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1 **Effect of ecological factors on fine-scale patterns of social structure in African**
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 (*Carcinus 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

151 catch, and because lions become more susceptible to interspecific competition from
152 spotted hyaenas (*Crocuta crocuta*) that frequently cooperate to move lions at fresh
153 kills (Kruuk 1972). In general, group size has fitness benefits apart from resources,
154 the demands of protecting their young and themselves against encounters with
155 neighbouring prides (Packer 1986; Mosser & Packer 2009) and maintaining a long-
156 term territory (Packer *et al.* 1990; Mosser & Packer 2009) can result in lions forming
157 larger groups. Here we argue that fitness benefits might shape the tendency for
158 members of a given pride to remain cohesive or to split into smaller subgroups, which
159 is a much more flexible strategy than adding or removing members from the pride.
160 Social bonds are therefore likely to form the basis of how species such as lions
161 respond socially to ecological processes. We expect to observe a trade-off between
162 maintaining fewer but stronger bonds when conditions are good and maintaining more
163 but weaker bonds when conditions are poor and more challenging.

164

165 In this study, we combine data on the fine-scale patterns of association among
166 individuals across multiple prides of African lions with data on the prey herds in each
167 pride's territory within Hwange National Park, Zimbabwe. We consider a herd of
168 prey to represent a resource patch available to lions (Carr & Macdonald 1986), and
169 the abundance, dispersion, and richness of these patches (see Table S1) as important
170 attributes that can influence the opportunities for social interactions (Tanner &
171 Jackson 2012). Resource richness is measured by the herd size and body size of
172 mixed herds of prey. Breaking down prey availability into different axes allows us to
173 better understand the effects of prey availability on fine scale patterns of association,
174 distinguishing our study from many of its predecessors that used only prey abundance
175 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 km² 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 km² 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

