

Proximity to humans affects local social structure in a giraffe metapopulation

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Abstract

1. Experimental laboratory evidence suggests that animals with disrupted social systems express weakened relationship strengths and have more exclusive social associations, and that these changes have functional consequences. A key question is whether anthropogenic pressures have a similar impact on the social structure of wild animal communities.
2. We addressed this question by constructing a social network from 6 years of systematically collected photographic capture–recapture data spanning 1,139 individual adult female Masai giraffes inhabiting a large, unfenced, heterogeneous landscape in northern Tanzania. We then used the social network to identify distinct social communities, and tested whether social or anthropogenic and other environmental factors predicted differences in social structure among these communities.
3. We reveal that giraffes have a multilevel social structure. Local preferences in associations among individuals scale up to a number of distinct, but spatially overlapping, social communities, that can be viewed as a large interconnected metapopulation. We then find that communities that are closer to traditional compounds of Indigenous Masai people express weaker relationship strengths and the giraffes in these communities are more exclusive in their associations.
4. The patterns we characterize in response to proximity to humans reflect the predictions of disrupted social systems. Near bomas, fuelwood cutting can reduce food resources, and groups of giraffes are more likely to encounter livestock and humans on foot, thus disrupting the social associations among group members. Our results suggest that human presence could potentially be playing an important role in determining the conservation future of this megaherbivore.

KEYWORDS

anthropogenic disruption, community detection, *Giraffa camelopardalis*, Giraffe, social network analysis

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1 | INTRODUCTION

Sociality provides the channel through which information, genetic material and diseases spread through populations (Kurvers, Krause, Croft, Wilson, & Wolf, 2014; Sih, Spiegel, Godfrey, Leu, & Bull, 2018). Social interactions among group members can be critical for survival and reproduction in group-living species (Alberts, 2019; Alexander, 1974) and are essential for the persistence of social units (Dunbar & Shultz, 2010). Social behaviour of animals can respond to changes in the environment (Edenbrow et al., 2011) or habitat configuration (He, Maldonado-Chaparro, & Farine, 2019; Lattanzio & Miles, 2014; Leu, Farine, Wey, Sih, & Bull, 2016). Increasingly, this environment includes disturbances arising from proximity to humans (Belton, Cameron, & Dalerum, 2018). Repeated, minor and indirect disruptions, such as human presence and encroachment into natural habitats, might accumulate to have cryptic negative effects on social behaviour. These effects might be especially prominent in animals with larger space requirements and a history of hunting or harassment by humans, and therefore lower tolerance to human presence.

There is increasing evidence that human activities can have far-reaching consequences for social species by disrupting group structure, and subsequently impacting group function (Foley & Faust, 2010; Parsons, Balcomb, Ford, & Durban, 2009; Shannon et al., 2013). African elephants exposed to traumatic events such as selective killing of older family members were unable to discriminate between the calls of conspecifics (Shannon et al., 2013) and displayed less discriminating social behaviour (Gobush & Wasser, 2009). However, human impacts could also be more subtle. Socially stable colonies of zebra finches *Taeniopygia guttata* that were experimentally split and then recombined expressed weaker relationship strengths and were more exclusive in their social associations, despite experiencing no long-term change in group membership. This change in social structure then resulted in lower group foraging efficiency (Maldonado-Chaparro, Alarcon-Nieto, Klarevas-Irby, & Farine, 2018). In another study, tree lizards *Urosaurus ornatus* living in frequently burned compared with unburned habitats were more aggressive and interacted more often with each other (Lattanzio & Miles, 2014). Spotted hyena *Crocuta crocuta* clans that experienced the highest human activity interacted less with other clan members (Belton et al., 2018). Together, these studies suggest a link between externally mediated social disruptions and social function.

