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1 **Giraffe (*Giraffa camelopardalis*) social networks in areas of contrasting human**  
2 **activity and lion density**

3

4 **Giraffe networks, human activity and lion density**

5

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26 **Abstract**

27 The adaptive value of close social bonds and social networks has been demonstrated in a variety of  
28 vertebrate taxa. While the effect of predators on populations is well established, disturbance by  
29 humans is increasingly being identified as affecting the behaviour and reproductive success of  
30 animals and can have significant impacts on their survival. We used a concurrent analysis of two  
31 adjacent giraffe *Giraffa camelopardalis* populations in Kenya to determine whether human activities  
32 and high predation affected their social networks. One study site was a premier tourist destination  
33 with a high volume of human activity in the form of tourist traffic and lodge infrastructure, alongside  
34 a high density of lions which preferentially prey on giraffe calves; the other was a private wildlife  
35 conservancy with minimal human activity and no lion population. Giraffes in both networks showed  
36 preferred associations and avoidances of other individuals, which were independent of space use.  
37 Bond strength was lower in the population exposed to high levels of human activity and lions, and  
38 the network had lower density and clustering, and shorter path lengths, suggesting that it was more  
39 fragmented. We suggest that human activity and predator density may influence the patterns of  
40 social interactions in giraffes and highlight the importance of understanding the impact of tourism  
41 and management on the survival and success of wild animal populations.

42

43

44 **Keywords**

45 *Giraffa camelopardalis*, human disturbance, predation, predator density, social behaviour, social  
46 bonds, social networks, wildlife tourism

47

48

## 49 1 INTRODUCTION

50 The effects of predator presence on the behaviour of African ungulates are well established (Valeix  
51 et al. 2009a, b; Périquet et al. 2010; Creel et al. 2014; Ripple et al. 2014); however, there has been  
52 limited investigation into how these behavioural changes may influence the structure of social  
53 organisation of prey species, or the changes in network structure. Since social networks offer fitness  
54 benefits and may influence an individual's survival (Silk 2007a, 2009; Brent et al. 2015; Goldenberg  
55 et al. 2016) and risk of disease (Drewe 2009; MacIntosh et al. 2012; VanderWaal et al. 2014a;  
56 Adelman et al. 2015), understanding how the social organisation of prey species responds to  
57 predation risk is an important, yet almost completely neglected, area of biology. Furthermore, it is  
58 well recognised that populations of African mammals are in decline (Craigie et al. 2010; Ogutu et al.  
59 2011; Ceballos et al. 2017), yet there is also an increasing appetite and economic justification for  
60 tourism in protected areas (Beale & Monaghan 2004), which is likely to impose significant  
61 disturbance on populations of resident animals (Green & Giese 2004; Kerbiriou et al. 2009). Given  
62 that disturbance by humans through tourism is increasing, it is critical that we understand how such  
63 disturbance affects the social organisation of animals to ensure species protection and balance this  
64 with the increasing economic justification for tourism in protected areas (Beale & Monaghan 2004).  
65 In this paper, we present a population-level analysis of the social organisation of an African ungulate  
66 species with variable social organisation, the giraffe *Giraffa camelopardalis*, comparing two adjacent  
67 populations exposed to different levels of human activity and density of lions.

68 Fission-fusion social organisation, whereby group size and composition are constantly changing,  
69 characterises many taxa and is considered to be an adaptive response to changing environmental  
70 conditions (Green & Giese 2004; Aureli et al. 2008). Such a flexible social system is likely to have  
71 arisen as animals seek to balance the costs and benefits associated with grouping (Krause & Ruxton  
72 2002). Social bonds are considered to be a product of these trade-offs, whereby individuals gain  
73 benefits from associating with or avoiding other individuals (Palombit et al. 1997; Connor et al. 2000;

74 Silk 2007b); close bonds provide benefits such as enhanced infant survival (Silk et al. 2009),  
75 increased lifespan (Silk et al. 2010), lower stress levels (Crockford et al. 2008; Wittig et al. 2008) and  
76 reduced levels of aggression within groups (Haunhorst et al. 2017). Despite the prevalence of fission-  
77 fusion social organisation in animals, and a large body of research investigating the causes, costs and  
78 benefits of different patterns of social organisation, the conclusions about what drives social  
79 structure remain highly variable (Patriquin et al. 2010). Even for the same species, different studies  
80 reach different conclusions, demonstrating the highly responsive nature of networks to local factors  
81 (Leu et al. 2016).

82 Most animals do not exist in isolation and so it is beneficial to consider social organisation at a  
83 network level (Whitehead 2008). The application of network theory to the study of animal social  
84 organisation has allowed rapid advances in our understanding of population-level behaviour (Krause  
85 et al. 2007; Kurvers et al. 2014; Brent et al. 2015). A social network approach is useful because it  
86 provides a validated, quantitative approach to characterise both individual- and population-level  
87 social structure (Krause et al. 2007). Studying the social network of populations allows greater  
88 insight and understanding of processes which support disease transmission (VanderWaal et al.  
89 2014a; Mejía-Salazar et al. 2017), social learning (Hobaiter et al. 2014), and the evolution of social  
90 strategies (Cameron et al. 2009; Brent et al. 2015).

91 The environmental factors affecting fission-fusion organisation in mammals include climate,  
92 resource availability and distribution, predation risk, group size and human influences (Lehmann &  
93 Boesch 2004; Couzin 2006; Lehmann et al. 2007; Sundaresan et al. 2007; Aureli et al. 2008; Kelley et  
94 al. 2011), but the factors influencing fission may differ from those driving fusion. For example, in  
95 African elephants *Loxodonta africana*, fission events are driven by resource availability and  
96 distribution, but fusion events are influenced by genetic relatedness (Archie et al. 2006, 2008; Chiyo  
97 et al. 2011). Variation in the effects of environmental variables on patterns of social organisation  
98 have also been found in brown bats *Eptesicus fuscus* (Willis & Brigham 2004; Metheny et al. 2008),

99 meerkats *Suricata suricatta* (Drewe et al. 2009; Madden et al. 2009), bottlenose dolphins *Tursiops*  
100 *truncatus* (Parsons et al. 2003; Möller & Harcourt 2008; Frère et al. 2010), chimpanzees *Pan*  
101 *trogodytes* (Lehmann et al. 2007; Langergraber et al. 2009), red ruffed lemurs *Varecia rubra* (Vasey  
102 2007) and humans *Homo sapiens* (Marlowe 2005).

