



Social connectedness and movements among communities of giraffes vary by sex and age class

Juan M. Lavista Ferres^a, Derek E. Lee^{b,c}, Md Nasir^a , Yu-Chia Chen^d, Avleen S. Bijral^a, Fred B. Bercovitch^{e,f}, Monica L. Bond^{c,g,*} 

^a Microsoft AI For Good Research Lab, Redmond, WA, U.S.A.

^b Department of Biology, Pennsylvania State University, University Park, PA, U.S.A.

^c Wild Nature Institute, Concord, NH, U.S.A.

^d Department of Electrical and Computer Engineering, University of Washington, Seattle, WA, U.S.A.

^e Wildlife Research Center, Kyoto University, Kyoto, Japan

^f Department of Animal, Wildlife, and Grassland Sciences, University of the Free State, Bloemfontein, South Africa

^g Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

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Many social mammals form discrete social communities within larger populations. For nonterritorial, polygynous, size-dimorphic species, sex- and age-class differences in life-history requirements might mediate differences in social connectedness and transitions among communities. We conducted social network analysis and community detection with an extensive data set of 1081 individually identified wild giraffes, *Giraffa camelopardalis*, over 5 years to test predictions that adult males and young of both sexes show greater social connectedness (degree, closeness and betweenness centrality) and transition more often among social communities than adult females, which form stronger and more stable relationships. We also expected that young animals would be more socially connected than adults. Using both static and dynamic network clustering techniques, we detected four distinct mixed-sex social communities, which we termed 'super-communities' to differentiate this apex level of social organization from intermediate-level female-only communities. Most (~70%) giraffes remained within their same super-community, and those (usually adult males) that visited a different super-community often returned to their original super-community. Males – both adults and calves – had higher social centrality scores than females, and adult males were closer to all other individuals in the network and transitioned among super-communities twice as often as females and calves, reflecting their roaming reproductive strategy of seeking females in oestrus. Of all age and sex classes, young males had the most social ties and highest betweenness (moved most often among groups), which we attributed to social exploration prior to natal dispersal. Overall, female giraffes have stronger social associations than males, but males exceed females in measures of social connectedness, reflecting differences in reproductive and life-history profiles. Our findings suggest that giraffe translocations that do not consider sociality are likely to break up established social associations and potentially reduce fitness.

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Male and female mammals often have different life-history strategies (Clutton-Brock, 2016; Dobson & Oli, 2007; McCullough, 1999; Trivers & Willard, 1972). In polygynous mammals where males provide no care of offspring, males maximize their fitness by defending a group of females, defending sexually receptive females within a group or defending territories containing resources that attract females, while female behaviour is driven by mate selection

and the requirements of raising young (Clutton-Brock, 2016; Emlen & Oring, 1977; Trivers & Willard, 1972). In many mammal species, females form social groups in which members feed together, travel together, cooperate to avoid male harassment and cooperatively raise or protect offspring (Clutton-Brock & Iason, 1986). Sociospatial behaviour also differs by sex, with female mammals tending towards philopatry while males tend to disperse (Clutton-Brock & Lukas, 2012; Greenwood, 1980; Wolff, 1994). Younger males often form unstable bachelor groups (Marjamäki et al., 2013; Ruckstuhl & Festa-Bianchet, 2001), and older males may become more solitary as they age (VanderWaal et al., 2014). In size-dimorphic mammals,

* Corresponding author.

E-mail address: monica@wildnatureinstitute.org (M. L. Bond).

the developmental trajectory of females and males follows different age-related patterns, with the former maturing earlier and living longer than the latter (Clutton-Brock, 2016). Therefore, sex and age differences in life-history requirements likely mediate differences in social behaviour, including the degree to which an individual is connected within its network of associates.

Social groups in a variety of taxa frequently merge and split in a fission–fusion fashion for foraging efficiency, predator avoidance or information transfer (Aureli et al., 2008). These fission–fusion dynamics of groups can be embedded within larger discrete and stable social communities, where associations are more frequent within than among communities (Bond et al., 2020; Lusseau et al., 2006; Papageorgiou et al., 2019; VanderWaal et al., 2014). Social connectedness and transitions among communities likely vary by age class and sex in response to differences in life history, but such information is generally lacking for long-lived species because long-term, large-scale studies of populations of individually identified animals are necessary to evaluate the structure and dynamics of complex social networks.

Giraffes, *Giraffa camelopardalis*, are large (800–1200 kg), long-lived, iteroparous, size-dimorphic browsing ruminants that inhabit African savanna woodlands (Dagg, 2014; Shorrocks, 2016). Giraffes live in fission–fusion societies with group size and composition fluctuating and mediated by kinship, sex, age proximity, familiarity, reproductive state, season and ecological – including anthropogenic – factors (Bercovitch & Berry, 2009, 2013; Bond et al., 2019; Hart et al., 2020; Muller et al., 2018; Wolf et al., 2018). Giraffes are an excellent study species for exploring social complexity and movement patterns because their basic fission–fusion society forms nonrandom clusters of individuals that exhibit distinct social structure, with individuals ranging over relatively extensive areas (Brown and Bolger, 2020; Knüsel et al., 2019; Le Pendu & Ciofolo, 1999; Leuthold & Leuthold, 1978). Home range overlap is obviously required for individuals to coalesce into a group, but the degree of home range overlap among giraffes accounts for only a fraction of the variation in their social associations (Carter, Seddon et al., 2013; Deacon & Bercovitch, 2018; VanderWaal et al., 2014). Females maintain long-term bonds with other females, males have less stable associations with each other, and adult males are more likely to be solitary than are females and younger males (Bercovitch & Berry, 2013; Bond et al., 2019; Bond, König et al., 2021; Carter, Seddon et al., 2013; Carter, Brand et al., 2013; VanderWaal et al., 2014). The association patterns of giraffes create a structured social network characterized by multiple levels of organization (Bond et al., 2020; Grueter et al., 2020; VanderWaal et al., 2014). VanderWaal et al. (2014) documented five ‘cliques’ embedded in three ‘subcommunities’, which were themselves embedded in two spatially separated ‘communities’ of approximately 30 and 50 adult females in a relatively small population of reticulated giraffes (*G. c. reticulata*). Bond et al. (2020) and Bond, König, et al. (2021) revealed social organization among female-only associations in a metapopulation of 540 adult female Masai giraffes (*G. c. tippelskirchi*) that consisted of more than a dozen communities each composed of approximately 60–90 females that were spatially overlapping but socially discrete.

Mixed-sex associations among giraffes, and how they contribute to population social structure, are not well understood. Reproduction influences social relationships, with females often coalescing into nursery groups when calves are born around the same date (Langman, 1977; Saito & Idani, 2016). Younger males form bachelor herds or sometimes follow older males (Berry & Bercovitch, 2014), while older males often range alone, covering large distances in search of oestrous females (Pratt & Anderson, 1985). The roaming reproductive strategy of older males might provide a mechanism that links female communities together. Furthermore, relatively

little is known about sex differences in social associations as giraffes mature from calves into young adults. Carter, Brand, et al. (2013) showed that as juvenile female Angolan giraffes (*G. c. angolensis*) <18 months of age matured to >4 years, they increased their number of female associates and had more associates than older females, possibly reflective of a dispersal phase. In the same giraffe population, Castles et al. (2019) found that gregariousness (average group size) of males decreased after approximately age 4, but no age differences in betweenness, a measure of how much an individual acts as a connector to others in their network (Kolaczyk & Csárdi, 2020). These studies provide a foundation for testing predictions about age and sex differences in social connectedness among giraffes in other populations.

Here we investigated patterns of social connectedness and movements across mixed-sex ‘super-communities’ in a meta-population ($N > 1000$) of free-roaming Masai giraffes (Lee & Bolger, 2017) that we systematically studied over 5 years. We have previously reported (Bond et al., 2020; Bond, König, et al., 2021) that adult female social networks in our study area are organized into more than a dozen communities. Our first objective here was to expand upon that analysis by exploring the structure of super-communities composed of multiple age and sex classes, and by analysing movement patterns of males and females among super-communities. Our second objective was to compare the connectedness of male and female juveniles and adults with others in their social network. To achieve this aim, we quantified three measures of network centrality to represent connectedness: degree (number of associates), closeness (geodesic distance to other associates) and betweenness (number of shortest paths passing through the individual; Kolaczyk & Csárdi, 2020). We did not examine the strength of social associations with other individuals, but rather the degree of social connectedness within the network. Animals with many loose associations have a higher degree of social connectedness than do animals with fewer but stronger associations (see Ellis et al., 2019).

We tested the following three predictions based on age- and sex-related differences that have been reported among giraffes.

(1) Adult males (a) have higher social connectedness, (b) move more often among super-communities and (c) travel farther distances than adult females, given their roaming reproductive strategy.

