

Original Article

Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*)

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It is increasingly recognized that association patterns of most gregarious animals are nonrandom. However, nonrandom patterns can emerge in any population that exhibits spatial structure, even if individuals associate randomly. In species that lack clearly differentiated social relationships characteristic of socially complex mammals, space use patterns must be considered alongside association patterns in order to establish whether nonrandom association patterns are determined by underlying social structure or are merely an artifact of spatial structure. In this study, we simultaneously consider space use and association patterns for a wild population of reticulated giraffe. We examined whether the giraffe's flexible fission–fusion association patterns were embedded in higher levels of social organization. We identified multilevel social organization in which individuals were members of social cliques. Cliques were embedded in larger subcommunities, which in turn were embedded in communities. The frequency with which 2 individuals were observed together was positively correlated with the extent to which their home range overlapped, implying an underlying role of shared space use in determining association patterns. However, membership in cliques and subcommunities was relatively unrelated to space use patterns for males. For females, space use played a much larger role in determining multitiered social organization, which is consistent with a matrilineal-based society characterized by female philopatry. Although giraffe social interactions are highly fluid in nature, it is apparent that association patterns in giraffe are not the result of random fission–fusion events but are embedded within a structured social network characterized by multiple levels of organization.

Key words: association patterns, community structure, data cloud geometry, network analysis, social structure, spatial overlap.

INTRODUCTION

The ecological basis of social organization has had a long history of investigation in behavioral ecology, and it is now understood that ecological factors, such as predation and the distribution of resource, play a crucial role in shaping social structure (Alexander 1974; Rubenstein and Wrangham 1986; Isbell and Young 2002). Animal social structures that are characterized by fission–fusion dynamics exhibit frequent coalescing and dividing of group members into smaller subgroups (Langman 1977; Leuthold 1979; Couzin 2006; Aureli et al. 2008). Fission–fusion dynamics are thought to allow animals to respond to changing environmental conditions and

flexibly balance conflicting demands. They allow animals to form larger groups when there are reproductive, foraging, or antipredator benefits, but to minimize costs of intragroup competition if the benefits of grouping change. Flexible grouping dynamics are exhibited in a broad range of taxa, including shoaling fish (Hoare et al. 2004; Kelley et al. 2011), bats (Popa-Lisseanu et al. 2008; Kerth et al. 2011), primates (Kummer 1968; Symington 1990), carnivores (Schaller 1972; Wolf et al. 2007; Smith et al. 2008), ungulates (Aycrigg and Porter 1997; Cross et al. 2005; White et al. 2010), elephants (Moss 1988; Weitemyer et al. 2005; Archie et al. 2006b), and marine mammals (Lusseau 2003; Pearson 2009).

Understanding how fission–fusion dynamics influence population structure has important implications for disease transmission (Keeling 1999; Craft et al. 2010; Griffin and Nunn 2012), information flow (McComb et al. 2001; Vital and Martins 2009), mating

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opportunities (Hashimoto et al. 2001), and gene flow (Altmann et al. 1996). Although fission–fusion societies are sometimes thought to occur only in species with higher cognitive abilities due to the need to maintain social bonds (Aureli et al. 2008), it is increasingly recognized that fission–fusion dynamics can emerge through self-sorting of individuals with similar needs and motivations (Couzin 2006; Ramos-Fernández et al. 2006). Fission–fusion dynamics can result from simple foraging models with no description of how actors should behave socially (Ramos-Fernández et al. 2006). Thus, in species with less obvious social relationships than species such as chimpanzees (*Pan troglodytes*: Goodall 1986) or elephants (*Loxodonta africana*: Moss 1988; Wittemyer et al. 2005; Archie et al. 2006b), it can be difficult to determine whether observed fission–fusion dynamics are socially mediated or merely an artifact of foraging patterns or space use.

Ungulates typically exhibit highly flexible grouping patterns. Within-population variation in group size tends to be related to habitat type, resource abundance, and predation risk (Jarman 1974; Gosling 1986; Molvar and Bowyer 1994; Gude et al. 2006; Isvaran 2007; Barja and Rosellini 2008; Fortin et al. 2009). Sometimes flexible fission–fusion dynamics are embedded in higher levels of organization (white-tailed deer, *Odocoileus virginianus*: Aycrigg and Porter 1997; African buffalo, *Syncerus caffer*: Cross et al. 2005; impala, *Aepyceros melampus*: Murray 1982; feral cattle: Lazo 1994; plains zebra, *Equus burchelli*: Rubenstein and Hack 2004). For example, zebra social groups temporarily and nonrandomly fuse with other groups to form larger herds (Rubenstein and Hack 2004), and white-tailed deer fission–fusion dynamics are rooted within a genetically related community of females (Miller et al. 2010). As in deer, social structure in some ungulate species may be based on female locational philopatry, which may lead to bonds based on matrilineal relationships (Greenwood 1980; Murray 1982). In other ungulate species, there is little evidence of preferential bonds or higher levels of structure (Lott and Minta 1983; Schulte and Klingel 1991; Le Pendu et al. 1995), though it is possible that the higher levels of social organization are undetected in less studied species.

As yet, there is a little agreement in the literature as to the existence and extent of social structure in giraffe (*Giraffa camelopardalis*). Some studies concluded that giraffes lack social organization and that association patterns are random (Foster and Dagg 1972; Dagg and Foster 1976; Leuthold 1979; Le Pendu et al. 2000). This conclusion stemmed primarily from perpetually shifting grouping patterns observed among giraffe. Groups daily or even hourly coalesce into larger groups or break apart into smaller groups. An individual's associates may shift numerous times in the course of a day (Leuthold 1979; Pratt and Anderson 1982; Pellew 1984; Pratt and Anderson 1985; Bercovitch and Berry 2009a). Dagg and Foster (1976) and Le Pendu et al. (2000) stated that individual interactions were ephemeral and bonds nonexistent.