Detecting signals of natural versus anthropogenic influences on social relationships among individuals in their natural environment is challenging. It requires large-scale studies of individually identified animals across replicated social groups spanning multiple environmental gradients. Here, we addressed this challenge by collecting and analysing long-term data from a metapopulation of adult female Masai giraffes *Giraffa camelopardalis tippelskirchi* in Tanzania, and testing whether the environment—especially proximity to human settlements—shapes social structure. Giraffes are megaherbivores that can roam over vast areas, moving across ecologically heterogeneous landscapes that, increasingly, include anthropogenically modified

land and human settlements (Knüsel, Lee, König, & Bond, 2019; Lee & Bolger, 2017). Adult females maintain family-based long-term associations (Bercovitch & Berry, 2012; Carter, Seddon, Frère, Carter, & Goldizen, 2013) despite having fluid group membership via fission-fusion dynamics (Leuthold, 1979). Such associations have been proposed to result in a multilevel social structure (VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014), although the spatial reach of, and overlap among, giraffe social communities remains unknown.

In Tanzania, giraffes are generally tolerated by humans because they do not cause conflict with farmers or livestock. Hunting of giraffes is illegal, but poaching for meat and body parts occurs (Kiffner, Peters, Stroming, & Kioko, 2015). Despite the public tolerance and hunting restrictions, Masai giraffe populations throughout their range have declined 50% in recent years (Bolger et al., 2019). Several reasons have been suggested, including poaching, habitat loss and fragmentation, lion *Panthera leo* predation on calves, and changes in food supply (Lee, 2018; Muller, 2018; Strauss, Kilewo, Rentsch, & Packer, 2015). Disruption to social systems also may be a contributing factor in population declines, but, to date, anthropogenic effects on social structure of giraffes remain unclear. One recent study by Muller, Cuthill, and Harris (2019) reported differences in network metrics across two separated, small, enclosed populations of Rothschild's giraffes in Kenya. They found that relationships were weaker and more exclusive in a population inhabiting an area with a high volume of tourists and lions, compared to another population inhabiting an area with no lions and a low volume of tourists. However, Muller et al. (2019) did not statistically compare the network characteristics of the two populations, and the effects of natural predation and human disturbance from tourism could not be discriminated due to the lack of replication beyond the two populations. In our study area, overlapping (i.e. replicated) communities of giraffes occurred along a gradient of proximities to human settlements, enabling us to test the effects on social structure from human presence. Giraffes do not flee from and appear to be tolerant of tourist vehicles in protected areas, so we did not consider tourism traffic in the protected areas to disrupt social structure.

In this paper, we examine whether proximity to human settlements can affect the social relationships of adult female giraffes. We focused on adult females because they form longer term associations with other females than do adult males, and show stronger preferences in their associations (Bercovitch & Berry, 2012; Carter, Brand, Carter, Shorrocks, & Goldizen, 2013). Moreover, adult females have more stable association rates than maturing and dispersing subadult females (Carter, Brand, et al., 2013). Giraffes in Tanzania are poached using machetes (Kiffner et al., 2015) or snares (Strauss et al., 2015) and are intolerant of people approaching them on foot. Further, livestock herders are often accompanied by dogs, which chase giraffes (MLB and DEL, pers. obser.). Thus we expect being near to human settlements and the consequent presence of humans on foot could disrupt the natural social behaviours of giraffes by scattering—thus splitting—members of a group. People often cut wood for fuel, which may reduce local food resources for giraffes and further contribute to disruption of their social behaviours during foraging. Based on the results of Maldonado-Chaparro et al. (2018), we predict that if

giraffes cannot maintain as large group sizes because groups living near humans are repeatedly disturbed, they should preferentially associate with fewer individuals, thus reducing the average relationship strength and being more exclusive in their social associations, likely because instability increases the costs of maintaining many concurrent relationships. To test this prediction, we constructed social networks using individual-based photographic capture–recapture data systematically collected over 6 years from a metapopulation of 1,139 wild adult female giraffes in a large and ecologically diverse area of northern Tanzania: the Tarangire Ecosystem (TE). Our study area spans two national parks, a private ranch and unprotected village lands (Figure 1). Because these areas are unfenced, individuals can move across the entire area. While the parks are protected, village lands are not, and these are experiencing rapid land-use changes such as conversion of natural savanna habitats to farmland (Lee, Bond, Kissui, Kiwango, & Bolger, 2016; Msoffe et al., 2011).