103 Disturbance by humans is increasingly being recognised as having significant effects on the  
104 behaviour and reproductive success of animals (Manor & Saltz 2003; Green & Giese 2004;  
105 Hebblewhite et al. 2005; Stankowich 2008; Bonnot et al. 2013) and can adversely affect the survival  
106 and management of wild populations (Carney & Sydeman 1999). Numerous studies have found that  
107 human activities can disrupt breeding (Giese 1996), influence mortality rates (Feare 1976; Wauters  
108 et al. 1997) and scare animals away from preferred feeding sites (Gander & Ingold 1997). How  
109 human disturbance influences social behaviour at a population level has been less well studied, but  
110 is likely to be associated with the disruption or prevention of natural behaviours. To date, few  
111 studies have used a network approach to investigate how human activity influences the structure or  
112 function of animal social networks. However, a study of how human activity affects the social bonds  
113 of spotted hyaenas *Crocuta crocuta* found that clans in areas with high levels of human activity  
114 showed lower density (less connectivity in the network), suggesting weaker social bonds (Belton et  
115 al. 2018). The disruption of typical social structures may have important fitness implications for  
116 individuals, but it is not clear how human activity influences these processes. Likewise, the impact of  
117 predators on populations of prey species is well documented (Ripple & Beschta 2003; Creel et al.  
118 2014), but it is not clear how predator density might influence social organisation at a population  
119 level. Only one previous study has attempted to quantify the effects of predation on network  
120 structure; the authors studied guppies *Poecilia reticulata* in a lab system (Kelley et al. 2011). They  
121 found that under predation, networks were higher in strength and connectedness, and individuals  
122 had more associates, than fish and networks under a low risk of predation. Groups under high  
123 predation risk also stayed together for longer, while groups under low risk disbanded more regularly  
124 (Kelley et al. 2011).

125 As a large, conspicuous fission-fusion species, giraffes present the ideal opportunity to study social  
126 structure dynamics. Social network methods have highlighted their non-random patterns of  
127 association (Bercovitch & Berry 2013a; Carter et al. 2013a, b; Malyjurkova et al. 2012), although  
128 there is no clear consensus on many aspects of giraffe social behaviour, and network structure has  
129 yet to be linked to fitness in this species. That said, one study has highlighted how the social network  
130 of giraffes influences their risk of exposure to pathogens (VanderWaal et al. 2014a). Giraffes inhabit  
131 a wide variety of landscapes and habitats throughout eastern and southern Africa, and their fission-  
132 fusion social system potentially allows them to adapt their behavioural strategies to local  
133 environmental differences.

134 Giraffe populations exist in a wide range of habitats, from deserts to woodland and savannah  
135 environments, and mean group size ranges from three to nine, depending on season, location and  
136 availability of conspecifics (Muller et al. 2018a). However, most studies examining social behaviour  
137 in giraffes focus on single, isolated populations, making it difficult to draw general conclusions about  
138 this species' behavioural ecology. Comparing same-species networks under differing environmental  
139 conditions is an important tool in developing greater understanding of mechanisms underlying  
140 collective and social behaviour (Voelkl & Noë 2008; Sueur et al. 2009, 2011), although this is  
141 currently lacking for giraffes. Given that predator density influences the population demography of  
142 giraffes (Muller 2018) and that population demography has a strong influence on patterns of social  
143 organisation (Faust 2006; Flack et al. 2006; Silk et al. 2006; Williams & Lusseau 2006; Kanngiesser et  
144 al. 2011), we suggest that general conclusions drawn from single-population studies must be  
145 interpreted with caution, since these results may represent how a specific social network responds  
146 to a particular set of circumstances that are not generalisable to other populations.

147 In this study, we aim to examine the effects of disturbance on the social network structure of  
148 giraffes. We compare two populations of wild giraffes, each subjected to different levels of  
149 disturbance by human activity and predator presence. One population was classified as being under



150 'high disturbance' and the other under 'low disturbance' (see Methods for justification). We  
151 compare two aspects of sociality between the populations: first, the motivation to bond with  
152 conspecifics, and second, how the results of bonding are manifested within the social network. The  
153 two available studies investigating network changes under predation (Kelley et al. 2011) and  
154 disturbance by humans (Belton et al. 2018) found varied results, so it is difficult to use these studies  
155 to predict what may happen in giraffes exposed to both pressures. However, given the evidence that  
156 disturbance by tourism disrupts normal group behaviour in animals (Green & Giese 2004; Lusseau &  
157 Bejder 2007; Ranaweera et al. 2015), we predict that the social network of giraffes exposed to  
158 high levels of disturbance will be more fractured, and we test four hypotheses. High levels of  
159 disturbance will lead to i) lower bond strength, ii) lower density, as individuals disband following  
160 disturbance, iii) a lower number of sub-communities representing a more fractured society, and iv)  
161 shorter path length as individuals move around more due to high levels of disturbance by humans.  
162 Comparing two different wild populations presents several challenges since there are multiple  
163 factors which can vary between them, but they also present an opportunity to begin to understand  
164 the relative influence of different variables on social organisation. Performing a concurrent analysis  
165 of two populations has great value, especially if the populations are close and data collection and  
166 analytical methods are kept consistent (Farine & Whitehead 2015); this is the approach we take  
167 here.

