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2 **lions**

3

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28

29   **Abstract**

30   1. Environmental variations can influence the extent to which individuals interact

31   with other individuals by changing the value of grouping. It is well known that many

32   species can form and disband groups, often in response to the distribution and

33   abundance of resources.

34   2. While previous studies showed that resources influence the broad-scale structure of

35   animal groups, knowledge gaps remain on whether they affect the fine-scale patterns

36   of association among individuals within groups.

37   3. We quantify association patterns in African lions while simultaneously monitoring

38   the abundance and distribution of prey. We test how social and ecological factors,

39   including individual trait (age, sex, reproductive state) similarity, prey availability

40   (prey abundance, dispersion, herd size and body size), interspecific competition, and

41   vegetation cover affect within-pride social structure in African lions.

42   4. In general, a greater abundance of dispersed smaller prey resulted in prides being

43   consistently divided into subgroups with weaker cohesion among pride members. By

44   contrast, low abundance and aggregated small herds of prey resulted in stronger

45   connections among individuals. We found interesting trade-offs in individual

46   decisions to associate generally (equally across all other members of the pride) when

47   resources are aggregated and rich, and associating more exclusively (in subgroups of

48   preferred associates) when resources are scarce. Further, lions preferentially

49   associated equally across the pride when prey were large, providing some evidence

50   that the composition of hunting parties might be important when prey are more

51 difficult to catch.

52 5. Our study provides evidence that ecological factors can shape both global and fine-

53 scale properties of animal social systems, even when species live in seemingly

54 consistently structured societies. Our findings suggest that the decisions by lions in

55 the compromise between having few strong connections and having many weaker

56 connections is strongly determined by ecological conditions. More broadly, our study

57 reveals how fission-fusion dynamics and ecological factors can play out

58 simultaneously across multiple levels of sociality.

59

60 **Key words**

61 Animal social networks, dynamic networks, ecological factors, fission-fusion,

62 heterogeneity, lion, null models, prey availability

63

64 **Introduction**

65 One important goal in animal ecology is to understand the relationship between

66 environmental factors and animal population abundance, spatial distribution, and

67 social structure (Solomon 1949). Studies across different taxa have demonstrated that

68 resource availability is an important determinant of the broad-scale structure of

69 animal societies, with most of these studies showing that animal group size is

70 generally larger when food resources are more abundant and of a higher quality (see

71 Hanya & Chapman 2013; Macdonald & Johnson 2015 for reviews). In particular Nel,

72 Loutit, Braby and Somers (2013) found that where food patches were rich, fairly

73 clumped and heterogeneous, black-backed jackals (*Canis mesomelas*) group sizes

74 were large and territory sizes small. In group-living animals, interactions among pairs

75 or subgroups of individuals within a group (Hinde 1956; Macdonald, Yamaguchi &

76   Kerby 2000; Krause & Ruxton 2002), and the outcome of these interactions can be

77   interpreted as a network of social relationships (Whitehead 2008; Farine & Whitehead

78   2015). The nature, number, and strength of these relationships are complex and can

79   mediate the benefits, such as food sharing, that individuals accrue from living in

80   groups, particularly in times of need (Carter, Farine & Wilkinson 2017). Earlier

81   attempts at understanding the interactions among individuals in a carnivore social

82   structure, using the example of farm cats (*Felis catus*), were analytically

83   unsophisticated. However, they offered some insights into patterns of social structure

84   of group living carnivores (see Macdonald, Apps, Carr & Kerby 1987). Modern tools

85   in ecology and evolution are now allowing us to understand better the patterns of

86   animal social structure (i.e. the patterns in social relationships) at a finer level of

87   social organization (Tanner & Jackson 2012; Farine *et al.* 2015a), including in

88   carnivores (e.g. Ellwood *et al.* 2017). Understanding the processes generating

89   variation in social structure across populations is critical for understanding the effects

90   of sociality (Ilany & Akçay 2016). Yet, there is still only preliminary understanding

91   of how ecological variables shape the fine-scale patterns of animal social structure

92   (He, Maldonado-Chaparro & Farine 2019) and the implications of these on the overall

93   group social structure and stability.

94

95   A number of postulates have been put forward to explain social structure in different

96   animal populations, including predation risk for explaining the grouping patterns of

97   females in non-human primates (Sterck, Watts & van Schaik 1997), kinship for

98   shaping spatial layout of group living animals (Hirsch, Stanton & Maldonado 2012),

99   and homophily (individual preferences for associating with like individuals) for

100   shaping which individuals interact most strongly (Farine 2014). Social network

101　analysis has been instrumental in testing these postulates. At its base, social network

102　analysis quantifies the strength of associations or interactions among each pair of

103　individuals in a social group or population (Whitehead 2009). It allows us to

104　understand complex social and ecological interactions in animal communities (Croft,

105　James & Krause 2008; Farine & Whitehead 2015) by providing metrics that quantify

106　social structure at different levels of organization, i.e. within individuals, groups and

107　populations. Some pioneering studies have used social network analysis to reveal

108　details of the relationship between food availability and patterns of animal social

109　structure. For example, Tanner and Jackson (2012) found that European shore crab

110　(*Carcius meana*) individuals aggregated into cohesive stable subgroups when

111　resources were clumped. Additionally, Foster *et al.* (2012) showed that when prey

112　were abundant, the killer whale (*Orcinus orca*) population was characterized by a

113　highly interconnected social network. Nevertheless, our understanding of the

114　relationship between resources and social structure remains superficial. How do

115　different aspects of food availability, such as the size and distribution of prey items,

116　affect the finer-scale patterns of associations among individuals, in particular their

117　decisions to form or disband subgroups?

118

119　In species that exhibit a form of fission-fusion social organization, the average size of

120　subgroups, the amount of cohesion they show, and even their sexual composition are

121　expected to vary depending mainly on food distribution and mating systems

122　(Symington 1988). One species that has been widely reported as exhibiting within-

123　group fission-fusion dynamics by forming subgroups is the African lion (*Panthera*

124　*leo*) (Schaller 1972). Individuals within these subgroups form very close associations

125　(Van Orsdol, Hanby & Bygott 1985), and subgroup membership can potentially be

126   influenced by the attributes of different individual lions, such as their age, sex and

127   reproductive state. For instance, female lions often form highly stable maternity

128   groups that are effective in defending their cubs against infanticidal males from

129   outside the pride and subgroup (Packer, Scheel & Pusey 1990). However, the

130   interactions between individuals within a group are also likely to vary with ecological

131   conditions. Although lions engage in a wide variety of important social activities,

132   such as cooperative hunting (Scheel & Packer 1991), mutual defence of kills (Cooper

133   1991) and cooperative defence of territory and young (Mosser & Packer 2009), it has

134   been suggested that lion sociality might be influenced by resource availability

135   (Macdonald, Mosser & Gittleman 2010; Mbizah, Valeix, Macdonald & Loveridge

136   2019). For example, habitat quality was suggested as a major driver of lion social

137   organisation in the Serengeti National Park, Tanzania (Mosser, Fryxell, Eberly &

138   Packer 2009), and the number of prey herds visiting a waterhole determines

139   maximum lion group size in Hwange National Park, Zimbabwe (Valeix, Loveridge &

140   Macdonald 2012). These studies provide evidence that the general structure of lion

141   populations (group size) is linked to overall resource availability (food abundance).

142

143   The dynamics of resource availability especially the abundance, richness, type, and

144   distribution of prey might also influence finer-scale lion social structure. For example,

145   when prey are abundant, we expect that there will be less competition for food,

146   meaning that lions will gain fewer benefits from being in larger groups. As a result,

147   they should preferentially remain with close associates. Extensive work on baboons

148   has shown that the strength of close associations can increase fitness (Silk *et al.* 2010;

149   Alberts 2019). When prey are scarce, then we expect lions to associate with a greater

150   number of their other pride members, because prey are more difficult to locate and

catch, and because lions become more susceptible to interspecific competition from

spotted hyaenas (*Crocuta crocuta*) that frequently cooperate to move lions at fresh

kills (Kruuk 1972). In general, group size has fitness benefits apart from resources,

the demands of protecting their young and themselves against encounters with

neighbouring prides (Packer 1986; Mosser & Packer 2009) and maintaining a long-

term territory (Packer *et al.* 1990; Mosser & Packer 2009) can result in lions forming

larger groups. Here we argue that fitness benefits might shape the tendency for

members of a given pride to remain cohesive or to split into smaller subgroups, which

is a much more flexible strategy than adding or removing members from the pride.

Social bonds are therefore likely to form the basis of how species such as lions

respond socially to ecological processes. We expect to observe a trade-off between

maintaining fewer but stronger bonds when conditions are good and maintaining more

but weaker bonds when conditions are poor and more challenging.

In this study, we combine data on the fine-scale patterns of association among

individuals across multiple prides of African lions with data on the prey herds in each

pride's territory within Hwange National Park, Zimbabwe. We consider a herd of

prey to represent a resource patch available to lions (Carr & Macdonald 1986), and

the abundance, dispersion, and richness of these patches (see Table S1) as important

attributes that can influence the opportunities for social interactions (Tanner &

Jackson 2012). Resource richness is measured by the herd size and body size of

mixed herds of prey. Breaking down prey availability into different axes allows us to

better understand the effects of prey availability on fine scale patterns of association,

distinguishing our study from many of its predecessors that used only prey abundance

as a measure of food availability.

176

177   The availability of resources is also modulate by interspecific competition and habitat

178   structure. Spotted hyaenas are lion's main competitor, and they frequently cooperate

179   to mob lions (Kruuk 1972) especially at fresh lion kills. Furthermore at higher hyaena

180   to lion ratio, hyaenas can successfully seize food from lions (Lehmann *et al.* 2017).

