

Key players and hierarchical organization of prairie dog social networks



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ABSTRACT

The use of social network theory in evaluating animal social groups has gained traction in recent years. Despite the utility of social network analysis in describing attributes of social groups, it remains unclear how comparable this approach is to traditional behavioral observational studies. Using data on Gunnison's prairie dog (*Cynomys gunnisoni*) social interactions we describe social networks from three populations. We then compare those social networks to groups identified by traditional behavioral approaches and explore whether individuals group together based on similarities. The social groups identified by social network analysis were consistent with those identified by more traditional behavioral approaches. However, fine-grained social sub-structuring was revealed only with social network analysis. We found variation in the patterns of interactions among prairie dog social groups that was largely independent of the behavioral attributes or genetics of the individuals within those groups. We detected that some social groups include disproportionately well-connected individuals acting as hubs or bridges. This study contributes to a growing body of evidence that social networks analysis is a robust and efficient tool for examining social dynamics.

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1. Introduction

In the study of social animals, there is growing interest in complex emergent properties of group structure. Social network analysis (SNA) has been increasingly used to study the social dynamics of animal systems (Bergmuller et al., 2010; Brent et al., 2011; Lusseau, 2003; Lusseau and Newman, 2004; Newman, 2003). It is a unifying conceptual framework that can be applied comparatively across all social taxa—from microbes to humans. Social networks can help to identify features of species that are indiscernible (or even invisible) based on studies of individuals or behaviors alone (Croft et al., 2004; Lusseau and Newman, 2004). In other cases, there exists substantial intra-specific variation among networks based, in part, on group attributes, individual differences, and ecological factors (Faust and Skvoretz, 2002; Guimarães et al., 2007; Bhadra et al., 2009; Madden et al., 2009). Furthermore, differences in social networks, whether among taxa or social groups, almost necessarily lead to differences in the spread of diseases, decision making strategies, information or, in some cases, food, through networks (Croft et al., 2004; Drewe et al., 2009; Hamede et al., 2009; Jacobs et al., 2011; Kasper and Voelkl, 2009; Madden et al., 2009).

A key challenge with SNA is how to relate their results to the much larger literature on social interactions that relies on other approaches to distinguish social groups. Prior to the widespread use of SNA, behavioral studies explored social interactions and social groups dynamics using informal clustering techniques (e.g., Hinde, 1976). Our understanding of the social systems of most organisms rests on such traditional approaches. Can the results from these earlier studies be related to those of social network analysis? This question seems to have not been well considered, particularly in the social mammals where research has tended to divide social groups into hierarchical categories. Such groups are constructed out of the existence of interactions among individuals but also the nature of those interactions and whether they are negative, positive, reproductive, relate to food sharing, or have some other defining features. The advantages of SNA are frequently highlighted (e.g., Proulx et al., 2005; Sueur et al., 2011; Wey et al., 2008), but whether SNA builds on, replaces, or conflicts with other approaches is unclear.

Gunnison's prairie dogs, *Cynomys gunnisoni*, are large, diurnal, highly social ground squirrels whose range is limited to the grasslands of the Colorado Plateau (Hall and Kelson, 1959). Gunnison's prairie dogs colonies contain a variable number of territories occupied by distinct social groups, ranging from 3 to 15 individuals (Travis et al., 1995; Verdolin and Slobodchikoff, 2010) akin to small groups of social insects (e.g., *Temnothorax albigipennis*:

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Dornhaus and Franks, 2006), primate groups (Chapman and Chapman, 2000), or hunter gatherer societies (Hamilton et al., 2007). Traditionally, ecologists have distinguished prairie dog social groups using behavioral and spatial observations of known individuals over time (King, 1955; Slobodchikoff, 1984; Travis and Slobodchikoff, 1993; Verdolin, 2007), with a strong emphasis on negative interactions, where negative interactions among individuals imply those individuals are from different social groups (Slobodchikoff, 1984; Travis and Slobodchikoff, 1993; Verdolin, 2007). The designation of the size of groups and the identity of individuals within groups also often relies on data on mating behavior and behavioral time allocation (e.g., time spent being vigilant versus feeding; Slobodchikoff, 1984; Travis and Slobodchikoff, 1993; Travis et al., 1995; Verdolin, 2007). The resulting identification of distinct social groups within a site can be robust with regard to individual interactions, but tends to result in a categorical classification of groups, in which individuals either are or are not members of groups and any patterning in social structure above or below the standard social group is either not described or, if described, is in terms of the behavior of individual species and their histories.

