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1 **Giraffe (*Giraffa camelopardalis*) social networks in areas of contrasting human**

2 **activity and lion density**

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

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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.

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44   **Keywords**

45   *Giraffa camelopardalis*, human disturbance, predation, predator density, social behaviour, social

46   bonds, social networks, wildlife tourism

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1 INTRODUCTION

The effects of predator presence on the behaviour of African ungulates are well established (Valeix

et al. 2009a, b; Périquet et al. 2010; Creel et al. 2014; Ripple et al. 2014); however, there has been

limited investigation into how these behavioural changes may influence the structure of social

organisation of prey species, or the changes in network structure. Since social networks offer fitness

benefits and may influence an individual's survival (Silk 2007a, 2009; Brent et al. 2015; Goldenberg

et al. 2016) and risk of disease (Drewe 2009; MacIntosh et al. 2012; VanderWaal et al. 2014a;

Adelman et al. 2015), understanding how the social organisation of prey species responds to

predation risk is an important, yet almost completely neglected, area of biology. Furthermore, it is

well recognised that populations of African mammals are in decline (Craigie et al. 2010; Ogutu et al.

2011; Ceballos et al. 2017), yet there is also an increasing appetite and economic justification for

tourism in protected areas (Beale & Monaghan 2004), which is likely to impose significant

disturbance on populations of resident animals (Green & Giese 2004; Kerbiriou et al. 2009). Given

that disturbance by humans through tourism is increasing, it is critical that we understand how such

disturbance affects the social organisation of animals to ensure species protection and balance this

with the increasing economic justification for tourism in protected areas (Beale & Monaghan 2004).

In this paper, we present a population-level analysis of the social organisation of an African ungulate

species with variable social organisation, the giraffe *Giraffa camelopardalis*, comparing two adjacent

populations exposed to different levels of human activity and density of lions.

Fission-fusion social organisation, whereby group size and composition are constantly changing,

characterises many taxa and is considered to be an adaptive response to changing environmental

conditions (Green & Giese 2004; Aureli et al. 2008). Such a flexible social system is likely to have

arisen as animals seek to balance the costs and benefits associated with grouping (Krause & Ruxton

2002). Social bonds are considered to be a product of these trade-offs, whereby individuals gain

benefits from associating with or avoiding other individuals (Palombit et al. 1997; Connor et al. 2000;

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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   *troglodytes* (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; Ranaweerage 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^2, 1670 m asl) surrounding Lake Elementeita; LNNP is a

179   National Park (size 188 km^2, 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^2) compared to more typical densities of 0.08 to 0.14 lion/km^2 (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

13

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

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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.

4 DISCUSSION

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

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

Measures of whole network structure generally supported our predictions and indicated that the network exposed to high disturbance was more fragmented than the network with low disturbance.

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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

	Observed network	Random network	P value
SC: whole network			
Mean SRI value	0.125	0.083	<0.001
Mean CV	116.938	75.373	<0.001
SC: filtered network			
Mean SRI value	0.126	0.095	<0.001
Mean CV	95.081	64.118	<0.001
LNNP: whole network			
Mean SRI value	0.088	0.053	<0.001
Mean CV	130.369	93.768	<0.001
LNNP: filtered network			
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
SC: whole network	0.728	0.822	0.243
SC: filtered network	0.831	0.877	0.362
LNNP: whole network	0.614	0.757	0.219
LNNP: filtered network	0.669	0.767	0.243