Animals often associate in groups that merge and split over time in a fission–fusion process, but may form social communities of individuals that interact frequently with each other in an area (Shizuka & Farine, 2016). Our first objective was to determine whether adult female giraffes form discrete communities of individuals that associate more frequently within the larger metapopulation, and if so, how many communities are there and how modular are they? Partitioning the giraffe metapopulation that spans the TE into multiple distinct communities then allowed us to accomplish our second objective, to identify natural and anthropogenic factors that explain variation

in sociality. We modelled the community-level relationship strength and social exclusivity as functions of social and environmental factors, including local giraffe population density, vegetation fertility and distance to two different types of human settlements, bomas and towns. Bomas are dispersed family compounds of huts constructed with natural materials, and towns consist of dense concentrations of concrete structures. Bomas in our study area are occupied by Indigenous pastoralist Masai people who typically do not poach giraffes for meat, but may kill lions and other carnivores to protect livestock (Kissui, 2008) and lion and spotted hyena densities are significantly lower in adjacent village lands than in the parks (Lichtenfeld, 2005). Towns are much rarer, but also much more densely populated by people, typically surrounded by farmlands and inhabited by bushmeat poachers (Kiffner et al., 2015). We hypothesized that social communities of giraffes living closer to both types of human settlements would exhibit weaker relationship strengths and more exclusive social associations—a signature of a disrupted social environment according to Maldonado-Chaparro et al. (2018).

2 | MATERIALS AND METHODS

2.1 | Study area

The TE in northern Tanzania is in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km² (Prins, 1987).

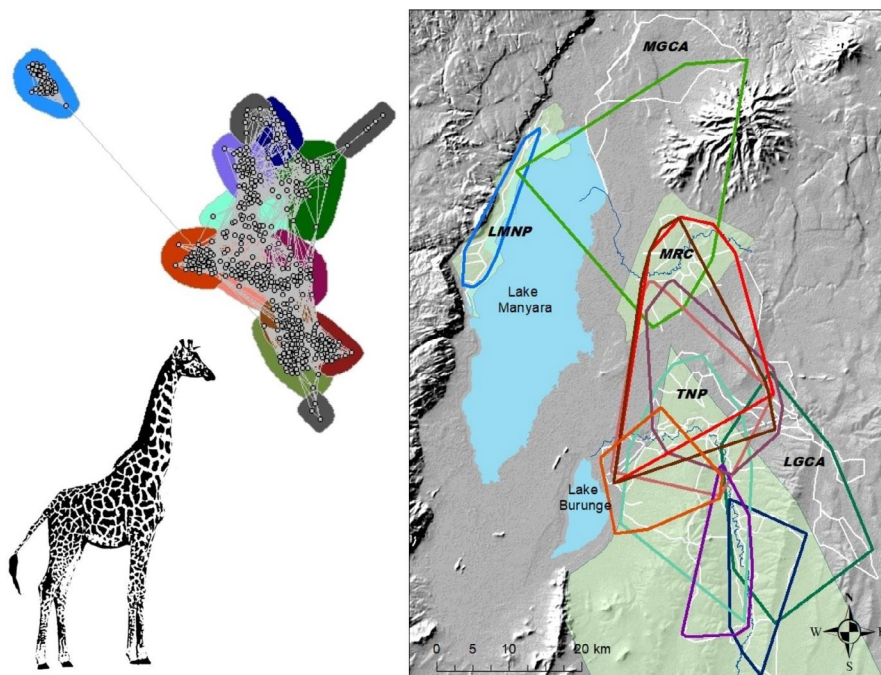


FIGURE 1 Community structure of a social network of 540 wild adult female giraffes (left) and minimum convex polygons showing spatial overlap of 11 communities (right) in the Tarangire study area, northern Tanzania. Communities were identified with the cluster-walktrap community-detection algorithm. White lines are roads and tracks surveyed for giraffes from 2011 to 2016, blue lines are rivers, light blue areas are alkaline lakes and green areas are national parks and conservancies. LMNP, Lake Manyara National Park; TNP, Tarangire National Park; MRC, Manyara Ranch Conservancy; MGCA, Mtwambu Game Controlled Area; LGCA, Lolikisale Game Controlled Area. Communities 1 = dark green, 2 = bright blue, 3 = navy blue, 5 = aquamarine, 6 = olive green, 7 = salmon, 8 = purple, 9 = dark pink, 10 = red, 13 = brown, 14 = orange. In the network, communities 4, 11 and 12 are dark grey and contained too few individuals for analysis

The TE experiences three precipitation seasons per year (short rains = October–January, long rains = February–May and dry = June–September). The main vegetation communities in the TE are *Acacia tortilis* parkland, *Acacia-Commiphora* woodland, gall *Acacia drepanolobium* woodland, *Combretum-Dalbergia* woodland and open grassland (Lamprey, 1963). The TE has undergone 3% annual human population growth between 2003 and 2012, which added nearly 800,000 people (Tanzanian National Bureau of Statistics (TNBS), 2013), increased illegal poaching, caused habitat loss and fragmentation, and reduced connectivity for wildlife (Msoffe et al., 2011).