Although SNA has been used recently for a variety of social species, its application has focused primarily on individual measurements or full network measurements. When SNA methods are used to find intermediate (within network) structure in the full networks, these methods are referred to as community detection (Leu et al., 2010; Lusseau, 2003; Lusseau and Newman, 2004; Maryanski, 1987). The use of community detection techniques in the analysis of social networks has recently gained traction (Porter et al., 2009). Often network structure is not obvious by simply looking at a list of interactions, or a resulting graph of interactions. Community detection permits a researcher to identify social groups by discerning which individuals in the network have more connections to the other individuals within the group than to individuals outside the group.

If a network-based approach to exploring the social dynamics of Gunnison's prairie dog—or any other species—produces social groupings similar to traditional methods, social network analysis can add to the insights of traditional approaches in several ways. First, comparing social network properties among groups may highlight subtle variation in social structure not readily observable or quantifiable by conventional behavioral studies (Faust and Skvoretz, 2002; Traud et al., 2011; Wolf et al., 2007). Second, network analyses can also reveal emergent properties of social groups, including identifying individuals with central roles—such as the dolphin social brokers—and characterizing variability in group cohesion or hubs, individuals who are connected to an unusually high number of other organisms (Bezanson et al., 2008; Croft et al., 2005; Gero et al., 2013; Lusseau, 2003; Lusseau and Newman, 2004; Madden et al., 2009; Naug, 2008). Third, SNA may provide a method for testing the hypothesis that individuals may group together based on similarities, differences, or random associations (Galef and Laland, 2005; Pedersen et al., 2006; Pepper, 2000; Reader and Biro, 2010; Rendella and Whitehead, 2001; Ross, 2001). On the other hand, if SNA produces fundamentally different social group clusters than traditional behavioral approaches, it might imply that the two methods describe potentially distinct information and social processes.

Here, we generated social network matrices using data on positive social interactions of Gunnison's prairie dogs. We then used community detection analysis to discern distinct social groups simply from the network data and compared them to social groups identified by traditional behavioral approaches (Traud et al., 2011). Next, we used SNA to examine whether there were features of Gunnison prairie dog social behavior detectable only through SNA or behavioral studies alone. Based on the differences

we found between SNA and traditional methods, we expanded our analysis to further explore aspects of sociality not detectable by traditional methods.

2. Methods

2.1. Study area

A detailed description of live-trapping, handling, and marking methods are available in Verdolin (2007). A Scientific Collector's Permit (Arizona Game and Fish Permit no. SP742094) was obtained prior to trapping and all procedures were in compliance with Stony Brook University IACUC (IACUC no. 2009-1745, Stony Brook University). Individuals were trapped with veterinary supervision from mid-February (upon emergence from hibernation) through August at two colonies, Country Club (CC) and Humane Society (HS), with two 1 ha-plots delineated per colony and separated by road. These distinct sites are referred to as CCI, CCII and HSI, HSII, respectively. For our purposes we consider these to be separate populations, as individuals from each plot within a colony did not co-mingle. AVID[®] identification microchips were implanted subdermally in all captured animals for permanent identification. Individuals were also marked with black Lady Clairol[®] semi-permanent hair dye for visual identification. Data for the analyses presented here are based on data collected from March to August 2004 and reflects data collected from mutually exclusive populations on three sites: HSI, HSII, and CCI.

For each population, all behavioral observations were made by JLV alternately in the morning from 0700 to 1000 h and afternoon from 1500 to 1800 h, during the times when prairie dogs were most active (as in Longhurst, 1944). With the exception of days when trapping occurred, JLV made observations at least every other day at each site from March 7 to August 15, 2004, for a total of 396 h of observation. Prairie dogs that consistently exhibited mutually tolerant behaviors with one another, such as greet-kisses and co-feeding, were assigned to the same social group (see Verdolin, 2007 for details).

2.2. Determination of social group membership

This study uses previously published social groups determined using traditional methods where the dataset included: (1) the home range overlap of individuals, (2) all occurrences of a mutually tolerant positive interactions such as greet-kissing and co-feeding (within 1 m of each other), and (3) all occurrences of aggressive interactions, which was any interaction that resulted in fights or chases (see Verdolin, 2007). Because aggressive interactions are infrequent (e.g., 0.016 events/h among males), and rarely occur within a social group ($N = 5$ in 396 h of observation), aggressive interactions are typically used to determine who does *not* belong to the social group (see Verdolin, 2007). This approach followed common behavioral sampling approaches for social vertebrates (Altmann, 1974; Hinde, 1976).

