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1 **Group sizes of giraffes in Kenya: the influence of habitat,**

2 **predation and the age and sex of individuals**

3 Zoe Muller[*], Innes C. Cuthill, Stephen Harris

4 School of Biological Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue,

5 Bristol BS8 1TH, UK.

6 *Corresponding author: Zoe Muller. Email: muller.zoe@gmail.com

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14   **Abstract**

15   Giraffe group sizes appear to vary in response to localised ecological and environmental factors, but

16   there has been little investigation of how social factors or predation risk affect group size in giraffes.

17   We studied two adjacent, enclosed populations of Rothschild's giraffes in Kenya, and used 591

18   records of groups to determine the relative influence of a series of variables on group size. One

19   population was free from any risk of predation, while the other area contained a high density of

20   lions. Mean group size was smaller in the population with lions, but a series of GLMMs accounting

21   for habitat and age/sex class of individuals showed that the presence of high numbers of juveniles in

22   the area free from lions artificially inflated group sizes. Removing juveniles from the analysis showed

23   that contrary to the existing creche hypothesis, adult females were found in smaller groups when

24   they had calves. We found no evidence that predation risk influenced grouping behaviour. Rather,

25   recruitment and habitat type had a stronger influence on group sizes, but the results were complex

26   and varied between different age and sex classes of individual. We conclude that predation is not an

27   important driver of giraffe grouping, and that further research is necessary to understand the

28   complex behaviour and ecology of this prominent yet understudied species.

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Introduction

Temporal and spatial variation in animal groups arises as individuals balance the costs and benefits of group living to maximise fitness (Rodman, 1981; Krause & Ruxton, 2002; Thaker *et al*., 2010). By living in groups animals gain protection from predators, knowledge about the location of resources and access to mating opportunities, although these benefits must be traded off against costs such as increased competition for resources, aggression and risk of disease (Hamilton, 1964; Pulliam, 1973; Krause & Ruxton, 2002; Beauchamp, 2003). The grouping behaviour of a species is often modified by the additive effects of environmental and social factors (Price & Stoinski, 2007; White, Proffitt & Lemke, 2012; Creel, Schuette & Christianson, 2014), and fission-fusion societies are especially adept at altering their group sizes when conditions change (Estevez, Andersen & Nævdal, 2007). Such behavioural and group-level plasticity enables fission-fusion species to respond rapidly to changes in local conditions, and achieve an optimal balance between the costs and benefits of grouping (Aureli *et al*., 2008).

Protection from predators is one of the most frequently cited benefits of grouping, and predation has a strong and multifarious influence on the lives of prey species. As well as the direct risk of being predated, the presence of predators can reduce reproductive success and affect the population growth of prey species (Werner *et al*., 1983; Zanette *et al*., 2011; Creel *et al*., 2014). Reduced reproduction rates as a consequence of perceived predation risk (Zanette *et al*., 2011) may occur due to animals altering the time they invest in vigilance and foraging behaviours (Brown & Kotler, 2004) or by changing patterns of habitat use, which influences their ability to forage successfully (Sih & McCarthy, 2002; Creel *et al*., 2014). The presence of predators typically elicits increased vigilance and grouping behaviour (Krause & Ruxton, 2002; Creel & Winnie, 2005; Creel *et al*., 2014) but the strength and consistency of these responses varies between species (Creel *et al*., 2014). Increasing group size with increasing predation risk is reported across a variety of taxa (Crook & Gartlan, 1966; Seghers, 1974; Clutton-Brock & Harvey, 1977; Wrona & Dixon, 1991; Price & Stoinski, 2007).

59 Giraffes are an interesting species in which to study group living; early studies described giraffes as

60 groups of random individuals with no long-lasting associations (Dagg & Foster, 1976; Leuthold, 1979;

61 Le Pendu, Ciofolo & Gosser, 2000). However, new approaches and techniques have altered our

62 understanding of their social structure and motivations for associating, and have identified linear

63 hierarchies (Horová, Brandlová & Gloneková, 2015) and long-lasting preferred associations driven by

64 kinship (Bercovitch & Berry, 2013a), home range overlap (VanderWaal *et al*., 2013), social

65 preferences (Carter *et al*., 2013a) and age proximity (Bercovitch & Berry, 2013b; Carter *et al*.,

66 2013b).