(2) Younger males and females (first seen as calves <1 year old) have higher social connectedness than adult females, but not adult males, given that adult female giraffes form long-term bonds with a subset of individuals in the population (communities), adult males roam among female groups and young animals explore their social environment as they mature.

(3) Younger males and females have similar social connectedness, given that both sexes explore their social environment.

METHODS

Study Area

The Tarangire Ecosystem in northern Tanzania is in the eastern branch of the Great Rift Valley and encompasses roughly 30 000 km² (Prins, 1987). The region experiences three distinctive seasons per year (short rains = October–January; long rains = February–May; dry = June–September). The main vegetation communities in the Tarangire Ecosystem are *Vachellia (Acacia) tortilis* parkland, *Vachellia-Commiphora* woodland, gall *Vachellia drepanolobium* woodland, *Combretum-Dalbergia* woodland and open grassland (Lamprey, 1963). Our study area is in the core of the

Tarangire Ecosystem, consisting of a 1500 km² area spanning five administrative units with differing management activities (see Results, Fig. 1). The two national parks, Tarangire (TNP) and Lake Manyara (LMNP), have high levels of wildlife protection including exclusion of livestock and human settlements and regular anti-poaching patrols; Manyara Ranch Conservancy (MRC) has intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols, but with large numbers of livestock and herders present during the daytime. Lolikisale (LGCA) and Mtowambu Game Controlled Areas (MGCA) have the lowest levels of wildlife protection and allow livestock, human settlements and sport hunting (although hunting of giraffes is prohibited). None of the administrative units are fenced, and all units are connected by movements of adult female giraffes (Lee & Bolger, 2017).

The Rift Valley escarpment, forming the western boundary of the study area, is a steep cliff that restricts giraffe movements in that direction. Few wild large mammals are present east of Makuyuni town, west of TNP and south of LMNP due to high human and livestock population density and intensive agriculture. Giraffes cross the two 2-lane asphalt roads in the study area (Lee & Bolger, 2017).

Field Data Collection

Each giraffe has a coat pattern that is unique and unchanging from birth to death (Foster, 1966). We used a Canon camera body

with a 100–400 mm lens to photograph, and later identify, individual giraffes from their unique patterns. From May 2011 until October 2016, we conducted 30 daytime, fixed-route transect surveys along a network of dirt tracks to collect photographic mark–resight data on three primary sampling periods per year near the end of each season (January–February, May–June, September–October). We sampled according to Pollack's (1982) robust design, with each primary sampling period composed of two independent, consecutive secondary sampling periods during which all transects in the study area were driven once. Transect density throughout the study area was high (0.42 km/km²) relative to the average adult female giraffe home range size of 114 km² (Knüsel et al., 2019). Driving speed was maintained between 15 and 20 km on all transects, and all surveys included the same two observers and driver. Each secondary survey took approximately 10 days.

When giraffes were encountered, we 'marked' (or resighted) each animal by approaching to within 150 m distance and photographing them on the right side for individual identification. We attempted to find and photograph all members of all groups we encountered. Giraffe groups have been defined in multiple ways but share a common foundation (Bercovitch & Berry, 2013). The groups consist of individuals that coordinate movements and activity, with the distances between individuals in a group less than between groups. Using an absolute distance between giraffes to define a group is problematic because interindividual distances within a group change when the group moves from dense thickets to more open areas (F. B. Bercovitch, personal observation). In the Tarangire Ecosystem, we have found that the most appropriate definition of a group is one or more giraffes foraging or moving together and >500 m from the next nearest giraffe (Bond et al., 2019).

We used physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics and height to categorize giraffes into three age classes: calves (<1 year), subadults (1–3 years) or adults (>3 years). Giraffes mature sexually at about 4 years of age, so we considered individuals >3 years to be adults (Lee & Strauss, 2016). Younger sexually mature males probably do not successfully mate in the presence of older dominant males, which may result in differential sociality of younger versus older adult males, but we were unable to divide adults into different age classes because we did not know the age of individuals that we first saw as adults. For each photograph, we recorded the animal's age class (calf, subadult, adult), sex (male, female) and the GPS location of the group. We did not analyse subadults here due to insufficient numbers of individuals in this age class for social network analysis (see below). To identify individuals, we used Wild-ID, a computer program that matches unique patterns from photographs and is known to perform with little misidentification error in large giraffe data sets (Bolger et al., 2012).

We carried out the field research with permission from the Tanzania Commission for Science and Technology (COSTECH), Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA) and Manyara Ranch Conservancy.

Social Network Construction

In network terminology, individuals are called 'nodes' and associations among individuals are called 'edges'. Social network analysis generates an association matrix based on edges between nodes, with edges in a weighted network representing repeated associations over time. We determined associations between giraffes using the 'gambit of the group' approach – the presence of two individuals in the same group (Franks et al., 2010). We defined the association rate among individuals (edge weights) using the

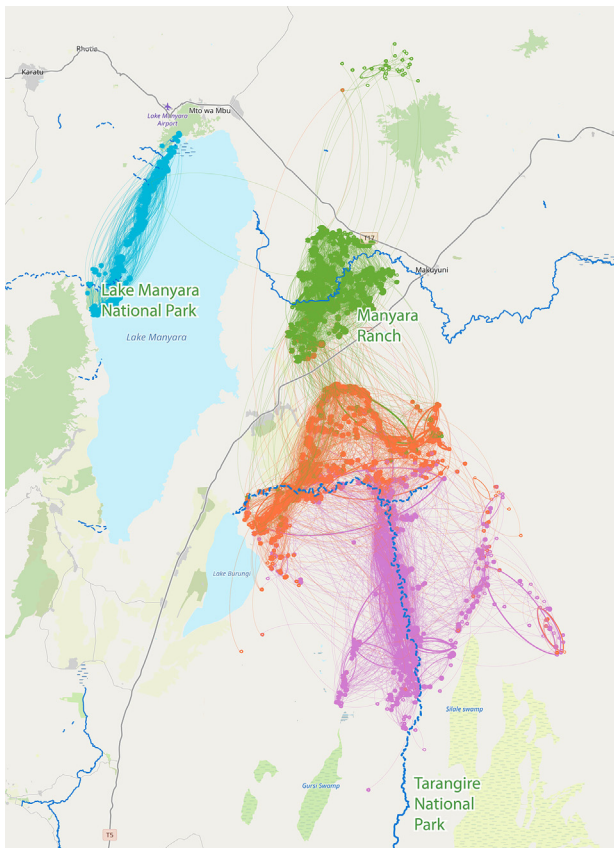


Figure 1. All observations and connections for Masai giraffes in the Tarangire Ecosystem, Tanzania during 2011–2016, with colour indicating super-community identifier (blue = west, green = north, orange = central, purple = south). Blue lines are rivers (northern is Makuyuni, southern is Tarangire), grey lines are tarmac roads, green polygons are forests and stippled green is swamp.

simple ratio index (Cairns & Schwager, 1987; Hoppitt & Farine, 2018). The simple ratio index represents the propensity for two individuals to be observed in the same group given that the group contains at least one of the individuals (Farine & Whitehead, 2015). Because individual level network metrics can vary with sampling effort, we sought to reduce sampling error by collecting individual data with equal sampling intensity and effort (Farine & Whitehead, 2015).

Our survey design involved driving each transect once during each secondary sampling period (~10 days); thus, each animal had the opportunity to be detected only one time during that period. However, on rare occasions some animals might be observed twice, for example in the late afternoon and again the following morning near an area where we camped. It is not possible to statistically account for this bias in detectability because it is not systematic, and multiple sightings of the same animals close in time are not independent. We therefore used only the first detection per individual giraffe for each secondary sampling period to reduce sampling bias and avoid nonindependence of observations. We further removed individuals with fewer than six observations to improve the accuracy of our network (Davis et al., 2018). None of the 118 individuals first seen as subadults had more than five detections in our data set, so we did not include this age class in our analyses. See Appendix, Fig. A1 for histogram of detections for each age and sex class.

Comparing Social Metrics

We computed three social network centrality metrics of giraffes from the weighted network, including degree, closeness centrality and betweenness centrality, in Gephi and Python using NetworkX (Hagberg et al., 2008). All three metrics assess the 'social connectedness' of an individual within its network. Degree centrality is defined as the number of edges a giraffe has and represents the number of its associates, i.e. the more associates, the more central in the network (Wey et al., 2008). Closeness centrality, calculated as the average of the shortest path length from a node to every other node in the network, shows how close an individual is to every other individual in its network (Golbeck, 2013) and reflects the potential influence on the entire network. The betweenness centrality for each pair of nodes is the number of the shortest paths between every other pair of nodes in the network that pass through the focal node and is useful for pinpointing individuals that tend to move among groups, indicating how important the animal is as a point of social connection (Wey et al., 2008).