Recent work suggests that giraffe populations have more complex structure than previously thought (Pratt and Anderson 1982; Fennessy 2004; Bashaw et al. 2007; Shorrocks and Croft 2009; Bercovitch and Berry 2012; Carter et al. 2012). Association patterns appear to be nonrandom and female giraffe exercise social preferences, which are partly determined by shared space use and genetic relatedness (Carter et al. 2009; Bercovitch and Berry 2012). Although it has been suggested that giraffe sociality may be characterized by fission–fusion grouping dynamics embedded within a larger social community (Pratt and Anderson 1982; Bashaw et al. 2007; Bercovitch and Berry 2009a, 2012; Carter et al. 2012), it is still unclear whether giraffe exhibit higher levels

of social structure, as seen in some other fission–fusion species (Symington 1990; Wittemyer et al. 2005; Wolf et al. 2007; Fortuna et al. 2009; Mourier et al. 2012). While much of the previous work has focused on quantifying variation in pairwise association indices (Leuthold 1979; Pratt and Anderson 1985; Le Pendu et al. 2000; Fennessy 2004; Carter et al. 2012), we apply social network analysis to uncover multilevel social organization. Social network analysis provides a more sophisticated technique for analyzing association patterns because it not only takes into account direct (dyadic) interactions, but also indirect connections between individuals (Wey et al. 2008; Sih et al. 2009; Makagon et al. 2012). Even though dyadic association indices among giraffe are low (Leuthold 1979; Le Pendu et al. 2000), network analysis may reveal social organization if it allows for the detection of clusters of individuals within the network that interact more frequently with one another but more rarely with others.

In this study, we analyze a giraffe social network consisting of more than 1000 observations of giraffe groups and more than 200 known individuals to gain an unprecedented level of detail into the social structure of the giraffe, with a specific focus on identifying multiple levels of social organization. We then compare the social structure to the spatial distribution of the population to determine whether the observed social structure arises as an artifact of individual space use or whether it is a social phenomenon in that aspects of social structure cannot be explained from space use alone.

METHODS

Study site and population

This study was conducted in Ol Pejeta Conservancy (OPC), a 364 km² semiarid wildlife reserve located on the equator (0°N, 36°56'E) approximately 220 km north of Nairobi, Kenya. It is part of the larger Laikipia plateau (altitude 1800 m), which extends from Mount Kenya to the Aberdares Mountains. The reserve is a grassland–woodland mosaic, with the dominant woody species being *Acacia drepanolobium* and *Euclea divinorum*. OPC receives on average 900 mm of rainfall per year (Birkett 2002), with peak rainfall occurring in March–April and October–November. During the study period (2011), however, monthly rainfall during the dry season was above average and exhibited less seasonal variation than in normal years (Ol Pejeta Conservancy, unpublished data). Large mammals found on Ol Pejeta include lions (*Panthera leo*), spotted hyena (*Crocuta crocuta*), leopards (*Panthera pardus*), elephants (*L. africana*), cheetah (*Acinonyx jubatus*), buffalo (*S. caffer*), black and white rhinoceros (*Diceros bicornis*, *Ceratotherium simum*), Grevy's and plains zebra (*Equus grevyi* and *E. burchelli*), Thomson's and Grant's gazelle (*Gazella thomsonii* and *G. granti*), impala (*A. melampus*), and oryx (*Oryx gazella*).

Across their geographic range, there are several features that emerge as characteristic of giraffe sociality. Giraffes are usually found in groups of, on average, 3–5 individuals, with approximately 20–25% of groups being larger than 6. Groups larger than 30 are extremely rare but do occur. Adult males are commonly found alone, whereas adult females are almost always in groups (Dagg and Foster 1976; Leuthold 1979; Le Pendu et al. 2000; van der Jeugd and Prins 2000; Fennessy 2004; Bercovitch and Berry 2009a; Shorrocks and Croft 2009). Adult males adopt a roaming strategy searching for females in estrus (Dagg and Foster 1976; Pratt and Anderson 1985). Breeding tends to be relatively aseasonal, though birthing peaks sometimes occur (Fennessy 2004; Bercovitch and Berry 2009b). Females with calves often pool their young into

crèches that may persist for several months (Langman 1977; Pratt and Anderson 1979).

All giraffe at OPC were recognized using individually unique spot patterns along their necks. At the time of this study, OPC had a population of 212 reticulated giraffe. We believe that this population estimate represents a complete census of the population because all giraffe were observed approximately once per week and only 2 new adults were discovered in the entire last 5 months of the study. Giraffes were aged according to height estimates and age-associated behaviors. This aging scale was adapted from the literature (Langman 1977; Pratt and Anderson 1979; Fennessy 2004). Neonates (<3 months old) still had attached umbilical cords, and the length of the neck was short relative to the height of the shoulder. Juveniles (3 months to 1.5 years) were larger than neonates, but still accompanied their mother. Activity budgets of juveniles begin to resemble an adult's. Subadults (1.5–4 years) no longer consistently accompany their mothers, but were smaller than adults. Adults (>4 years) coincide approximately with the onset of sexual maturity and adult size. At the conclusion of the study period, OPC's giraffe population consisted of 160 adults, 20 subadults, 21 juveniles, and 11 neonates. The number of giraffe classified as subadults was likely underestimated because of older individuals being erroneously classified as adults. The population exhibited a 50:50 sex ratio.