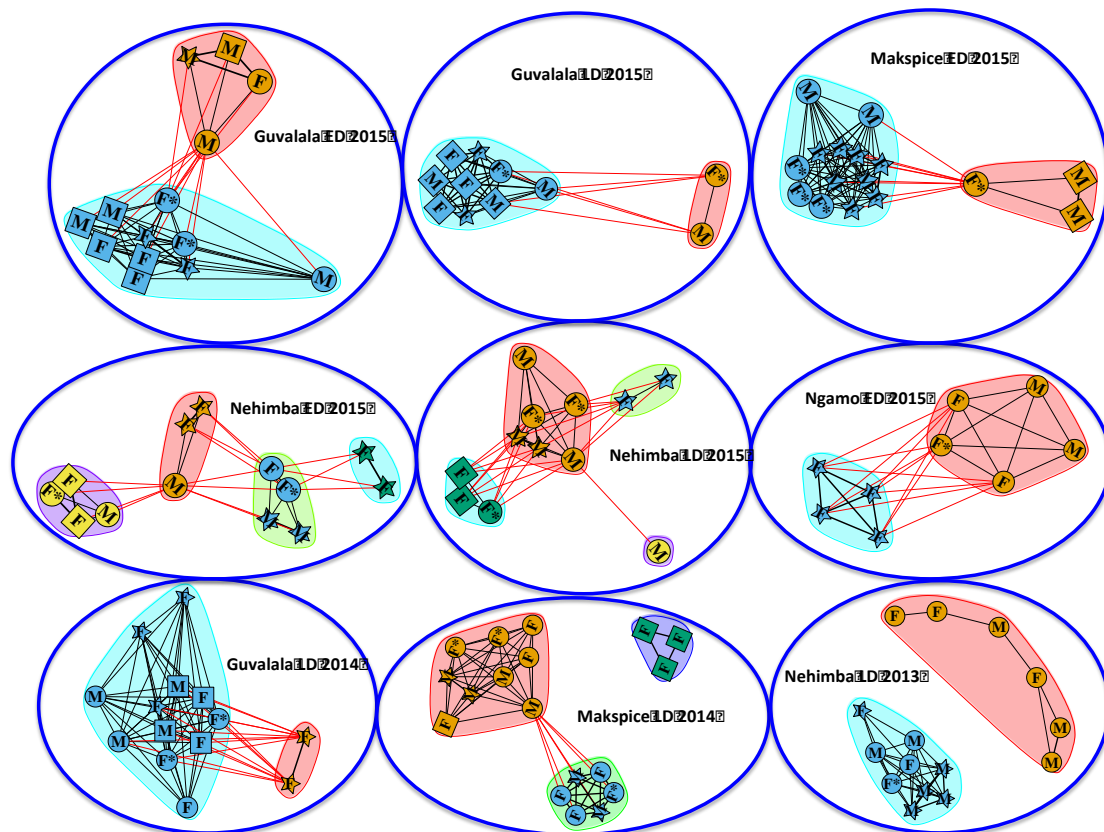
352 **Results**

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 ± 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



370

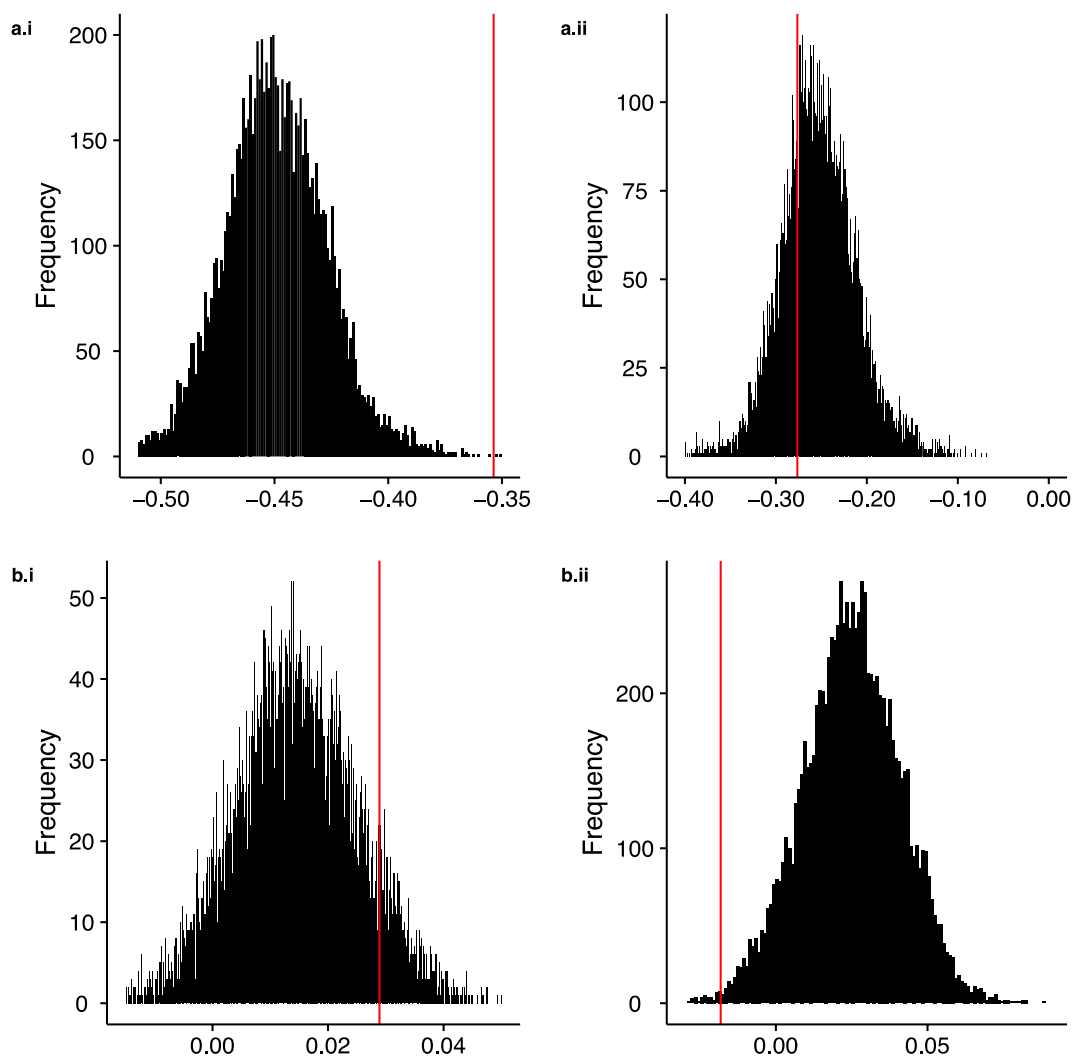
371 **Fig. 1** Subgrouping patterns across a total of four prides, two distinct seasons (early
 372 dry season (ED) and late dry season (LD)) and three years (2013 to 2015). Pride
 373 identity, season and year are noted in each network. Each node, representing an
 374 individual lion, is assigned to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