For all three metrics, we compared the results between sexes (females versus males) and by age class (calves versus adults). To measure the statistical significance of the results, we used a bootstrap process (Lusseau et al., 2008). We computed 1000 bootstraps of the observations by resampling the giraffes (nodes of the network) with replacement and calculated the social network metrics at each iteration. We report the mean, standard deviation and 95% confidence intervals of the observed metrics over the bootstrap replicates for each sex and age class, and the nonoverlapping confidence intervals for these comparisons indicate statistical significance. For consistency of comparing the metrics across sex and age classes with different sample sizes, we used the normalized versions of all centrality metrics. The normalization factor was chosen to be a linear or quadratic form of the size of the network n . More specifically, for degree and closeness centrality, the factor was $(n-1)$ while $(n-1)(n-2)/2$ was used for betweenness centrality.

Community and Super-community Detection

We distinguish between a 'community' of adult female-only associates (Bond et al., 2020) and what we term here as a mixed-sex 'super-community'. Both communities and super-communities are subgroups of animals that associate more with each other than with the rest of the network (Girvan & Newman, 2002), but a community is based upon the association indices only between adult females, while a super-community is based upon associations among all four age and sex classes. To provide the strongest evidence for the community delineations, we used a range of methods to identify communities and assess the robustness of community membership assignments. We adopted two different methods for community and super-community detection: an algorithm based on a static graph, where we used all associations throughout the 5 years of data (Blondel et al., 2008), and a dynamic graph, where we created a social network that changed over time (Chen et al., 2019). We used a geolocation layout to visualize the social network as coordinates, with the average latitude and longitude of each giraffe during a given survey (based on its location if a singleton, or the centre of its group formation if it was in a group) during the 5 years of observations. The data visualization was performed in Gephi (Bastian et al., 2009) and Power BI (Power BI | Microsoft Power Platform, <https://powerbi.microsoft.com/en-us/>).

The static algorithm, commonly known as the Louvain method (Blondel et al., 2008), is a greedy optimization approach that attempts to optimize the modularity of partitions of the network. For the network that could change over time, we used the dynamic clustering method (Chen et al., 2019), which is based on a time-dependent extension of the approximate-likelihood stochastic block model estimation framework. The extension is made possible by modelling the parameters of the static model as stochastic processes; estimators of the parameters are obtained with the efficient auto-differentiation algorithm in a maximum a posteriori manner. The procedure iteratively refines cluster membership based on an initial clustering for each time step while ensuring cluster membership stability over time. The dynamic block model we used here is a sequence of networks and clusters of giraffes observed at every 4-month time step. We initialized the clusters for each time step by performing spectral clustering on the static network (created by using all associations over 5 years), then ran the method to obtain the cluster membership for every giraffe at every 4-month time step.

To determine the number of communities and super-communities for the static algorithm, we used modularity Q (Newman, 2006), a well-known metric that measures the strength of the partitioning of a network into modules. We chose the optimal number of super-communities by maximizing the modularity Q value while varying the time resolution parameter (Lambiotte et al., 2008) of the static algorithm, which controls the partitioning. For the dynamic network approach, we used the eigengap statistic (von Luxburg, 2007) instead of modularity Q , since the former performs better for sparse networks and is well suited to our data because the giraffe networks at every time step were not densely connected.

To analyse the stability of the selected communities and super-communities, we ran the algorithm over 1000 replicate networks that contained perturbations created by a bootstrap process of sampling with replacement. We computed community assortativity (r_{com}) (Shizuka & Farine, 2016), a measure to capture the robustness of super-community membership assignments, across these replicate networks. In addition, we calculated average

modularity Q and frequency for each possible number of communities over all replicate networks. For all-age mixed-sex populations, we experimented with different values of the resolution parameter (Lambiotte et al., 2008) of the static algorithm and chose a resolution of 2, which generated the most stable super-communities, i.e. the maximum r_{com} .

Lastly, we measured the home range of each super-community using the minimum convex polygon (MCP) based on the outermost locations of all giraffes in each super-community (Burt, 1943).

Comparing Movements and Transitions

We calculated distances moved by giraffes and tested for Markov properties, which assess how much each location depends upon the previous location. We also compared the transition probabilities among super-communities by sex and age class.

To calculate the distances travelled by giraffes, we took the first observation of every individual as a centre point, then computed the distances to all additional observations of that individual relative to that centre point. We calculated the mean and quantiles of the distances moved around the centre point using the bootstrap process with 1000 replicates, and calculated P values using bootstraps to compare differences among age and sex classes (Boos, 2003).

We also analysed movements more broadly with a Markov transition model with covariates. To quantify the differences in how female and male calves and adults moved, we added age $_i$ *sex $_i$ interaction terms in the transition model, as well as an additional covariate of the individual's vicinity (other individuals nearby, also termed 'neighbourhood'). Our location data are derived from our longitudinal study (Diggle et al., 2002), wherein detections for individuals are collected over an extended period, but individuals are not detected during every survey. As such, we additionally accounted for the correlation between location measurements for individual giraffes in the model. Specifically, we introduced a covariate and refer to it as a lagged mean location, as described in the next section. The aim was to test for a difference in dependence on the previous location for females and males for different age classes. For example, a stronger dependence on the previous lag (higher corresponding coefficient) would indicate a more constrained movement and thus would allow us to make inference about variance in movement in space for the different categories (calf versus adult, male versus female).

Notation and model

Let $L_{it} = [X_{it}, Y_{it}]$ correspond to the location coordinates for the i th giraffe at the t th time step (each secondary observation with 4-month periods between them); $Z_i = [age_i, sex_i]$ be the covariates associated with the i th giraffe; and N_t be the total number of observed giraffes at time t . Finally, let $\underline{L}_{it} = [\underline{X}_{it}, \underline{Y}_{it}]$ be the weighted mean location defined as:

$$\underline{L}_{it} = \sum_{j=1, j \neq i}^{N_t} w_{ij}^t L_{jt}, \text{ where } w_{ij}^t \propto \exp(- (L_{it} - L_{jt})^T B_t (L_{it} - L_{jt}))$$

The covariate \underline{L}_{it} is a weighted average of all giraffe locations at time t , and the weights are normalized relative to i th giraffe's location and gives a higher weight to individuals closer to it.

The Markov transition model is:

$$L_{it} = \Lambda L_{it-1} + \Theta Z_i + E_{it},$$

$$E_{it} = \alpha E_{it-1} + \varepsilon_{it},$$

$$\varepsilon_{it} \sim N(0, \sigma^2 I)$$

where the errors ε_{it} are assumed to be independent and normally distributed. Making the sequence E_{it} dependent on the previous time step explicitly introduces a dependence on the previous location of the giraffe (Tsay, 1984). The dependence on the lagged and weighted mean location captures the impact of the giraffe's neighbours at the previous time step. The size of this neighbourhood is controlled by the bandwidth matrix B , and only individuals closer to the i th giraffe will matter. Individuals too far away will have a negligible contribution to the weighted average. The way B is chosen mirrors the selection of a bandwidth matrix for bivariate density estimation and is estimated for data points at each time separately (Duong & Hazelton, 2003). Intuitively, this covariate attempts to measure how giraffe movement is constrained by neighbours or other group members. Note that the model in its form is bivariate but is separated into two models for estimation, one for each coordinate. Such models are also referred to as linear link models with autoregressive errors and were estimated using the nlme package in R (Pinheiro et al., 2017).

Finally, to quantify movements between super-communities, we used the dynamic graph and computed the transition probabilities of giraffes moving from one super-community at time T to another super-community at time $T + 1$. We used a chi-square test to test for statistically significant sex differences in super-community transitions between age classes.

RESULTS

Our data set was composed of 1081 giraffes that had been observed at least six times during the 5-year observation period. Of these, 65% were female and 35% were male, and 73% were adults and 27% were calves (Table 1).

Comparing Social Metrics

Means, standard deviations and 95% confidence intervals of normalized values of social metrics among age and sex classes are presented in Table 2.