Our study area is at the core of the TE, where we sampled a 1,500 km² area spanning five administrative units with differing management activities (Figure 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. Lolkisale (LGCA) and Mtowambu Game Controlled Areas (MGCA) have the lowest levels of wildlife protection and allow sport hunting, livestock and human settlements. 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. Two 2-lane asphalt roads cross the study area, but giraffes can cross these (Lee & Bolger, 2017).

2.2 | Field data collection

Each giraffe has a coat pattern that is unique and unchanging from birth to death (Foster, 1966). We used a Canon EOS 7D Mark II with a 100–400 mm lens to photograph, and later identified, individual giraffes from their unique coat markings. From May 2011 until October 2016, we conducted 31 daytime, fixed-route transect surveys along a network of dirt tracks to collect photographic capture–mark–recapture data on three primary sampling periods per year near the end of each precipitation season (January–February, May–June and September–October). We sampled according to Pollock's 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 (Pollock, 1982). Transect density throughout the study area was high (0.42 km/km²) relative to average adult female giraffe home range (115 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 'captured' (or 'recaptured') 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; however, some individuals inevitably escaped detection or identification (see Appendix S1). For each photograph, we recorded the animal's age class (calf, subadult, adult), sex (male, female) and the GPS location of the group. 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: calf (<1 year), subadult (1–3 years) or adult (>3 years). Giraffes mature sexually at about 4 years of age, so we considered individuals >3 years to be adults (Lee & Strauss, 2016). In our analysis, we used only females that were adults during the first year of our study. Our sample included most of the adult females in the study area, as 80% were identified by the end of 2012 (Figure S1). 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 datasets (Bolger, Morrison, Vance, Lee, & Farid, 2012). We defined a group as one or more giraffes that were foraging or moving together, but were not moving past each other in opposite directions, and were ≥ 500 m from the next nearest giraffe. Giraffe groups were usually self-defining as the distances between individuals were substantially less within groups than between groups.

2.3 | Social network construction

We used the 'gambit of the group', the presence of two individuals in the same group, to define associations between adult female giraffes and construct a social network (Franks, Ruxton, & James, 2010). We defined the association rate among individuals (the edge weights) using the simple ratio index (Hoppitt & Farine, 2018), which 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). Higher edge weights represented a greater propensity for two individuals to be seen in the same groups. Because individual-level network metrics can vary with sampling effort, population size and population density, we sought to reduce sampling error by collecting individual data with equal sampling intensity and effort (Farine & Whitehead, 2015). We used only one detection per individual giraffe for each secondary sampling period (~10 days) to avoid non-independence of observations and to reduce sampling bias. We further removed individuals with fewer than six observations to improve the accuracy of our network (Davis, Crofoot, & Farine, 2018).

We created the social network using the package *asnipe* (Farine, 2013) for R version 3.4.3 (R Core Team, 2017). We show that our results are consistent when using the alternative and commonly used half-weight index, and when using alternative thresholds (≥ 8 and ≥ 10 detections) for the number of observations (Farine & Whitehead, 2015; Appendix S1). We also used methods recommended by Whitehead (2008) to explore the robustness of our network (Appendix S2).