379

380 *Prey abundance*

381 The strength of division of prides into subgroups significantly increased (i.e.
 382 subgroups became clearer and more consistent) with increase in prey abundance
 383 (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)

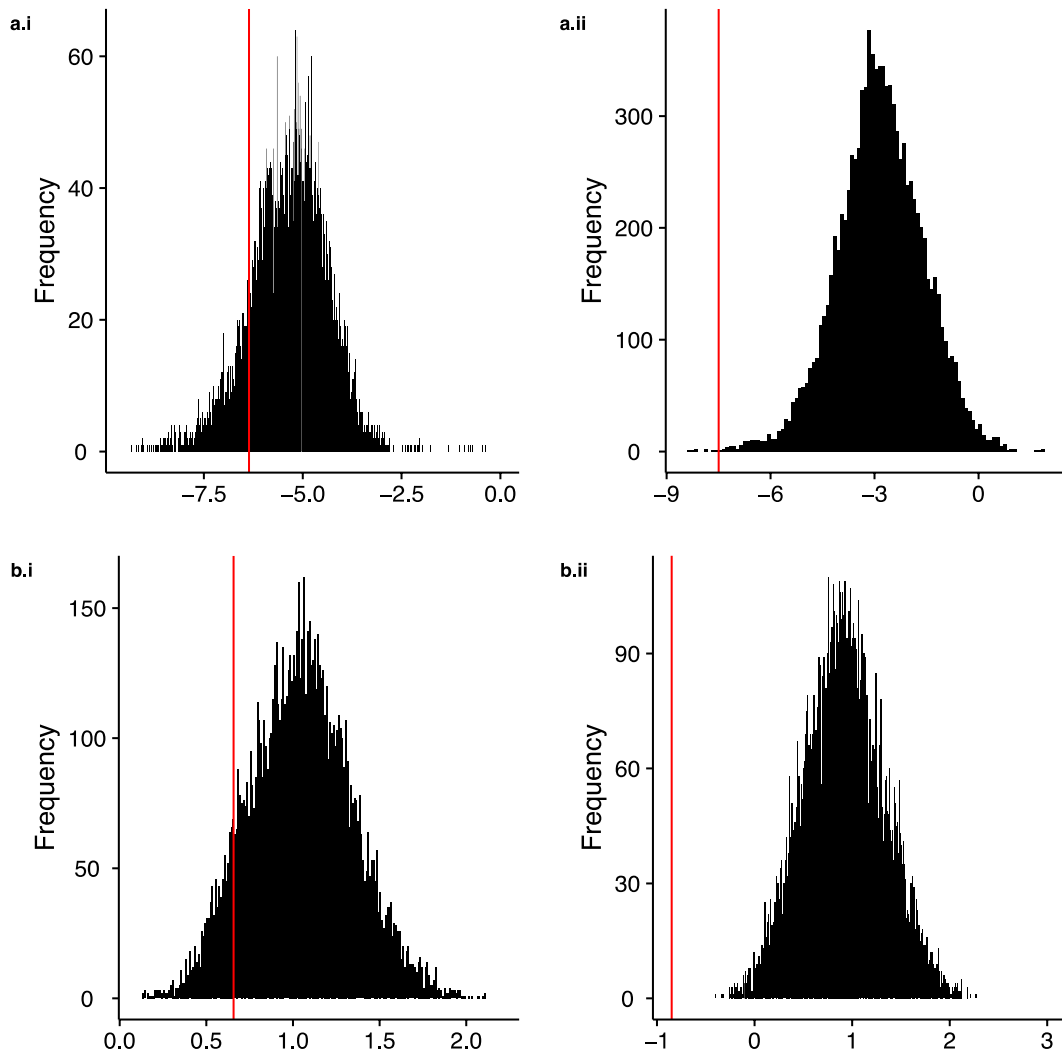
395 prides and (ii) subgroups and b) network density (gregariousness among individuals)
396 within (i) prides and (ii) subgroups. The distribution of the coefficients of the
397 regression slope of the random networks (black lines) and the observed network (red
398 line).