168

## 169 **2 METHODS**

170 All experimental protocols and procedures employed in this study were approved by the University  
171 of Bristol Animal Welfare and Ethical Review Board (project number UB/11/003), the Kenya National  
172 Council for Science and Technology and the Kenya Wildlife Service.

173

### 174 **2.1 Study areas**

175 We studied two populations of Rothschild's giraffes *Giraffa camelopardalis rothschildi*; one was  
176 enclosed within Soysambu Conservancy (SC) and one was enclosed within Lake Nakuru National Park  
177 (LNNP), both of which are located south of Nakuru, Kenya between 00°22'S and 36°23'E. SC is a  
178 private wildlife conservancy (size 190 km<sup>2</sup>, 1670 m asl) surrounding Lake Elementeita; LNNP is a  
179 National Park (size 188 km<sup>2</sup>, 1759 m asl) surrounding Lake Nakuru. The two study sites are adjacent  
180 with a shared 7.8 km boundary along the west fenceline of SC and the east fenceline of LNNP (Figure  
181 1). An electrified game fence, across which no large mammals could pass, was a physical barrier  
182 between the two study sites. The climate, topography, soil types, vegetation and the diversity of  
183 flora and fauna found in each area are similar and they are part of the same biome and microclimate  
184 (Nicholson 1996; Omondi 2011).

185 There are two notable differences between the study sites: (1) the density of lions, *Panthera leo*, and  
186 (2) the levels of human activity. Lions are the only predator to pose a significant threat to giraffes  
187 (Hirst 1969; Pienaar & De 1969; Foster & Dagg 1972; Dagg & Foster 1976; Strauss & Packer 2013). At  
188 the time of this study, LNNP contained 56 lions (Ogutu et al. 2012), which is a high density (0.3  
189 lion/km<sup>2</sup>) compared to more typical densities of 0.08 to 0.14 lion/km<sup>2</sup> (East 1984; Creel & Creel  
190 1997). Preferential preying of lions upon giraffes has been identified as a problem in LNNP, along  
191 with observations of lions feeding on giraffe calf carcasses in the park (Kenya Wildlife Service 2002;  
192 Brenneman et al. 2009). During the same time, SC was free of lions and had been for several  
193 decades (Hugh George Cholmondeley, owner of Soysambu Ranch, personal communication).  
194 Additionally, the levels of human-related disturbance also varied between sites; LNNP is classified as  
195 a 'Premium Park' (Maingi et al. 2016) and is the second largest revenue-producing National Park in  
196 Kenya. In 2012 it received 253,500 visitors (Muthoka et al. 2017). It has an extensive road network,  
197 contains five large tourist lodges and several campsites. In contrast, SC is a privately owned and  
198 managed conservation area, which changed its main use from a private cattle farm to a wildlife  
199 conservation area in 2009. It was an under-utilised area for ecotourism (Kenya Wildlife Service 2004)  
200 and received significantly fewer visitors per year than LNNP. At the time of this study, there was an

201 average of 1 tourist vehicle per day in SC (Z. Muller, personal observation), the area had a limited  
202 road network and no tourism infrastructure.

203 To acknowledge differences in predator density and levels of human activity between sites, and  
204 because we could not discriminate between effects of predation and human disturbance with only  
205 these two populations, we used more general descriptions of ‘low disturbance’ for SC and ‘high  
206 disturbance’ for LNNP. We accept that we were unable to quantify predation risk in each population,  
207 but human-related disturbance and tourism can be considered a form of predation risk (Frid & Dill  
208 2002; Amo et al. 2006; Geffroy et al. 2015). Furthermore, high levels of human activity have been  
209 shown to alter the structure of networks (Belton et al. 2018), which supports our decision to refer to  
210 the two populations in terms of varying levels of disturbance.

211

## 212 2.2 Data collection

213 We carried out a three-month pilot study in each site (SC: March-May 2010; LNNP: March to May  
214 2011) to identify, sex and age all individuals, and to develop an appropriate definition for ‘group’.  
215 We also used this time to determine a distance threshold in which giraffes could be approached by  
216 vehicle without being alarmed by our presence; this was typically 100 m – 500 m. Giraffes were well  
217 habituated to the presence of vehicles, and we took care to respect this distance threshold during  
218 data collection so as not to influence their natural behaviour. However, it was not necessary to get  
219 so close to groups since we used a zoom lens to obtain digital photographs of group members, and  
220 binoculars to verify numbers, so data were usually collected from a much greater distance than the  
221 ‘disturbance’ threshold (typically >500 m to 1 km, depending on road layout and visibility). Following  
222 the pilot study, data were collected for nine months in each study site (SC May 2010 – January 2011;  
223 LNNP May 2011 – January 2012). All giraffes were individually identified (ID) using unique coat  
224 patterns (see Muller (2018) for full details of ID methodology and site map). Each study site was  
225 segmented into quarters. Giraffes were searched for by driving transects along the road network in