Behavioral data on individuals was obtained using focal sampling (Altmann, 1974). Focal samples were conducted for 5 min. During the focal sample, the location of the focal animal and all occurrences of social interactions were recorded. Four such focal samples were taken in sequence. Active individuals were chosen for observation, with the qualification that no individual was observed more than once in a daily time block (see Verdolin, 2007 for more details). During the observation period, each focal sample was recorded using a Sony Digital camcorder. For this study, JLV analyzed the videotaped focal samples to extract data, with the behavior of the focal animal recorded every 5 s. We used vigilance, feeding, and moving behavior in our analyses. Vigilance behavior included both posting and scanning, where posting is a

stationary bipedal alert posture and scanning is quadrupedal scanning of the environment with the head above a 90° angle (Verdolin and Slobodchikoff, 2002). Feeding was defined as actively consuming a food item and moving was measured as movement from one location to another. The proportion of time that the focal animal spent engaged in each behavior was then calculated. In the case of multiple observations of the same individual, the average time spent in each behavior was calculated. Trappability was also considered a behavioral trait and was calculated as the proportion of times an individual was trapped given the trapping period.

Given the low rate of agonistic interactions among group members, we wanted to assess whether we could determine group membership using SNA solely on the basis of positive interactions among individuals. In Gunnison's prairie dogs, greet-kiss behavior is a distinct, easily observable interaction that, when not followed by agonistic behavior (e.g., fights, chases) signals a mutually tolerant behavior indicative of social group membership (King, 1955; Travis and Slobodchikoff, 1993; Travis, 1994; Slobodchikoff et al., 2009). We did not include the CCI site in the analyses because an insufficient number of focal samples were made on prairie dogs from that population to include them in the behavioral analysis. Two additional social groups on CCI were not included because they were primarily determined by spatial location and the number of interactions was insufficient for this analysis.

2.3. Determination of community membership

We used the number of greet kisses recorded over a period of six months, which is to say, we considered a subset of the data available from field observations of these prairie dogs, excluding all behavioral observations except for data on who greet-kissed with whom and how often (see above). Although a fine-scale temporal (e.g., monthly) analysis of social network structure would have been desirable, the frequency of positive interactions was too sparse to permit this approach. Based on these data, we created a matrix for each site where all individuals are listed on both the horizontal and vertical axes and each entry in the matrix became the integer corresponding to the number of interactions between each pair of prairie dogs, making this an undirected weighted network. We used the R package igraph to identify network communities using multilevel community detection (Blondel et al., 2008; Csardi, 2005). This algorithm is a modularity-maximizing algorithm. Modularity is a measure of number of ties within a group minus the expected number of ties within that group given the network. This process works in two steps, which are then iterated, where each prairie dog is first placed into its own community and each community's neighbors are then checked to see if merging two communities resulted in a gain in modularity. The second step of this algorithm is to treat each community as an individual prairie dog, summing ties within the community to make a weighted self-loop and then summing ties between communities to make weighted ties. The first step is then repeated with this new network. This process is iterated until no gains in modularity can be made. The resulting set of communities then has optimal modularity. This algorithm maximizes this modularity while also taking the weights of ties into account, or the numbers of greet kisses between each pair of prairie dogs.

2.4. Comparison of traditional and SNA approaches

In many studies, once communities are identified through SNA, traits of individuals are then compared to those communities to test for correlation between traits and communities. For example, Traud et al. (2011) tested for communities in the Caltech 2005 Facebook network. The traits of users were then compared within

and among communities where it was found that users are most likely to be in groups of friends by House, or dormitory (Traud et al., 2011). We took advantage of this approach to test whether social network communities predicted traditional behavioral groups. To compare these two sets of classifications, we first calculated the Rand similarity coefficient in Equation 1 for the pair of classifications (Rand, 1971).

$$\frac{w_{11} + w_{00}}{M} \quad (1)$$

where M was the total number of possible pairs of prairie dogs in the site, $n(n-1)/2$, n was the total number of prairie dogs in the site we were testing, w_{00} was the number of pairs of prairie dogs, where both prairie dogs were in different communities and in different social groups, w_{11} was the number of pairs of prairie dogs where both prairie dogs were in the same community and both prairie dogs were in the same social group. Put simply, the Rand coefficient is the proportion of pairs whose social relationship was consistent in each type of analysis. The Rand coefficient can take on any value between and including zero and one, where one is perfect agreement and zero being the worst possible match. When the Rand coefficient value is less than one, but not zero, it is unclear how well the two groupings match.