67 However, some of the most basic elements of giraffe ecology remain unknown. Variation in giraffe

68 group sizes is believed to be a result of adaptive responses to local environmental and social

69 conditions, such as habitat type and season (Ciofolo, 1995; Leuthold, 1979; van der Jeugd & Prins,

70 2000; Brand, 2007), sex of group members (Bercovitch & Berry, 2014) and the presence of predators

71 (Creel *et al*., 2014). Lone individuals are common, mean group size is typically 3 to 9 individuals

72 (Table 1). Groups are smaller in the presence of predators (Creel *et al*., 2014), suggesting that

73 protection from predators is not a driver of grouping. Vigilance scanning increases as the number of

74 males in a group increases (Cameron & du Toit, 2005), suggesting that there are reduced foraging

75 costs for being in groups. It is generally accepted that females with calves congregate to form creche

76 groups (Langman, 1977; Leuthold & Leuthold, 1978; Horwich *et al*., 1983; Pratt & Anderson, 1985),

77 but this has never been explicitly tested. Fundamental questions about the adaptive advantages of

78 grouping in giraffes are still unanswered.

79 In this study, we aim to further explore the hypothesis that giraffes group for predator-protection

80 benefits. We also test the effects of habitat on group size, since giraffes should be more vulnerable

81 in some habitats than others, which may affect grouping decisions. Lastly, we test the influence of

82 the age/sex of individuals on grouping behaviour, since individuals of different age and sex class may

83 have different strategies and motivations to form or disband from groups (Bercovitch & Berry, 2014).

84

Materials and Methods

86

Study sites and data collection

88 We collected group size data at two locations in the Great Rift Valley region of Kenya: Soysambu

89 Conservancy (SC) is a 190km^2 wildlife conservancy surrounding part of Lake Elementeita (00°46'S,

90 036°23'E; 1670m asl), and Lake Nakuru National Park (LNNP) is a 188km^2 National Park surrounding

91 Lake Nakuru (0°22'S 36°05'E; 1759m asl). Both areas are enclosed and separated by an electrified

92 game-proof fence along the 7.8 km shared boundary along the south-eastern boundary of LNNP and

93 western boundary of SC (Fig. 1).

94 The risk of predation is a notable difference between the two areas. Lions are the only predator to

95 pose a significant threat to giraffes (Hirst, 1969; Pienaar, 1969; Foster & Dagg, 1972; Dagg & Foster,

96 1976; Strauss & Packer, 2013). In 2011, LNNP contained 56 lions (Ogutu *et al*., 2012), which is a high

97 density (0.3 lion/km^2) compared to more typical densities of 0.08 and 0.14 lion/km^2 (East, 1984;

98 Creel & Creel, 1997). Preferential preying of lions upon giraffes has been identified as a problem in

99 LNNP (Kenya Wildlife Service, 2002; Brenneman *et al*., 2009). At the time of this study, SC was free

100 of lions and had been for several decades (5th Baron Delamere, pers. comm.). This information is the

101 basis of our assertion that giraffes in LNNP were exposed to a higher risk of predation than those in

102 SC.

103 Data were collected for nine consecutive months in each study site (SC May 2010 to January 2011;

104 LNNP May 2011 to January 2012), matched by time of year to reduce seasonal or climatic effects as

105 far as possible. We searched for giraffe groups by driving a 4x4 vehicle at 20km/hr along pre-defined

106 routes through each study site. Each route was driven in a randomised order and direction between

107   sunrise at 06:30 and sunset at 18:30 (UTC + 3h Standard Time), and the whole study site was

108   searched each day.

109   A group of giraffes was defined as all individuals within 1km of each other and engaged in generally

110   similar behaviour (Foster, 1966; Foster & Dagg, 1972; Leuthold, 1979; Le Pendu *et al*., 2000; Carter,

111   2013). Each group was observed for a minimum of 30 minutes, to ensure that all group members

112   were seen and reliably identified.