226 each area, using a 4x4 vehicle. All areas (i.e. the entire study site) were searched each day. Roads  
227 taken and direction driven were randomised. Data collection started at 06:30 hrs and ended at 18:30  
228 hrs (UTC + 3 h Standard Time). Upon sighting an individual or group of giraffes the vehicle was  
229 stopped at an appropriate distance so as not to influence their behaviour. There is no standard  
230 definition of group size for giraffes. Previous studies use either inter-individual distance thresholds,  
231 which ranged from 100 m (Jeugd & Prins 2000), through 400-500 m (Leuthold 1979; Carter 2013;  
232 VanderWaal et al. 2014b), to 1000 m (Foster 1966; Pratt & Anderson 1985), or similarity of  
233 behavioural state (Backhaus 1961; Shorrocks & Croft 2009). However, a common theme was that  
234 giraffe groups are self-defining; distances within groups are substantially smaller than distances  
235 between groups (Shorrocks & Croft 2009; Carter 2013; VanderWaal et al. 2014b). During the pilot  
236 phase we also found that groups were self-defining; the proximity of individuals within a group was  
237 typically up to 200 m, but inter-group distances were always above 1 km. We also noted that group  
238 members typically were synchronised in their behaviour. Therefore, we set the definition of a group  
239 as 'all individuals within 1 km of each other and engaged in generally similar behaviour'. The  
240 individual ID of all group members was recorded. We sampled each group for exactly 30 min to  
241 standardise observation time between groups and ensure that all members of the group had been  
242 recorded. We categorised each data point using a 'reliability score' of 1: certain that all group  
243 members had been observed; 2: unsure if all group members had been observed; or 3: certain that  
244 all group members had not been observed. Only data points of score 1 were used in the analyses to  
245 ensure complete accuracy of identifications of group membership. Data reliability score was not  
246 influenced by habitat type or complexity; there were equal proportions of scores for each habitat  
247 type/complexity. All methods and the data collection procedure were standardised between sites to  
248 ensure consistency and comparability of data sets. At the time of this study, SC contained 77  
249 giraffes: 26 females, 25 males and 26 calves (individuals < 1 year), and LNNP contained 89 giraffes:  
250 44 females, 40 males and 5 calves (Muller 2018).

### 251 2.3 Social network analysis

252 Data from each population were analysed separately, since each network was discrete with no  
253 migration between populations. Associations were defined using the gambit of the group, whereby  
254 all individuals within a group were said to be associated (Croft et al. 2008) and associations were  
255 symmetrical (i.e. if A is associated with B, then B is also associated with A). We created an adjacency  
256 matrix (an NxN matrix describing the edges in the network) for each site and populated this with the  
257 pair-wise associations observed between each pair of individuals. The pair-wise associations (edge  
258 weights, or cell values in the adjacency matrix) were calculated using the Simple Ratio Index (SRI)  
259 (Cairns & Schwager 1987; Whitehead 2008; Hoppitt & Farine 2018), which estimates the proportion  
260 of time that two individuals spent together. We calculated the SRI using the formula:  $SRI = X / (Y_A +$   
261  $Y_B - X)$ , where A and B are individuals in a dyad,  $Y_A$  and  $Y_B$  are observations of individuals A and B  
262 respectively, and  $X$  is the interactions between A and B. The SRI accounts for sample size and  
263 number of observations of each individual and provides a quantitative measure of the frequency of  
264 co-occurrence while also controlling for effort: 0 indicates animals that were never observed  
265 together and 1 indicates animals always observed together (Whitehead 2008)). To quantify bond  
266 strength between individuals (hypothesis i), we examined i) the mean edge weight i.e. SRI value  
267 describing strength of association between two individuals, and ii) the coefficient of variation (CV) of  
268 edge weights for all individuals in the network. High SRI and CV values represent focused association  
269 with specific individuals, i.e. individuals with high SRI and CV values have few, preferred associates  
270 (strong bonds). Low SRI and CV values represent more non-specific patterns of association, where  
271 individuals associate more freely with a wider set of conspecifics (weaker bonds) (Whitehead 2008;  
272 Leu et al. 2016).

273 Since there were differences in the calf cohort between the two study sites (Muller 2018), we ran  
274 the analyses twice for each population, once on the whole network and once on a filtered network  
275 which excluded calves, to understand the influence of demography on the network. We did this to  
276 mitigate the effects of demographic differences between the two sites, to understand the possible  
277 influence of different proportions of calves in each network, and because calves are unlikely to

278 contribute towards adult grouping decisions (Cameron & du Toit 2005; Muller et al. 2018a). That  
279 said, exclusion of calves does not remove the effects of their presence on adult decisions.

280 We calculated further measures to quantify properties of other elements of the network. Density  
281 (hypothesis ii) is the number of observed associations in a network, divided by the possible number  
282 of associations (Farine & Whitehead 2015). A low density score indicates that few individuals  
283 associate within social groups (Madden et al. 2009), while a high density score indicates that many  
284 of the possible associations have occurred, and animals are highly social among and between  
285 groups. Density is standardised by the maximum weight in the network, and is calculated based on  
286 the frequency of the interactions within the network (Whitehead 2008). To test hypothesis iii, we  
287 calculated clustering coefficient, which measures the extent to which an individual is connected to  
288 other individuals. It describes how many cliques are in a network: high clustering coefficient values  
289 indicate highly connected groups of individuals (Newman 2003; Whitehead 2008). To test hypothesis  
290 iv, we calculated path length as a measure of how connected or separated each individual is. Path  
291 length quantifies the number of edges connecting a pair of nodes, i.e. how many individuals are  
292 required to connect two non-directly connected individuals (Wey et al. 2008). We used weighted  
293 path lengths, which accounts for the SRI values between individuals in the network. All analyses  
294 were done in R (R Core Development Team 2017) using the *asnipe* (Farine 2013) and *igraph* (Csárdi  
295 & Nepusz 2006) packages.

#### 296 2.4 Statistical significance testing using permutation tests

297 Due to the non-independent nature of network data, null models were used as a way of testing  
298 hypotheses. Null models use observed networks to randomly generate comparable networks  
299 containing the same number of nodes and edges, and replicate observed patterns of association, but  
300 without the process of interest. By comparing observed networks to null models, non-social factors  
301 which influence the associative behaviour of animals can be accounted for (e.g. home range overlap,  
302 temporal effects, etc.) and specific hypotheses about social processes can be tested (VanderWaal et