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



411

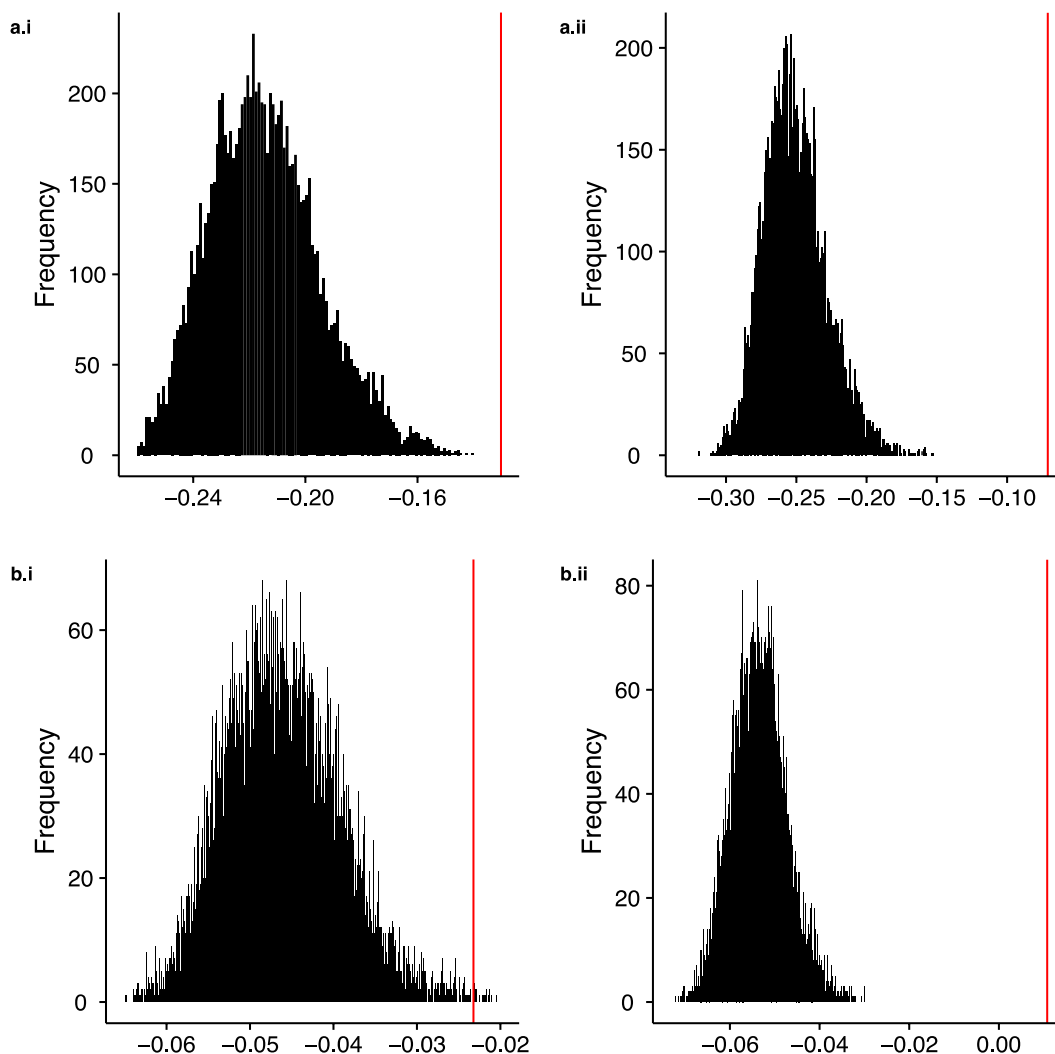
412 **Fig. 3** The relationship between nearest neighbour index of prey herds (index of prey
 413 dispersion) and a) mean weighted degree (strength of connections among individuals)
 414 within (i) prides and (ii) subgroups and b) network density (gregariousness among
 415 individuals) within (i) prides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

