

1 **Effect of ecological factors on fine-scale patterns of social structure in African**  
2 **lions**

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26

27 **Abstract**

28 1. Environmental variations can influence the extent to which individuals interact with  
29 other individuals by changing the value of grouping. It is well known that many species  
30 can form and disband groups, often in response to the distribution and abundance of  
31 resources.

32 2. While previous studies showed that resources influence the broad-scale structure of  
33 animal groups, knowledge gaps remain on whether they affect fine-scale patterns of  
34 association among individuals within groups.

35 3. We quantify association patterns in African lions while simultaneously monitoring  
36 the abundance and distribution of prey. We test how social and ecological factors,  
37 including individual trait (age, sex, reproductive state) similarity and prey availability  
38 (prey abundance, dispersion, herd size and body size) affect within-pride social  
39 structure in African lions.

40 4. We found that individual decisions about associates depended on resource  
41 availability with individuals associating equally across all members of the pride when  
42 prey herds were scarce, aggregated or large bodied, and associating more exclusively  
43 (in subgroups of preferred associates) when prey herds were abundant, dispersed or  
44 small bodied. Individuals within lion prides seemed to be buffering against changes in  
45 prey availability by modulating their strength and density of connections with  
46 conspecifics when prides split into subgroups. The strength and density of connections  
47 among individuals within subgroups was greater when prey herds were large and lower  
48 when prey herds were dispersed or large bodied.

49 5. Our findings suggest that individual lions are making social decisions at both the  
50 subgroup level and the pride level, with decisions representing putatively fitness-

51 enhancing strategies. Individuals were typically shifting between having few strong  
52 connections and having many weaker connections depending on prevailing ecological  
53 conditions, with prey abundance, dispersion and body size having the greatest impact  
54 on decisions about splitting into subgroups. The maintenance of connections within  
55 prides and subgroups in the face of ecological change suggests that the fission-fusion  
56 nature of lion prides might be essential for the long-term maintenance of social  
57 connections even when short-term conditions do not allow them. More broadly, our  
58 study reveals how fission-fusion dynamics and ecological factors can simultaneously  
59 have an effect on animals across multiple levels of sociality.

60

61 **Key words**

62 Animal social networks, dynamic networks, ecological factors, fission-fusion,  
63 heterogeneity, lion, null models, prey availability

64

65 **Introduction**

66 One important goal in animal ecology is to understand the relationship between  
67 environmental factors and animal population abundance, spatial distribution, and social  
68 structure (Solomon, 1949). Studies across different taxa have demonstrated that  
69 resource availability is an important determinant of the broad-scale structure of animal  
70 societies, with most of these studies showing that animal group size is generally larger  
71 when food resources are more abundant and of a higher quality (see Hanya & Chapman,  
72 2013 ; Macdonald & Johnson, 2015 for reviews). In group-living animals, within-group  
73 interactions and the outcome of these interactions can be interpreted as a network of  
74 social relationships (Farine & Whitehead, 2015; Whitehead, 2008). The nature,  
75 number, and strength of these relationships are complex and can mediate the benefits,

76 such as food sharing, that individuals accrue from living in groups, particularly in times  
77 of need (Carter, Farine, & Wilkinson, 2017). Earlier attempts at understanding the  
78 interactions among individuals in a carnivore social structure, using the example of  
79 farm cats (*Felis catus*), did not involve complex analysis, however this offered some  
80 insights into patterns of social structure of group living carnivores (see Macdonald,  
81 Apps, Carr, & Kerby, 1987). Modern tools in ecology and evolution are now allowing  
82 us to better understand the patterns of animal social structure (i.e. the patterns in social  
83 relationships) at a finer level of social organization (see Ellwood et al., 2017; Farine,  
84 Firth, et al., 2015; Tanner & Jackson, 2012). Understanding the processes generating  
85 variation in social structure across populations is critical for understanding the  
86 evolution of sociality (Ilany & Akçay, 2016). Yet, there is still only preliminary  
87 understanding of how ecological variables shape the fine-scale patterns of animal social  
88 behavior (He, Maldonado-Chaparro, & Farine, 2019) and the implications of these on  
89 the resulting emergent group social structure and stability (Cantor & Farine, 2018).