303 al. 2014a; Adelman et al. 2015; Farine 2017). To test if bond strength in each observed network was  
304 significantly different from what would be expected by chance (hypothesis i), the mean SRI and CV  
305 values for the observed network were compared to a distribution of mean SRI and CV values  
306 generated using 1000 permutations of the network data (Manly 2006). We used pre-network data  
307 permutations as these types of null model can account for inherent structure in the observed data,  
308 and are the most reliable at detecting real effects i.e. they reduce type I and type II error rates; see  
309 Farine (2017) for a full review. Our null models controlled for sampling period and spatial  
310 distribution of individuals to ensure that the distribution of individuals in the null models remained  
311 consistent with the patterns in the observed data. This accounts for the influence of any space-  
312 related factors (i.e. individual home ranges, habitat type or space use) and sampling-period factors  
313 (weather, resources abundance) and creates a null model in which the structure of the data (space  
314 and time) are retained, but individual variation is not (Aplin et al. 2015; Spiegel et al. 2016; Muller et  
315 al. 2018b). This ensures that the only process which is randomised is the process of interest, i.e. the  
316 social associations - who is observed with whom - and allowed us to make inferences about social  
317 organisation independent of temporal or spatial variables. To control for effects of spatial  
318 distribution, we split the study area into 40 grid squares, each measuring 0.1 latitude x 0.02  
319 longitude and data swaps in the null model were restricted to within each spatial grid, so that data  
320 were only swapped between individuals that were observed in the same location during the same  
321 time period (Aplin et al. 2015). The observed variance in latitude and longitude were 0.8 and 1.1 of a  
322 decimal degree respectively.

323 A  $p$ -value was obtained by comparing the observed mean SRI and CV value to the distribution of the  
324 mean SRI and CV values from the 1000 random networks ( $p$ -values stabilised after ~200  
325 permutations of the observed data, so 1000 permutations was sufficient to ensure the  $p$ -values were  
326 representative). To assess how the other network measures (density, clustering coefficient, path  
327 length) differed between the two networks (SC and LNNP), we compared the network-level  
328 observed mean values between populations. We did not test these using null models for the

329 following reasons: i) SRI and CV permutations are the most effective values to establish if the  
330 observed networks are non-random (Whitehead 2008; Farine & Whitehead 2015); ii) density and  
331 bond strength would have been the same as the null model (Belton et al. 2018); and iii) our  
332 hypotheses focus on the differences between the network structure of the two populations, not  
333 their comparisons to random *per se*. All analyses were performed on all four networks: whole and  
334 filtered (calves excluded) for each study site.

### 335 **3 RESULTS**

#### 336 3.1 Patterns of association

337 The SC and LNNP whole networks are visualised in Figures 2 and 3 respectively. The whole SC  
338 network contained 1861 connected dyads and 695 unconnected dyads; after filtering out calves,  
339 there were 1059 connected and 216 unconnected dyads. The whole LNNP network contained 2405  
340 connected and 1511 unconnected dyads; after filtering out calves, there were 2331 connected and  
341 1155 unconnected dyads. The mean number of associates per individual for each whole network  
342 was 51.7 in SC and 54.0 in LNNP. When calves were removed, this fell to 41.5 in SC and was little  
343 changed, at 55.5, in LNNP. Since there were 50 adults/subadults and 22 calves in SC, and 79  
344 adults/subadults and 5 calves in LNNP, most individuals in each population encountered each other  
345 during the study period.

346 Both networks were non-random; in all cases (both study sites, whole and filtered networks) the  
347 observed mean SRI and mean CV value were significantly greater than would be expected by chance,  
348 based on corresponding values from the null models (Table 1).

#### 349 3.2 Network metrics

350 In both the whole and the filtered networks, density, clustering coefficient and path length were all  
351 higher in SC compared to LNNP (see Table 2). Within networks, all metrics increased when calves  
352 were removed.



#### 353 4 DISCUSSION

354 Association patterns in both populations were significantly different to those that would be  
355 expected by chance, indicating that giraffes showed preferences to associate with and avoid specific  
356 individuals (Whitehead 2008). This supports the results of previous studies suggesting that giraffes  
357 live in social groups with familiar individuals (Bercovitch & Berry 2013a; Carter et al. 2013b), and  
358 suggests that the mechanisms driving individuals to associate with preferred conspecifics are not  
359 completely disrupted by high levels of disturbance by humans and predators. Currently there is  
360 considerable uncertainty over how giraffes choose to associate with conspecifics; the available  
361 evidence suggests that they group with others based on kinship, age, individual preferences or  
362 behavioural state (Bercovitch & Berry 2013a, b; Carter et al. 2013a, b; Muller et al. 2018b), and that  
363 shared space use plays a significant role in association patterns (Carter et al. 2013b; VanderWaal et  
364 al. 2014a). Our null models controlled for the spatial and temporal distribution of individuals,  
365 ensuring that the only element randomised was the association patterns between individuals. Since  
366 this removed any obvious factors which might confound our assessment of association choices, such  
367 as shared space use, sampling bias or habitat type, we can say that giraffes show non-random  
368 patterns of association independent of spatial or temporal variables.

369 Individuals in the area with low disturbance (SC) had stronger and more exclusive bonds (i.e. higher  
370 SRI and CV values) than those in the area exposed to high disturbance (LNNP) (hypothesis i). When  
371 calves were removed from each network, mean SRI increased (SC) or remained stable (LNNP) but  
372 the CV in both networks decreased. This suggests that the presence of calves weakens measures of  
373 bond strength at a network level. It could be that the presence of calves is not important for  
374 maintaining higher and more exclusive bonds at a network level, but this is more likely to reflect  
375 changes in the association patterns of mothers, which then contribute to the overall network means.  
376 Measures of whole network structure generally supported our predictions and indicated that the  
377 network exposed to high disturbance was more fragmented than the network with low disturbance.