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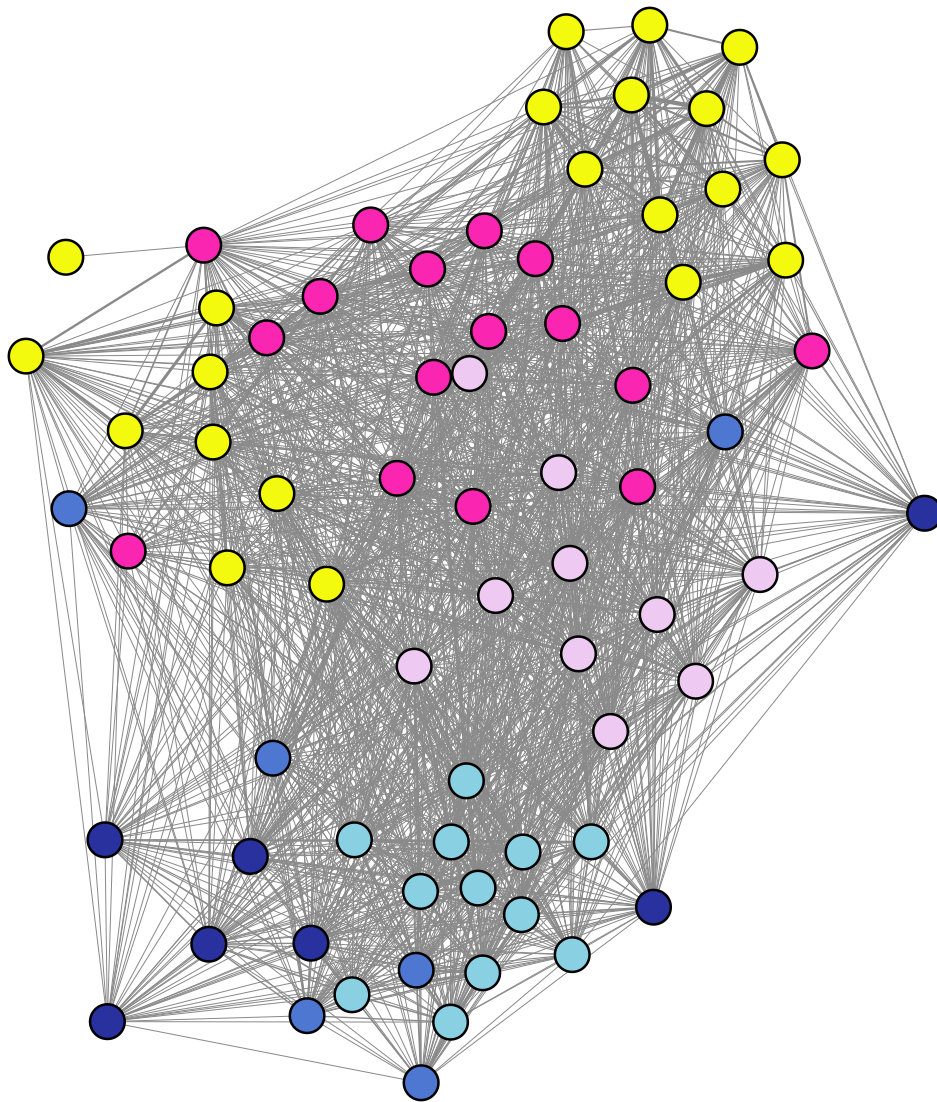
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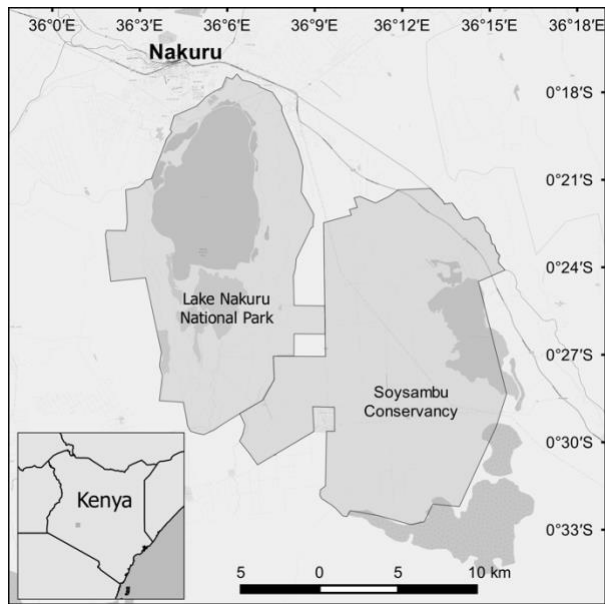
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941   FIGURE 1 Location of the study sites in the Great Rift Valley region of Kenya. Reproduced, with