Disappearances could usually be attributed to death rather than emigration because OPC is enclosed by a perimeter fence, eliminating immigration and emigration from the giraffe population except through a few narrow gaps in the fence. Of the 6 adults that disappeared between July 2010 and August 2011, 3 were observed in very poor condition prior to disappearing. The remaining 3 disappeared during the last few months of 2010 when the population was not being monitored.

Because of the large size of the reserve (364 km²), we do not expect ranging patterns to be significantly influenced by the fact that this population was fenced. In Kenya, cows and bulls live in overlapping home ranges that vary from 13 to 162 km² and from 16.5 to 164 km², respectively (Foster and Dagg 1972; Leuthold and Leuthold 1978). Home range sizes from the upper end of this range were from Tsavo National Park, which is significantly drier than OPC. In the other 2 locations for which average home range sizes have been estimated, mean home range size was less than 85 km² (Foster and Dagg 1972; Leuthold and Leuthold 1978).

Field observations

From 21 January to 2 August 2011, giraffe group composition and membership were recorded for all giraffe groups sighted while driving predetermined survey routes. Routes were determined so that a different part of the study area was surveyed each day, allowing for most of the study area to be surveyed once every 3 days. Routes were approximately 100 km in length, covered approximately 115 km² each, and traversed all habitat types. Observed giraffe groups were followed off-road until a complete census of the individuals present was accomplished. A group was defined as a set of individuals engaged in the same behavior, or moving in the same direction or toward a common destination, as long as each giraffe was no more than 500 m from at least one other group member. All individuals observed within a group were considered to be in association with every other member of the group. As group membership is constantly shifting (Le Pendu et al. 2000; Fennessy 2004), independence of observations was ensured by using only the first observation of an individual's group on a given day for social network analysis. Group sizes do not vary with time of day (Bercovitch and

Berry 2009a). During the study period, K.L.V. collected a total of 1089 observations of giraffe groups. On average, 30.7 giraffe were observed per day, distributed between 4 and 6 groups. Each individual giraffe was observed on average 31.1 times (approximately once per week). Given that nearly all giraffe were sighted approximately once per week, any giraffe that had not been seen between 1 July and 2 August was assumed to have died or left the study area and was excluded from analysis. Giraffe that were seen fewer than 5 times were also excluded ($n = 1$). Research was conducted under Institutional Animal Care and Use Committee protocol no. 15887 from the University of California, Davis.

Network construction

A social network was constructed from observed association patterns. Instead of the absolute number of times the animals were seen together, we controlled for varying resighting frequencies among individuals by calculating association strength (AS) as follows:

$$AS = \frac{Y_{ij}}{Y_{ij} + Y_i + Y_j},$$

where Y_{ij} is the number of times that individuals i and j were observed in the same group. Y_i and Y_j represent the number of times each individual was observed in a group where the other was absent. An association matrix was first constructed with each element AS_{ij} representing the AS between the i th and j th individuals, and then used to construct a network of associations between individuals. Pairs with nonzero AS were linked in the network, with links weighted according to the AS value.

We also constructed a “home range network” using the extent of home range overlap to connect individuals. Individual home ranges were mapped using the GPS locations recorded for each giraffe sighting. Home range boundaries were determined using a fixed-kernel utilization distribution of sightings (Worton 1989; Harris et al. 1999). Due to potential sensitivity to sample size, we used a 75% probability contour (kernel density isopleth) to exclude outlying observations and produce a core home range. Home range overlap between 2 individuals was defined as the number of 1-km² grid squares that fell within both individuals' home ranges, divided by the total size of both individuals' home ranges. These dyadic home range overlap values were used to connect individuals in the home range network.

Network and statistical analysis

We constructed 3 data sets to examine social organization in adults and subadults: female only ($N = 86$), male only ($N = 84$), and combined sex ($N = 170$). All statistical analyses were performed separately on each of these 3 data sets. Neonates and juveniles were excluded from all data sets used to examine social structure because animals of these age groups are nearly always found near or accompanying their mothers.

Data cloud geometry (DCG) methods (Fushing and McAssey 2010) were applied to the association matrix to identify social community structure at multiple scales. The DCG method utilizes the tendency of random walks to remain within clusters of highly connected nodes to quantify community structure in the network. Detailed methods are described elsewhere (Fushing et al. 2013). Essentially, this method employs regulated random walks with recurrence-time dynamics to detect information about the number

of clusters and the corresponding cluster membership of each individual at multiple scales based on local information provided by the similarity measure AS. The DCG algorithm makes it possible to monitor phase transitions (i.e., cluster splits) in order to obtain a meaningful tree topology (Fushing et al. 2013). Hierarchical levels $\{T_1, T_2, \dots, T_k\}$ correspond to phase transitions, which are then utilized to build the geometric hierarchy of the data cloud into a tree with $\{T_1, T_2, \dots, T_k\}$ hierarchical levels. The resulting hierarchical tree is termed a DCG tree (Fushing et al. 2013). In the DCG trees, shown in Figure 1, there are 3 hierarchical levels. For simplicity and convenience, we term clusters at the highest hierarchical level as communities (Level A clusters). Each community consists of multiple subcommunities (Level B clusters), and each subcommunity consists of multiple cliques (Level C clusters). Although cliques were identified using DCG algorithms, it is worth noting that the term “clique” also has a specific definition in network theory: a completely connected set of nodes (Wasserman and Faust 1994). In our analysis, only 3.5% of within-clique dyads were not connected (AS = 0) in females. For males, only 2.4% of within-clique dyads were not connected. Thus, social cliques defined by DCG very nearly meet the classic definition.