378 Fewer potential associations between individuals were realised (lower density) under the high  
379 disturbance (hypothesis ii). This indicates that the network is more segmented and individuals  
380 exhibit fewer social interactions between groups. This may be because individuals are forced to  
381 disband due to human- or predator-related disturbance, or that they cannot use the habitat as freely  
382 as those in SC, due to restrictions on space used imposed by human-related development, roads that  
383 are busy with high levels of tourist traffic throughout the area, or through avoiding areas which lions  
384 occupy. The network under high disturbance showed less connectivity (lower clustering coefficient;  
385 hypothesis iii) than the network under low disturbance, which, like density, may indicate the  
386 network is fractured with isolated sections and groups of individuals. We found shorter path length  
387 under high disturbance (hypothesis iv), which could be indicative of the more temporary nature of  
388 connections, as suggested by the low bond strength (edge weights). In LNNP, low path length could  
389 indicate the presence of smaller, more isolated groups which are not as strongly bonded as those in  
390 SC. Networks with small path lengths, all other things being equal, have a quicker spread of disease  
391 and information (Reppas et al. 2012), so perhaps shorter path lengths in areas of high pressure are  
392 beneficial, since information about disturbance or threat can be transmitted more quickly. The lower  
393 mean edge weight for giraffes in LNNP would support the possibility that giraffes are disbanded and  
394 moved between groups in LNNP more often than in SC.

395 While social networks can confer fitness benefits to individuals, it is not so clear what consequences  
396 arise from the disruption or disturbance of such mechanisms. In humans, poor access to social  
397 networks is associated with ill health and poverty (Belle 1983; Cattell 2001; Adato et al. 2006), but  
398 the effects of poor social integration have not been explicitly tested in other species. Given that,  
399 close bonds of adults and stable social structure have been shown to increase fitness and survival of  
400 offspring in multiple taxa (Silk et al. 2003, 2009; Cameron et al. 2009), it is plausible that the  
401 opposite means fitness reductions and reduced birth rates and survival of offspring. So, the low  
402 cohesion and high fragmentation of the network in LNNP could have fitness implications for that  
403 population. Coincidentally, the giraffe population in LNNP has very few calves (Muller 2018). This

404 was attributed to the high predation by lions (Brenneman et al. 2009), an obvious conclusion given  
405 that lion predation of giraffe calves is known to be high (58% of calves < 1 year in Tanzania are killed  
406 by lions (Pellew 1984; Strauss & Packer 2013), and because LNNP contains a high density of lions  
407 (Ogutu et al. 2012; Muller 2018). But if high predation by lions is the proximate cause of the lack of  
408 calves in the LNNP population, what is the ultimate cause? One hypothesis is that if social networks  
409 offer survival benefits to young, and those social networks are disrupted (potentially by high levels  
410 of disturbance, as demonstrated in hyaenas; Belton et al. 2018), could this disruption result in  
411 reduced survival of young? It is well established that stable social networks facilitate the survival of  
412 the young (Silk et al. 2003, 2009; Cameron et al. 2009; Stanton & Mann 2012; Brent et al. 2015,  
413 2017; Goldenberg et al. 2016; Lahdenperä et al. 2016), so it seems plausible that disruption of those  
414 networks could influence calf survival, and potentially explain the lack of calves in LNNP. There is  
415 evidence of alloparental care in giraffes; young calves are frequently left in a crèche system, cared  
416 for by adults other than their mother (Leuthold 1979; Pratt & Anderson 1979, 1985), there are  
417 several reports of allonursing (Pratt & Anderson 1985; Perry 2011; Gloneková et al. 2016, 2017) and  
418 females express distress behaviours following the death of another individual's calf (Bercovitch  
419 2012; Strauss & Muller 2013). The presence of social bonds between adults may therefore be  
420 important to facilitate the survival of calves, so the disruption of those bonds across the population  
421 in LNNP may have adversely affected the survival of calves.

422 An alternative hypothesis is that high lion predation was responsible for the removal of calves, and  
423 the lack of calves contributed to bond disruption in females. Maintenance of a high mean bond  
424 strength before and after filtering calves out of the network suggests that strong bonds exist  
425 between adults, and that mother-calf bonds are not the sole contributor to high mean bond  
426 strength at a network level. Disruption of social structure can have a severe impact on wider  
427 population processes within social species (Manor & Saltz 2003), making it possible that disruption  
428 of the giraffe network in LNNP has negatively affected the survival of calves. Understanding which  
429 comes first is a difficult question to answer: do strong bonds between adults lead to increased calf

430 survival, or does the presence of calves facilitate strong bonds between adults? Understanding the  
431 direction of such social processes, how these vary between species, and the implications for the  
432 success of individuals remains a central question in biology.

433 We also recognise that observed differences in network structure between our two study  
434 populations were due to factors other than levels of disturbance. For example, differences in the  
435 relative availability of conspecifics between the two sites (population demography; Muller 2018)  
436 may have influenced patterns of associations. Likewise, local differences in habitat structure and  
437 forage availability may have been influential but were outside the scope of this study. We highlight  
438 these limitations so that our results can be interpreted in the correct context, and so that future  
439 work can consider these aspects in their study design. We also recognise that studies like this would  
440 be able to draw stronger conclusions if networks structure could be linked to fitness and survival  
441 outcomes, but will require much longer-term data sets than we were able to collect.

## 442 **5 CONCLUSIONS**

443 We have demonstrated how the social networks and association patterns of the same species can be  
444 very different between populations, despite using the same study design, observer, data collection  
445 methodologies and analytical techniques. Such disparity in network structure between two  
446 populations suggests caution in drawing general conclusions about a species' behaviour from studies  
447 which focus on a single population. The comparison of networks has provoked some discussion  
448 (Faust & Skvoretz 2002; Faust 2006; Dubé et al. 2008), but we demonstrate its value in  
449 understanding how key environmental variables may influence the natural behaviour of species. We  
450 have demonstrated how the latest techniques in generating null models against which to test our  
451 hypotheses can be used to account for spatial and temporal factors, enabling the identification of  
452 true patterns of social preference. Studies of social behaviour which do not account for  
453 environmental factors in null models must be interpreted with caution, since social processes have  
454 not been isolated from the influence of external variables (Farine 2017).