181   Thus, the presence of hyenas could alter or reinforce the relationship between

182   resources and social decisions in lions. Habitat is also likely to play a role. Lions are

183   considered ambush predators that rely heavily on concealment to catch their prey

184   (Hopcraft, Sinclair & Packer 2005), consequently dense vegetation is important for

185   providing cover for stalking lions which may increase their chances of prey capture

186   (Loarie, Tambling & Asner 2013). We therefore investigate how broader ecological

187   factors can also drive patterns of fine scale social structure by including data on the

188   abundance of spotted hyaena and the percentage of vegetation cover in prides'

189   territories (see Table S1).

190

191   **Materials and Methods**

192   *Study area*

193   Hwange National Park covers approximately 15 000 km^2 of semi-arid dystrophic

194   savanna on Kalahari sands, on the north-western border of Zimbabwe. During the wet

195   season (November to February), various waterholes, rivers and pools are rain fed and

196   available to animals, but natural surface water then becomes scarce as the dry season

197   progresses and only pumped waterholes (~ 50), mostly in the North of the park,

198   maintain water availability. The end of dry season coincides with the lowest quantity

199   and quality of browsing and grazing resources. These differences in vegetation and

200   water distribution across the park result in differences in the distribution of herbivores

201   in terms of both assemblages and abundance (Chamaillé-Jammes, Charbonnel, Dray,

202   Madzikanda & Fritz 2016). We therefore commonly distinguish three seasons in

203   Hwange National Park: the wet season (November - February), the early dry season

204   (March - June) and the late dry season (July - October). Lion density is estimated at

205   around 3.5 lions/100 km^2 in the study area (Loveridge *et al.* 2016) and there is a

206   heterogeneous distribution of prey, both spatially and temporally (Chamaillé-Jammes

207   *et al.* 2016).

208

209   *Lion pride observations*

210   In this study, we used data from seven GPS-collared lions (two adult females and five

211   adult males) from four different prides for the study period 2013 - 2015. Lion prides

212   were located with the help of GPS radio-collars and at times opportunistically. The

213   prides were observed at least five times per month to record the size and composition

214   of their group at that time. When a group was observed, we recorded the pride name,

215   identity of individuals present, as well as their age, sex and reproductive state

216   (whether they had cubs). We also recorded their activities during observations and

217   these included resting, hunting, feeding and walking. All lion individuals are

218   recognizable by whisker patterns that are unique to each individual and natural

219   markings such as scars, muzzle spots and tooth irregularities (Pennycuick & Rudnai

220   1970). We looked at two aspects of lion group (1) pride (all the individuals within a

221   group) and (2) subgroup (individuals of a pride present at each observation). We

222   recorded all individuals present together as being connected (Whitehead & Dufault

223   1999; Farine 2015). The GPS collars recorded locations every two hours day and

224   night, and we regularly downloaded this positional data to estimate lion seasonal

225   home range. Only individuals that had collar data with fixes covering the whole

226   season were included in calculating seasonal home range.

227

228   *Ecological factors*

229   To measure prey availability, we conducted multi-species spoor (tracks made by

230   animals when they cross the roads) surveys from 2013 to 2015 during the early dry

231   season and the late dry season. Most of the available roads in the study area were used

232   as transects (n = 64 transects) and were between 9 and 55 km long. The 64 selected

233   transects were within areas that lions frequent. When a fresh spoor (less than 24hrs

234   old) was encountered, it was assessed for species and group size by highly skilled and

235   experienced trackers (see S1 Appendix for further details on the spoor survey

236   method). Only spoor from common lion prey species in the area was used in this

237   analysis. Information on prey availability was extracted for each lion home range in

238   each season (See S2 Appendix for further details). From the spoor surveys, we also

239   extracted information on the abundance of hyaenas within lion home ranges and then

240   calculated the ratio of hyaena abundance to lion pride size. We used a vegetation map

241   (Arraut, Loveridge, Chamaillé-Jammes, Valls-Fox & Macdonald submitted) to

242   calculate the percentage of vegetation cover within each lion home range. We re-

243   classed the original seven vegetation classes into two main classes; open vegetation

244   (grassland and bushed grassland) and closed vegetation (bushland, woodland

245   deciduous, mopane scrubland, mopane woodland and woodland evergreen) and

246   calculated the percentage of the closed vegetation within each lion home range.

247

248   *Social networks construction*

249   We used lion pride observational data to construct a social network for each pride in

250   each dry season in each year, with observations ranging from 16 to 66 observations

251 per season (Table S3). Thus, each social network represented the patterns of

252 associations within a pride over a four-month period. The social networks contained

253 each of the individuals in one pride as nodes and pairwise association indices as edge

254 weights. Because we did not have complete data on observations of all groups

255 simultaneously, we had to convert the number of associations into an association rate

256 (the propensity for individuals to be seen together). To calculate these edge weights,

257 we used the Simple Ratio Index as an estimate of the proportion of time two

258 individuals spent together (Cairns & Schwager 1987; Hoppitt & Farine 2017). The

259 Simple Ratio Index is defined as $x / (y_a + y_b + y_{ab} + x)$, where x is the number of

260 observations of two individuals together, y_a is the number of observations with only

261 individual a, y_b is the number of observations with only individual b. y_{ab}, the number

262 of simultaneous observations of individuals a and b, was not relevant to our study.

263 This ratio ranges from 0 for two individuals never seen in the same subgroup and 1

264 for two individuals always seen in the same subgroup. Animals that died during a

265 season were not included in that season's network.

266

267 *Social network analysis*

268 We first used the multiple regression quadratic assignment procedure (MRQAP) to

269 test if the tendency of lions to associate with individuals of the same sex, same age or

270 same reproductive state had an effect on lion social structure. MRQAP tests the

271 matrix equivalent of a linear regression and are widely used for hypothesis testing in

272 networks (Farine 2017). We conducted a separate MRQAP for each pride in each

273 season with association as the dependent matrices and age based homophily, sex

274 based homophily and reproductive state based homophily as the independent

275 variables. The homophily matrices were constructed by assigning similar pairs a value

276   of 1, while dissimilar pairs received a value of 0. We conducted these tests using the

277   MRQAP function with a custom null model option in 'asnipe' package in the

278   statistical software R (Farine 2013). The null model consisted of 10 000 permutations

279   (see below)

280

281   To quantify the division of prides into subgroups and the nature of connections within

282   prides and within subgroups, we used three network metrics: modularity, mean

283   weighted degree and network density. Modularity describes the separation of

284   networks into structural communities, or subgroups of individuals that are more

285   connected among themselves than they are to others (Girvan & Newman 2002).

286   Herein, we call these network-based communities "subgroups". A higher modularity

287   implies that a group tends to break into distinct subgroups with stronger connections

288   between individuals within a subgroup but weaker connection between individual in

289   different subgroups (Newman 2004). Mean weighted degree is defined as the average

290   sum of the weight of edges surrounding each node in a network; it measures the

291   strength of connections among individuals in a group and a high mean weighted

292   degree means most individuals were seen together most of the time. Network density

293   is the ratio of the number of edges (nonzero edges) in the network over the total

294   number of possible edges between all pairs of nodes. A high network density

295   represents greater gregariousness among individuals with individuals being connected

296   to more conspecifics. We represented the resulting subgroup assignments by giving

297   different colours of nodes to each subgroup within a pride using the community

298   detection algorithm (Fig. 1). All network measures were calculated in R using igraph

299   (Csardi & Nepusz 2006).

300

301   *Hypothesis testing*

302   We first preliminarily tested for the correlation between the four measures of prey

303   availability, and the correlations were generally moderate to low ($-0.59 \leq r \leq 0.62$),

304   still each measure was analysed separately. All analysis were done in the statistical

305   software R (Bates, Mächler, Bolker & Walker 2015) using linear mixed effects

306   regression analysis and the identity link in the lme4 package. We assessed the

307   relationship between the different network metrics (modularity, mean weighted

308   degree and network density for each pride and subgroup network) and (i) the four

309   measures of prey availability, (ii) a measure of interspecific competition (ratio of

310   hyaena abundance to lion pride size), and (iii) a measure of vegetation cover

311   (percentage of closed vegetation). The network metric was the response variable

312   while the above ecological variables that can potentially influence lion social structure

313   were the fixed effects; with lion pride ID included as the random effect. Using the

314   null model procedure described below, we also generated 10 000 randomised versions

315   of each network, and ran the same regression with each of these randomised

316   networks. We then calculated P-values for each fixed effect by calculating the number

317   of coefficients of the regression slopes from the randomised networks that were

318   greater than or equal to the corresponding coefficient of the regression slopes using

319   the observed network, divided by the number of random networks generated and

320   corrected for a two-tailed test (Farine 2017). The regression coefficients were scaled

321   (by subtracting the mean and dividing by the standard deviation) to make the strength

322   of the effect comparable between the pride level and the subgroup level. All analysis

323   were done in R statistical software (R Core Team 2019).