418

419 *Patch richness (mean prey herd size)*

420 Mean prey herd size, an index of patch richness, had no significant effect on the
 421 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).
427



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

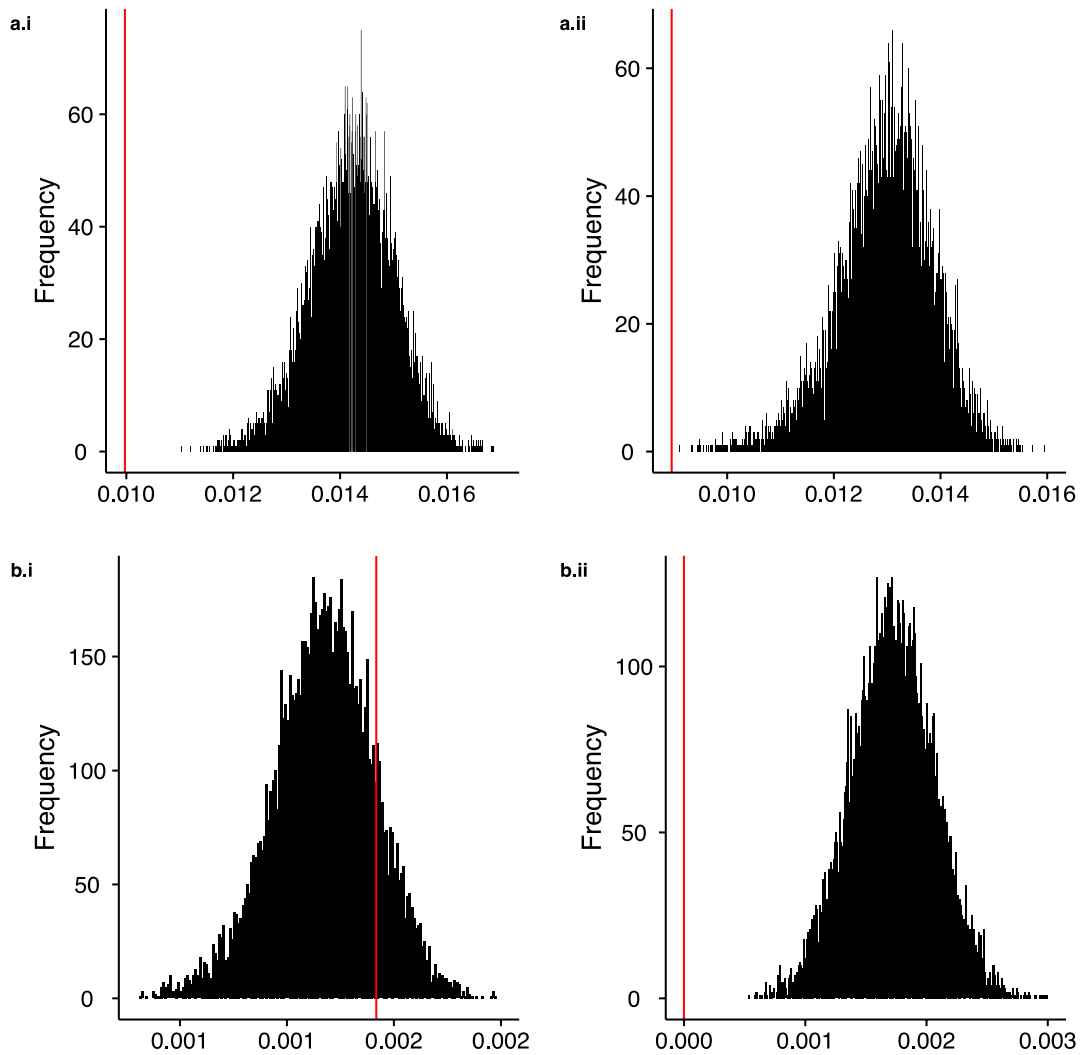
441 5a.ii). Mean prey body size had no significant effect on gregariousness when