Degree distribution

On average, one giraffe was connected to 65 other giraffes. Male giraffes had higher degree than female giraffes, both for adults (males = 85 associates, females = 47 associates) and calves (males = 91 associates, females = 73 associates). Moreover, both male and female calves had a higher mean degree than adult females,

Table 1

Distribution by sex and age class of a sample of Masai giraffes used in network analysis in the Tarangire Ecosystem, Tanzania during 2011–2016

| | Females | Males | Total |
|--------|-----------|-----------|-----------|
| Adult | 538 | 252 | 790 (73%) |
| Calves | 161 | 130 | 291 (27%) |
| Total | 699 (65%) | 382 (35%) | 1081 |

Table 2
Mean, SD (in parentheses) and 95% confidence intervals, CI [in brackets] of normalized centrality metrics, by sex and age class of Masai giraffes in the Tarangire Ecosystem, Tanzania during 2011–2016. Mean and CI calculated over 1000 bootstrap replicates

| | Females | Males | Total |
|-------------------------------|------------------------------------|------------------------------------|------------------------------------|
| Degree centrality | | | |
| Adult | 0.0438 (0.0014) [0.0411–0.0466] | 0.0788 (0.0018) [0.0753–0.0822] | 0.0371 (0.0014) [0.0344–0.0398] |
| Calves | 0.0674 (0.0007) [0.0661–0.0687] | 0.0842 (0.0005) [0.0833–0.0851] | 0.0640 (0.0013) [0.0614–0.0665] |
| Total | 0.0419 (0.0014) [0.0392–0.0446] | 0.0596 (0.0019) [0.0560–0.0633] | 0.0351 (0.0014) [0.0322–0.0379] |
| Closeness centrality | | | |
| Adult | 0.2317 (0.0044) [0.2230–0.2403] | 0.3133 (0.0030) [0.3074–0.3193] | 0.2722 (0.0044) [0.2636–0.2807] |
| Calves | 0.2282 (0.0024) [0.2236–0.2328] | 0.2865 (0.0013) [0.2840–0.2890] | 0.2913 (0.0032) [0.2850–0.2976] |
| Total | 0.2406 (0.0042) [0.2325–0.2488] | 0.3120 (0.0032) [0.3056–0.3183] | 0.2816 (0.0040) [0.2738–0.2894] |
| Betweenness centrality | | | |
| Adult | 0.0039 (0.0001) [0.0037–0.0042] | 0.0057 (0.0001) [0.0055–0.0058] | 0.0021 (0.0001) [0.0020–0.0022] |
| Calves | 0.0138 (0.0002) [0.0134–0.0142] | 0.0178 (0.0001) [0.0175–0.0181] | 0.0063 (0.0001) [0.0061–0.0065] |
| Total | 0.0029 (0.0001) [0.0027–0.0030] | 0.0041 (0.0001) [0.0040–0.0043] | 0.0015 (0.0001) [0.0015–0.0016] |

and male calves had a higher mean degree than male adults. We report the normalized metrics in Table 2 to compare among networks of different sex and age classes due to the variation in sample sizes.

Closeness centrality

Overall, males (0.3120) had greater closeness centrality than females (0.2406), and male adults (0.3133) had greater closeness centrality than male calves (0.2865), but female adults (0.2317) and female calves (0.2282) did not significantly differ.

Betweenness centrality

Betweenness centrality of calves (3671) was significantly higher than adults (1224), and male calves (10 387) showed significantly higher betweenness centrality than female calves (8041). Similar to degree, we report the normalized version of this metric in Table 2 to compare across different sex and age classes.

Giraffe Social Network

The giraffes' social graph was fully connected; however, two distinct subgraphs were joined by only one edge created by a single female giraffe (Fig. 1). The social network had a diameter of 6 (greatest distance between any pair of nodes) and a radius of 2 (the minimum among all the maximum distances between a node to all other nodes), and the average path length was 2.6 (the average number of steps along the shortest paths for all possible pairs of network nodes; Brandes, 2001).

Community and Super-community Detection

We found that four was the most frequent number of super-communities based on their count of occurrences in 1000 replicates (Appendix, Table A1). Four super-communities also produced highly stable community structures with r_{com} values of at least 0.85 in all resolutions greater than 2 (Appendix, Table A2). Hence, we adopted the four super-community structure in the entire giraffe population for the rest of the analyses.

Dynamic algorithm super-community detection based on the eigengap statistic consistently generated four super-communities

for the entire giraffe population. The all-age mixed-sex super-communities identified by both the static and dynamic algorithms were similar (Fig. 2), with both algorithms detecting four spatially distinctive super-communities that we referenced as south, centre, north and west, respectively (Table 3). Although neither algorithm considered the geographical location of each giraffe as part of mapping the super-community's structure, both algorithms produced four geographically separate super-communities. The similar results for both the static and dynamic approaches underscore the validity and consistency of the delineation.

We detected multiple adult female-only social communities from the same population, with r_{com} being the greatest with eight communities and modularity Q being the greatest with seven communities (Appendix, Tables A3, A4). All-female communities were entirely contained within one of the four super-communities; in other words, female communities did not span the boundaries of the super-communities.

The spatial area (MCP) of each super-community was as follows: south = 507.6 km², centre = 122.7 km², north = 421.3 km², west = 56 km².

Comparing Movements and Transitions

Distances moved

Mean distances travelled by sex and age class are presented in Table 4. Measured from the first position for every sequential pair of observations, adult males travelled on average 1.5 times the distance that adult females and calves travelled ($P < 0.001$; Fig. 3). Adult males also travelled 1.3 times farther than male calves ($P < 0.001$). The difference between the distance travelled by adult females and female calves was not significant ($P = 0.176$). The P values are based on statistical tests to compare the movements among different age and sex classes. We also show the mean and quantiles of the different classes in Table 4.

Not only did adult male movements cover a greater amount of area, but the area covered was more diffuse and wide-ranging than that covered by adult females (Fig. 4). The scatterplots in Fig. 5 reveal that males had a relatively wider spread than females. The comparison of coefficients for lag_x and lag_y with coefficients for lag_x : SexM and lag_y : SexM reveal that the dependence on the previous location was ~5% and ~7% less for males than for females, respectively. The estimation results are shown in Table A5 of the Appendix. Thus, it appears that the movement of males was less constrained than that of females in general. Additionally, the interaction of age class and sex with lagged location shows that, for male calves, location significantly depended on the previous location.

Transitions among super-communities

Giraffes in the west super-community, which was isolated from the others, did not transition to any other super-community during the 5-year study period (other than a single female), so we did not consider the west super-community for further transition analysis. During the 5 years of observations, 70% of the giraffes stayed in the same super-community and never transitioned to another super-community, while 27% visited one new super-community and 3% visited all three super-communities (north, centre and south; Table 5). Of the 34 giraffes that visited all three super-communities, 25 were adult males: even though adult males comprised only 23% of all giraffes, they represented 74% of the giraffes that transitioned among the three super-communities. Only 1.3% of adult females, compared with 11.0% of adult males, visited all three super-communities. Adult males were significantly more likely to visit other super-communities than were adult females ($\chi^2_1 = 31.919$,

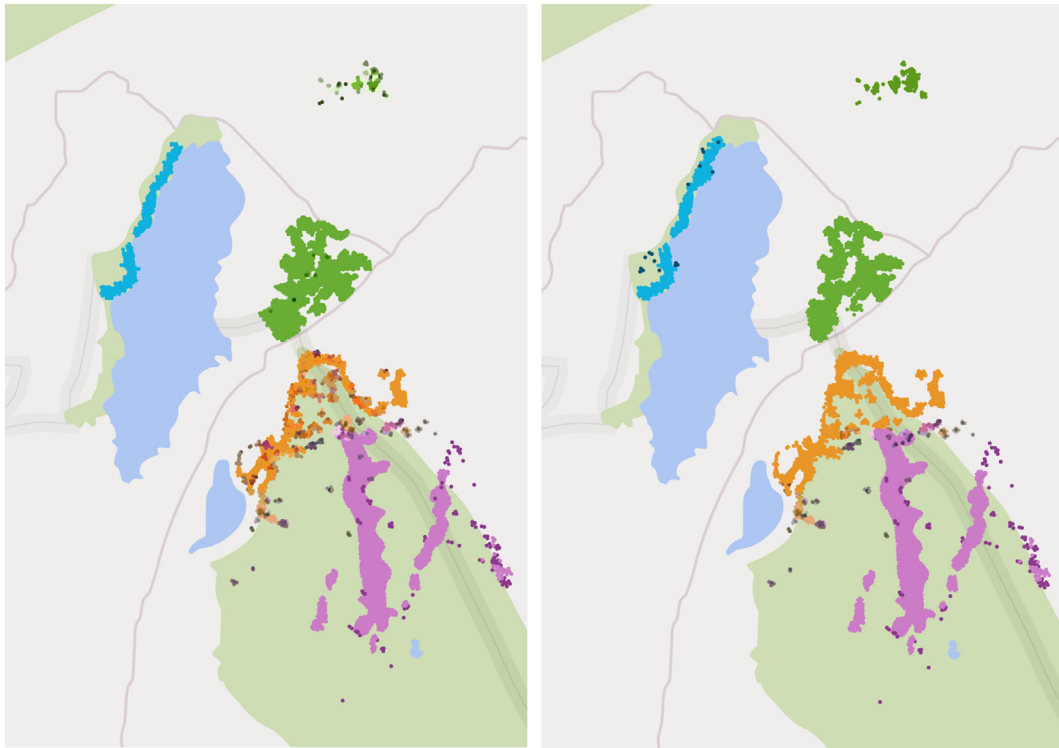


Figure 2. Static (left) and dynamic (right) network clustering yielded identical super-communities of giraffes.