2.4 | Characterizing community structure

Our first objective was to identify and characterize social communities of interacting giraffes in the metapopulation. We used the cluster-walktrap community-detection algorithm to divide the metapopulation into communities using package `IGRAPH` for R (Csárdi & Nepusz, 2006). The strength of the partitioning of the network into discrete communities can be described using a modularity coefficient known as Q (Newman, 2003), where higher Q values reflect more dense connections within than between communities (Newman, 2006; Shizuka & Farine, 2016). Here we present results from the cluster-walktrap algorithm, but we also ran three other community-detection algorithms and compared Q values for each of the three datasets (Table S1). We tested whether the metapopulation was more structured into communities than expected by chance given our observation data by noting whether the value of Q from the observed network fell outside the 95% range of Q values calculated from 1,000 randomly generated networks from permuted data (Shizuka & Farine, 2016). The p -value was equivalent to the number of times the observed Q (Q_{observed}) was higher than the distribution of Q values from the randomized networks (Q_{random}). We provide more details on the randomization procedure below.

We also tested the robustness of our community detection using the approach described by Shizuka and Farine (2016). This procedure estimates the effect of sampling effort as the probability that a pair of giraffes that were assigned to the same community in the observed network was assigned to the same community in 1,000 bootstrapped replicate networks. The test statistic, r_{com} , approaches 1 when all bootstrap replicates result in the exact same community assignments as the observed community, with more robust data having higher r_{com} values. We calculated r_{com} with package `ASSORTNET` for R (Farine, 2014).

2.5 | Identifying the predictors of between-community differences in social structure

Our second objective was to explore social and environmental factors that might underpin differences in relationship strength and social exclusivity among the discrete communities of giraffes. That is, we split the metapopulation network into replicated but distinct social networks that represent each community, thus making community networks the units of analysis in our study. We then calculated the relationship strength of the females in a community (the mean of the weights of the edges connected to a given female) and how socially differentiated the relationships are (using the coefficient of variation—or CV—of the edge weights). A higher mean edge weight means that females are more likely to be observed with their associates in a given observation, thus corresponding to having stronger relationships. The CV characterizes the spread of the values, and a higher CV corresponds to females having distinct strong and weak relationships (and thus more exclusive relationships), while a lower CV corresponds to females having more equal relationships across all of their associations.

We used linear models (family = Gaussian) to estimate the effects of social and environmental predictor variables on first, relationship strength and second, social exclusivity, calculated for each community network. Predictors included (a) the local giraffe population density within the community (PopDen), equivalent to the number of all adult females ever seen within the boundaries of a community's home range (regardless of community membership or number of detections; $N_{\text{total}} = 1,139$), divided by that community's home range size (km^2); (b) the average distance (in km) between all locations of all individuals in a community to the nearest boma (Dist_boma) or town (Dist_town); and (c) the proportion of grasslands on volcanic soils (Prop_gv) within each community's home range. Volcanic soils are particularly fertile, which may enhance forage quality (Mizota, Domon, & Yoshida, 1992), and in our study area volcanic soil grasslands had the highest giraffe calf survival (Lee et al., 2016). We postulate that adult female giraffes might congregate in areas with high forage nutritional quality and form stronger relationships with others utilizing these resources. These explanatory variables represented potential social, anthropogenic and vegetation influences on social structure (Table 1; Table S2). See Appendix S3 for methods used to generate spatial data.

We estimated the significance of each predictor by comparing the coefficient value of the model fitted to the observed community network to the distribution of coefficient values generated by fitting the model to randomized networks generated by the pre-network permutation test as described below.

TABLE 1 Effects of covariates on relationship strength (mean edge weight)^a and social exclusivity (edge weight CV)^b of 11 adult female Masai giraffe communities in Tanzania, 2011–2016. p -value is the number of times the coefficient generated from 50,000 randomized networks (relationship strength) and 10,000 randomized networks (social exclusivity) was greater than the coefficient from the observed network. Significant p -values are given in bold

	Estimate	SE	t-value	p_{rand}
Giraffe population density				
Relationship strength	0.002	0.007	0.218	0.810
Social exclusivity	-0.105	0.093	-1.128	0.998
Distance to boma				
Relationship strength	0.003	0.002	1.757	0.000
Social exclusivity	-0.057	0.026	-2.172	0.016
Distance to town				
Relationship strength	0.000	0.001	0.383	0.258
Social exclusivity	0.002	0.013	0.119	0.987
Proportion grasslands on volcanic soils				
Relationship strength	0.020	0.021	0.957	0.084
Social exclusivity	-0.439	0.282	-1.554	0.919

^aModel = `glm(mean edge weight ~ PopDen + Dist_boma + Dist_town + Prop_gv, family = gaussian)`.