There are several advantages of the DCG technique compared to other commonly used community-finding algorithms. Unlike some algorithms, it does not require ties to be binary and instead utilizes the weighted nature of the association index. Compared with traditional hierarchical clustering methods, DCG trees are more robust, less sensitive to measurement errors, and provide information on the intrinsic scales embedded within the data cloud (Fushing and McAssey 2010; Fushing et al. 2013). Fushing et al. (2013) showed that DCG algorithms more accurately accounted for spatial clustering in the giraffe population compared to classic hierarchical clustering. Specifically, hierarchical clustering grouped a number of individuals dwelling on the west side of the river into the same spatial cluster as animals on the eastern side. In contrast, the DCG method accurately grouped these animals with other animals living on the same side of the river. In this study, DCG algorithms were applied separately to the male and female social networks, as well as to the combined sex data set. The algorithm was also performed on the home range network to identify neighborhoods of individuals that clustered spatially. Clustering trees generated by DCG can be used to examine multilevel social organization.

Significance of network clustering configurations (DCG trees) was determined using Monte Carlo tests. Multiple levels of clustering are present in a DCG tree. Thus, to test the significance of the DCG tree involves testing the clustering structure at each hierarchical level T_k . We achieved this by sampling 1000 random clustering configurations at each level T_k ($k = 1, \dots, K$). In these random permutations, the number and size of clusters matched the observed DCG clustering configuration, but individual membership was randomly allocated. At each hierarchical level T_k , within-cluster tie strength (WCTS) was calculated for each cluster by taking the average AS among animals within the same cluster. The observed mean $WCTS_k$ of all clusters at level T_k was compared with the permuted distribution of mean $WCTS_k$. This distribution was generated by calculating mean $WCTS_k$ for the randomized clustering configurations. P values were calculated as the percentage of permuted $WCTS_k$ that were more extreme than the observed $WCTS_k$. $WCTS_k$ was considered significant if it fell in the 95% percentile of the permuted distribution of $WCTS_k$ ($P < 0.05$). When $P < 0.05$, it indicates that at level T_k , the DCG approach produced clusters that were significantly denser than randomly generated clusters.

In addition, we examined the significance of each distinct cluster in each level by comparing $WCTS_{kl}$ with the 95% percentile of 1000 permuted $WCTS_{kl}$ values, where $WCTS_{kl}$ is the within-cluster tie strength of the l th cluster identified within level T_k . For example, are members of a particular cluster more densely connected than those in the random clusters generated in the procedure above? Although the population could exhibit significant clustering at a given level T_k , not all individuals must be involved in “significant clusters” that are significantly denser than random clusters.

Finally, we analyzed whether the association strength between 2 individuals was correlated with the extent to which their home ranges overlapped. Because of the nonindependent nature of network data, we used MR-QAP (multiple regression quadratic assignment procedure (Krackhardt 1988; Dekker et al. 2007) to determine the effect of shared space use on AS (arcsine transformed). MR-QAP is a variation of the Mantel test that allows a dependent matrix (in this case, the association matrix) to be regressed against independent matrices (home range overlap matrix). After performing a standard regression analysis across the corresponding cells of each matrix, the procedure randomly permutes the rows and columns of the dependent matrix and recomputes regression coefficients 1000 times. This generates a distribution of coefficients against which the observed coefficients are compared in order to generate P values (Krackhardt 1988). Because early analysis indicated that age may be a critical factor influencing grouping patterns in males, 0/1 dummy variables were included in the male MR-QAP representing the age combination present in the dyad: younger–younger, younger–older, and older–older. The younger class included both subadult males and younger adult males. Ages were subjectively determined by height, coloration, and ossicone size (Pratt and Anderson 1982). All statistical analyses were performed in R (v 2.15.0, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Giraffe group sizes ranged from 1 to 44 individuals (mean: 5.42 ± 0.19 individuals, mode: 1). Giraffe observed alone were nearly always adult males (84% of lone giraffe sightings) although females were sometimes observed alone in the days prior to being observed with very young calves. Approximately 27.4% groups were greater than 6 animals, and 12.1% of groups were greater than 12. The average home range size was 95.7 ± 3.3 km² for adult males, 64.2 ± 3.4 km² for adult females, 110.0 ± 8.8 km² for subadult males, 70.5 ± 15.2 km² for subadult females, 51.0 ± 7.7 km² for juveniles, and 17.9 ± 3.4 km² for neonates. Population density was approximately 0.6 giraffe/km².

In each subset of the data (adult and subadult females, adult and subadult males, males and females combined), community structure algorithms identified 3 hierarchical levels of clustering in which several social cliques were embedded in higher order subcommunities, which were in turn embedded in larger communities (Figures 1 and 2). In the female network, for example, 5 cliques were embedded in 3 subcommunities, and 2 of these subcommunities (B.2 and B.3) were embedded into a single community cluster (A.2). In the combined sex analysis, 7 out of 8 social cliques consisted primarily of animals of the same sex (>70% of membership was 1 sex). Therefore, we focused on single-sex networks in subsequent analyses.