We then compared the Rand coefficient to the distribution of possible Rand coefficients using randomization tests (Edgington and Onghena, 2007). This allowed us to empirically calculate the P -value corresponding to the degree of matching between communities and social groups (Edgington and Onghena, 2007) (Table 1). Due to the slightly biased nature of the distribution of Rand coefficients for these small networks, we used randomization tests as opposed to z -scores, which assume a normal distribution of Rand coefficients. P -values were calculated empirically using Monte Carlo simulations. To find the P -values for each Rand statistic, we iterated n (10,000) times, randomizing the communities and calculating the Rand statistic for the random communities paired with the actual social groups. We then counted the number of times that the iterated Rand statistic was larger than the observed Rand statistic for the actual social network communities and the social groups. The approximate P -value is then calculated as $(r+1)/(n+1)$ (North et al., 2003).

To test for differences in behavioral traits among the communities we used the proportion of time an individual spent being vigilant (e.g., posting, scanning), feeding, moving (Loughry, 1992; Verdolin and Slobodchikoff, 2002), and trappability. We separated the different behavior and trappability scores for each individual into categorical variables from the quartiles for that behavior. We compared communities to prairie dog behavioral traits using Rand Similarity coefficients and randomization tests in the same manner as described above, see also (Traud et al., 2011).

Table 1

The number of identified traditional behavioral social groups was fewer than the number of social network communities based on SNA; most social groups include >1 communities (see Fig. 1). P -values are based on the Rand similarity coefficient and randomization tests.

Site	# Traditional behavioral groups	# Social network communities	P -value
CCI	4*	8**	<0.001
HSI	5	5	<0.001
HSII	5	6	<0.001

* There were 6 identified social groups, but two were excluded from this analysis because they were determined primarily by spatial location (see Methods for details).

** One of the 8 groups was a single individual that was not assigned to a social network community due to a lack of recorded social interactions.

2.5. Quantification of social network structural features

We present a description of degree centrality and betweenness centrality for the communities and identify key individuals that act as hubs (individuals who disproportionately connect individuals within social groups) and/or bridges (individuals who serve to connect social groups with no other connections). Both degree centrality and betweenness centrality are measures of the importance of an individual in a given network (Opsahl et al., 2010). Degree centrality is the number of interactions each individual participates in and we used it to classify hubs, or individuals with a significantly higher degree centrality than the rest of the network they were a part of. Prairie dogs with a significantly higher degree centrality were classified as hubs. Individuals with a degree centrality outside the range of 95% of the degree centralities of the network were regarded as hubs. Betweenness centrality is a measure of the number of paths that are required to pass through a prairie dog to get from one prairie dog to all other prairie dogs in the network and uncovers

individuals that act as bridges between communities that would otherwise be unconnected. We measured betweenness centrality to quantify whether or not a prairie dog acts as a bridge between networks. Prairie dogs with a significantly higher betweenness centrality than the rest of the prairie dogs in the network were considered bridges. We calculated significance for betweenness centrality similarly to that of degree centrality: individuals with a betweenness centrality outside the range of 95% of the betweenness centralities for that network are classified as bridges. Bridges were also visually confirmed. We tested whether hubs and bridges occurred more than expected at random by simulating Erdos Renyi random networks with the same number of prairie dogs and the same number of interactions and then calculating the number of hubs and bridges for this distribution of networks (Erdős and Rényi, 1959). We then calculated the *P*-value for the empirical number of hubs or bridges. For these *P*-values, we used a similar process to the one described above for the *P*-values associated with Rand coefficients, only we used a random network for each iteration instead of the randomized