90

91 A number of postulates have been put forward to explain social structure in different  
92 animal populations. These include predation risk for explaining the grouping patterns  
93 of females in non-human primates (Sterck, Watts, & van Schaik, 1997), kinship for  
94 shaping spatial layout of group living animals (Hirsch, Stanton, & Maldonado, 2012),  
95 and homophily (individual preferences for associating with like individuals) for  
96 shaping which individuals interact most strongly (Farine, 2014). Social network  
97 analysis has been instrumental in testing these postulates. At its base, social network  
98 analysis quantifies the strength of associations or interactions among each pair of  
99 individuals in a social group or population (Whitehead, 2008). It allows us to  
100 understand complex social and ecological interactions in animal communities (Croft,

101 James, & Krause, 2008; Farine & Whitehead, 2015) by providing metrics that quantify  
102 social structure at different levels of organization, i.e. within individuals, groups and  
103 populations. Some pioneering studies have used social network analysis to reveal  
104 details of the relationship between food availability and patterns of animal social  
105 structure. For example, Tanner and Jackson (2012) found that European shore crabs  
106 (*Carcinus maenas*) aggregated into cohesive stable subgroups when resources were  
107 clumped. Additionally, Foster et al. (2012) showed that when prey were abundant, the  
108 killer whale (*Orcinus orca*) population was characterized by a highly interconnected  
109 social network. Nevertheless, our understanding of the relationship between resources  
110 and social structure remains superficial. How do different aspects of food availability,  
111 such as the size and distribution of prey items, affect the finer-scale patterns of  
112 associations among individuals, in particular their decisions to form or disband  
113 subgroups?

114

115 Species that exhibit a form of fission-fusion social organization frequently change their  
116 group size and composition within the lifetime of members as groups split (fission) or  
117 merge (fusion) (Couzin & Laidre, 2009). In these species, the average size of  
118 subgroups, the amount of cohesion they show, and even their sexual composition are  
119 expected to vary depending mainly on food distribution (Cortes-Avizanda et al., 2011;  
120 Sueur et al., 2011; Symington, 1988). One species that has been widely reported as  
121 exhibiting within-group fission-fusion dynamics by forming subgroups is the African  
122 lion (*Panthera leo*) (Schaller, 1972). Pride composition is mostly constant, with most  
123 changes taking place when new males take over the pride (Packer & Pusey, 1983). By  
124 contrast, subgroup membership within a pride can change continuously. Some  
125 individuals can maintain close associations within subgroups, and this tendency for

126 stability can be driven by attributes such as age, sex and reproductive state (Schaller,  
127 1972; Van Orsdol, Hanby, & Bygott, 1985). For instance, female lions often form stable  
128 maternity subgroups that are effective in defending their cubs against infanticidal males  
129 from outside the pride and subgroup (Packer, Scheel, & Pusey, 1990). Also highly  
130 unstable and dynamic subgroups can be formed during hunting, when pride members  
131 briefly come together to execute a hunt (Stander, 1992a). However, the interactions  
132 between individuals within a pride are also likely to vary with ecological conditions.  
133 Although lions engage in a wide variety of important social activities, such as  
134 cooperative hunting (Scheel & Packer, 1991), mutual defence of kills (Cooper, 1991)  
135 and cooperative defence of territory and young (Mosser & Packer, 2009), it has been  
136 suggested that lion sociality might be linked to, or influenced by, resource availability  
137 (Macdonald, Mosser, & Gittleman, 2010; Mbizah, Valeix, Macdonald, & Loveridge,  
138 2019).