113

114   *Individual covariates: sex and age*

115   In line with previous studies (Foster, 1966; Foster & Dagg, 1972; Pratt & Anderson, 1979, 1985;

116   Young & Isbell, 1991; van der Jeugd & Prins, 2000; Le Pendu *et al*., 2000) we used four age classes:

117   juvenile (<12 months), subadult (12 months to <4 years), adult (≥4 years) and big bulls (mature adult

118   males with dark coats and skull nodules, ≥9 years old) (Pellew, 1984; Pratt & Anderson, 1985; van

119   der Jeugd & Prins, 2000; Berry & Bercovitch, 2012). All giraffes were individually identified, sexed

120   and verified: see Muller (2018) for complete methodology.

121

122   *Habitat types*

123   Habitat was classified into three categories: *Acacia* woodland, mixed woodland and open plain.

124   *Acacia* woodland was any wooded area comprising ≥85% *Acacia* species. Mixed woodland was any

125   wooded area comprising ≤85% *Acacia* species, and typically contained mixed tree and shrub species

126   including *Euphorbia* spp*., Acacia* spp. and *Olea africana* (Mutangah, 1994). Open plain was any open

127   savannah or grassland area.

128

129   *Data Analysis*

130   Records of group size were used in a one-way ANOVA to assess differences in mean group size, and

131   in a Generalized Linear Mixed Model (GLMM) to determine which factors (population, age/sex class,

132   habitat type, individual ID) affected group size across the two study populations. Population, age/sex

133   class and habitat type were set as fixed effects. We accounted for the fact that individual giraffes

134   could be seen in different groups by including 'giraffe (individual ID)' and 'group' as random effects

135   to control for the non-independence of the group data. Since the group size distribution for each

136   population was positively skewed (Fig. 2) we used a GLMM with a negative binomial error structure,

137   which is appropriate for count data that are over-dispersed (Ridout *et al.*, 1998; Gschlößl & Czado,

138   2008; Lindén & Mäntyniemi, 2011). The outcome of the GLMM was the group size in which an

139   individual was found for a particular observation. Since individuals were observed repeatedly in

140   different groups, individual was included as a random effect. An additional random effect for group

141   was included since individuals within are not independent. All analyses were carried out in R 3.4.3

142   using the lme4 and gamlss.mx packages (R Development Core Team, 2013; Bates *et al.*, 2014).

143

144   **Results**

145   There were 77 giraffes in SC (7 big bulls, 6 male adults, 12 male subadults, 16 female adults, 10

146   female subadults and 26 juveniles) and 89 giraffes in LNNP (11 big bulls, 19 male adults, 10 male

147   subadults, 40 female adults, 4 female subadults and 5 juveniles); see Muller (2018) for discussion.

148   We collected 591 records of group size: 298 groups in SC, 293 in LNNP. Group sizes were larger in SC

149   (mean = 7.8, SD = 7.2, 95% CI 6.7, 9.1, min = 1, max = 37) than LNNP (mean = 5.3, SD = 5.5, 95% CI

150   4.7, 5.9, min = 1, max = 28). Lone individuals were common and accounted for 17.5% of all giraffe

151   groups in SC and 24.7% in LNNP. Of these lone individuals, 84.9% and 76.6% were males in SC and

152   LNNP respectively. Mean group sizes were not significantly different between habitat types within

153   each population; SC: *Acacia* woodland = 11.6, mixed woodland = 6.2, open plain = 7.3 ($F_{(2, 47)}$ =

154   2.432, p = 0.099); LNNP: *Acacia* woodland = 4.8, mixed woodland = 4.9, open plain = 6.3 ($F_{(2, 309)}$ =

155 2.145, *p* = 0.119), but the proportion of groups observed in each habitat type differed between the

156 two populations; in LNNP, 29% of groups were observed in *Acacia* woodland, 39% in Mixed

157 woodland and 32% in open plain. In SC, 20% of groups were observed in *Acacia* woodland, 55% in

158 mixed woodland and 25% in open plain.