$N = 707$, $P < 0.00001$), while sex differences in travelling to non-natal super-communities were absent among calves ($\chi^2_1 = 0.104$, $N = 272$, $P = 0.750$).

Within any 4 months between observation sessions, ~90% of the giraffes stayed in their super-community, while ~10% moved to other super-communities (Fig. 6). Most movements occurred between the centre and north super-communities (Fig. 6) despite the tarmac road dividing the two (Fig. 2). Males transitioned more often than the females (14% versus 7%), and the adult males moved three times more often than the calves (19% versus 6%). The calves moved only through the centre super-community: they were not observed on consecutive occasions in the south and north super-community. The adult females' movements were similar to the calves' movements (7% versus 6%). However, transitions did not follow Markovian properties because 90% of transitions returned to the origin while 10% did not.

DISCUSSION

Sexual selection has mediated sex differences in life-history trajectories in many size-dimorphic mammals, including giraffes. Given sex-related differences in reproductive strategies, we expected that adult male giraffes would have the highest social connectivity of any age and sex class, and the most amount of travel among super-communities, as a consequence of their roaming reproductive strategy (Bercovitch et al., 2006). We confirmed both patterns. Adult male giraffes lack the strong and stable social associations of adult females (Bercovitch & Berry, 2013; Carter, Seddon, et al., 2013; Carter, Brand, et al., 2013; Prehn et al., 2019; VanderWaal et al., 2014), but in our metapopulation, they had the highest closeness centrality of all age and sex classes, and thus were closer to every other individual in the network. In addition, they moved farther distances and transitioned between super-communities more often than females. These patterns likely

reflect the adult male giraffe's strategy of roaming widely in search of females in oestrus (Leuthold, 1979; Pratt & Anderson, 1985).

We predicted no sex differences in social connectedness among immature giraffes, but that younger animals would exhibit a higher connectedness than adult females. We found that young males had greater connectedness than young females, contrary to our expectations. We also discovered that male calves had higher betweenness – moving more among groups – and more social ties than adult males, adult females or female calves, presumably as they began to explore their social and ecological surroundings prior to natal dispersal. Our findings confirm that immature animals engage in exploring their social environment, and we suggest that the sex differences in their connectedness reflect sex differences in dispersal patterns (see below).

Our fundamental finding is that the metapopulation of giraffes residing in the Tarangire Ecosystem is characterized by an upper level of social complexity heretofore unknown. The metapopulation consisted of four super-communities of mixed sexes and ages, with three of the four numbering approximately 300 individuals (and one numbering 100). These super-communities contained discrete yet often overlapping adult female social communities ranging in size from 60 to 90 individuals. The super-communities and female communities are built upon fission–fusion dynamics that yield constantly changing group

Table 3

Number and percentage of Masai giraffes grouped by socially defined super-community in the Tarangire Ecosystem, Tanzania during 2011–2016

| Super-community | Females | | Males | | Total |
|-----------------|-----------|-----------|-----------|-----------|-------|
| | Adult | Calves | Adult | Calves | |
| South | 144 (43%) | 42 (13%) | 121 (36%) | 28 (8%) | 335 |
| Centre | 166 (53%) | 57 (18%) | 52 (17%) | 40 (13%) | 315 |
| North | 170 (52%) | 47 (14%) | 55 (17%) | 58 (18%) | 330 |
| West | 58 (57%) | 15 (15%) | 24 (24%) | 4 (4%) | 101 |
| Total | 538 (50%) | 161 (15%) | 252 (23%) | 130 (12%) | 1081 |

Table 4

Statistics of mean distances moved from first detection (km) by sex and age class of Masai giraffes in the Tarangire Ecosystem, Tanzania during 2011–2016

| | Mean | 5th percentile | 25th percentile | 75th percentile | 95th percentile |
|--------------|------|----------------|-----------------|-----------------|-----------------|
| Adult female | 4.1 | 1.7 | 2.6 | 5.1 | 8.5 |
| Calf female | 4.0 | 1.5 | 2.6 | 5.4 | 8.6 |
| Calf male | 5.2 | 2.0 | 2.9 | 6.6 | 12.2 |
| Adult male | 6.8 | 2.4 | 4.0 | 8.9 | 14.4 |

formations, with an average of about five to six giraffes, but ranging from singletons to upwards of 65 individuals (Bond et al., 2019), as documented in other locations in Africa (Bercovitch & Berry, 2009; Leuthold, 1979; Muller et al., 2018; VanderWaal et al., 2014; Wolf et al., 2018). Adult males have a low strength of social associations, given that they do not form extensive bonds with other giraffes, but have a high degree of connectedness, given that they travel frequently among groups and communities. Within this multilayered social network, adult males were more likely to visit multiple super-communities than were females or juveniles, yet 90% of all individuals that transitioned among super-communities still returned to their original super-community. These nuances of the multilevel society of giraffes reflect sex and age differences in reproductive life-history patterns.

Social Connectedness and Reproductive Strategies

Adult males and females

Adult female giraffes live in smaller home ranges than males and maintain closer and more stable social bonds with a subset of other females that have overlapping home ranges, while older adult males have weaker social bonds with both females and other males and engage in a solo pursuit of sexually receptive females (Bercovitch & Berry, 2013; Carter, Seddon, et al., 2013; Carter, Brand, et al., 2013; Prehn et al., 2019; VanderWaal et al., 2014). Solitary adult males tend to move regularly among female groups, inspecting females to determine reproductive status and guard females in oestrus (Leuthold, 1979), which in turn increases the number of conspecific connections for both females and males. However, older males are also found in groups with younger males (bachelor herds), further increasing their number of ties compared with females (Bercovitch & Berry, 2013).

Male reproductive success relies upon finding and mating with receptive females. Female giraffes give birth at 20-month intervals (del Castillo et al., 2005), and near the equator, births are evenly distributed throughout the year (Bercovitch & Berry, 2010; Dagg, 2014; Foster & Dagg, 1972; Lee et al., 2017; Sinclair et al., 2000). Moreover, females are sexually receptive for only a few days during each ~2-week cycle (Bercovitch et al., 2006; Pratt & Anderson, 1985), so oestrous females are a limited resource for males. In the Tarangire Ecosystem, female home ranges average 114 km² (Knüsel et al., 2019), and females in a South African population tended to show relatively low home range overlap with other females (Deacon & Bercovitch, 2018). Thus, female giraffes in oestrus are widely dispersed over space and time, so adult males continuously roam alone seeking females in different groups that are reproductively available. The adult male strategy of roaming among female groups to seek mating opportunities results in periodic hormone-induced rutting behaviour approximately every 2 weeks, a temporal scale that would overlap with local cycling females (Bercovitch et al., 2006; Pratt & Anderson, 1985; Seeber et al., 2013). African elephant, *Loxodonta africana*, males adopt a similar roaming strategy, with older males in musth increasing both their walking speed and daily distance travelled while searching for sexually receptive females (Taylor et al., 2019).

Male mammals need to access oestrous females in order to be reproductively successful, but often behavioural or environmental constraints make finding and defending females energetically costly for males (Clutton-Brock et al., 1982). In species where oestrous females are spatiotemporally dispersed, males may have large and often overlapping home ranges in which they attempt to encompass as many females as possible within that range (Bond & Wolff, 1999; Madison, 1985; Wolff, 1985) and thus are not thought to be territorial. In seasonally breeding species, such as red deer, *Cervus elaphus* (Clutton-Brock et al., 1982) and rhesus macaques, *Macaca mulatta* (Bercovitch, 1992), males accumulate fat reserves prior to the mating season, but the energetic demands of male reproductive strategies in nonseasonally breeding species such as giraffes are not met by a 'fattening phenomenon'. The energetic costs to giraffe males of a roaming reproductive strategy and mate guarding could be minimized because giraffes are unusual among browsers in that they ruminate while walking (Shorrocks, 2016).