324

325   *Null models*

326   Social data are typically non-independent (Croft, Madden, Franks & James 2011), in

327   order for one individual to have a connection, it requires another to do so as well. We

328   used null models to estimate the statistical significance in the relationships between

329   the ecological variables and the connections among individuals within prides and

330   within subgroups. Null models allow us to account for confounding non-social factors

331   that affect the observations of co-occurrences among individuals, such as sampling

332   effort, so that only the signal of social factors that shapes the social network are

333   evaluated when estimating significance (Farine & Whitehead 2015; Farine 2017). We

334   first did a pre-network permutation test in the 'asnipe' package (Farine 2013) to

335   compare the mean weighted degree, network density and modularity of the study

336   pride networks to that of a random pride networks. Pre-network permutations work by

337   sequentially swapping observations of pairs of individuals between groups for each

338   iteration of the randomization to increasingly randomize the observed data (Bejder,

339   Fletcher & Brager 1998). After each swap, the associations among all individuals are

340   recalculated and the above three network measures recalculated. We conducted

341   10,000 such swaps, thus generating a null distribution from 10,000 randomised

342   networks. We then re-ran the same null model procedure but restricted swaps to only

343   occur within the subgroups that were identified within each network (i.e. within each

344   pride). We calculated the mean weighted degree and network density for each

345   subgroup networks and compared to that of random subgroup networks from the

346   previous null model. Conducting this analysis allowed us to determine whether

347   individuals are trading-off within-subgroup social investment versus pride-level social

348   investments because in the first null model the associations were re-distributed across

349   subgroups, whereas in the second null model the associations remained within

350   subgroups.

351

Results

353 We first generated a baseline understanding of social structure in four lion prides by

354 testing whether individual traits influence patterns of associations among individuals

355 in replicated networks, each representing four months of observations in one of two

356 dry seasons (see Methods). While there was a correlation between the individual trait

357 (age, sex and reproductive state) similarity and the probability for individuals to be

358 observed together (Table S2) in some prides, the adjusted R^2 value for the relationship

359 between similarity in individual traits and association patterns among individuals

360 within lion prides was generally low (except for Ngamo pride) (see Table S2).

361

362 We then tested whether prides exhibited structured patterns of subgrouping. We found

363 that the seasonal networks for each pride could be statistically partitioned into two,

364 three, or four subgroups (Table S3; Fig. 1). Season itself had no significant effect on

365 modularity (the strength of division of a network into subgroups, estimate $\pm$ SE = -

366 0.08 $\pm$ 0.13; t (7) = -0.62; p = 0.56). We then tested whether seasonally-varying

367 ecological factors could explain patterns of structure, including subgrouping, in the

368 networks.

369
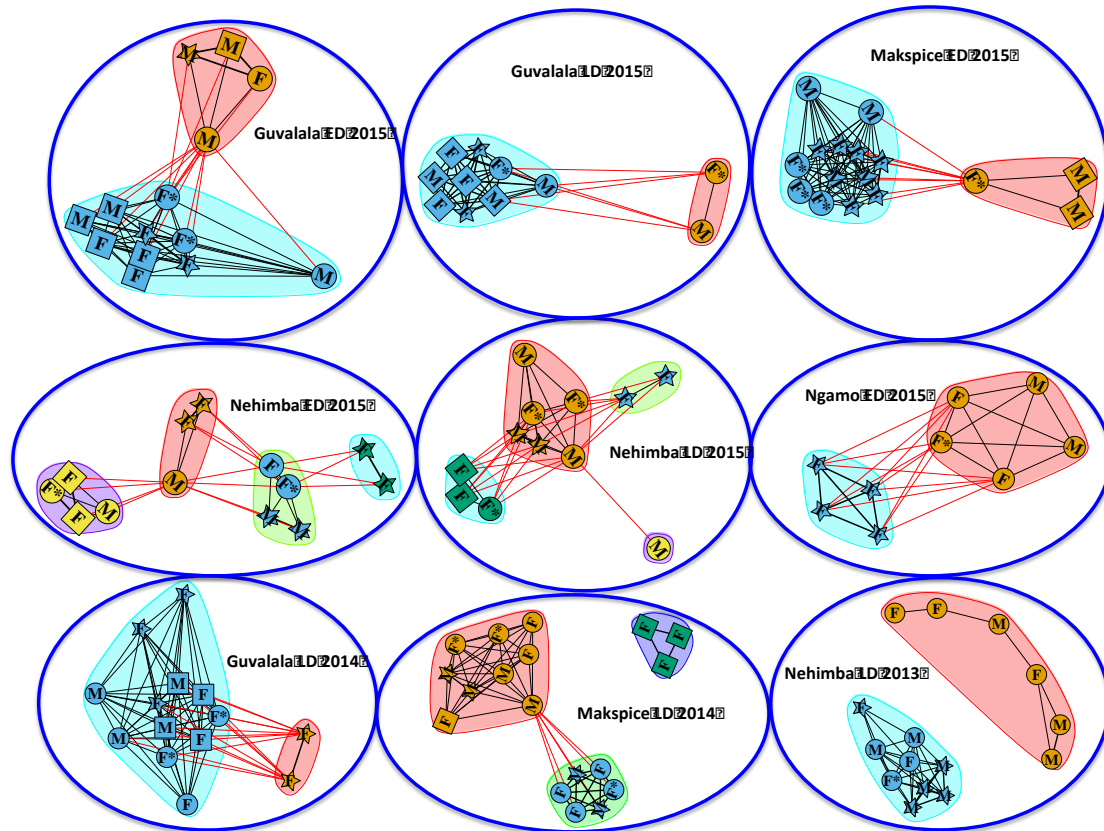
Fig. 1 Subgrouping patterns across a total of four prides, two distinct seasons (early dry season (ED) and late dry season (LD)) and three years (2013 to 2015). Pride identity, season and year are noted in each network. Each node, representing an individual lion, is assigned to a subgroup, which is denoted by node colour and coloured bubbles. The shape of the node donates lion age group (circle = adult, square = sub-adult and star = cub), the letter of the node indicates lion sex (M = male, F = female) and the * indicates the reproductive state (F* = females with cubs). Edge weights are proportional to the association index.

Prey abundance

The strength of division of prides into subgroups significantly increased (i.e. subgroups became clearer and more consistent) with increase in prey abundance (Table S4). Furthermore, the connections among individuals within prides became

384 significantly weaker with increasing prey abundance (Fig. 2a.i). However, this was

385 not significant when calculating strength of connections exclusively within subgroups

386 (Fig 2a.ii). Prey abundance had no significant effect on the gregariousness among

387 individuals (how many individuals were connected to, or network density) when

388 measured at the level of pride (Fig. 2.b.i) but an increase in prey abundance decreased

389 the gregariousness among individuals when measured at the level of the subgroups

390 (Fig. 2.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

391
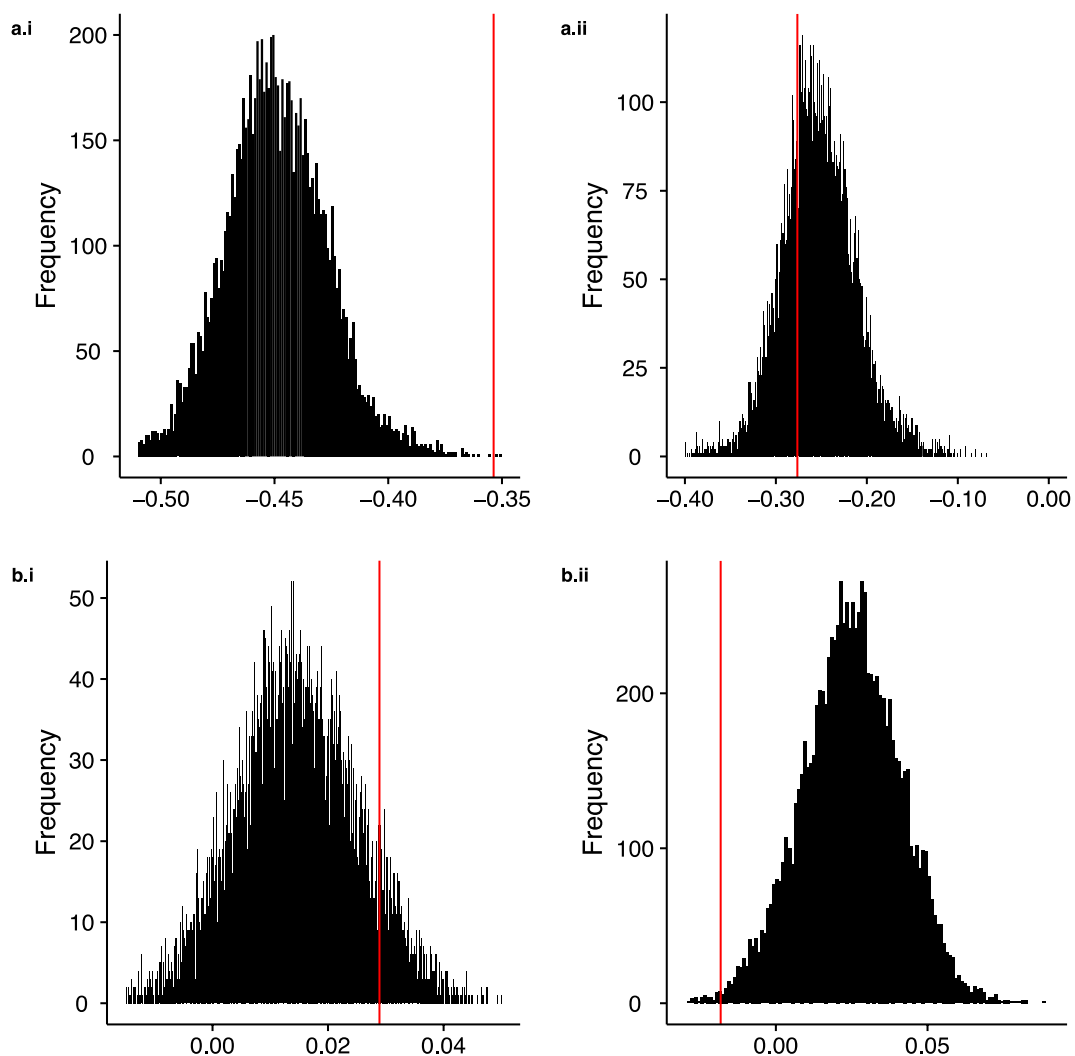
392

393 **Fig. 2.** The relationship between number of prey herds/km (index of prey abundance)