^bModel = `glm(edge weight CV ~ PopDen + Dist_boma + Dist_town + Prop_gv, family = gaussian)`.

Comparing network metrics among our giraffe communities was appropriate because all data were collected identically, ensuring observed differences were likely to be biological rather than methodological (Farine, 2017; Farine & Whitehead, 2015). However, it was recently suggested that using pre-network permutation is essential to avoid spurious inference (Farine & Aplin, 2019). That is, rather than directly comparing network metrics to each other (e.g. by directly interpreting the coefficient values of the linear model), which is not possible (Anderson, Butts, & Carley, 1999), we compared the observed differences among communities to the distribution of differences drawn from all of the random networks generated using the same observation data.

2.6 | Permutation tests for hypothesis testing

The non-independent nature of social network data violates the assumptions of many statistical methods (Croft, Madden, Franks, & James, 2011; Farine, 2017). Null models can be used to generate patterns expected from the data in the absence of the process of interest (Farine, 2017). We used a modification (Whitehead, 1999) of the Monte Carlo permutation test (Bejder, Fletcher, & Bräger, 1998) to generate randomized networks for hypothesis testing. The algorithm involves sequentially swapping observations of two individuals seen in different groups. In doing so, it inherently controls for many aspects of how the data were collected by generating random networks based on the same number of individuals, where each individual has the same number of observations, controlling for individuals' distributions in space and time, and maintaining the same distribution of group sizes (Farine, 2017). From these networks, we created a distribution of coefficient values from which we obtained a *p*-value that represented the proportion of times the coefficient values from the permuted networks were more extreme than those of the observed networks (Farine, 2017). We performed pre-network permutations using package *ASNIPE* for R (Farine, 2013).

To control for time, we restricted all swaps to occur within the same 20-day primary sampling period ($n = 16$ periods). To control for space, we constrained swaps to occur only between groups observed in the same administrative unit (TNP, MRC, LMNP, LGCA, MGCA). After each swap, we recalculated the edge weights in the network and reran exactly the same statistical procedure as we applied to the observed data. For tests determining the community social structure within the metapopulation and assessing robustness of community assignments, we conducted the permutation procedure on the whole network with 1,000 randomizations. When testing models about predictors of social structure within communities, we conducted the permutation procedure in each community independently (i.e. never swapping individuals across communities because we were interested in understanding within-community processes) and fit the model to 50,000 (relationship strength) or 10,000 (social exclusivity) randomized networks. The difference in the number of permutations reflects differences in how long the *p*-values took to stabilize (see Bejder et al., 1998).

For descriptive statistics, we calculated the 95% confidence intervals using 100 bootstrapped replicates of our observation data.

3 | RESULTS

3.1 | Community detection

Our social network comprised 540 adult females (with ≥ 6 detections over 6 years from a total of 1,944 unique group observations; see Section 2, Appendix S1; Table S1). Applying a cluster-walktrap algorithm (see Table S1 for a quantitative comparison of different algorithms) revealed 14 distinct communities of socially associated giraffes in this social network. Using a permutation test, we confirmed that communities in this giraffe population are more structured than expected by chance ($Q_{\text{observed}} = 0.742$, $Q_{\text{random}} = 0.661$, $p < 0.001$), and a bootstrap test revealed that our community assignment was robust ($r_{\text{com}} = 0.749$). Both the Q_{observed} and r_{com} values for our community assignments were relatively high (Shizuka & Farine, 2016), indicating strong community structure and high community fidelity with a low propensity for individuals to mix with other communities. Three of the communities contained ≤ 6 individual giraffes. We omitted these three communities from further analysis due to small sample sizes. The remaining 11 communities contained a mean of 47.8 individuals ($SD = 16.2$, range = 14–70; Table S2). Many of these communities overlapped considerably in space (Figure 1). All communities produced calves, so we did not consider presence versus absence of calves as an influence on social structure.