Sex differences in reproductive strategies among giraffes include different movement patterns, whereby females tend to remain clustered within their community and males move more often between communities and super-communities. Adult male giraffes not only move among female groups within communities to assess their oestrous status, but also occasionally move between super-communities, generating the highest centrality scores of any sex and age class. Adult males were also less constrained in their movements than adult females, with each successive location less dependent upon their previous location, indicating their movement patterns were more diffuse. Overall, more than 90% of giraffes were detected in the same super-community at the beginning and end of our 5-year study period, and 70% never transitioned at all, suggesting strong social fidelity for all age and sex classes, but adult males transitioned between super-communities twice as often as females and calves. Half of the adult male population visited at least one other super-community. Given the size of female giraffe home ranges, the asynchronous nonseasonal breeding and the limited time for conception, giraffe bulls would be expected to wander far and wide to maximize their reproductive success, and this behaviour links the female social communities into a larger mixed-sex

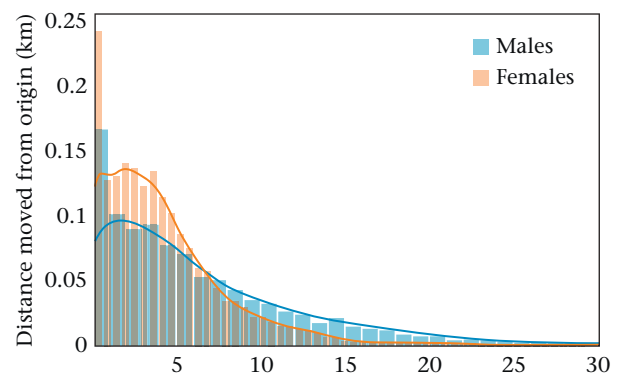


Figure 3. Mean distances moved from first detection (km) for male and female giraffe adults and calves.

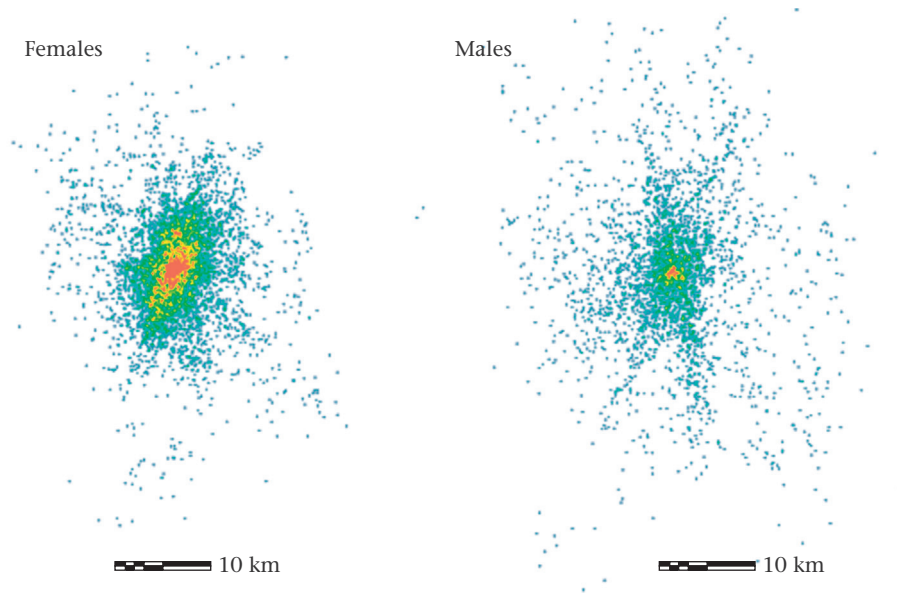


Figure 4. Spatial distribution of movements from the first position for every sequential pair of observations of female and male giraffe adults and calves.

super-community as well as occasionally linking super-communities.

Young males and females

We also examined the social connectedness and mobility of giraffes that we first detected as calves in order to determine the extent to which young males and females might display sex differences. Our study period was 5 consecutive years, so most calves aged into subadults during this time. We had predicted male and female calves would have similar social connectedness, as subadults of both sexes had more associates than their adult counterparts in a Namibian population of giraffes (Carter, Seddon, et al.,

2013; Castles et al., 2019). However, in all centrality metrics, our sample of young males were more socially connected than young females.

We attribute the higher social connectedness of young males to a manifestation of natal dispersal explorations. Most mammal species tend towards male-biased dispersal and female-biased philopatry (Clutton-Brock & Lukas, 2012; Dobson, 1982; Greenwood, 1980; Wolff, 1994). We suggest that these young male giraffes had begun exploring socially, joining bachelor herds, and possibly learning more about female distribution within the population prior to dispersal. Success of dispersal may be improved by acquiring information about the socioecological environment

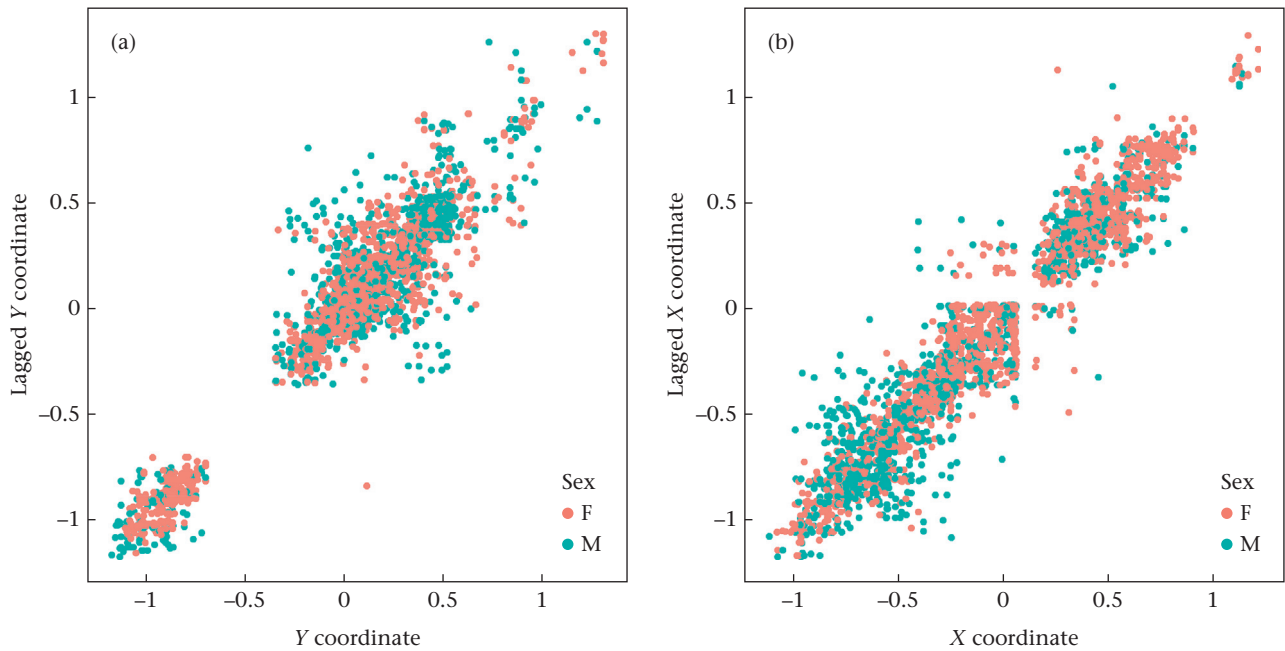


Figure 5. Scatterplots showing (a) Y coordinates against the lagged Y coordinates and (b) X coordinates against the lagged X coordinates for male and female giraffes. More spread indicates a relatively weaker dependence on the previous location.

Table 5

Number and percentage of dynamic network transitions among super-communities for 1081 Masai giraffes in the Tarangire Ecosystem, Tanzania during 2011–2016

| Category | Females | | | Males | | | Grand total |
|------------------------------------|-----------|-----------|-----------|-----------|----------|-----------|-------------|
| | Adult | Calves | Total | Adult | Calves | Total | |
| Stayed in the same super-community | 349 (73%) | 117 (80%) | 466 (75%) | 117 (51%) | 99 (79%) | 216 (61%) | 682 (70%) |
| Visited 1 other super-community | 124 (26%) | 27 (18%) | 151 (24%) | 86 (38%) | 26 (21%) | 112 (32%) | 263 (27%) |
| Visited all 3 super-communities | 6 (1%) | 2 (1%) | 8 (1%) | 25 (11%) | 1 (1%) | 26 (7%) | 34 (3%) |
| Total | 479 | 146 | 625 | 228 | 126 | 354 | 979 |

through periodic forays or sorties before attempting permanent dispersal (Conradt et al., 2001; Roper et al., 2003). Armansin et al. (2020) noted that for social species, resistance to dispersal into new social groups is lower when social connections already exist. For example, subadult male primates often disperse into social groups with which they have previously had contact (e.g. common marmosets, *Callithrix jacchus*, Lázaro-Perea, 2001; ursine colobus monkeys, *Colobus vellerosus*, Teichroeb et al., 2011). Periodic interactions with non-natal social groups prior to natal dispersal likely play a role in dispersal decisions and allow subadults to assess neighbouring groups and evaluate breeding opportunities before permanently departing (Lázaro-Perea, 2001). In our study population, young male giraffes engaged in sorties into non-natal adult female social communities and subsequently returned to their original community prior to final natal dispersal (Bond, Lee et al., in press). The highest degree and betweenness values for male giraffe calves compared to young females, and to male and female adults, reflects this reproductive life-history strategy.