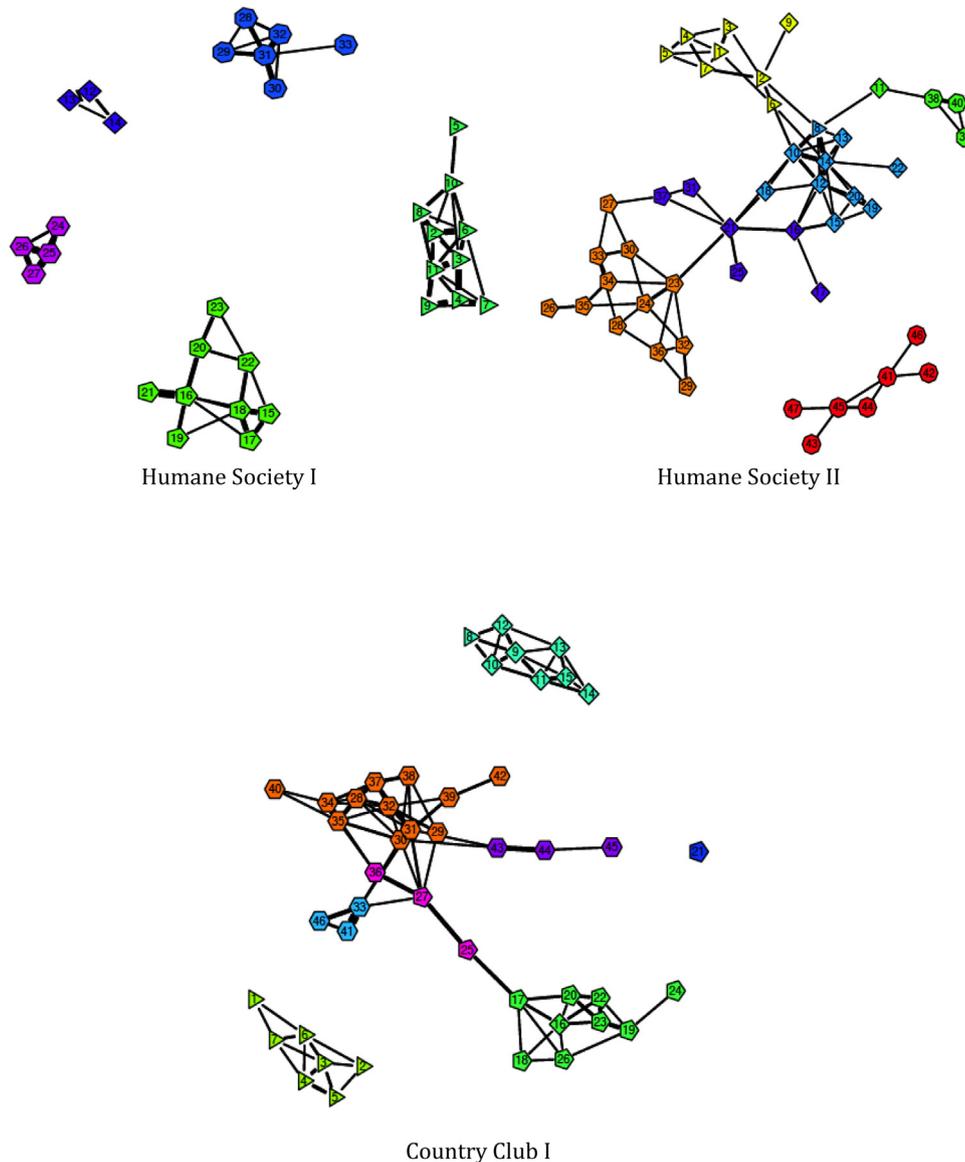


Fig. 1. Interaction networks for the three prairie dog populations analyzed in this study. Shapes indicate the social group. Colors indicate the community. Thickness of lines between shapes indicate number of interactions between prairie dog pairs (colors indicate groups based on network analysis, shapes indicate groups based on traditional behavioral approaches, color and shape groups are similar indicating a good match between social network communities and traditional behavioral groups (numbers identify specific individuals)).

communities. Lastly, we tested whether degree centrality and betweenness centrality were correlated with age, sex, and group size using a generalized linear model (GLM) in JMP Pro 10[®] (Dryad doi:10.5061/dryad.sh85t).

3. Results

A total of 220 focal samples for 80 prairie dogs were collected. In addition, a total of 5, 5, and 4 social groups were identified using behavioral observations and spatial locations for populations HSI, HSII, and CCI, respectively. Network analysis resulted in three different weighted networks, where each connection between a pair of prairie dogs was weighted by the number of interactions between the prairie dogs in that pair (Fig. 1). Overall, CCI, HSI, and HSII, consisted of 46, 32, and 47 prairie dogs respectively, and had average contacts of 4, 3.56, and 3.57 per prairie dog respectively with network densities of 0.089 (CCI), 0.11 (HSI), and 0.078 (HSII).

For each of the three populations, the Rand coefficient similarity values for community and group assignments were significantly different from random ($P < 0.001$), indicating agreement between social groups identified using SNA and those identified using traditional methods. However, with the exception of HSI, SNA detected additional social groups thereby uncovering subgroups (Table 1).

Although there were general differences in behavioral traits across social groups, the Rand similarity coefficient suggested that only individuals within social groups in the HSI population were more similar to each other in the proportion of time spent feeding ($P < 0.01$) (Table 2).

Across all three plots, we identified key individuals that acted as hubs within the network and individuals that were bridges between groups. In CCI, individuals 30, 31, and 32 were quantified as hubs (having a significantly higher degree centrality than the rest of their network), with the numbers of contacts for these individuals being 9, 9, and 8 respectively compared to the average of $4 (\pm 1.96SD)$. In HSI, only one hub was present, individual 11, with 7 contacts compared to the network average of $3.56 (\pm 1.63SD)$. Lastly, HSII had 3 hubs, individuals 10, 12, and 14, with contacts numbering 8, 9, and 10 respectively compared to a network average of $3.57 (\pm 2.12SD)$. CCI had significantly more hubs than expected at random (CCI: $P < 0.05$) while HSII and HSI did not have significantly more than expected at random (HSII: $P < 0.07$; HSI: $P < 0.39$).