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

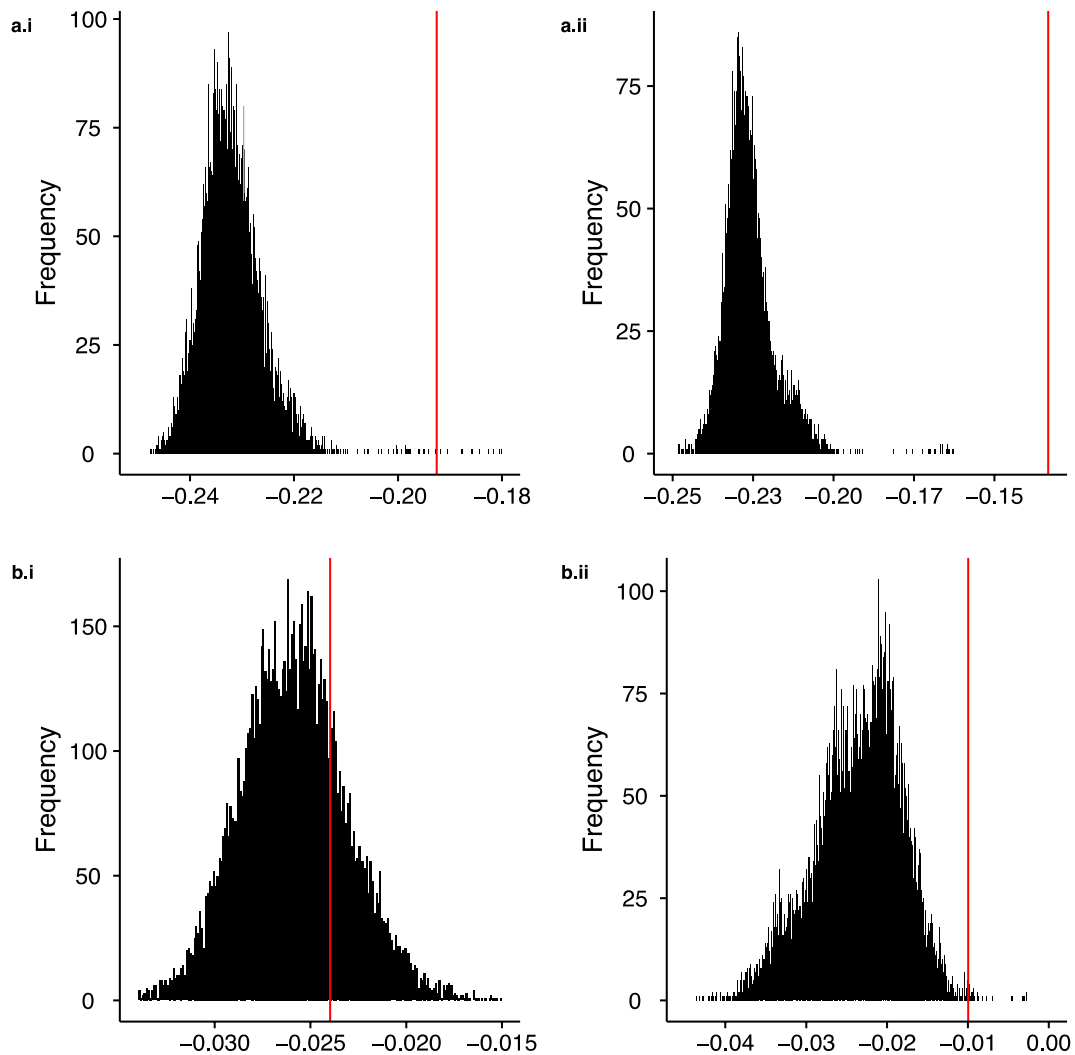
447 **Fig. 5** The relationship between mean prey body size (index of patch richness) and a)
 448 mean weighted degree (strength of connections among individuals) within (i) prides
 449 and (ii) subgroups and b) network density (gregariousness among individuals) within
 450 (i) prides and (ii) subgroups.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