159 A GLMM with population, habitat type and age/sex class as fixed effects and giraffe (individual ID)

160 and group as random effects showed that the age/sex * habitat type * population interaction was

161 significant (LRT chi-squared = 33.10, df = 20, *p* = 0.0329) (Fig. 3). We investigated the source of the

162 interaction by analysing the effects of habitat type and population for each age/sex category

163 separately (Table 2). There was no significant habitat * population interaction for adult males, bulls,

164 adult females or juveniles. Group sizes tended to be highest in open plain (significantly higher than

165 mixed woodland for all four of these age-sex categories), lowest in mixed woodland and

166 intermediate in *Acacia* woodland.

167 For bulls, adult females and juveniles (but not adult males), group sizes were higher in SC than LNNP.

168 For subadult males and subadult females there were significant Habitat * Population interactions.

169 For subadult males, this was because group sizes were higher in SC than LNNP only for *Acacia*

170 woodland; mixed woodland showed a non-significant trend in the same direction (*p* = 0.0712). For

171 subadult females the pattern was more complex; groups sizes were significantly higher in SC than

172 LNNP in *Acacia* woodland, but the reverse was true for mixed woodland.

173

174 *Analysis without juveniles*

175 To remove the artefacts of the presence of more juveniles *per se*, most notably in SC, driving up

176 group size, we repeated the GLMM without including juveniles in the counts. The AgeSex * Habitat *

177 Population interaction was significant (LRT = 31.66, d.f. = 16, *p* = 0.0111; Fig. 4), so we investigated

178 the source of the interaction by analysing the effects of habitat type and population for each age/sex

179   category separately (Table 3). For adult males, bulls and adult females, there was no significant

180   Habitat * Population interaction, so we can readily interpret the main effects. Group sizes tend to be

181   highest in open plain (significantly higher than mixed woodland for all three of these age/sex

182   categories), with *Acacia* woodland intermediate. For bulls, but not adult males or females, group

183   sizes were higher in SC than LNNP. For subadult males and females there were significant Habitat *

184   Population interactions. For subadult males, this was because group sizes were higher in SC than

185   LNNP only for *Acacia* woodland. For subadult females, the pattern was more complex; group sizes

186   were significantly higher in SC than LNNP in *Acacia* woodland, but the reverse was true for mixed

187   woodland. Mean group sizes are displayed in Fig. 4.

188

189   *Analysis of groups sizes in females with and without calves*

190

191   To determine whether groups were bigger in SC due to the presence of more juveniles pushing up

192   mean group size, or if females were altering their behaviour because they had calves, we analysed

193   group sizes in females with and without calves. We refer to a female's status as having dependent

194   calves or not as Parity. The response variable was group size not including calves. The Parity x

195   Habitat * Population interaction was not significant (LRT = 0.70, d.f. = 2, *p* = 0.7034), so we then

196   tested the two way interactions. Of these, only Population * Habitat was significant (Population *

197   Parity: LRT = 0.26, d.f. = 1, p = 0.6121; Parity * Habitat: LRT = 2.59, d.f. = 2, p = 0.2745; Population *

198   Habitat: LRT = 13.49, d.f. = 2, p = 0.0012). The Population * Habitat interaction has already been

199   analysed so is not discussed further here. The main effect of Parity was also significant (LRT = 4.14,

200   d.f. = 1, p = 0.0417). Females with calves were found in smaller groups (by about 1 animal; Fig. 5),

201   but this did not interact with the habitat and population differences already identified.

202

203 **Discussion**

204 Knowledge of a species' behaviour and ecology is important for management and conservation

205 (Sutherland, 1998) yet despite their prominence, giraffes are understudied in relation to other

206 African mammals. Information about the social organisation of giraffes is confusing and

207 contradictory, and factors influencing grouping behaviour are poorly understood. It is widely

208 perceived that grouping behaviour in mammals is an anti-predator response, with most mammals

209 exhibiting larger group sizes with increasing predation risk (Elgar, 1989; Wrona & Dixon, 1991;

210 Krause & Ruxton, 2002). Our overarching hypothesis was that if predation is a driver of grouping

211 behaviour in giraffes, then group sizes should be larger in the area with a high density of lions

212 (LNNP). We set out to quantify the relative influence of habitat type, social factors and risk of

213 predation risk on giraffe grouping behaviour.