Another important characteristic found in these networks was the existence of bridges. In CCI, prairie dogs 17, 25, 27, and 30 were identified as bridges (Fig. 1). The average betweenness centrality for this network is $29.37 (\pm 51.57SD)$, while the betweenness centralities for these prairie dogs are 168, 180, 194.8 and 171.5 respectively. HSI had only one bridge, prairie dog 16. The average betweenness was $3.63 (\pm 5.29SD)$, while this individual's betweenness was 21.8. Similarly, in HSII, individuals 10 and 21 were bridges, with values of 242.6 and 381.5 respectively, while the average betweenness for the network was $52.92 (\pm 76.45SD)$. Simulation results revealed that CCI had significantly more individuals that were bridges than expected by random chance alone (CCI: $P < 0.009$). In contrast, the number of bridges in HSI and HSII was not significantly different from random (HSI: $P < 0.14$; HSII: $P < 0.64$).

Table 2

P-values for the comparison of social network communities to the observed prairie dog behavioral traits.

Network	Trappability	Vigilance	Feeding	Moving
CCI	0.20	0.77	0.09	0.14
HSI	0.17	0.18	0.01*	0.91
HSII	0.62	0.08	0.95	0.19

* $P < 0.05$.

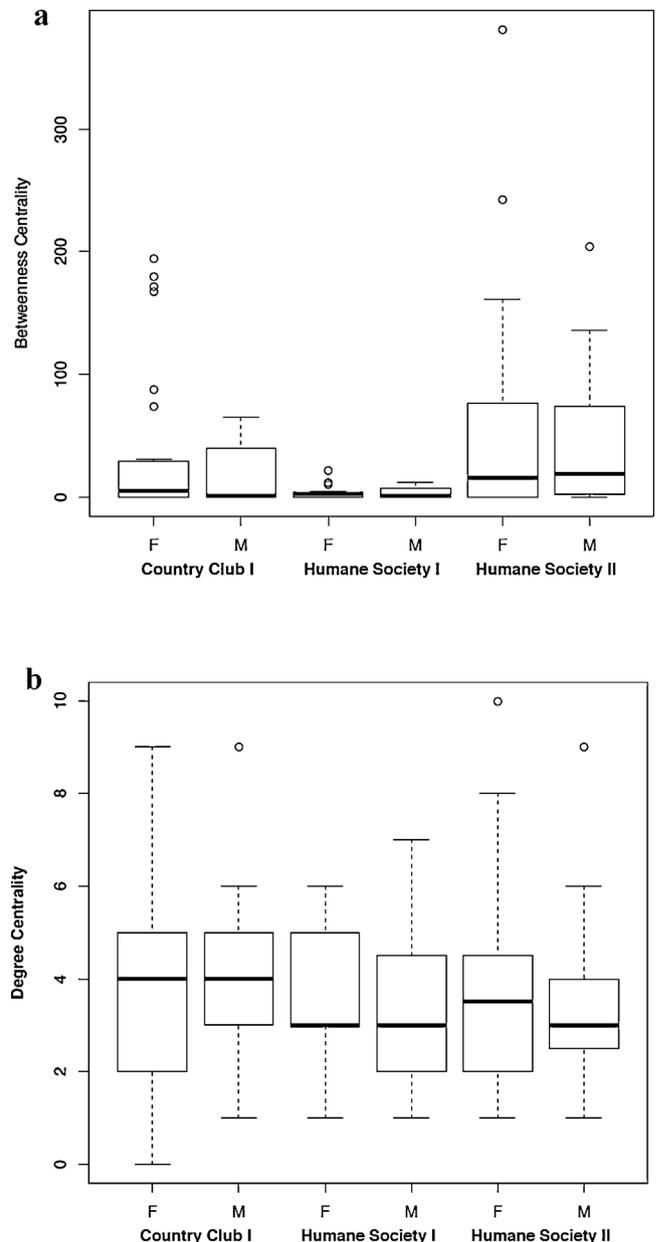


Fig. 2. (a) Betweenness centrality quartiles for all colonies separated by both site and sex. CCI had four female outliers matching the number of bridges in this network, HSI had three female outliers, only one of these is classified as a bridge, and HSII had two female outliers and one male outlier, but only the two females were bridges. (b) Degree centrality quartiles for all colonies separated by site and then by sex. In CCI, three individuals were classified as hubs; one male was an outlier. In HSI, none of the prairie dogs were outliers, even though one was classified as a hub. In HSII two of the three classified hubs are outliers, one male and one female.