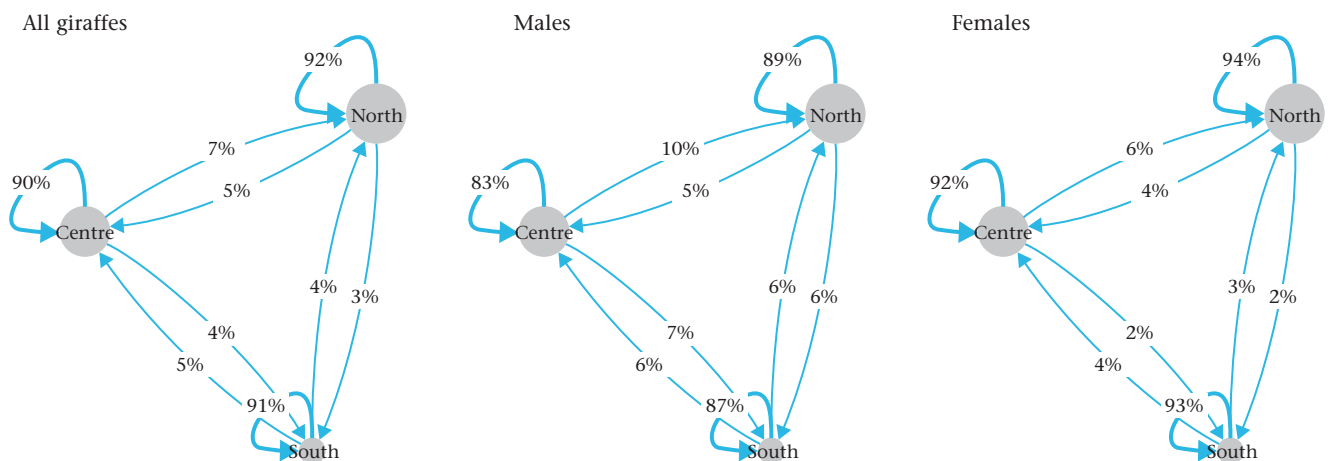
Giraffe Communities and Super-communities

As in many other social mammals, giraffe societies consist of distinct multilevel social networks (here, adult female communities and mixed-sex super-communities) within a larger population (Bond et al., 2020; VanderWaal et al., 2014; this study). Super-community boundaries in the Tarangire Ecosystem appear to be somewhat correlated with landscape features, such as Lake Manyara and the town of Mtowambu, which together physically and socially separated the west super-community from the rest of the population (see Fig. 1), although those features did not constitute an absolute barrier given that one female did transition. The north and the central super-communities were separated by a busy tarmac road and agricultural lands, but the highest rates of transitions actually were between these two super-communities,

demonstrating that individuals will regularly traverse across farmlands and tarmac roads if necessary to meet their life-history requirements. However, only a small proportion of individuals were recorded moving between these two super-communities, raising the possibility that such anthropogenic disturbances to the landscape could hinder male roaming reproductive strategies, and therefore limit genetic diversity in the metapopulation. The Tarangire National Park giraffe population was further divided into two super-communities, the centre and the south, which approximately followed the Sand River and the northern bend of the Tarangire River (see Fig. 1). Both the Sand and Tarangire Rivers are regularly crossed by giraffes at most times of the year (D. E. Lee & M. L. Bond, personal observations), so further research is needed to better understand why the giraffe super-communities split in this area.

The super-community with the fewest number of individuals (101) was located in the small, geographically isolated Lake Manyara National Park and had a home range of only 56 km², which was smaller than the home ranges of some individual giraffes in this population (Knüsel et al., 2019). The limited size of this super-community presents a risk of stochastic events such as a disease outbreak or inbreeding effects. The regular movements of individuals, especially males, between super-communities could reduce the risks of inbreeding. It remains to be seen what genetic structure exists among these super-communities, and whether efforts to maintain connectivity between Lake Manyara National Park and Manyara Ranch are needed to preserve or bolster the genetic diversity of the west community.

Of the four giraffe super-communities, three were composed of remarkably similar numbers of individuals (range 315–335), differing by no more than 20 individuals despite large differences in the amount of landscape occupied (MCP range 122.7–507.6 km²). This data set omits individuals seen fewer than six times. When we attributed all giraffes in our population to a super-community

**Figure 6.** Transition rates among super-communities for all giraffes, male giraffes and female giraffes.

based on the membership of others in their groups, the actual population of each super-community was 792, 814, 919 and 155 for the south, centre, north and west super-communities, respectively, confirming the consistent population sizes. The similarity in population size across three super-communities that differ widely in home range area offers intriguing evidence that there may be some optimal number of giraffes within a super-community that is regulated by both habitat availability and carrying capacity, but that may also be mediated by social, cultural or cognitive constraints (Grueter et al., 2020). For example, feral goats, *Capra hircus*, formed cliques of individuals whose size was consistent across networks despite significant differences in ecology, climate, demographic structure and genetics (Stanley & Dunbar, 2013).

The only previous study of giraffe multilevel social organization (VanderWaal et al., 2014) found a smaller community size than in our study, but their population was much smaller than our population. However, both studies, using different methods, revealed that the core giraffe fission–fusion social system is embedded in a larger complex multilevel society. Given that different analytical techniques were applied to different subspecies residing in different ecological systems, we suggest that our findings are robust and that giraffes across Africa have evolved a complex society that contains multiple layers of organization.

Multilevel social organization with nested social units have been documented for a variety of animal species, and a nomenclature to describe the nested assemblage of levels was suggested by Grueter et al. (2020). Giraffe social structure could be summarized as core units of ever-changing group formations based upon fission–fusion dynamics that are modulated largely by kinship, sex and age proximity, with individuals coalescing into ‘cliques’ that are embedded in successively larger, nested, upper levels called ‘sub-communities’ and ‘communities’, to the apex level of ‘super-communities’ in a metapopulation. Regardless of the terminology adopted, our findings indicate the extent to which the evolution of sociality has followed similar trajectories among animals.

Conclusions

The sex differences in life-history strategies among polygynous mammals are reflected in differences in rates of sexual maturation (Blackenhorn, 2005; Clutton-Brock & Isvaran, 2007) and life expectancy (Clutton-Brock & Isvaran, 2007). As a consequence of sex differences in reproductive development, reproductive strategies and life-history trajectories, we had expected that sex differences also characterized degrees of social connectedness and movement patterns, especially among mammals residing in fission–fusion societies where social groups can be composed of same-sex, mixed-sex or solitary individuals, with or without young, and we indeed found this to be the case.

The consistency in both community and super-community size (with the exception of the smaller west super-community in the nearly insular Lake Manyara National Park) suggests that giraffes in this population form modular female-based communities that are themselves embedded into one of a few larger super-communities, each with similar demographic structure in terms of age and sex distribution.

Our study not only reveals that giraffes reside in super-communities, but that different measures of social complexity map onto sex differences in reproductive and life-history profiles. Adult female giraffes have much stronger social associations than males, but adult males exceed females in measures of social connectedness. Such findings reveal how adult females have more close, and fewer loose, bonds with individuals than adult males, while males have more loose, and often no close, bonds with individuals than females. These patterns most likely reflect the

roaming reproductive strategies of males and the propensity of females to establish nursery groups and establish long-lasting ties with relatives and ‘friends’.

Earlier reports that giraffes have a fluid and constantly shifting social structure (Foster & Dagg, 1972; Le Pendu et al., 2000; Leuthold, 1979; van der Jeugd & Prins, 2000) were superficially correct, but failed to understand that the root of the flexibility is nonrandom social associations between individual giraffes. Giraffes live in a complex, structured society with a foundation composed of fission–fusion groups mediated by social, ecological, reproductive, temporal and anthropogenic factors operating in tandem, not independently (Bercovitch & Berry, 2013; Bond et al., 2019). Adult male roaming reproductive strategies connect adult female communities and occasionally link up mixed-sex super-communities, which should maximize genetic diversity of the metapopulation. Given that the Masai giraffe is categorized as an endangered subspecies on the IUCN Red List (Bolger et al., 2019) and resides in a multilayered complex social system, preserving giraffe habitats and promoting co-existence with people (Lee, 2018; Lee & Bond, 2018) are likely to be more productive for conservation than translocating a limited number of individuals to new areas, which would destabilize social relationships and potentially reduce fitness.