To visualize the significance of the DCG trees, we depicted the AS matrix as a heatmap in which darker shading indicates higher

AS values for the i th and j th giraffe (Figure 1). Darkly shaded blocks in the heatmap highlight clusters with denser connections among individuals. In Figure 1A, for example, females are grouped into 2 clusters at the community level, A.1 and A.2. Each of these clusters corresponds to a darker portion of the heatmap of the AS matrix,

which means the within-cluster tie strength is high for both A.1 and A.2. In contrast, the area of the heatmap corresponding to associations between individuals of different communities is relatively lighter in color, indicating low tie strength between A.1 and A.2. At the subcommunity level, A.2 is split into 2 clusters (B.2 and

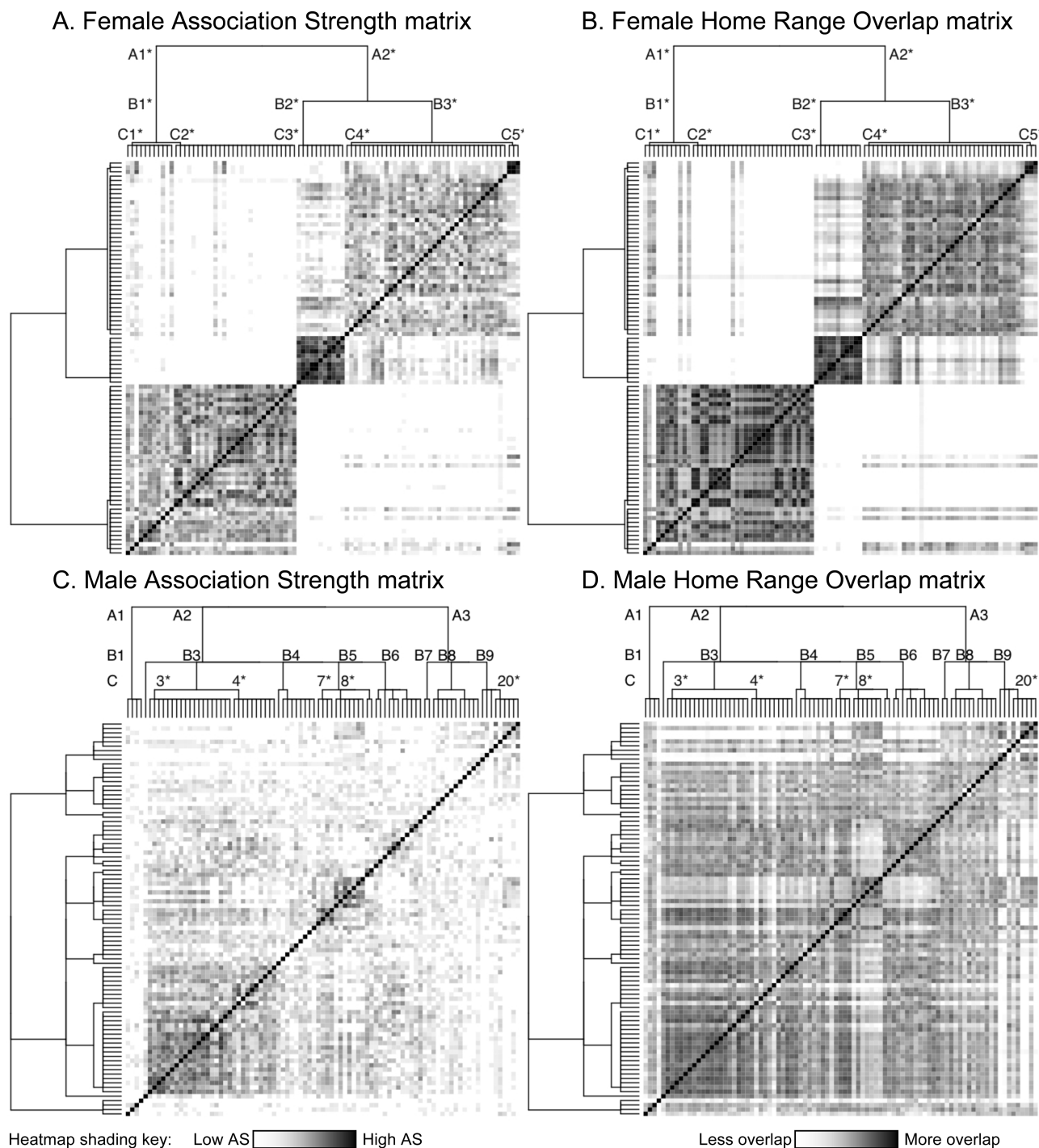


Figure 1

Multitiered DCG trees depict social clustering for female giraffes (A and B) and male giraffes (C and D). Heatmap matrices show AS (A and C) and home range overlap (B and D) for each pair of individuals. The social DCG tree is used to determine the order of individuals for both the association strength and home range overlap matrices. Darker shading indicates higher values of AS or overlap. Trees on the horizontal and vertical axes are identical. Organizational levels are denoted with letters (Communities = A, subcommunities = B, cliques = C), and asterisks indicate clusters that were significantly better connected than random expectations.