We found that age, sex, group size, and age \times sex interaction were not significant predictors of degree centrality (GLM: whole model: $R^2 = 0.04$, $F_{4, 120} = 1.21$, $P < 0.31$) or normalized betweenness centrality (GLM: whole model: $R^2 = 0.03$, $F_{4, 120} = 0.89$, $P < 0.47$) (Fig. 2a and b).

4. Discussion and conclusions

We found that the majority of the prairie dogs were placed in social network communities that were consistent with their traditional behavioral social group placement (Fig. 1). More importantly, the Social Network Analysis (SNA) approach also recovered additional structure within those groups, as well as

previously undetected structure within those social groups. Within network-based social groups, individuals were subdivided into smaller subunits of individuals that mostly interact with each other in ways apparent only when using SNA.

Prairie dog social networks also showed variation within and among populations in both colonies. For example, HSI social network communities lacked subgroups, suggesting that social groups were more cohesive in this location. Differences in environmental conditions and selective pressures impacting organisms often lead to social patterns that are conditional on the circumstances experienced by a given population at any point in time (e.g., paper wasps: [Gadagkar, 2001](#); sharks: [Jacoby et al., 2010](#); birds: [Jetz and Rubenstein, 2011](#); primates: [Lehmann and Dunbar, 2009](#); rodents: [Randall et al., 2005](#); [Verdolin, 2007](#)). We suspect that variation in ecological and historical processes, coupled with group specific social dynamics may contribute to the diversity we see in social networks across prairie dogs colonies. In addition, although individuals within social groups were not, on average, more closely related to each other than individuals between social groups ([Verdolin and Slobodchikoff, 2008](#)), some individuals within social groups were related. Community detection may be picking up on these details and suggests many directions for further study. This implies that prairie dog social groups within colonies act as societies with distinct membership.

In addition to detecting subgroups, SNA also detected interactions among social groups ([Fig. 1](#)). These interactions were hidden in traditional analyses that simply categorically considered prairie dogs as either in or not in groups. Behavioral and social variability in this species has traditionally been under-emphasized in the search for simplistic universal categorical descriptions and ignores the social complexity and variability that is likely driven largely by environmental differences (e.g., [Hoogland et al., 2012](#)). In reality, while some social groups really are discreet groups in which information (and pathogens) move in a relatively closed system, other groups are more connected such that both pathogens and information may be more likely to be moving readily both within and among what would be regarded as traditional social groups. However, some of these bridges may be temporary in nature. For example, on CCI individuals 25 and 27 were identified as bridges, but were actually individuals transitioning from one social group to another. Without detailed behavioral observations documenting social group transfer SNA might not detect that some bridges are short-lived.

In Gunnison's prairie dogs, the origin of social groups remains somewhat mysterious. Current research provides convincing evidence that many social systems, including that of Gunnison's prairie dogs, display significant sensitivity to resource availability and distribution (e.g., [Verdolin, 2009](#); [Jetz and Rubenstein, 2011](#); [Schradin et al., 2012](#); [Botero and Rubenstein, 2012](#)). While, in many cases, some individuals within social groups are related, this is not always the case. Differences in relatedness among social groups must at least in part be a function of complexities of dispersal patterns, wherein individuals who disperse short distances lead to non-random within group relatedness ([Pizzimenti, 1975, 1981](#); [Robinson, 1989](#); [Slobodchikoff, 1984](#); [Travis and Slobodchikoff, 1993](#); [Travis et al., 1995](#); [Verdolin, 2007](#); [Verdolin and Slobodchikoff, 2008](#)). Kinship within social groups may actually be an artifact of the combination of sociality and occasional short-distance dispersal events in this species. Instead, as has been proposed by [Hunt \(2007\)](#) for social wasps, colony-level selection population genetics and environmental factors may be driving social evolution in this species.

One additional hypothesis that has emerged to explain social grouping patterns is that within colonies individuals that share social traits tend to group together (one might also imagine the

opposite, that individuals whose social traits are complimentary group).

Do shared behavioral traits explain social group formation and networks in prairie dogs? To address this question, we compared the social network groups within colonies to the observed prairie dog behavioral traits. Although we found variation in a suite of behavioral traits among groups, when we compared social network groups and behavioral traits, we found that only one site (HSI) showed significant assortment of individuals within groups for feeding. Therefore, it seems unlikely that behavioral similarities and/or differences among individuals are strong enough to drive social group formation and network patterns in prairie dogs. Rather, the variation across social networks in behavioral traits may be a function of idiosyncratic differences among colonies. Alternatively, differences in personality, along a bold-shy axis, may contribute to network attributes ([Croft et al., 2009](#)), and is an important direction for future inquiry in this system.