394 and a) mean weighted degree (strength of connections among individuals) within (i)
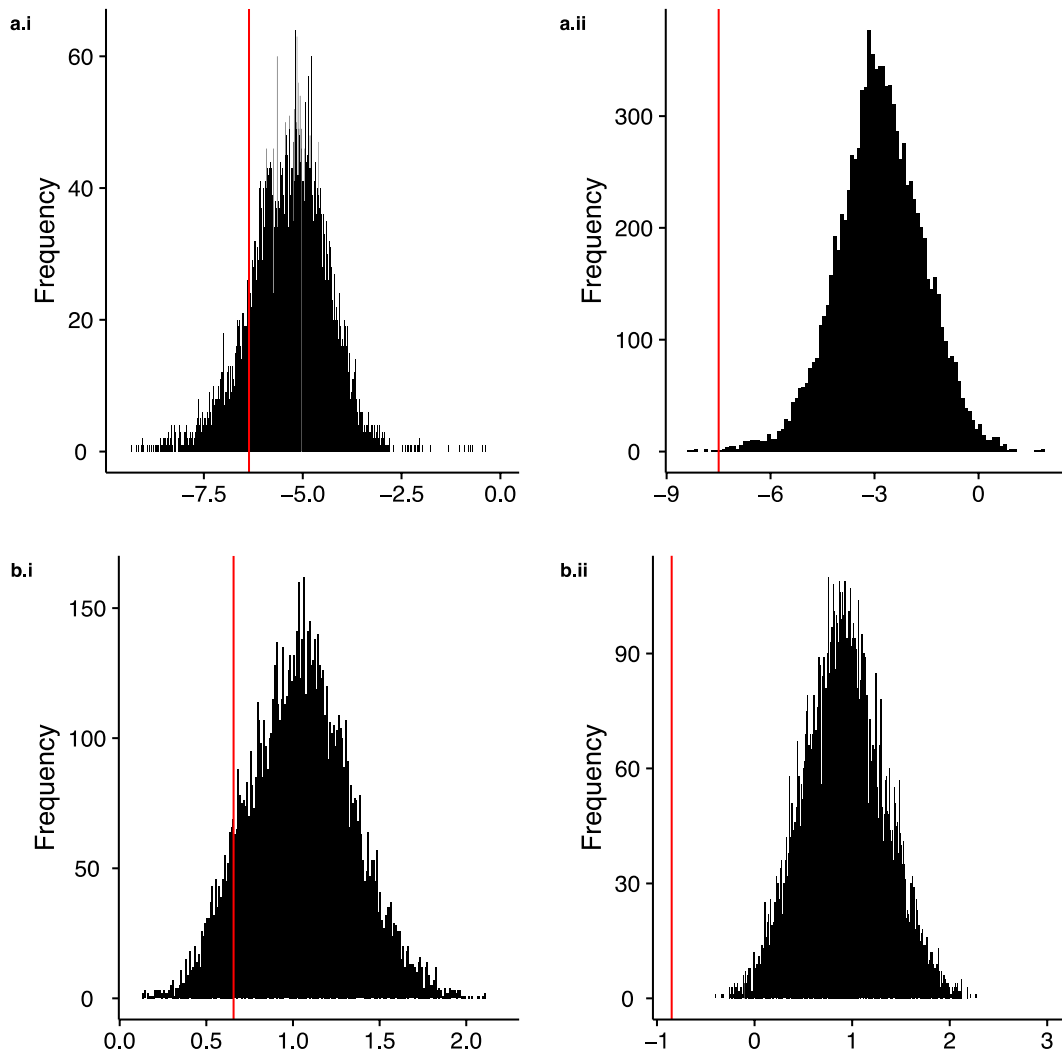
395   prides and (ii) subgroups and b) network density (gregariousness among individuals)

396   within (i) prides and (ii) subgroups. The distribution of the coefficients of the

397   regression slope of the random networks (black lines) and the observed network (red

398   line).

399

400   *Prey dispersion*

401   The strength of division of prides into subgroups significantly increased (i.e.

402   subgroups became clearer and more consistent, resulting in a higher modularity score)

403   with increase in prey dispersion (Table S4). Prey dispersion had no significant effect

404   on the strength of connections among individuals at the pride level, but significantly

405   increased the strength of connections among members of subgroups (Figs. 3a.i and

406   3a.ii). Prey dispersion had no significant effect on the gregariousness among

407   individuals when measured at the level of pride (Figs. 3.b.i) but an increase in prey

408   dispersion decreased the gregariousness within subgroups (Figs. 3.b.ii; see Figure S1,

409   Table S4, S5 and S6 for full results).

410

Fig. 3 The relationship between nearest neighbour index of prey herds (index of prey dispersion) and a) mean weighted degree (strength of connections among individuals) within (i) prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups. The distribution of the coefficients of the regression slope of the random networks (black lines) and the observed network (red line).

Patch richness (mean prey herd size)

Mean prey herd size, an index of patch richness, had no significant effect on the division of prides into subgroups (Table S4). The strength of connections among

422 individuals decreased at both the pride- and subgroup-level when prey herd size

423 increased (Figs. 4a.i; 4a.ii). Increase in prey herd size resulted in significant decrease

424 in gregariousness among individuals within prides (Fig. 4.b.i), and a significant

425 increase in gregariousness within subgroups (Fig. 4.b.ii; see Figure S1, Table S4, S5

426 and S6 for full results).

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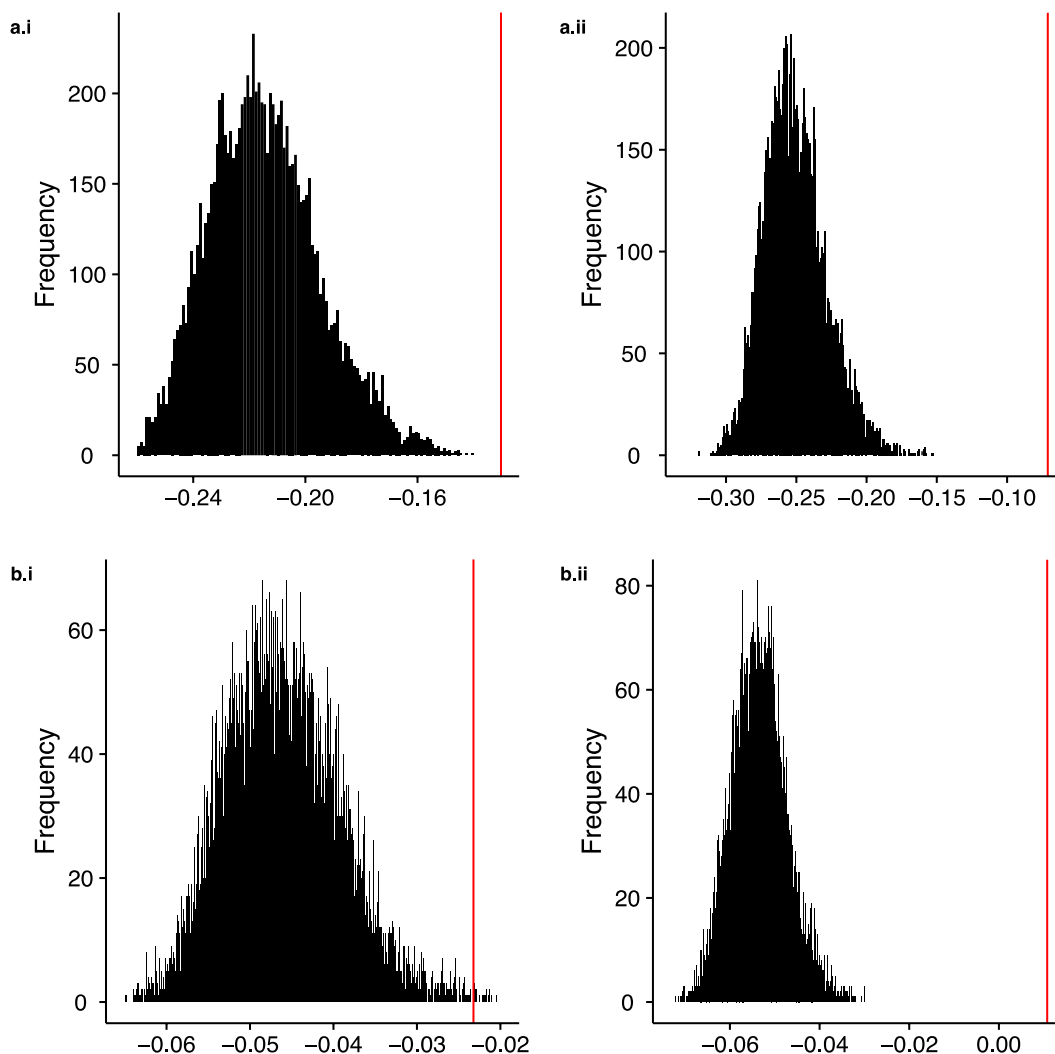
428

429 **Fig. 4** The relationship between mean prey herd size (index of patch richness) and a)

430 mean weighted degree (strength of connections among individuals) within (i) prides

431 and (ii) subgroups and b) network density (gregariousness among individuals) within

432 (i) prides and (ii) subgroups. The distribution of the coefficients of the regression

433   slope of the random networks (black lines) and the observed network (red line).