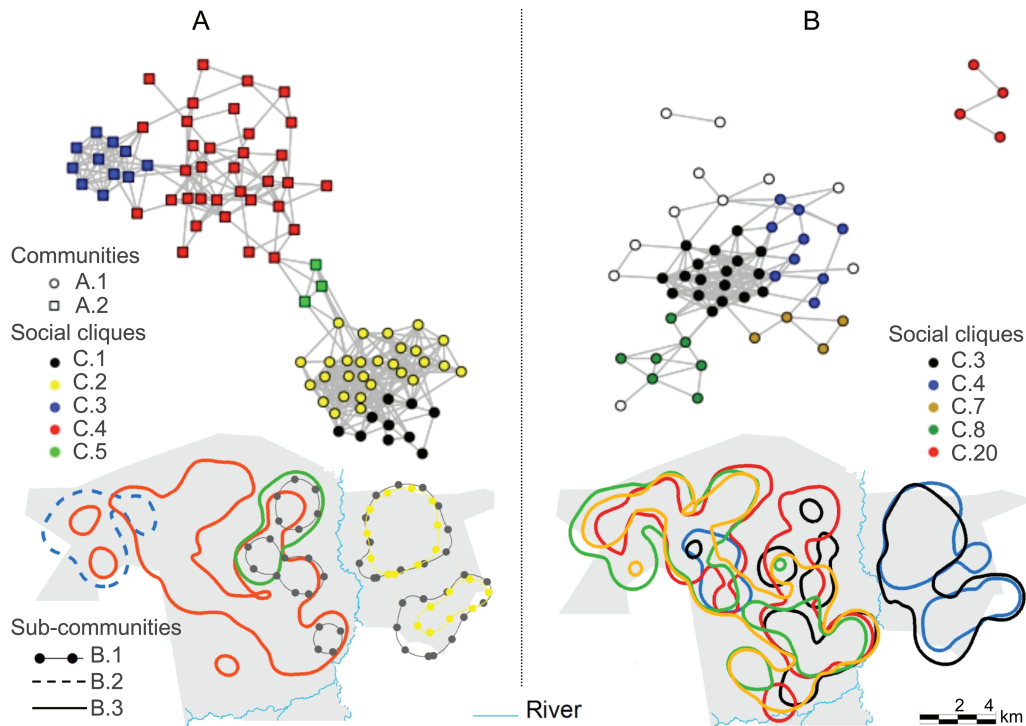


Figure 2

Social network and map of social clique home ranges for (A) females and (B) males. For visualization purposes, network edges have been filtered at the population mean AS + 1 SD. Edges with lower AS are not included in this figure. Some males were involved in no dyads that exceeded this threshold and thus become isolates in the filtered network. Isolated individuals (31 males) are not pictured. White nodes indicate males that were not members of significant clusters (≥ 4 members and $P < 0.05$ in randomization tests).

B.3). Associations within B.2 and B.3, respectively, correspond to even darker blocks in the heatmap, which illustrates that there are 2 densely connected finer-scale clusters within community A.2. These patterns are well captured by the multileveled DCG tree. Further hierarchical levels can be observed and interpreted similarly. Additional heatmaps were constructed to illustrate whether individuals in the same social clusters also tended to have high levels of home range overlap (Figure 1B,D).

For females, clustering at each hierarchical level was significant. In addition, each distinct community, subcommunity, and clique was significantly denser than randomly generated clusters (Figure 1A,B). For males, only clustering at the social clique level was significant. However, not all cliques were significantly denser than randomly generated clusters (Figure 1C,D).

The percentage of observations in which 2 individuals were seen together was highly correlated with shared space use (Figure 3). When age was included in the male MR-QAP, younger adults and subadults had significantly higher AS with males of the same age group than with older males ($\beta = 0.06$, $P < 0.01$), whereas older males had lower AS with other older males than with younger males ($\beta = -0.02$, $P < 0.01$). Female social organization appeared to closely correspond with shared space use; when pairwise home range overlap values were organized according to the social clustering trees, the block-like patterns depicted for home range overlap were highly similar to the social patterns (Figure 1A,B). This was not the case for male communities; there was little correspondence between social clustering and home range overlap (Figure 1C,D). Moreover, when we ran community-finding algorithms on the home range network to assess spatial clustering, only 32.6% of

male pairs assigned to the same spatial neighborhood were also in the same social clique. Thus, social and spatial communities were not analogous for males. In contrast, 89.3% of female dyads that were assigned to the same spatial neighborhood were also in the same social clique.

This difference between males and females is also apparent through a comparison of the degree to which social clique home ranges overlap (Figure 2). Figure 4 shows the average home range overlap between animals in the same versus different clusters. If social clustering were determined by space use alone, we would expect home range overlap to be higher for individuals in the same community than across communities. Consequently, grid cells along the table's diagonal should display higher values, as seen for female communities and subcommunities. At finer scales of social organization (cliques), however, females of different communities exhibited home range overlap $>35\%$ (cliques C.1 and C.2). Some female cliques were almost completely encompassed within the home range of another clique (C.5 by C.1 and C.4; Figure 2A). The home ranges of male cliques were also highly overlapping (Figures 2 and 4). Thus, although home range overlap and association strength are correlated, space use did not seem to determine social structure in males or to completely determine clique-level social organization in females.

DISCUSSION

The social structure identified in this study is the first quantitative evidence of multiple levels of social organization in the giraffe and confirms earlier suggestions that giraffe fission–fusion dynamics are embedded in higher levels of organization

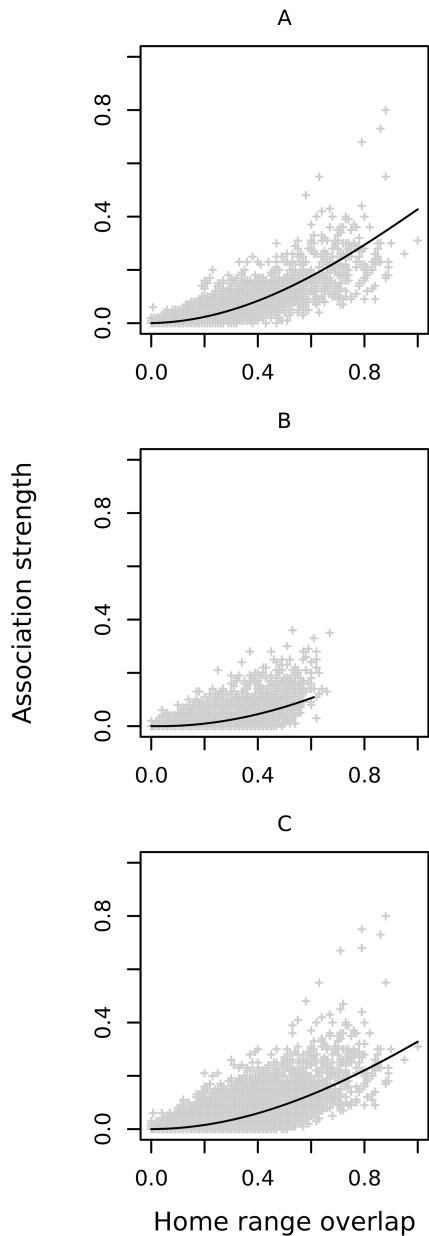


Figure 3
Effect of home range overlap on association strength for (A) adult and subadult females, (B) adult and subadult males, and (C) combined dataset. MR-QAP regression lines of the effect of home range overlap on association strength (arcsine transformed) are shown for the adult and subadult males ($\beta = 0.58$, $P < 0.01$), females ($\beta = 0.70$, $P < 0.01$), and combined datasets ($\beta = 0.61$, $P < 0.01$).