We also detected non-random variation among individual in their connectedness (degree). In a subset of social groups/communities in each population, some individual prairie dogs were more well connected than would be expected by chance, so-called hub individuals. For others, their betweenness centrality was significantly greater than expected, and these individuals act as bridges between networks ([Fig. 2a and b](#)). Central individuals (hubs) play a critical role in maintaining group cohesiveness and their removal can sometimes alter group dynamics substantially ([Flack et al., 2005](#); [Kanngiesser et al., 2011](#); [Manno, 2008](#)). In some species, males and females differ in their role in social networks, particularly with regard to their likelihood of being hubs or bridges. For example, in meerkats, the dominant female will act aggressively toward a subset of females, while other subordinate females are involved in initiating fewer aggressive acts ([Madden et al., 2009](#)). Similarly, in many female bonded primates, dominant females have disproportionately higher degree centrality than subordinates ([Lehmann and Dunbar, 2009](#); [Ramos-Fernandez et al., 2009](#)). Network attributes of individuals in Gunnison's prairie dogs do not, however, appear to be determined primarily by sex. The lack of dominance hierarchies in both male and female Gunnison's prairie dogs ([Verdolin, 2007](#)), may explain why sex and age were not significant predictors of degree centrality.

In Gunnison's prairie dogs, as in dolphins ([Lusseau, 2007](#); [Lusseau and Newman, 2004](#)) and primates ([Lehmann et al., 2010](#)), some individuals acted as bridges across communities, as measured by their betweenness centrality. Yet age and sex were not significantly statistically correlated with betweenness centrality. Interestingly, however, these individuals were all female, suggesting that in Gunnison's prairie dogs it is females who connect different social groups, even though the individuals who serve as hubs within social groups can be both female and male. As pointed out earlier two of the females identified as bridges actually were dispersing to neighboring groups. In Gunnison's prairie dogs both males and females disperse, but males tend to disperse between populations while females disperse within populations ([Robinson, 1989](#)). This difference in dispersal patterns may explain why all the bridges were females and also suggests that some females may act as temporary bridges while others are permanent ones. What is unclear is why these individuals are more connected and what factors influence the stability of bridges in these populations. Unlike in other species, where network centrality measures are correlated with group size ([Lehmann and Dunbar, 2009](#); [Madden et al., 2009](#); [Wittig et al., 2008](#)), there was no relationship between degree and betweenness centrality measures and group size in our populations.

Here, we demonstrate considerable variation in the structure of prairie dog social groups. Previous observational and experimental work has linked this variability to ecological factors ([Pizzimenti,](#)

1975; Slobodchikoff, 1984; Travis and Slobodchikoff, 1993; Travis et al., 1995; Verdolin, 2007, 2009). The results of this study suggest that fine-scale network interactions may be a consequence of the particular set of individuals that comprise a given social group. Although age, sex, group size, did not significantly predict key individuals within networks, the presence of individuals that act as hubs or bridges highlights the potential importance of some individuals to act as strategic players in prairie dog social dynamics. Statistically, these connected individuals almost certainly have a disproportionate effect on the movement of information, food, and disease through the network, but their uniqueness was invisible using traditional approaches. It would be interesting to investigate whether the removal of such individuals substantially alters the social network properties of a given group. We also detected similarities in behavioral traits within social network communities, although the traits varied among colonies. While grouping may have non-random features, the rules that govern such non-randomness are far from clear. In the future it would be interesting to explore what role individual variation in personality (e.g., behavioral syndromes) plays in social network structure. It is possible that integrating behavioral traits will reveal an optimum distribution of personality types within a given social network. Such investigation may also reveal fitness differences among social networks depending on the particular types of individuals that make up a given social group. Our results show that SNA analysis can be used in lieu of traditional behavioral observation methods. Not only does SNA detect statistically similar group structure, but also identifies important sub-structuring not readily apparent. More importantly, the structure of social networks can be determined on relatively short time-scales, such that they are adapted to the immediate internal and external needs of the group (Bhadra et al., 2009). However, one potential drawback of using SNA to the exclusion of more detailed behavioral observations is the potential to misidentify dispersing individuals as bridges. More generally, our work suggests that at least in this system, and we suspect others, social network approaches can build upon rather than compete with more traditional approaches of identifying and studying social groups.

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