Author Contributions

J.M.L.-F., D.E.L. and M.L.B. conceptualized the study. D.E.L. and M.L.B. collected field data and performed data curation. J.M.L.-F., M.N., Y.-C.C. and A.S.B. performed formal analysis and visualization. D.E.L., M.L.B., F.B.B., J.M.L.-F. and M.N. wrote the original draft. All authors contributed to review and final editing.

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Appendix

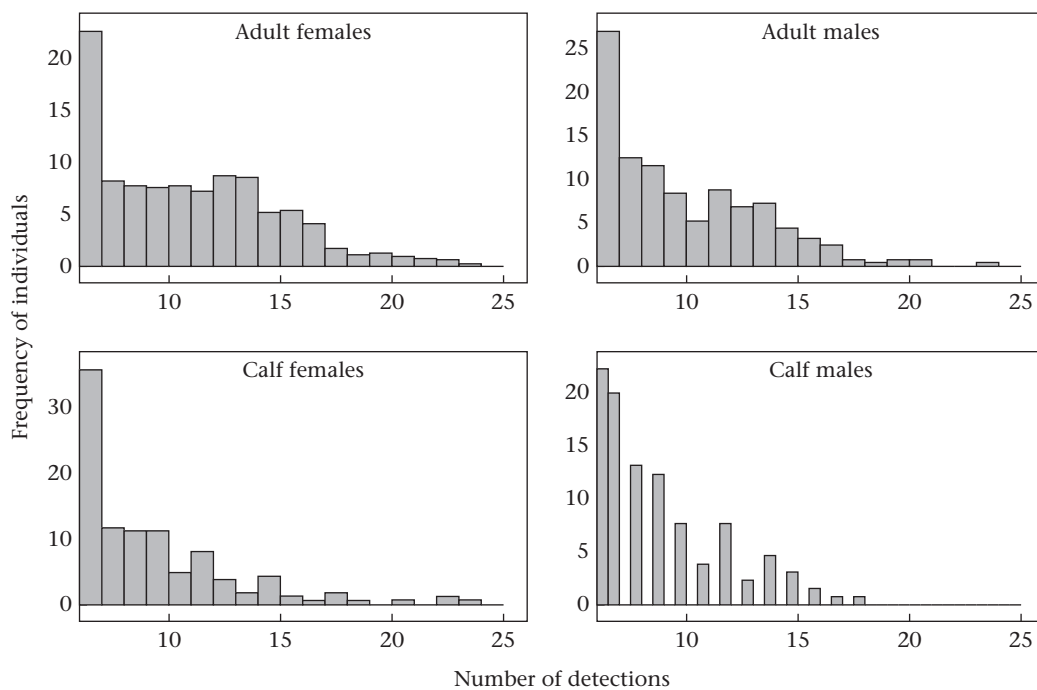


Figure A1. Range of the number of detections for 1081 Masai giraffe calves ($N = 538$ adult females, 252 adult males, 161 calf females, 130 calf males) used in social network analysis in the Tarangire Ecosystem, Tanzania during 2011–2016.

Table A1

The number of bootstraps replicates (out of 1000) with a given number of super-communities and resolution parameter

| Number of super-communities | res=1 | res=1.5 | res=2 | res=2.5 | res=3 | res=3.5 |
|-----------------------------|------------|------------|------------|------------|------------|------------|
| 3 | 0 | 0 | 0 | 2 | 15 | 49 |
| 4 | 0 | 71 | 477 | 756 | 820 | 806 |
| 5 | 4 | 633 | 413 | 211 | 153 | 137 |
| 6 | 253 | 267 | 104 | 30 | 12 | 8 |
| 7 | 470 | 27 | 6 | 1 | 0 | 0 |
| 8 | 238 | 2 | 0 | 0 | 0 | 0 |
| 9 | 35 | 0 | 0 | 0 | 0 | 0 |

Bold values denote the highest count across different numbers of communities for a given resolution.

Table A2Community assortativity (r_{com}) metric for different values of the resolution parameter and number of communities

| Number of communities | res=1 | res=1.5 | res=2 | res=2.5 | res=3 | res=3.5 |
|-----------------------|-------|---------|-------|---------|-------|---------|
| 3 | – | – | – | 0.369 | 0.374 | 0.381 |
| 4 | – | 0.734 | 0.899 | 0.883 | 0.870 | 0.860 |
| 5 | 0.689 | 0.871 | 0.895 | 0.881 | 0.882 | 0.855 |
| 6 | 0.793 | 0.879 | 0.896 | 0.899 | 0.897 | 0.856 |
| 7 | 0.809 | 0.884 | 0.899 | 0.869 | – | – |
| 8 | 0.830 | 0.808 | – | – | – | – |
| 9 | 0.845 | – | – | – | – | – |
| All | 0.810 | 0.858 | 0.897 | 0.881 | 0.861 | 0.825 |

The bottom row shows the r_{com} for all bootstraps combined.**Table A3**Community assortativity (r_{com}) metric for different numbers of communities or super-communities (all age and sex classes) and different subpopulations

| Sex and age class | Number of communities or super-communities | | | | | |
|-------------------------|--|--------------|--------------|--------------|--------------|--------------|
| | 3 | 4 | 5 | 6 | 7 | 8 |
| Adult female | – | 0.734 | 0.921 | 0.932 | 0.950 | 0.955 |
| Adult male | 0.910 | 0.909 | 0.934 | – | – | – |
| Adult all | – | 0.743 | 0.794 | 0.879 | 0.913 | – |
| Calves female | – | 0.938 | 0.944 | 0.952 | 0.944 | – |
| Calves male | – | 0.553 | 0.788 | 0.787 | – | – |
| Calves all | – | 0.622 | 0.789 | 0.832 | – | – |
| All female | – | 0.720 | 0.902 | 0.925 | 0.924 | 0.937 |
| All male | 0.495 | 0.886 | 0.924 | – | – | – |
| All (super-communities) | – | 0.899 | 0.895 | 0.896 | 0.899 | – |

Bold values represent the highest community assortativity (r_{com}) for different sex and age classes.**Table A4**Modularity Q for different numbers of communities or super-communities and different sex and age classes

| Sex and age class | Number of communities or super-communities | | | | | |
|-------------------------|--|-------|--------------|--------------|--------------|--------------|
| | 3 | 4 | 5 | 6 | 7 | 8 |
| Adult female | – | 0.681 | 0.711 | 0.718 | 0.724 | 0.722 |
| Adult male | 0.523 | 0.582 | 0.601 | – | – | – |
| Adult all | – | 0.660 | 0.670 | 0.683 | 0.686 | – |
| Calves female | – | 0.643 | 0.658 | 0.685 | 0.697 | – |
| Calves male | – | 0.600 | 0.637 | 0.655 | – | – |
| Calves all | – | 0.629 | 0.646 | 0.655 | – | – |
| All female | – | 0.677 | 0.710 | 0.717 | 0.721 | 0.723 |
| All male | 0.504 | 0.600 | 0.613 | – | – | – |
| All (super-communities) | – | 0.656 | 0.676 | 0.683 | 0.690 | – |

Bold values represent the highest modularity Q for different sex and age classes.**Table A5**

Model output for each location coordinate

| Regression results | Dependent variable | |
|----------------------------|---------------------|---------------------|
| | prod_x(1) | prod_y(2) |
| lag_x | 0.925** (0.036) | 0.049 (0.036) |
| hig_y | 0.126** (0.042) | 0.734** (0.042) |
| SexF | 0.001 (0.003) | -0.002 (0.003) |
| SexM | -0.011** (0.004) | -0.006 (0.004) |
| minAgeC | 0.001 (0.005) | 0.009* (0.005) |
| lagged_mean_x | 0.027 (0.036) | -0.073* (0.036) |
| lagged_mean_y | -0.159** (0.042) | 0.227** (0.042) |
| lag_x:SexM | -0.054** (0.012) | -0.049** (0.012) |
| lag_y:SexM | -0.044** (0.012) | -0.072** (0.012) |
| lag_x:minAgeC | -0.012 (0.014) | -0.014 (0.014) |
| lag_y:minAgeC | -0.010 (0.014) | -0.006 (0.014) |
| SexM:minAgeC | 0.010 (0.008) | 0.003 (0.009) |
| lag_x:SexM:minAgeC | 0.067** (0.022) | 0.058** (0.022) |
| lag_y:SexM:minAgeC | 0.061** (0.023) | 0.068** (0.023) |
| Observations | 4841 | 4841 |
| Log likelihood | 3230.803 | 3166.898 |
| Akaike's information crit. | -6431.606 | -6303.796 |
| Bayesian information crit. | -6334.376 | -6206.566 |

The interactions with lagged locations were highly significant and reveal differing dynamics of male and female movement. * $P < 0.05$; ** $P < 0.01$.