942   permission, from Muller, et al. 2018. Journal of Zoology 306, 77–87. Base map provided by Google
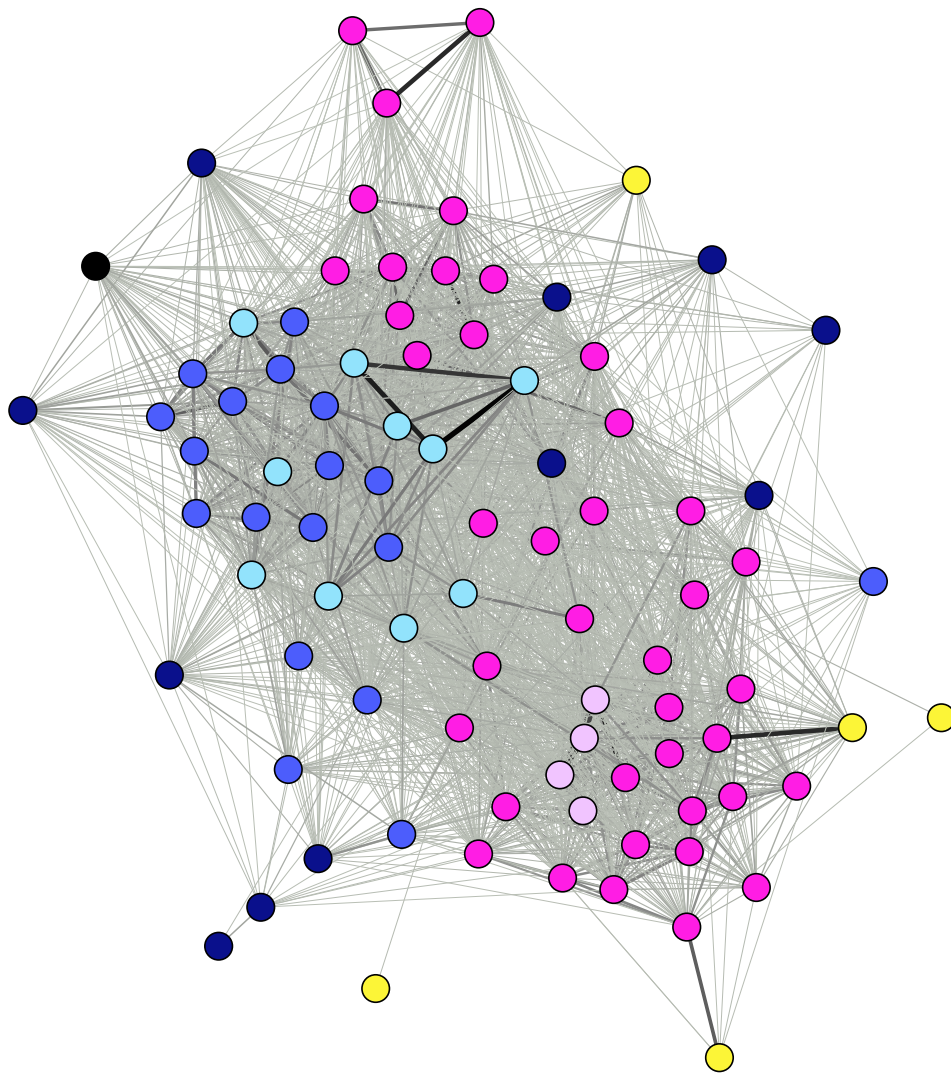
943   Maps 2018.

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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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FIGURE 3 Visualisation of the whole network in LNNP. Nodes are coloured by sex: mature bulls =

dark blue; adult males = mid-blue; subadult males = light blue; adult females = dark pink; subadult

females = light pink; calves = yellow. Edges are undirected and weighted by the association index

(Simple Ratio Index); darker lines represent stronger relationships between individuals.

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