434

435   *Patch richness (mean prey body size)*

436   The strength of division of prides into subgroups decreased with an increase in mean

437   prey body size, meaning that individuals tended to associate more evenly with all

438   other members of their pride (Table S4). The strength of connections among

439   individuals within prides and subgroups increased significantly with an increase in

440   mean prey body size, with this effect being stronger within subgroups (Figs. 5a.i and
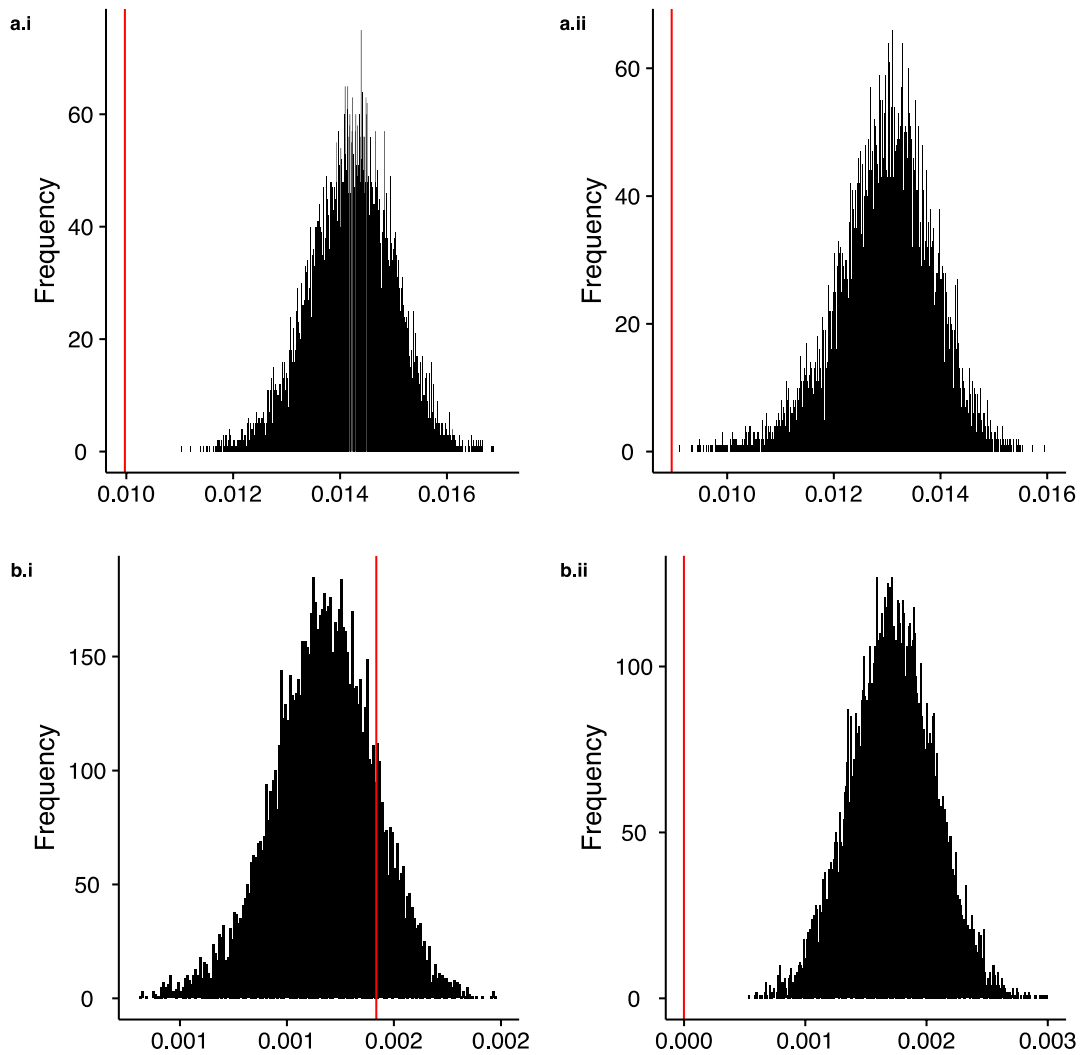
441   5a.ii). Mean prey body size had no significant effect on gregariousness when

442   measured at the level of pride (Fig. 5.b.i) but an increase in mean prey body size

443   significantly decreased the gregariousness among individuals when measured at the

444   level of the subgroups (Fig. 5.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

445

446

Fig. 5 The relationship between mean prey body size (index of patch richness) and a) mean weighted degree (strength of connections among individuals) within (i) prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups. The distribution of the coefficients of the regression slope of the random networks (black lines) and the observed network (red line).

Interspecific competition

The strength of division of prides into subgroups significantly increased (i.e. subgroups became clearer and more consistent) with an increase in interspecific competition (Table S4). The strength of connections among individuals significantly

457 decreased, for both pride and subgroups, when interspecific competition increased

458 (Figs. 6a.i; 6a.ii). Interspecific competition had no significant effect on the

459 gregariousness within prides (Fig. 6.b.i), but an increase in interspecific competition

460 significantly decreased the gregariousness among individuals within subgroups (Fig.

461 6.b.ii; see Figure S1, Table S4, S5 and S6 for full results).
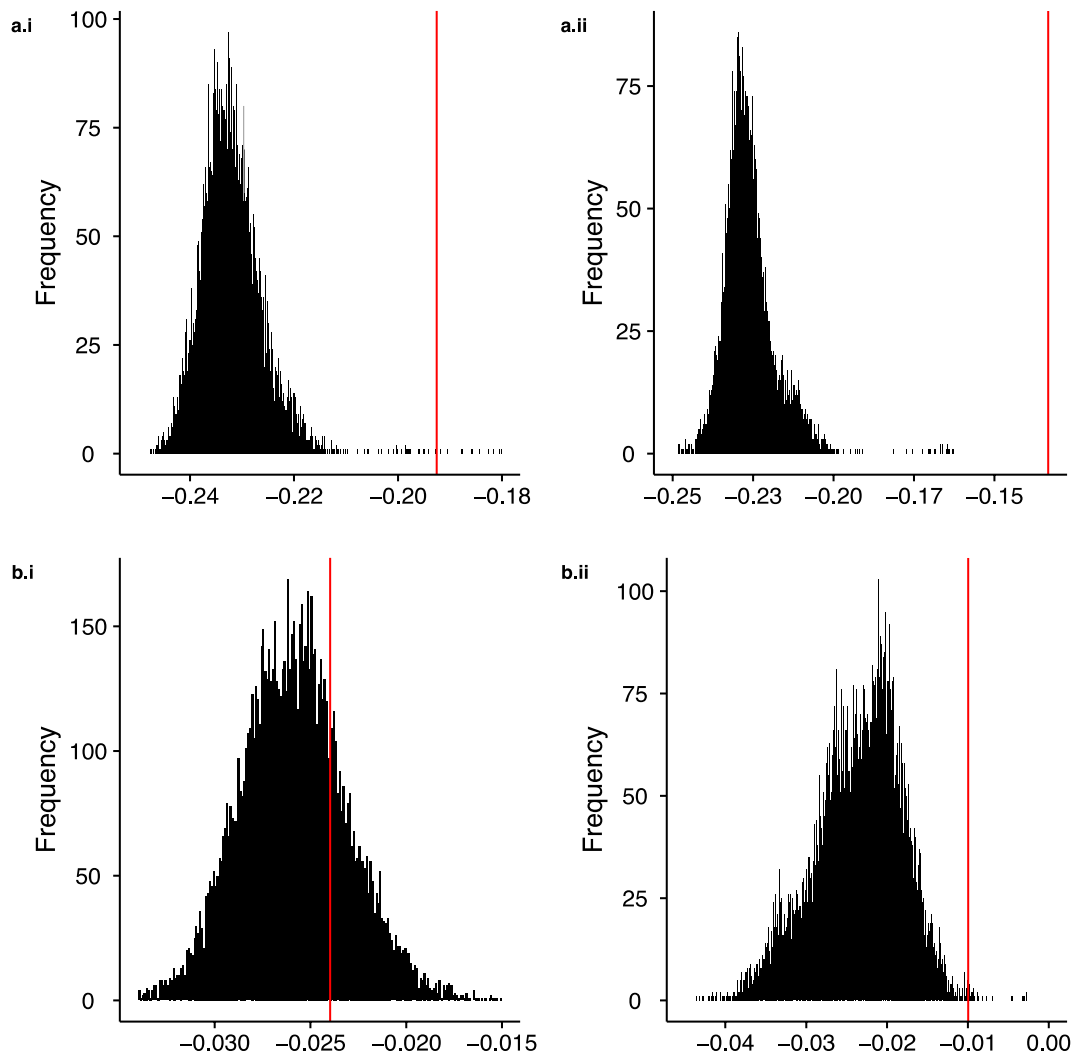
462

463 **Fig. 6** The relationship between ratio of hyaenas to lions (interspecific competition)

464 and a) mean weighted degree (strength of connections among individuals) within (i)

465 prides and (ii) subgroups and b) network density (gregariousness among individuals)

466 within (i) prides and (ii) subgroups. The distribution of the coefficients of the

467 regression slope of the random networks (black lines) and the observed network (red

468   line).