452

453 *Interspecific competition*

454 The strength of division of prides into subgroups significantly increased (i.e.
 455 subgroups became clearer and more consistent) with an increase in interspecific
 456 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

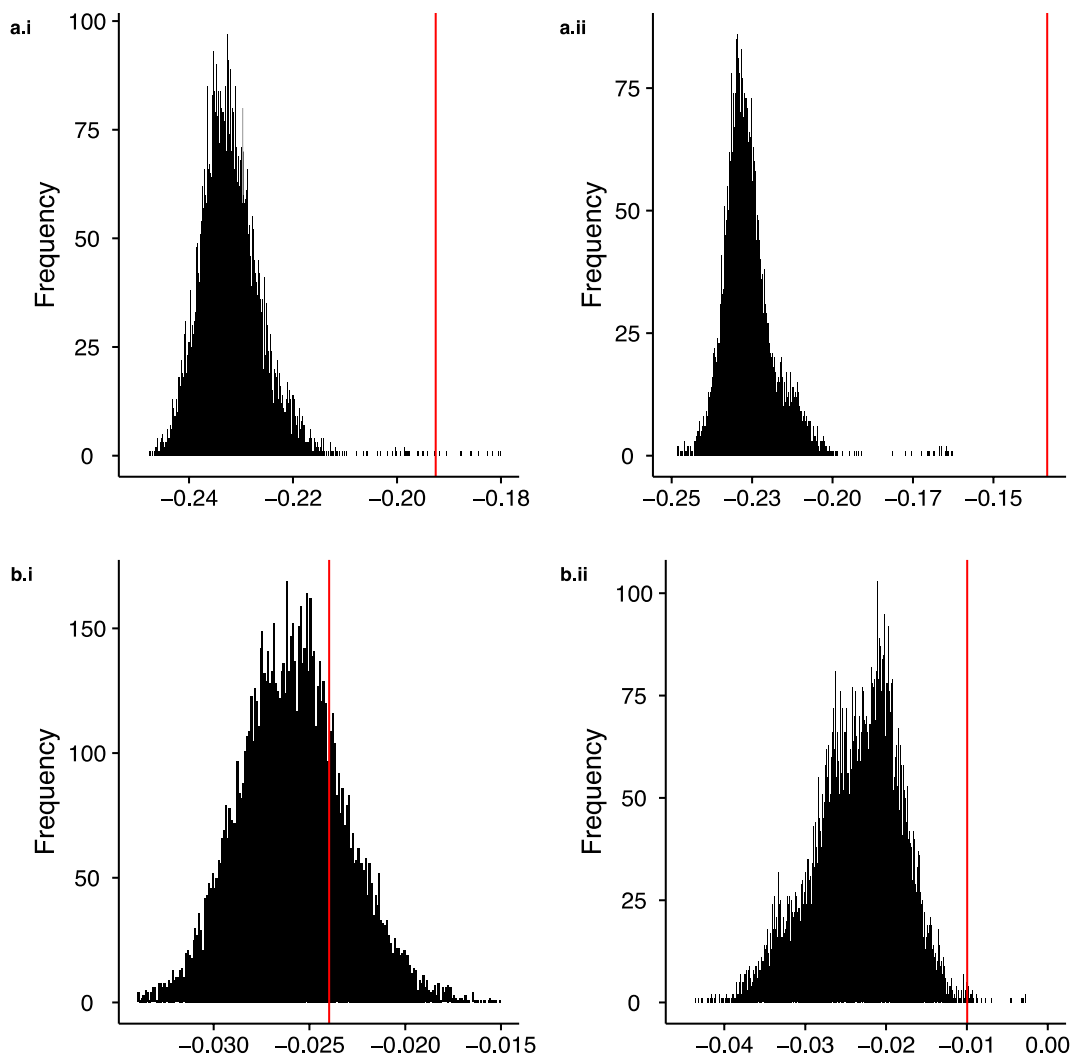
473 was not significant either within prides or within subgroups (Figs. 7a.i and 7a.ii). An