Fission–fusion dynamics, where adult female giraffes form subgroups containing a few other members from their community and where membership fluctuates over time, resulted in relatively weak relationship strengths. The mean relationship strength (edge weight, calculated using the simple ratio index) among giraffes across the whole metapopulation was 0.004 ($SD = 0.022$, 95% CI = 0.00016–0.006). Even among associated individuals, relationship strength was relatively low (mean non-zero edge weight = 0.058, $SD = 0.234$, 95% CI = 0.006–0.110). However, differences in relationship strength among communities varied extensively (range = 0.019–0.078; Table S2). Within each of the 11 of the giraffe communities we studied, the observed mean edge weight and observed CV values were significantly higher than expected by chance (Table S2). Together, these results signify that adult female giraffes exhibit preferred and avoided relationships within communities that overlap in space and time with other communities.

3.2 | Predictors of within-community social structure

Communities of adult female giraffes closer to bomas have weaker average edge weights, suggesting that they have weaker relationship strengths among all the members of the community (Table 1). The edge weight CV of communities also increased significantly with proximity to bomas, indicating that giraffes in communities closer

to traditional human compounds exhibit stronger relationships but with fewer other females, indicating greater exclusivity in their social associations (Table 1). Local giraffe population density, distance to towns and proportion of grasslands on volcanic soils had no discernible influence on variation in community-level social structure (Table 1).

4 | DISCUSSION

Our observations of groups of adult female Masai giraffes in the TE revealed that they form somewhat discrete, relatively large social communities that overlap substantially in space, resulting in an interconnected metapopulation. We find that the relationships among individuals within those communities are affected by the presence of traditional human settlements. Communities of giraffes that live closer to bomas have weaker relationship strengths among all community members, and have more exclusive social associations with fewer other females, in line with our predictions. Proximity to humans therefore appears to play a potentially important role in mediating the patterns of social associations between female giraffes in northern Tanzania.

The large spatial scale, lack of fences, and variation in human influences refers to the study area, and the large number of individuals refers to the study population. Relationships were weaker among all community members, and social exclusivity was higher in communities closer to bomas. But what could cause these patterns? The disruption in the equality of relationships could be a result of human habitat modification such as fuelwood cutting near bomas, competition with livestock, or wariness of humans, driving female giraffes to move more often and, when doing so, fission into smaller groups. The greater difficulty in maintaining group cohesion under such conditions could then cause individuals to form more exclusive associations with fewer other individuals from their community. But why would giraffes venture near to bomas at all? Previous research on the same population observed that adult female groups with calves were more likely to be closer to bomas than groups without calves (Bond, Lee, Ozgul, & König, 2019), possibly due to significantly lower predator densities on village lands compared with protected areas (Lichtenfeld, 2005). Female giraffes may therefore face a trade-off between maintaining cohesion within their social community and reducing predation risk to their calves. Although in the current study we did not detect an effect of distance to towns on relationship strength or social exclusivity, a previous study found that adult females have larger home ranges when living closer to towns (Knüsel et al., 2019). We documented the closest observation of a giraffe group to a town was 0.35 km, and the next-closest distance of a group was 1.01 km. In contrast, the closest group to a boma was 0.02 km, and we recorded 289 groups within 1.01 km of a boma. Because adult females appear to avoid towns altogether, there was no meaningful variation in distance to such large settlements among communities, and we could not detect an influence of proximity to towns on social structure.

Our results suggest an indirect effect of human presence on megaherbivore social structure that reflects recent findings of various effects of anthropogenic disturbances on social structure in a diverse range of taxa. Hyenas living in areas of a national park with higher levels of human activity had less dense social networks, indicating animals interacted less with other clan members (Belton et al., 2018). Giraffes in a population with high levels of tourism and a high density of lions appeared to have weaker associations and more exclusive relationships than in a population without lions and few tourists (Muller et al., 2019). The results of that study, while remaining unclear due to a lack of statistical support, do align with our theory-driven prediction, and our statistically significant findings, that disturbances can disrupt social structure. In a key experimental study, induced social instability (temporarily splitting otherwise stable groups) resulted in more exclusive, but overall weaker relationships among members of zebra finch colonies. This change in social structure then adversely affected collective actions, such as foraging efficiency (Maldonado-Chaparro et al., 2018). In our study, we found that variation in social structure of giraffe communities along a gradient of human presence matched exactly the predictions of the zebra finch study, with the members of communities living closer to bomas having weaker relationship strengths and more exclusive social associations. In giraffes, functionally important collective actions might involve making decisions about movements (Berry & Bercovitch, 2015), synchronizing activities across larger groups (Muller, Cantor, Cuthill, & Harris, 2018) and sharing care of young (Langman, 1977). If changes in social relationships translate to decreased effectiveness in performing these collective actions, then proximity to traditional human settlements could, indirectly, have negative effects on fitness.