469

470   *Vegetation cover*

471   Vegetation cover had no significant effect on division of prides into subgroups (Table

472   S4). The effect of vegetation cover on the strength of connections among individuals
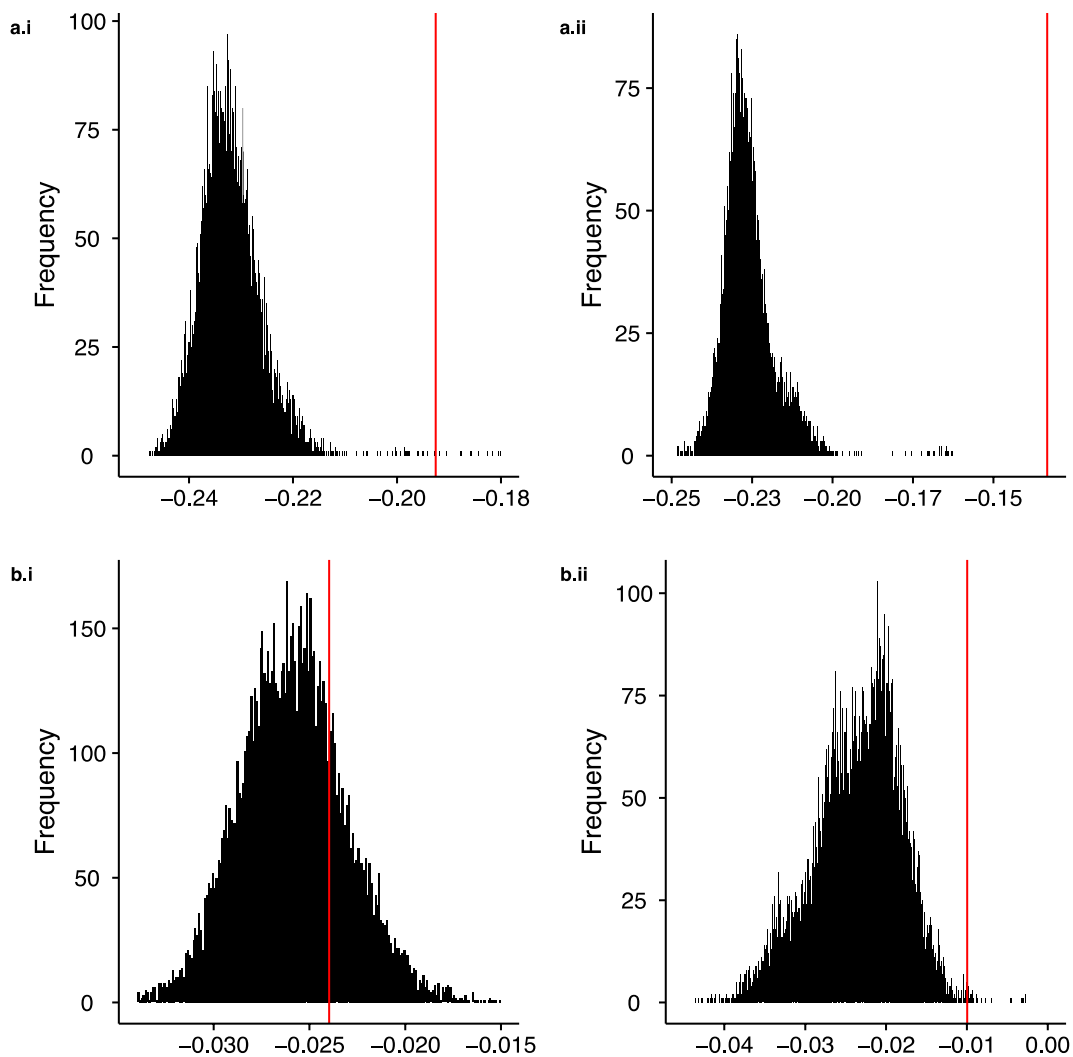
473   was not significant either within prides or within subgroups (Figs. 7a.i and 7a.ii). An

474   increase in vegetation cover resulted in a significant increase in gregariousness among

475   individuals within subgroups (Figs. 7.b.i, 7.b.ii; see Figure S1, Table S4, S5 and S6

476   for full results).

477

478

479   **Fig. 7** The relationship between percentage of closed vegetation (vegetation cover)

480   and a) mean weighted degree (strength of connections among individuals) within (i)

481   prides and (ii) subgroups and b) network density (gregariousness among individuals)

482   within (i) prides and (ii) subgroups. The distribution of the coefficients of the

483   regression slope of the random networks (black lines) and the observed network (red

484   line).

485

486   **Discussion**

487   Our study extends prior studies on the role of ecological factors in determining broad

488   population structure by demonstrating their effects on the fine scale patterns of

489   association among individuals at two scales: within groups and within subgroups.

490   More specifically, our study revealed that an increase in prey abundance, prey

491   dispersion, interspecific competition and a decrease in prey body size resulted in

492   clearer and more consistent subgroups. These ecological factors also affected the

493   strength, total amount, and variability in subgroup membership among individuals

494   within a pride. Our study therefore provides evidence that ecological factors can

495   shape both global and fine-scale properties of animal social systems, even when

496   species live in seemingly consistently structured societies (e.g. with defined and long-

497   lasting territories).

498

499   Individuals of similar characteristics often band together to form cliques, for example

500   coalition males in cheetahs (*Acinonyx jubatus*) come together to increase their

501   chances of holding territories (Caro & Collins 1986). Our network analyses captured

502   some fundamental properties of lion behaviour, including the general propensity for

503   lions to associate with individuals of the same sex. In lions, females often come

504   together to defend their cubs against nomadic males (Packer & Pusey 1983) whereas

505   males form coalition to take over and protect territories (Schaller 1972; Packer 1986).

506   However, overall our results suggest that the effect of individual trait similarity alone

507   explains relatively little of the variance in subgroup composition. One pride did show

508   consistent significant effects, but this is likely to be because this was a highly

509   gregarious pride composed of only adult males and females and their cubs, which was

510   quite unique to this particular pride.

511

512   Our key finding is that different axes of resource availability explained patterns of

513   social structure within groups and within subgroups. As the amount of available food

514   increased, prides tended to divide into subgroups. The excess available food might

515   provide individuals with an opportunity to invest more into strengthening bonds with

516   close associates within their subgroups rather than maintaining weaker bonds with all

517   pride members. Research in vampire bats (*Desmodus rotundus*) has highlighted that

518   strongly connected associates are the primary source of help when an individual is

519   going hungry (Carter *et al.* 2017). Subgroups of lions were also more gregarious when

520   food was scarce, capturing their tendency to maximize foraging efficiency by

521   searching in groups (Lachlan, Crooks & Laland 1998). Searching in groups is also

522   useful for sharing information about the resources as shown in other studies that

523   personal information and experience may be used to optimize search pattern and can

524   be useful in locating food patches (Aplin, Farine, Morand-Ferron & Sheldon 2012).

525   These results are in contrary to what Foster *et al.* (2012) discovered for killer whales

526   for which the associations between individuals in a group were stronger and the

527   network highly interconnected when food was abundant.

528

529   The dispersion of resources potentially increases searching behaviour (Sogard & Olla

530   1997; Valeix *et al.* 2010), thus limiting the opportunity for social interactions between

531   individuals at the pride level (Tanner & Jackson 2012). When resources are dispersed

532   across the landscape, prides tended to break into subgroups. We found that this led to

533   prides that were socially fragmented. Persistent separation between subgroups within

534   a pride reduces encounter rates and contacts among individuals across different

535   subgroups, which could have impacts on processes such as mate choice and other

536   social behaviours (Banks, Piggott, Stow & Taylor 2007; Krause, Lusseau & James

537   2009). Further, weaker associations between subgroups can make the pride less stable

538   (Beisner, Jackson, Cameron & McCowan 2011) and susceptible to other

539   anthropogenic and stochastic influences (Snijders, Blumstein, Stanley & Franks

540   2017). Recent experiments that involved temporarily splitting colonies of zebra

541   finches found that social instability increased social exclusivity (i.e. subgrouping)

542   and, as a result, decreased the collective performance of colonies in terms of foraging

543   efficiency (Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby & Farine 2018).

544   When resource patches become more aggregated, for example through clustering of

545   prey herds in patches of specific habitats or around waterholes (Valeix *et al.* 2009),

546   lion prides tend to use these resource patches intensively (Valeix *et al.* 2010). This

547   aggregation of prey appears to allow regular associations among pride members,

548   leading to highly connected pride members with little subgrouping within prides.

549   Golden jackals (*Canis aureus*) have also been reported to aggregate around clumped

550   food sources resulting in a larger and more cohesive group (Macdonald 1979).

551

552   Prey herd size had no significant effect on the strength of the division of the pride into

553   subgroups, however the overall strength of connections among individuals, within

554 both prides and subgroups, decreased with increase in the size of prey herds. This

555 result is contrary to what we were expecting since larger prey herds can potentially

556 provide a chance for several predators within a group to make a kill or for more than

557 one individual to be killed from the herd (e.g. Creel & Creel 2002). Our results might

558 instead be interpreted in terms of lion foraging behaviour where both prides and

559 subgroups avoid hunting large prey herds because the increased vigilance by very

560 large groups reduces the attack success rate (Kenward 1978; Cresswell & Quinn

561 2011) which could make it difficult for lions to hunt successfully, especially buffalos

562 which have been known to mob predators and kill lions (Mangani 1962; Estes 1991).

563 In Serengeti lions have been shown to prefer smaller prey herds over large herds

564 (Scheel 1993).