214 Group size distribution was positively skewed in both populations with a high frequency of lone

215 individuals, as in other studies (Foster & Dagg, 1972; Leuthold, 1979; van der Jeugd & Prins, 2000; Le

216 Pendu *et al*., 2000; Bercovitch & Berry, 2010; VanderWaal *et al*., 2014). Lone individuals were more

217 frequent in LNNP, probably due to the higher proportion of adult males (33% big bulls and adult

218 males, vs. 17% in SC) which frequently roam alone (Foster & Dagg, 1972; Dagg & Foster, 1976;

219 Bercovitch & Berry, 2014). Mean group size was smaller in LNNP, which is the opposite of what we

220 expected, if predation was a driver of aggregations in giraffes. However, further analysis which

221 accounted for habitat type, individual covariates and population, showed that the relationship

222 between these variables and group size was complex.

223 To account for the effects of juveniles pushing up group sizes in SC, re-analysis after removal of

224 juveniles confirmed that there was a significant influence of age/sex on group size. We found

225 significant interactions between age/sex, habitat and population, but these patterns were also

226 complex. Group sizes for males (adult males, subadult males and bulls; Fig. 4) were largest in the

227 open plain habitat type, and generally smaller in LNNP. For females (adult and subadult), results

228   were mixed (Fig. 4). Our hypothesis that group sizes will be larger in the area with a high risk of

229   predation was not supported, and our results highlight the complexity of factors contributing to

230   group size in giraffes.

231   The hypothesis that females form larger groups when they have calves was not supported, and the

232   opposite was true; females were found in smaller groups when they had calves. We found no

233   evidence that increased mean group size in SC was due to females altering their behaviour to group

234   with others when they had calves. Because the calves are counted as group members it seems most

235   likely that the increased group size is solely because there are more calves, not because the females

236   are joining together with other females to form creches. Although calves are typically found with

237   their mothers, it appears unlikely that they contribute to their mother's decision to join or leave a

238   group. Therefore, group sizes are not constrained by demography – rather, adults maintain their

239   typical grouping patterns, but group sizes are smaller in LNNP due to the reduction in numbers of

240   juveniles (Brenneman *et al.*, 2009). Numerous sources in the literature describe how female giraffes

241   form creche groups to care for their young (Langman, 1977; Leuthold & Leuthold, 1978; Horwich *et*

242   *al.*, 1983; Pratt & Anderson, 1985) and some evidence of alloparental care has been reported (Dagg

243   & Foster, 1976; Pratt & Anderson, 1979; Gloneková, Brandlová & Pluháček, 2016). However, our

244   results show that contrary to popular belief, females with calves are found in smaller groups than

245   females without calves.

246   If giraffes gain predation protection benefits through grouping, then we would expect the group

247   sizes to be larger in LNNP across all habitat types. However we found no evidence for this, and our

248   results support previous studies which also reported smaller group sizes in the presence of predators

249   (Creel *et al.*, 2014), and that the rate of vigilance scanning in giraffes is not modified by changes in

250   group size (Cameron & du Toit, 2005).

251   Our study is the first to examine two separate populations of giraffes within the same biome to

252   attempt to understand the relative combined effects of predation, habitat and demographic factors

253 on grouping behaviour. We demonstrate that the presence of juveniles can artificially inflate group

254 size results, and we suggest caution of over-interpretation of studies which do not account for this.

255 We suggest that predator avoidance is not the main driver of giraffe grouping behaviour, but rather

256 that social and habitat factors are likely to play an important role. We identify that removal of

257 juveniles is potentially a problem in enclosed environments with high lion densities, which alters the

258 greater social landscape for affected animal species. However, poor recruitment could also be due to

259 other factors which cannot be ruled out, i.e. disturbance of foraging or reproductive activities by

260 tourism, in-breeding factors, local environmental factors including food quality and availability, or

261 differences in female fecundity, sexual receptivity, or harassment by bulls. The incongruous nature

262 of group sizes of giraffes across Africa could be due to individuals adapting to local environmental

263 conditions, but it is becoming clear that social factors are also important influencing variables.