455 As wildlife populations become increasingly restricted to enclosed conservation areas, and wildlife  
456 tourism continues to experience significant growth, it is critical to understand how human activity  
457 and associated disturbance affect the social behaviour of wildlife populations. Further, as wildlife  
458 populations become increasingly enclosed and prey populations are confined to areas containing  
459 high predator density, we need to understand how this may influence social networks, which in turn  
460 might have an impact upon population dynamics and demography. We have provided evidence to  
461 suggest that disturbance by humans and predators may be disruptive to the social networks of  
462 giraffes, and introduce the hypothesis that such disruption is a contributory cause of reduced calf  
463 survival in LNNP. If this hypothesis is true, it raises difficult questions about balancing the need for  
464 species conservation and protection alongside commercial activities which support conservation,  
465 and the conservation of large predators alongside threatened prey species (Bercovitch 2018). We  
466 suggest that further work is needed to understand exactly how disturbance by humans and  
467 predators influences the social behaviour of animals, but more importantly, how subsequent  
468 changes in animal behaviour influence the survival, reproduction and evolution of those species. We  
469 also hope that our findings will serve as a caution to other researchers about the danger of drawing  
470 general conclusions about the social organisation of a species based on single-population studies,  
471 and act as a catalyst to promote wider discussion about the challenges and benefits of comparing  
472 networks.

473

474 **CONFLICT OF INTEREST**

475 The authors have no conflict of interest to declare.

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918 **TABLE 1** Mean non-zero edge weight (using the simple ratio index, SRI) and coefficient of variation  
 919 (CV) values for the observed and random networks for both study sites (Soysambu Conservancy, SC,  
 920 and Lake Nakuru National Park, LNNP) including all the network data ('whole network') or without  
 921 calves ('filtered network'). Significance was tested at the  $P < 0.05$  level, based on 1000 random  
 922 network permutations

	<b>Observed network</b>	<b>Random network</b>	<b>P value</b>
<b>SC: whole network</b>			
Mean SRI value	0.125	0.083	<0.001
Mean CV	116.938	75.373	<0.001
<b>SC: filtered network</b>			
Mean SRI value	0.126	0.095	<0.001
Mean CV	95.081	64.118	<0.001
<b>LNNP: whole network</b>			
Mean SRI value	0.088	0.053	<0.001
Mean CV	130.369	93.768	<0.001
<b>LNNP: filtered network</b>			
Mean SRI value	0.088	0.056	<0.001
Mean CV	121.451	86.444	0.004

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930 **TABLE 2** Network metrics for both study sites (Soysambu Conservancy, SC, and Lake Nakuru National  
 931 Park, LNNP) using network data including ('whole network') or without calves ('filtered network')

	Density	Clustering Coefficient	Path Length
<b>SC: whole network</b>	0.728	0.822	0.243
<b>SC: filtered network</b>	0.831	0.877	0.362
<b>LNNP: whole network</b>	0.614	0.757	0.219
<b>LNNP: filtered network</b>	0.669	0.767	0.243

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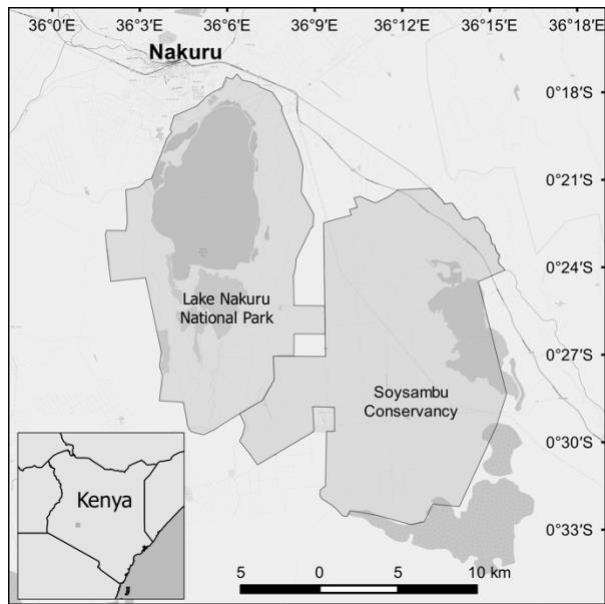
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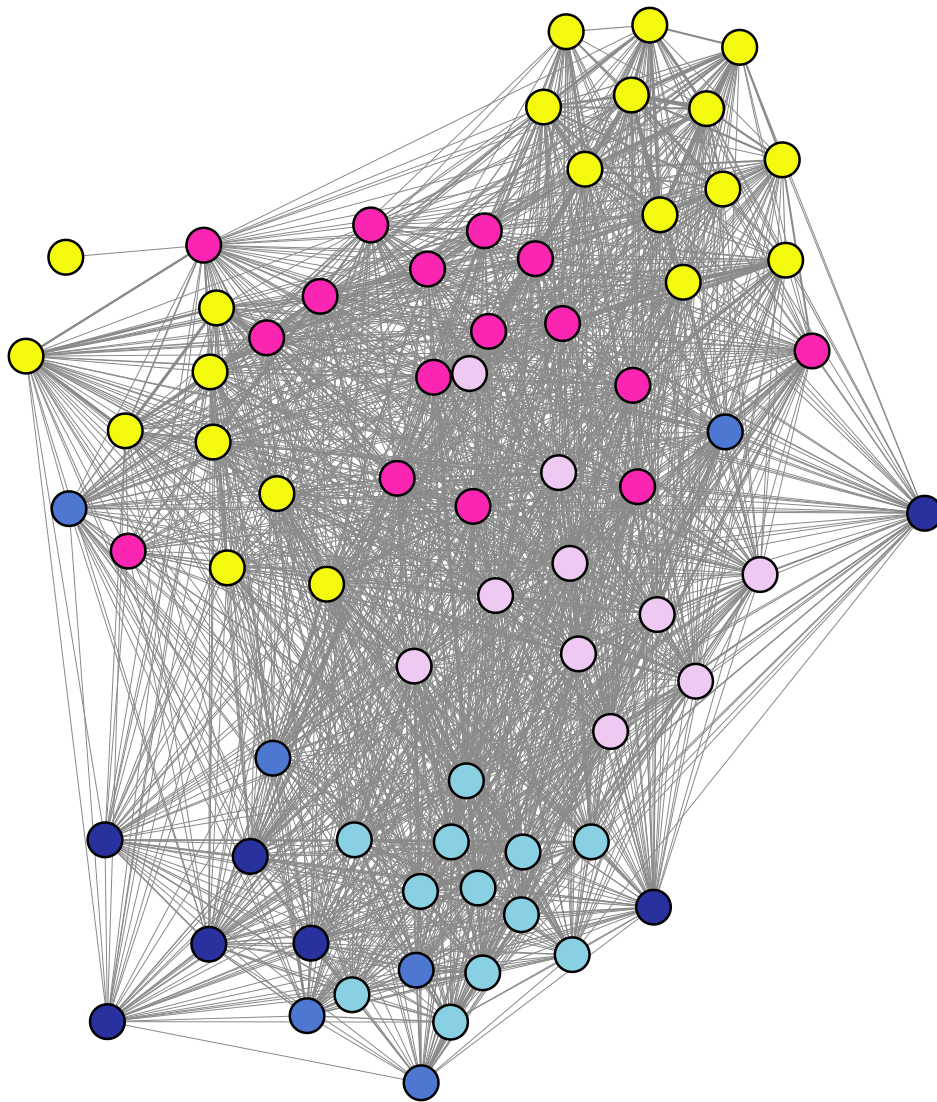
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940