565

566 We further found that the strength of division of prides into subgroups decreased with

567 increase in prey size. Large prey species (rich patches) such as buffalo, zebra, giraffe

568 or juvenile elephant can feed several lions, consequently, competition for prey within

569 the pride is likely to be minimal and individuals can associate frequently outside of

570 their close connections. Essentially, individuals in the pride tended to come together

571 more often (fusion), which could allow them to cooperatively hunt the large sized

572 prey (Scheel & Packer 1991) and increase success of prey capture (but see Caraco &

573 Wolf 1975; Packer *et al.* 1990) while minimizing energetic costs (Carbone, Teacher

574 & Rowcliffe 2007). Similarly, Kruuk (1972), and later Smith, Kolowski, Graham,

575 Dawes and Holekamp (2008), showed that when energy per resource patch is high,

576 hyaenas tend to congregate at such food patches and spend relatively more time with

577 conspecifics than alone. As a result the increased pride-level cohesion when prey is

578 large may also provide a number of other benefits to pride members, including

579 increased chances of communal defence of cubs (Packer & Pusey 1983) and territorial

580 defence (Grinnell 2002; Mosser & Packer 2009).

581

582 The strength of division of prides into subgroups increased with increase in

583 interspecific competition with the hyena. Furthermore, the gregariousness among

584 individuals in both subgroups and prides and the strength of their connections

585 decreased with increase in competition. This was contrary to our expectations of how

586 interspecific competition and predation risk would influence the fine scale animal

587 social structure. We expected cooperation to be higher and connections stronger

588 particularly in areas where there are higher densities of hyaenas as lions might need to

589 defend their kills from hyaenas (Cooper 1991). Perhaps our result is because the

590 cooperative mobbing behaviour by hyenas when they encounter lions (Lehmann *et al.*

591 2017) has the effect of weakening the bonds between individual lions and reducing

592 gregariousness.

593

594 As stalk-and-ambush hunters, vegetation cover has been shown to be an important

595 variable in the foraging behaviour and hunting success of lions (Funston, Mills &

596 Biggs 2001; Hopcraft *et al.* 2005) particularly for male lions (Loarie *et al.* 2013). In

597 our study, gregariousness among individuals within subgroups increased with

598 increase in vegetation cover. As expected of a stalk-and-ambush predator, lions would

599 spend more time and associate more with subgroup members, for a more coordinated

600 hunt in areas of good cover (Stander & Albon 1993; Hopcraft *et al.* 2005) where they

601 have a higher chance to successfully hunt prey like buffalo that are vulnerable to

602 predation in dense bush (Hay, Cross & Funston 2008).

603

604   The structure of the pride social networks, and the subgroups therein, captured the

605   trade-offs individuals face between associating generally (equally across the pride)

606   when resources are abundant and easy to find and catch, and associating more

607   exclusively (in subgroups of preferred associates) when resources are scarce or more

608   difficult to come by. Thus, we found seemingly consistent and predictable patterns of

609   ecological factors on different aspects of within-pride social structure. However, the

610   effect of ecological factors on the strength of connections and the frequency of

611   associations among individuals were often more pronounced within subgroups than at

612   the pride-level. Our results therefore suggest that the changes in pride structure under

613   different ecological conditions can be dramatic from the perspective of individuals.

614

615   Our findings could be important given that individual lions are highly dependent on

616   their pride mates for survival and reproduction (Packer, Pusey & Eberly 2001). Our

617   results also suggest that increasing pride-level connectance with decreasing prey

618   abundance is likely to arise from re-allocation of social associations from subgroups

619   to other group members. This contrasts with a more traditional view of hierarchical

620   societies in which higher-level organisation (here a pride) emerges from connections

621   among more stable lower levels (here subgroups). Drawing on our knowledge of

622   decision-making, our findings may insinuate that individual lions are making

623   decisions at both the subgroup level and at the pride level.

624

625   A number of studies have examined the relationship between ecological factors and

626   group size across a range of species, for example white-throated magpie-jays

627   (*Calocitta formosa*) (Langen & Vehrencamp 1998), river dolphins (Gomez-Salazar,

628   Trujillo & Whitehead 2012) and lions (Mbizah *et al.* 2019). Our findings suggest that

629   ecological factors can also influence the more complex fine-scale elements of social

630   dynamics within groups. Decisions about sociality are often optimized to maximize

631   individual fitness (Silk 2007; Farine, Montiglio & Spiegel 2015b) and in our study we

632   found that individuals compromise between having few strong connections and

633   having many weaker connections. These patterns mirror recent findings in vampire

634   bats showing that individuals exhibit patterns of social bet-hedging, maintaining both

635   stronger and weaker associations, which are differentially important in times of need

636   (Carter *et al.* 2017). We further show that the trade-off is driven by different axes of

637   variation in the underlying distribution of ecological resources. Our study therefore

638   provides evidence that ecological factors can shape fine-scale properties of animal

639   social systems at different scales, even when species live in structured societies that

640   outwardly appear to be consistent.

641

661 **Authors' Contributions**

662 M.M.M., D.R.F., M.V., J.E.H., D.W.M., A.J.L. conceived the ideas and designed the

663 methodology; M.M.M. collected the data; M.M.M and D.R.F analysed the data;

664 M.M.M. led the writing of the manuscript. All authors contributed critically to the

665 drafts and gave final approval for publication.

666

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Supplementary Information Text

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898 *S1 Appendix*

899 **The spoor survey method**

900 In this study prey availability was assessed using the spoor counting method, which is

901 an indirect method of estimating population abundance. This method assumes that the

902 intensity or frequency of animal signs is correlated to population size (Wilson &

903 Delahay 2001). Spoor counting has been extensively used for estimating carnivore

904 abundance (e.g. Funston *et al.* 2010), and has been found to be reliable for estimating

905 abundance of large herbivores as well (e.g. Silveira, Jacomo & Diniz 2003). Multi-

906 species spoor (animal track) count surveys were conducted from 2013 to 2015 during

907 the early dry season and the late dry season. Roads or routes, termed transects, were

908 divided into short segments, and these formed the units of the survey. Selected

909 transects were driven and spoor were identified with the help of highly skilled and

910 experienced trackers and care was taken to avoid double counting spoor. Vehicles

911 driven at a speed of 10 - 15 $km.h^{-1}$ served as an observation platform during spoor

912 surveys, with a driver, a recorder and a tracker sitting on a customized seat mounted

913 to the front of a vehicle. Roads were not swept before the surveys and surveys were

914 undertaken once per season for each of the five study sites.

915 When fresh spoor (less than 24h old) was encountered, it was assessed for

916 species, herd size, age class and sex. The experienced trackers were able to determine

917 if the spoor was fresh by the state and detail of the spoor, the shape and size of the

918 spoor aided in determining the species, its age and sex, while the number of spoors

919 around that area were counted to get the herd size. Only prey species and herd size

920 were used in the analyses and we are confident that our highly skilled and

921 experienced trackers could reliably assess these. Spoor were counted if they crossed

922 transects but subsequent re-crossings were ignored when the trackers judged from the

923 animal's movement patterns that these were apparently made by the same animal.

924 During the surveys, spoor of a range of herbivores and carnivores were identified to

925 the species level, but only spoor from lion prey species were used in this study. Prey

926 species included in the analysis were Burchell's zebra (*Equus quagga*), giraffe

927 (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala

928 (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), steenbok (*Raphicerus

929 campestris*), common duiker (*Sylvicapra grimmia*), sable (*Hippotragus niger*), roan

930 antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*)

931 and juvenile African elephant (*Loxodonta Africana*) (frequently recorded as prey

932 during drought years in Hwange; Loveridge, Hunt, Murindagomo & Macdonald

933 2006).

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935 *S2 Appendix*

936 **Prey availability within lion home ranges**

937 Lion home ranges were defined as the 90% probability contour of location

938 distribution using the fixed kernel density estimator (Powell 2000) and the reference

939 smoothing factor href (Hemson *et al.* 2005). Home range analyses was undertaken

940 using the 'AdehabitatHR' package in the statistical software R (Calenge 2006). We

941 used data from only one GPS collared lion per pride for each of the lion pride seasons.

942 Prey availability data from spoor counts were overlaid on lion home ranges in QGIS

943 (QGIS Development Team 2019) and the road transects that fell within each lion

944 home range were clipped. For each home range and each season, we calculated four

945 measures of prey availability, comprised of an index of prey abundance (number of

946 prey herds/km), an index of prey dispersion (nearest neighbour index of prey herds),
947 and two indices of patch richness (mean prey herd size and mean prey body size). The
948 nearest neighbour index was calculated in QGIS (QGIS Development Team 2019) by
949 measuring the distance between each prey herd and its nearest neighbour and then
950 averaging all these nearest neighbour distances. Prey body sizes were obtained from
951 Cumming and Cumming (2003).
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953 **Figures**

Ecological factors	Modularity	Weighted degree		Network density	
	Pride level	Pride level	Subgroup level	Pride level	Subgroup level
Prey abundance	*2.498*	*4.166*	-0.646	1.365	*-2.888*
Prey dispersion	*6.061*	-1.047	*-3.694*	-1.292	*-4.605*
Herd size	1.664	*4.165*	*7.708*	*3.269*	*11.655*
Prey size	*-7.443*	*-5.477*	*-4.507*	1.023	*-5.169*
Ratio hyena to lion	*4.231*	*6.547*	*12.435*	0.674	*2.721*
Vegetation cover	-1.387	-0.637	-1.408	-0.904	*-5.825*

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956 **Fig. S1** The scaled coefficients of the relationship between ecological factors and (i)
957 modularity (strength of division of a network into subgroups), (ii) mean weighted
958 degree (strength of connections among individuals) and (iii) network density
959 (gregariousness among individuals). The bold and italics coefficients indicate
960 significant relationships. For weighted degree and network density, the negative
961 relationships become more negative along the blue gradient and positive relationships
962 become more positive along the orange gradient.
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Supplementary Information Tables

Table S1. Description of the factors that may influence lion social structure and the
four hypotheses tested in this study: (i) individual trait similarity, (ii) prey availability,
(iii) interspecific competition, and (iv) vegetation cover.