(Pratt and Anderson 1982; Bashaw et al. 2007; Bercovitch and Berry 2009a; Carter et al. 2012). Individual giraffe exhibit the strongest social ties with a core group of others (their clique) but still maintain relatively high AS with members of their subcommunity. Individuals may sustain moderate amounts of association with members of their community, but AS is typically low with giraffe outside their community (Figure 1). Our analyses do not mean that members of cliques are always observed together or do not associate with other giraffe, but rather that these animals tend to be together more often than with animals

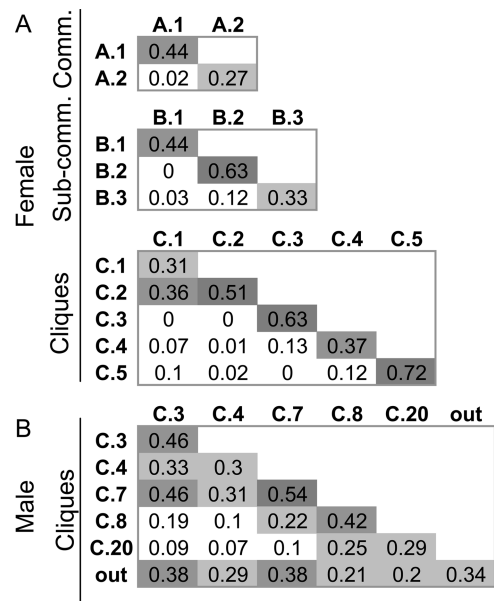


Figure 4
Average percent home range overlap of individuals within the same social community versus between communities. Shading is darker for higher levels of overlap. Community and subcommunity matrices are not shown for males because social clustering was not significant at these levels. For male cliques, only significant clusters are shown. Therefore, we generated an out-group metric, which is the average overlap between individuals of a clique to other giraffe in the same subcommunity but not the same clique. No out-group was provided for females because all females were part of significant clusters. Darker shading of cells on the diagonal of each table reflects where space use patterns correspond with social structure. For males, in contrast, average home range overlap for pairs of males in the same social clique is no higher than overlap among males belonging to different cliques.

that are not members of their clique. Association strength within clusters may not necessarily be substantially higher than across clusters, but there is high transitivity within clusters, indicating that individuals linked to a common neighbor are themselves likely to be linked (i.e., the friend of my friend is also my friend, Wasserman and Faust 1994).

Although several authors suggest that giraffe social organization is characterized by fission–fusion dynamics embedded in higher level communities (Bashaw et al. 2007; Bercovitch and Berry 2009a; Carter et al. 2012), these conclusions have stemmed from observed variation in group sizes, shifting group membership, and pairwise association indices without putting such interactions into the context of a larger social network. Thus, they suggested that community structure might exist without defining the multileveled nature of the organization, as we were able to demonstrate here. Pratt and Anderson (1982) described an apparent social division in their study populations, but the division was not quantified rigorously. Such divisions have not been reported elsewhere, but that may be due to small sample sizes. Community structure in a loosely social species like the giraffe may be difficult to readily observe without large sample sizes and the application of new analytical tools. Shorrocks and Croft (2009) conducted a preliminary analysis of giraffe social networks. However, the conclusions they were able to make about the nature of giraffe social organization were limited. The maximum number of observations that any individual was resighted was 4 instances, and the maximum number of times they observed repeated associations among individuals

was twice (Shorrocks and Croft 2009). In their network, an average individual in their network was connected to a total of 5 other giraffe. This number is far below the total number of connections exhibited by an average individual in our population (~ 98 connections), but similar to the average group size observed both here and in other populations (Dagg and Foster 1976; Leuthold 1979; Le Pendu et al. 2000; van der Jeugd and Prins 2000; Fennessy 2004; Bercovitch and Berry 2009a; Shorrocks and Croft 2009). Thus, the network observed in their 4-week study was more of a snapshot of association patterns in time rather than an overall description of giraffe social organization. In comparison, we recorded nearly 1100 groups and observed each individual approximately 30 times with some pairs recorded together up to 34 times, allowing giraffe social organization to be rigorously analyzed.

Males and females can be considered to occupy separate social networks, given that 7 of 8 social cliques were primarily single sex in the combined analyses. Although most observed giraffe groups contain both males and females, the repeated observations and transitivity that are necessary to classify individuals into clusters tend to occur only within sexes. Giraffe populations also exhibit sexual segregation by habitat, with cow-calf groups preferring open habitats and bulls being more commonly observed in denser habitats (Young and Isbell 1991; Ginnett and Demment 1999; Bercovitch and Berry 2009a).