941 FIGURE 1 Location of the study sites in the Great Rift Valley region of Kenya. Reproduced, with  
 942 permission, from Muller, et al. 2018. *Journal of Zoology* 306, 77–87. Base map provided by Google  
 943 Maps 2018.

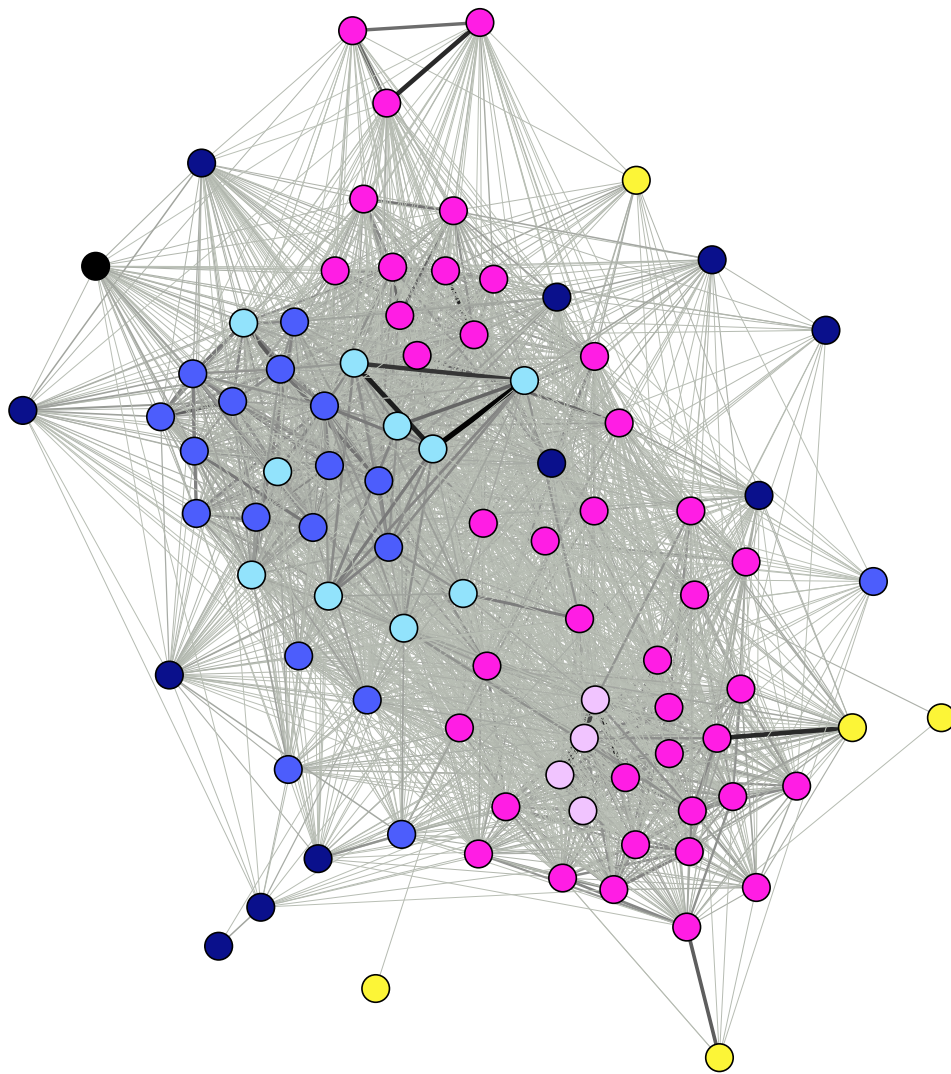
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946 FIGURE 2 Visualisation of the whole network in SC. Nodes are coloured by sex: mature bulls = dark  
947 blue; adult males = mid-blue; subadult males = light blue; adult females = dark pink; subadult  
948 females = light pink; calves = yellow. Edges are undirected and weighted by the association index  
949 (Simple Ratio Index); darker lines represent stronger relationships between individuals.

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951

952 FIGURE 3 Visualisation of the whole network in LNNP. Nodes are coloured by sex: mature bulls =  
953 dark blue; adult males = mid-blue; subadult males = light blue; adult females = dark pink; subadult  
954 females = light pink; calves = yellow. Edges are undirected and weighted by the association index  
955 (Simple Ratio Index); darker lines represent stronger relationships between individuals.

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