Description of Social and Ecological Factors
A. Social Factors
(i) Individual trait similarity
Sex - Grouping patterns of male lions may be influenced by their tendency to form coalitions that cooperate to compete with other coalitions for exclusive access to females (Packer & Pusey 1982). Grouping patterns of female lions is believed to be influenced by the need to protect their young and also maintain a long-term territory (Packer, Scheel & Pusey 1990).
Age - Age specific behaviour can also influence grouping patterns in lions. For example, subadult male lions may disperse from their natal pride and form coalitions with other dispersing subadult males (Van Orsdol 1981).
Reproductive state - In lions, lactating mothers tend to temporarily separate from the rest of the pride to forage and nurse their young (Packer *et al.* 1990).
B. Ecological Factors
(ii) Prey availability
Prey abundance - According to the prey abundance hypothesis, lions would be predicted to prefer areas of higher prey abundance (Hopcraft, Sinclair & Packer 2005), therefore individual lions may aggregate around these areas of high prey abundance
Prey dispersion - A measure of prey dispersion describes the distance lions have to travel to encounter prey or the effort involved in searching for prey. Lions would be expected to aggregate around areas of clustered prey patches, which are easily accessible (Valeix *et al.* 2010).
Prey herd size - A larger herd of prey might be considered a richer patch insofar as, all else being equal, it provides an opportunity for more than one lion to make a kill (in the Serengeti lions were observed sometimes to kill multiple prey when several lions attacked a herd and each captured an animal (Schaller 1972, page 251)) and also provides a higher chance of the lions finding a vulnerable individual within the herd. Larger preys herds are therefore expected to support larger lions groups.
Prey body size - A large bodied prey also might be considered a rich patch insofar as, for example, a single eland or giraffe could readily feed several lions, whereas a single gazelle could not. Availability of large prey would therefore promote large lions groups and strengthen group ties.
(iii) Interspecific competition
Hyaena to lion ratio - It is suggested that competition with hyaenas may impact the grouping patterns and social structure of lions (Cooper 1991). To avoid detection and encounters with hyaenas, lions may form smaller prides and also hunt smaller prey, so that they are less conspicuous (Périquet, Fritz & Revilla 2015). It is therefore likely that the ratio of hyaenas to lions may have an effect on lion social structure and grouping patterns.
(iv) Vegetation cover
Percentage of closed vegetation - As ambush predators, lions usually rely on cover when hunting (Hopcraft *et al.* 2005; Davidson *et al.* 2012). Dense vegetation would therefore provide cover for stalking lions and enable them to ambush their prey. The

increased chances of prey capture provided by the dense vegetation may increase the
frequency with which individuals come together to hunt.

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1035 **Table S2.** Multiple regression quadratic assignment procedure (MRQAP) results for
1036 the effect of individual trait (sex, age and reproductive state (Repro state)) similarity
1037 on the connections among lions in a pride in the nine-pride seasons from 2013 to
1038 2015. In bold are the significant P values.

Pride	Season/Year	Trait	β	P (β<=r)	P	R^2
Guvalala	Early dry 2015	Age	0.024	0.037	**0.073**	0.035
		Sex	-0.029	0.959	**0.082**	
		Repro state	0.173	0.000	**0.000**	
Guvalala	Late dry 2015	Age	0.188	0.001	**0.002**	0.012
		Sex	0.116	0.015	**0.031**	
		Repro state	-0.049	0.995	**0.009**	
Makspice	Early dry 2015	Age	0.067	0.058	0.116	0.035
		Sex	0.098	0.130	0.260	
		Repro state	0.033	0.102	0.204	
Nehimba	Early dry 2015	Age	0.043	0.131	0.262	0.030
		Sex	0.137	0.004	**0.007**	
		Repro state	-0.056	0.684	0.632	
Nehimba	Late dry 2015	Age	0.079	0.158	0.317	0.059
		Sex	0.136	0.003	**0.005**	
		Repro state	0.012	0.133	0.265	
Ngamo	Early dry 2015	Age	0.569	0.002	**0.004**	0.737
		Sex	0.180	0.000	**0.000**	
		Repro state	0.214	0.000	**0.000**	
Guvalala	Late dry 2014	Age	0.038	0.038	**0.077**	0.062
		Sex	0.075	0.242	0.484	
		Repro state	0.174	0.000	**0.001**	
Makspice	Late dry 2014	Age	0.142	0.046	**0.093**	0.062
		Sex	0.099	0.019	**0.038**	
		Repro state	0.013	0.851	0.299	
Nehimba	Late dry 2013	Age	-0.038	0.642	0.715	0.010
		Sex	0.015	0.332	0.663	
		Repro state	-0.193	0.899	0.202	

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Table S3. The number of pride observations (Obs), number of individuals in a pride (Indiv), number of subgroups (Sub), and the three network metrics; modularity (strength of division of a network into subgroups), mean weighted degree (strength of connections among individuals) and network density (gregariousness among individuals) for each pride, per season, per year.

Pride	Year	Season	Obs	Indiv	Sub	Modularity	Weighted degree	Network density
Guvalala	2015	Early dry	66	14	2	0.24	3.39	0.60
Guvalala	2015	Late dry	45	11	2	0.04	4.95	0.65
Makspice	2015	Early dry	29	16	2	0.09	4.37	0.66
Nehimba	2015	Early dry	16	13	4	0.52	2.00	0.35
Nehimba	2015	Late dry	23	12	4	0.30	1.76	0.50
Ngamo	2015	Early dry	33	9	2	0.37	2.52	0.62
Guvalala	2014	Late dry	31	14	2	0.07	3.71	0.77
Makspice	2014	Late dry	23	18	3	0.56	3.19	0.35
Nehimba	2013	Late dry	26	15	2	0.16	3.00	0.32

Table S4. The coefficient (β), P value (P), range of random coefficients (range from, range to), mean and standard deviation (SD) for the relationship between ecological factors and modularity (strength of division of a network into subgroups). In bold are the significant P values.

Ecological factors	β	P	Range from	Range to	Mean	SD
Prey abundance	0.036	**0.008**	-0.133	0.0643	-0.0091	0.0182
Prey dispersion (PD)	0.266	**0.008**	-2.815	0.8430	-1.0000	0.4917
PD Without-outlier	3.235	**<0.001**	-1.167	2.9525	0.3392	0.4777
Herd size	0.045	0.114	-0.006	0.0638	0.0259	0.0112
Prey size	-0.003	**<0.001**	-0.003	0.0011	-0.0005	0.0004
Ratio hyaena to lion	0.023	**<0.001**	-0.006	0.0217	0.0064	0.0039
Vegetation cover	-0.010	0.176	-0.023	0.0004	-0.0065	0.0027

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Table S5. The coefficient (β), P value (P), range of random coefficients (range from, range to), mean and standard deviation (SD) for the relationship between ecological factors and mean weighted degree (strength of connections among individuals) at the pride level and within subgroups. In bold are the significant P values.

Ecological factors	β	P	Range from	Range to	Mean	SD
Pride level						
Prey abundance	-0.354	**<0.001**	-0.539	-0.3504	-0.4494	0.0230
Prey dispersion	-6.360	0.272	-10.453	-0.3831	-5.3600	0.9548
Herd size	-0.130	**0.002**	-0.272	-0.0996	-0.2144	0.0202
Prey size	0.010	**<0.001**	0.009	0.0165	0.0141	0.0008
Ratio hyaena to lion	-0.193	**0.003**	-0.248	-0.1776	-0.2320	0.0060
Vegetation cover	0.094	0.464	0.079	0.1084	0.0962	0.0034
Subgroup level						
Prey abundance	-0.276	0.560	-0.432	-0.0683	-0.2535	0.0424
Prey dispersion	-7.497	**0.002**	-8.701	2.2460	-2.8376	1.2537
Herd size	-0.071	**<0.001**	-0.320	-0.1002	-0.2508	0.0226
Prey size	0.009	**<0.001**	0.009	0.0163	0.0130	0.0009
Ratio hyaena to lion	-0.133	**<0.001**	-0.248	-0.1629	-0.2263	0.0077
Vegetation cover	0.069	0.189	0.050	0.0942	0.0781	0.0066

Table S6. The coefficient (β), P value (P), range of random coefficients (range from, range to), mean and standard deviation (SD) for the relationship between ecological factors and network density (gregariousness among individuals) at the pride level and within subgroups. In bold are the significant P values.

Pride level	β	P	Range from	Range to	Mean	SD
Prey abundance	0.029	0.182	-0.025	0.0502	0.0145	0.0106
Prey dispersion	0.657	0.201	0.067	2.2194	1.0454	0.3004
Herd size	-0.023	**0.005**	-0.066	-0.0187	-0.0461	0.0070
Prey size	0.001	0.299	0.000	0.0020	0.0012	0.0002
Ratio hyaena to lion	-0.024	0.475	-0.036	-0.0150	-0.0259	0.0028
Vegetation cover	0.011	0.362	0.008	0.0173	0.0125	0.0014
Subgroup level						
Prey abundance	-0.018	**0.009**	-0.029	0.0966	0.0250	0.0162
Prey dispersion	-0.849	**<0.001**	-0.397	2.2734	0.9133	0.4126
Herd size	0.011	**<0.001**	-0.074	-0.0274	-0.0534	0.0061
Prey size	0.000	**<0.001**	0.000	0.0031	0.0017	0.0003
Ratio hyaena to lion	-0.010	**0.006**	-0.044	-0.0027	-0.0235	0.0055
Vegetation cover	0.006	**<0.001**	0.006	0.0189	0.0140	0.0014

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