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

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660

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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896 **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***

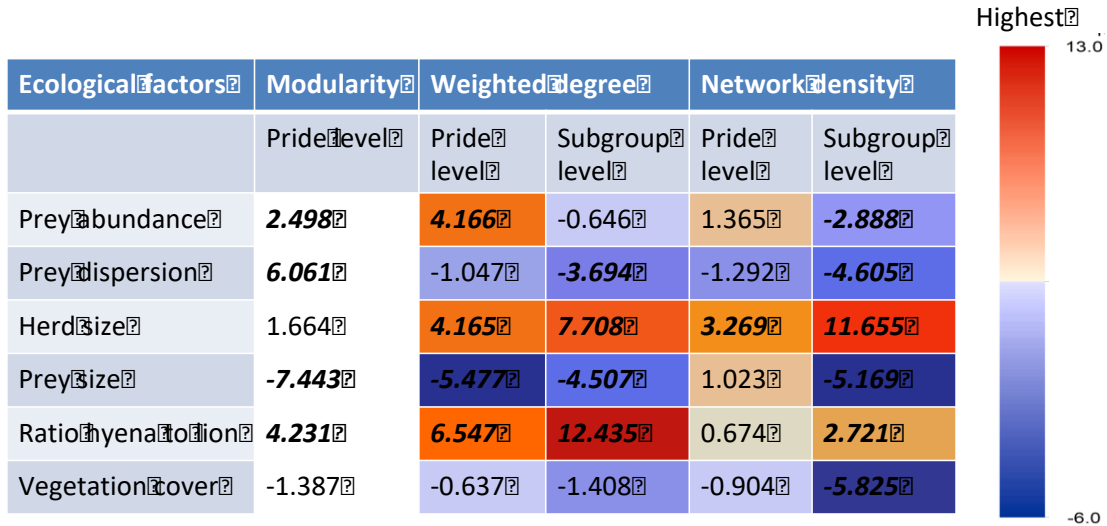
936 **Prey availability within lion home ranges**

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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Figures



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

982 **Supplementary Information Tables**

983

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

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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		R^2
				($\beta \leq r$)	P	
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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1044 **Table S3.** The number of pride observations (Obs), number of individuals in a pride
 1045 (Indiv), number of subgroups (Sub), and the three network metrics; modularity
 1046 (strength of division of a network into subgroups), mean weighted degree (strength of
 1047 connections among individuals) and network density (gregariousness among
 1048 individuals) for each pride, per season, per year.
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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

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1081 **Table S4.** The coefficient (β), P value (P), range of random coefficients (range from,
 1082 range to), mean and standard deviation (SD) for the relationship between ecological
 1083 factors and modularity (strength of division of a network into subgroups). In bold are
 1084 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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1120 **Table S5.** The coefficient (β), P value (P), range of random coefficients (range from,
 1121 range to), mean and standard deviation (SD) for the relationship between ecological
 1122 factors and mean weighted degree (strength of connections among individuals) at the
 1123 pride level and within subgroups. In bold are the significant P values.

Ecological factors	β	P	Range from	Range to	Mean	SD
<i>Pride level</i>						
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
<i>Subgroup level</i>						
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

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1152 **Table S6.** The coefficient (β), P value (P), range of random coefficients (range from,
 1153 range to), mean and standard deviation (SD) for the relationship between ecological
 1154 factors and network density (gregariousness among individuals) at the pride level and
 1155 within subgroups. In bold are the significant P values.

<i>Pride level</i>	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
<i>Subgroup level</i>						
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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