Papageorgiou, D., Christensen, C., Strauss, E.D. & Farine, D.R. (2022). A guide to designing GPS-based studies of animal societies. *bioRxiv*. https://doi.org/10.1101/2022.01.29.478280

Hoppitt, W.J.E. & Farine, D.R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.*, 136, 227–238.

Hubert, L. & Arabie, P. (1985). Comparing partitions. *J. Classif.*, 2, 193–218.

Iacopini, I., Petri, G., Barrat, A. & Latora, V. (2019). Simplicial models of social contagion. *Nat. Commun.*, 10, 2485.

Jolly, C.J. (2020). Philopatry at the frontier: A demographically driven scenario for the evolution of multilevel societies in baboons (Papio). *J. Hum. Evol.*, 146, 102819.

King, S.L., Connor, R.C., Krützen, M. & Allen, S.J. (2021). Cooperation-based concept formation in male bottlenose dolphins. *Nat. Commun.*, 12, 2373.

Klarevas-Irby, J.A., Wikelski, M. & Farine, D.R. (2021). Efficient movement strategies mitigate the energetic cost of dispersal. *Ecol. Lett.*, 24, 1432–1442.

Kopp, G.H., Fischer, J., Patzelt, A., Roos, C. & Zinner, D. (2015). Population genetic insights into the social organization of Guinea baboons (Papio papio): Evidence for female-biased dispersal. *Am. J. Primatol.*, 77, 878–889.

Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S. & Rutz, C. (2013). Reality mining of animal social systems. *Trends Ecol. Evol.*, 28, 541–551.

Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56–64.

Lotito, Q.F., Musciotto, F., Montresor, A. & Battiston, F. (2022). Higher-order motif analysis in hypergraphs. *Commun. Phys.*, 5, 79.

Lugo-Martinez, J., Zeiberg, D., Gaudelet, T., Malod-Dognin, N., Przulj, N. & Radivojac, P. (2021). Classification in biological networks with hypergraphlet kernels.

Bioinformatics, 37, 1000–1007.

Maldonado-Chaparro, A.A., Forstmeier, W. & Farine, D.R. (2021). Relationship quality underpins pair bond formation and subsequent reproductive performance. *Anim. Behav.*, 182, 43–58.

Musciotto, F., Battiston, F. & Mantegna, R.N. (2021). Detecting informative higher-order interactions in statistically validated hypergraphs. *Commun. Phys.*, 4, 1–9.

Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., *et al.* (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science.* 375, eabg 1780.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., *et al.* (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.*, 82, 911–921.

Nyaguthii, B.N. (2021). Cooperative breeding in the vulturine guineafowl (Acryllium vulturinum) at Mpala Research Center, Laikipia County, Kenya. University of Eldoret, Kenya.

Painter, J.N., Crozier, R.H., Poiani, A., Robertson, R.J. & Clarke, M.F. (2000). Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, Manorina melanophrys. *Mol. Ecol.*, 9, 1339–1347.

Papageorgiou, D., Christensen, C., Gall, G.E.C., Klarevas-Irby, J.A., Nyaguthii, B., Couzin, I.D., *et al.* (2019). The multilevel society of a small-brained bird. *Curr. Biol.*, 29, R1120–R1121.

Papageorgiou, D. & Farine, D.R. (2020). Shared decision-making allows subordinates to lead when dominants monopolize resources. *Sci. Adv.*, 6, eaba5881.

Papageorgiou, D. & Farine, D.R. (2021). Multilevel Societies in Birds. *Trends Ecol. Evol.*, 36, 15–17.

Portugal, S.J. & White, C.R. (2018). Miniaturization of biologgers is not alleviating the 5% rule. *Methods Ecol. Evol.*, 9, 1662–1666.

Psorakis, I., Roberts, S.J., Rezek, I. & Sheldon, B.C. (2012). Inferring social network structure in ecological systems from spatio-temporal data streams. *J. R. Soc. Interface*, 9, 3055–3066.

Sánchez-Tójar, A., Schroeder, J. & Farine, D.R. (2018). A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *J. Anim. Ecol.*, 87, 594–608.

Silk, M.J., Hodgson, D.J., Rozins, C., Croft, D.P., Delahay, R.J., Boots, M., *et al.* (2019). Integrating social behaviour, demography and disease dynamics in network models: applications to disease management in declining wildlife populations. *Philos. Trans. R. Soc. B Biol. Sci.*, 374, 20180211.

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

Städele, V., Van Doren, V., Pines, M., Swedell, L. & Vigilant, L. (2015). Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society. *J. Hum. Evol.*, 78, 103–113.

Strandburg-Peshkin, A., Farine, D.R., Couzin, I.D. & Crofoot, M.C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, 348, 1358–1361.

Strauss, E.D. & Holekamp, K.E. (2019). Social alliances improve rank and fitness in convention-based societies. *Proc. Natl. Acad. Sci.*, 116, 8919–8924.

Sunga, J., Webber, Q.M.R. & Broders, H.G. (2021). Influence of number of individuals and observations per individual on a model of community structure. *PLoS One*, 16, e0252471.

Tudisco, F. & Higham, D.J. (2021). Node and edge nonlinear eigenvector centrality for hypergraphs. *Commun. Phys.*, 4, 201.

Tung, J., Barreiro, L.B., Burns, M.B., Grenier, J.-C., Lynch, J., Grieneisen, L.E., *et al.* (2015). Social networks predict gut microbiome composition in wild baboons. *Elife*, 4, 1–18.

Voelkl, B. & Noë, R. (2008). The influence of social structure on the propagation of social information in artificial primate groups: A graph-based simulation approach. *J. Theor. Biol.*, 252, 77–86.

Wang, D., Forstmeier, W., Farine, D.R., Maldonado-Chaparro, A.A., Martin, K., Pei, Y., *et al.* (2022). Machine learning reveals cryptic dialects that explain mate choice in a songbird. *Nat. Commun.*, 13, 1630.

Webber, Q.M.R. & Vander Wal, E. (2019). Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Anim. Behav.*, 149, 77–87.

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University of Chicago Press.

Xiao, J., Li, Y., Chu, C., Wang, Y., Meiners, S.J. & Stouffer, D.B. (2020). Higher-order interactions mitigate direct negative effects on population dynamics of herbaceous plants during succession. *Environ. Res. Lett.*, 15, 074023.