264 Variations could also be due to unknown taxonomic differences, given the uncertainty and ongoing

265 debate over the taxonomic status of giraffes (Brown *et al*., 2007; Groves & Grubb, 2011; Bercovitch

266 & Deacon, 2015; Fennessy *et al*., 2016; Bercovitch *et al*., 2017). We highlight the need for further

267 research into this iconic species, and hope that our results contribute to the ongoing efforts to

268 understand giraffe behaviour and ecology.

269

279

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434

435   **Table 1** Published reports of giraffe group size data. NR = Not reported. [†]Study looked at males only.

436   * Excludes group sizes of *n*=1.

437

438   **Table 2** Results from separate GLMMs on effect of Habitat (H) and Population (P) for each age/sex

439   category (AdM: adult male; SubM: subadult male; Bull; AdF: adult female; SubF: subadult female;

440   Juv: juvenile). If the Habitat * Population interaction was significant, the main effects are not

441   interpretable and, instead, separate GLMMs for the effect of Population are presented (as SC vs

442   LNNP) for each habitat type (MW: mixed woodland; AW: *Acacia* woodland; OP: open plain). Values

443   in each cell are likelihood ratio tests (p-values in italics). If the Habitat * Population interaction was

444   not significant, main effects of Habitat and Population are presented, and separate analyses of

445   Population differences for each Habitat are not applicable (na). Instead, where the main effect of

446   Habitat was significant, t-tests (and p-values in brackets) of pair-wise contrasts between habitats are

447   presented. The degrees of freedom for Habitat and the Habitat * Population interaction was 2; for

448   Population and pair-wise Habitat contrasts d.f. = 1. Significant effects are in bold.

449

450   **Table 3** Results from separate GLMMs on effect of Habitat (H) and Population (P) for each age/sex

451   category (AdM: adult male; SubM: subadult male; Bull; AdF: adult female; SubF: subadult female). If

452   the Habitat * Population interaction was significant, the main effects are not interpretable and,

453   instead, separate GLMMs for the effect of Population are presented for each habitat type (MW:

454   mixed woodland; AW: *Acacia* woodland; OP: open plain). Values in each cell are likelihood ratio tests

455   (p-values in italics) and, where Habitat was significant, t-tests (and p-values in italics) of pair-wise

456   contrasts between habitats. If the Habitat * Population interaction was not significant, main effects

457   of Habitat and Population are presented, and separate analyses for each Habitat are not applicable

458   (na). The degrees of freedom for Habitat and the Habitat * Population interaction was 2; for

459   Population and pair-wise Habitat contrasts d.f. = 1. Significant effects are in bold.

Figure 1 Location of the study sites in the Great Rift Valley region of Kenya. Base map provided by Google Maps 2018.

Figure 2 Frequency distributions of samples of group size for each study population.

Figure 3 Mean group size of giraffes in each study site, split by age/sex class (AdM = adult male, SubM = subadult male, Bull = big bull, AdF = adult female, SubF = subadult female, Juv = juvenile) and habitat type (AW = *Acacia* woodland, MW = mixed woodland, OP = open plain).

Figure 4 Mean group size of giraffes in each study site, following removal of juveniles. Abbreviations as in Fig. 3.

Figure 5 Mean group size of adult females, with and without calves, split by study site and habitat type. Abbreviations as in Fig. 3.