Social stability and the patterns of social connections among members of a group or community have demonstrable and measurable consequences across a spectrum of group-living animals. The number of both weak and strong associations between female chacma baboons *Papio ursinus* influences fitness, with more strong associations predicting birth rate and more weak associations predicting infant survival and longevity (McFarland et al., 2017). For female savanna baboons *Papio cynocephalus*, adverse social circumstances in early life can significantly increase social isolation in adulthood, and reduce adult life span (Alberts, 2019). Adult rock hyraxes *Procapra capensis* that live in groups with more equal associations live longer (Barocas, Illany, Koren, Kam, & Geffen, 2011). Social integration among female horses increases foal birth rates and survival, and decreases harassment by males (Cameron, Setsaas, & Linklater, 2009). Experimentally induced chronic social instability alters alloparental care, and increases anxiety in female rodents and their offspring (Ebensperger et al., 2017; Pittet, Babb, Carini, & Nephew, 2017). In our study we find that proximity to traditional human settlements in a wild mammal population is correlated with the signatures of social systems that have experienced repeated disruptions resulting in instability (Maldonado-Chaparro et al., 2018).

Our study also revealed that giraffes can form distinct social communities within a larger scale metapopulation. The partitioning

of the metapopulation into discrete communities with relatively high modularity, meaning female giraffes associated with each other much more frequently within than between the communities, indicates clear social clustering even among individuals that share the same space. Multiple scales of social organization were documented in a population of reticulated giraffes *Giraffa camelopardalis reticulata* in Kenya (VanderWaal et al., 2014), where females exhibited the strongest social associations within a core group and maintained moderate associations with other members of their community, but had low association rates between their two identified communities. However, these two communities were geographically separated by a river. In our metapopulation, the presence of a lake and substantial geographical distance also split the insular LMNP community from all others (Figure 1), but the remainder of the communities showed extensive spatial overlap and yet were relatively discrete. Thus, we reveal the potential for a higher level of organizationally distinct but spatially overlapping set of social connections beyond the 'social cliques' of giraffes as described by VanderWaal et al. (2014). Social structuring is evidently an important feature of wild giraffe populations, with individuals exhibiting preferred and avoided associations beyond simply utilizing common areas (Carter, Seddon, et al., 2013). Associations among individuals are likely to be important for population persistence and should be considered when developing and implementing conservation measures for giraffes such as land-use plans and translocations.

5 | CONCLUSIONS

Megaherbivores—plant-feeding mammals that attain an adult body mass of at least 1,000 kg (Owen-Smith, 1988)—are ecological engineers that play a key role in shaping the vegetation of African savanna ecosystems (Dublin, Sinclair, & McGalde, 1990; Palmer et al., 2008; Waldram, Bond, & Stock, 2008). Despite their ecological importance, populations of giraffes and the other two terrestrial African megaherbivores, elephants and rhinoceroses, have declined precipitously over most of the continent (Ripple et al., 2015). The main direct threats to the largest herbivores are overhunting for meat and body parts, and eliminating habitat through deforestation and land cultivation (Ripple et al., 2015), but scientists still lack a fundamental understanding of how natural and anthropogenic factors affect social structures of wild populations. The social network approach that we used for giraffes, and our methods for statistical inference about the relationship between community social structure and natural and human influences, offers a framework for examining social structure under different environmental conditions, so that network structure of populations can be compared across a gradient of interest. Using this framework, we provide evidence for disruption of social structure by humans. We recommend that future studies examine this subtle yet potentially far-reaching effect on other social species and explore how social structure might influence fitness in wild populations.

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AUTHORS' CONTRIBUTIONS

M.L.B., D.E.L., A.O., B.K. and D.R.F. conceived the ideas and designed methodology; M.L.B. and D.E.L. collected the data; M.L.B. and D.R.F. analysed the data; M.L.B. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code used in this study are published in the Open Access Data Repository of the Max Planck Society: <https://dx.doi.org/10.17617/3.3s> (Bond, König, Lee, Ozgul, & Farine, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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