Male social cliques are akin to “bachelor herds” described in other ungulate species. Bachelor cliques observed in our population do not appear to be random collections of young males, but rather consist of males that are familiar with each other and are repeatedly observed together. Younger males tended to be observed in larger groups of other males, which may or may not also be accompanied by females. Older males tended to be found alone, in pairs, or with mostly female groups. Indeed, the MR-QAP analysis suggests that younger males actively prefer to associate with animals of similar age, whereas older males, which tend to dominate mating opportunities (Pratt and Anderson 1982), avoided associating with rivals. This follows the observations of Pratt and Anderson (1982). Carter et al. (2012) demonstrated a nonsignificant trend for males to have preferred social partners only when subadult males were included in the analysis, suggesting that older males do not exhibit social preferences. The most readily apparent clusters within our male social network (Figure 1C) tended to consist of younger males. Four of the five significant male cliques were comprised of at least $>70\%$ younger bulls, and 100% of cliques C.3 and C.7 were younger.

Any population that exhibits spatial structure and loose aggregations of individuals will likely exhibit social network structure, even if individuals merely associate randomly with individuals in spatial proximity. Indeed, association strength was highly correlated with home range overlap, which is unsurprising given that animals cannot possibly socially interact if they do not share space. Highly overlapping home ranges should lead to at least some interaction, whereas discontinuous home ranges rarely lead to interaction. However, there is a broad range of intermediate overlap where variation in association strength cannot be explained purely by home range overlap. Although home range overlap does explain a substantial amount of variance in association strength (adjusted $R^2 = 0.61$ for combined sex analysis), it is evident that there are numerous dyads with home range overlaps greater than 60% that associate no more frequently than dyads with only 20% overlap (Figure 3). These results mirror those of Carter et al. (2012).

Random associations among individuals with overlapping home ranges should lead to high levels of correlation between the structure of social and home range networks. Differences in the social network structure relative to the home range network emerge from behavioral choices by individuals. The decision to associate with a preferred set of individuals within one's spatial neighborhood will cause the home range network to be overlaid with an additional social layer representing spatiotemporal overlap (sharing the same space at the same time). Community-finding algorithms were performed on the home range network to assess if social clusters simply consisted of individuals that were clustered in the same spatial neighborhood. Only a third of male pairs assigned to the same spatial neighborhood were also in the same social clique. Thus, social and spatial communities were not analogous for males. In contrast, nearly 90% of female dyads that were assigned to the same spatial neighborhood were also in the same social clique. This suggests that female social organization has an underlying spatial basis, or conversely, that space use is highly influenced by social factors. Female communities A.1 and A.2 were geographically separated by a river, which females only rarely crossed. However, spatial separation between female subcommunities was evident despite no geographic barriers to movement (subcommunities B.2 and B.3; Figure 2), and the home ranges of female social cliques overlapped substantially in some cases (cliques C.1 and C.2; cliques C.1, C.4, and C.5; Figure 2). Although space use is correlated with association strength among females, these results suggest that finer-scale social structure (i.e., membership in subcommunities and cliques) does not emerge solely from patterns of space use.

Female social organization was much more strongly influenced by shared space use than male community structure (Figure 1). This relationship between female community structure and space use is consistent with matrilineal-based structure if 2 conditions are met: female philopatry and female-female bonds. Preferential associations among kin are not required to produce spatially based kin structure. Even in solitary species, female locational philopatry may lead to clustering of related animals on the landscape (Waser and Jones 1983). If females associate randomly with other individuals within their home range, philopatry alone may produce kin-based social structure even if bonds are not maintained between female kin (Waser and Jones 1983; Isbell 2004; Wolf and Trillmich 2008).

The fact that social cliques, in some cases, occupied highly overlapping home ranges suggests that females do not randomly associate with other females within their own home ranges. Recent work by Bercovitch and Berry (2012) indicates that female-female bonds do exist. Sister-sister pairs were more likely to associate, as were mothers with their adult daughters (Bercovitch and Berry 2012). Mothers were observed alone with their adult offspring of up to 10 years, and giraffe groups were observed with up to 3 generations of maternal kin (Bercovitch and Berry 2009a). Further evidence for kin-based bonds among female giraffe arises from the fact that female calves remain with their mothers longer than male calves (Pratt and Anderson 1979), though not all studies confirm this (Bercovitch and Berry 2009a). In a captive study, adult females were most affiliative with their subadult daughters (Bashaw et al. 2007). Fennessy (2004) described a small population of 17 giraffe that appeared to be divided into 2 core groups, each consisting of a cow and her calves. Finally, Carter et al. (2012) showed that female giraffe exhibiting social preference for one another were more related than expected by chance.

Although these studies suggest the existence of kinship-based social structure, genetic and long-term behavioral studies will be required to confirm whether multilevel social structure is matrilineally based and how this may influence the evolution and expression of other social behaviors. For example, mothers frequently pool their calves in nursery crèches in which 1 female often remains with the calves while the other mothers forage elsewhere (Langman 1977; Pratt and Anderson 1979). Even in the absence of an inclusive fitness explanation, female social cliques may set the stage for evolution of crèches by reciprocal altruism.

Giraffe social structure is highly fluid, which has historically made it difficult to identify social structure. The frequent fissioning and fusioning of giraffe groups has led to interpretations that giraffe social interactions are random and ephemeral in nature. Through the application of network analysis and DCG community-finding methods, however, we were able to discern structural social organization. The results presented here, taken together with other recent work on giraffe social behavior (Bercovitch and Berry 2012; Carter et al. 2012), lead us to reject the notion that giraffe lack social organization and that associations are simple random aggregations. While social interactions are highly fluid in nature, it is becoming increasingly clear that association patterns in giraffe are not the result of random fission–fusion events but are embedded within a structured social network characterized by multiple levels of organization. This has implications for giraffe conservation and for the evolution of social behavior. More generally, these results give us new insights into how social structure in fission–fusion species is influenced by underlying patterns of space use. Observations such as these are key for further elucidating how socioecological factors give rise to social structure in fission–fusion species.

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