Author (Year)	Age/Sex	HxP	Study site and region	AW-MW	Subspecies	OP-MW	OP-AW	Length, season of study (if reported)	SC - LNNP in MW	SC - LNNP in AW	SC - Total population size
Fennessy (2004)			Kunene Region, Northern Namib Desert, Namibia		*G. c. angolensis*			Long term data; 1981 to 2000	No		NR
Fennessy (2004)			Northern Namib Desert, Namibia - Khumib River (KR) - Hoarusib River (HR) - Hoanib River (HbR)		*G. c. angolensis*			Observed on a monthly basis over two-year period; 2002 and 2003	No		NR
Brand (2007)			Etosha National Park, Namibia		*G. c. angolensis*			May to December 2004, and March to December 2005	No		Estimated population 3550
Carter *et al.* (2013a)			Etosha National Park, Namibia		*G. c. angolensis*			May 2009 to June 2010	No		535 individuals in study area (3550 estimated in park)
Malyjurkova *et al.* (2014)			Bandia reserve, Senegal		*G. c. giraffa*			January to March 2013; dry season	Yes, 35km²		28
Ciofolo (1995)			Niger, 100km south-east of Niamey		*G. c. peralta*			June to November 1990	No		50 – 100 individuals
Le Pendu *et al*. (2000)			Niger, 100km south-east of Niamey		*G. c. peralta*			October 1996 to December 1997	No		63
Shorrocks & Croft (2009)			Mpala Research Centre, Laikipia, Kenya		*G. c. reticulata*			Two four-week periods in March/April 2005 and March/April 2006	No		133 individuals used in study (total population NR)
VanderWaal *et al.* (2014)			Ol Pejeta Conservancy, Laikipia, Kenya		*G. c. reticulata*			One year; 2011	Yes, 365km²		212
Bercovitch & Berry (2010)			Luangwa Valley, Zambia		*G. c. thornicrofti*			August 1971 to October 2005	No		600
Berry & Bercovitch (2015)†			Luangwa Valley, Zambia		*G. c. thornicrofti*			August 1971 to October 2005	No		600
Foster & Dagg (1972)			Nairobi National Park, Kenya		*G. c. tippelskirchi*			1965 to 1968	Yes, 117km²		250
Leuthold (1979)			Tsavo East National Park, Kenya		*G. c. tippelskirchi*			August 1970 to October 1974	No		Unknown
van der Jeugd & Prins (2000)			Lake Manyara National Park, Tanzania		*G. c. tippelskirchi*			June to October 1991; dry season	Yes, 325km²		101 individuals identified

AdM	3.00 0.2229	**16.01** *0.0003*	**2.20** *0.0278*	**4.01** *<0.0001*	1.63 *0.1029*	0.04 *0.8468*	na	na	na
SubM	**6.33** *0.0422*	na	na	na	na	na	3.25 *0.0712*	**11.03** *0.0009*	0.01 *0.9254*
Bull	1.88 *0.3901*	**10.90** *0.0043*	0.51 *0.6122*	**2.87** *0.0042*	**3.27** *0.0011*	**8.47** *0.0036*	na	na	na
AdF	0.88 *0.6455*	**59.48** *<0.0001*	**3.89** *0.0001*	**8.18** *<0.0001*	**3.28** *0.0011*	**30.35** *<0.0001*	na	na	na
SubF	**14.94** *0.0006*	na	na	na	na	na	**6.36** *0.0117*	**8.43** *0.0037*	2.41 *0.1204*
Juv	3.95 *0.1384*	**18.48** *<0.0001*	0.64 *0.5210*	**4.74** *<0.0001*	**2.49** *0.0131*	**26.60** *<0.0001*	na	na	na

Age/ Sex	HxP	Habitat	AW-MW	OP-MW	OP-AW	Population	SC - LNNP in MW	SC - LNNP in AW	SC - LNNP in OP
AdM	2.43 0.29615	**19.27** *0.0001*	**2.588** *0.0097*	**4.38** *<0.0001*	1.62 *0.1064*	1.61 *0.2051*	na	na	na
SubM	**6.09** *0.0477*	na	na	na	na	na	0.17 *0.6770*	**7.77** *0.0053*	0.17 *0.6731*
Bull	2.06 *0.3571*	**10.98** *0.0041*	0.23 *0.8204*	**3.18** *0.0015*	**3.31** *0.00098*	**4.12** *0.0424*	na	na	na
AdF	5.38 *0.0678*	**67.92** *<0.0001*	**5.31** *<0.0001*	**8.62** *<0.0001*	**2.37** *0.0178*	1.55 *0.2136*	na	na	na
SubF	**21.20** *<0.0001*	na	na	na	na	na	**18.81** *<0.0001*	**5.07** *0.0243*	0.23 *0.6288*

Study site

SC   LNNP