139

140 The dynamics of resource availability; especially the abundance, type, and distribution  
141 of prey might also influence finer-scale lion social structure and this can have profound  
142 behavioural, ecological and evolutionary impacts (Foster et al., 2012; He et al., 2019).  
143 For example, when prey is scarce, then we expect lions to associate less with their pride  
144 members to reduce competition for food and increase their own food intake (Packer et  
145 al., 1990). The benefits that can be gained from associating with pride members might  
146 shape the tendency for members of a given pride to remain cohesive or to split into  
147 smaller subgroups, which is a much more flexible strategy than adding or removing  
148 members from the pride. Social bonds are therefore likely to form the basis of how  
149 species such as lions respond socially to ecological processes. We expect to observe a  
150 shift back and forth in decisions by individual lions between maintaining fewer but

151 stronger bonds and maintaining more but weaker bonds depending on resource  
152 availability. In this study, we combine data on the fine-scale patterns of association  
153 among individuals across multiple prides of African lions with data on the prey herds  
154 in each pride's territory within Hwange National Park, Zimbabwe. We consider a herd  
155 of prey to represent a resource patch available to lions (Carr & Macdonald, 1986), and  
156 the abundance, dispersion, and type of these patches (see Table S1) as important  
157 attributes that can influence the opportunities for social interactions (Tanner & Jackson,  
158 2012).

159

## 160 **Materials and Methods**

### 161 *Study area*

162 Hwange National Park covers approximately 15 000 km<sup>2</sup> of semi-arid dystrophic  
163 savanna on Kalahari sands, on the north-western border of Zimbabwe. During the wet  
164 season (November to February), various waterholes, rivers and pools are rain fed and  
165 available to animals, but natural surface water then becomes scarce as the dry season  
166 progresses and only pumped waterholes (~ 50), mostly in the North of the park,  
167 maintain water availability. The end of dry season coincides with the lowest quantity  
168 and quality of browsing and grazing resources. We therefore commonly distinguish  
169 three seasons in Hwange National Park characterised by surface water availability and  
170 vegetation quality: the wet season, the early dry season (March - June) and the late dry  
171 season (July - October). However, for this study only the early dry and late dry season  
172 data was available as the study area is inaccessible during the wet season. Lion density  
173 is estimated at around 3.5 lions/100 km<sup>2</sup> in the study area (Loveridge et al., 2016).  
174 Differences in vegetation and water distribution across the park result in differences in  
175 the distribution of herbivores in terms of both assemblages and abundance (Chamaille-

176 Jammes, Charbonnel, Dray, Madzikanda, & Fritz, 2016).

177

178 *Lion pride observations*

179 For this study we used data from four different prides between 2013 – 2017. We located  
180 lion prides with the help of GPS radio-collars fitted to two adult females and five adult  
181 males, as well as opportunistically during other field work activities. The prides were  
182 observed at least five times per month to record their size and composition. Some prides  
183 were however not observed in some of the months and seasons during the study period.  
184 When a pride was observed, we recorded its name, identity of individuals present, as  
185 well as their age, sex and whether they had cubs. We also recorded their activities  
186 during observations, which included resting, hunting, feeding and walking. All lion  
187 individuals are recognizable by whisker patterns, natural markings such as scars,  
188 muzzle spots, and tooth irregularities that are unique to each individual (Pennycuick &  
189 Rudnai, 1970). We looked at two aspects of lion pride: (1) pride (all the individuals  
190 within a pride) and (2) subgroup (individuals of a pride present at each observation).  
191 We recorded all individuals present together as being connected (Farine, 2015;  
192 Whitehead & Dufault, 1999). The GPS collars recorded locations every two hours day  
193 and night, and we regularly downloaded these positional data to estimate lion seasonal  
194 home range. Only individuals that had collar data with fixes covering the whole season  
195 were included in calculating seasonal home range to avoid underestimation of home  
196 range size.

197

198 *Prey availability*

199 To measure prey availability, we conducted multi-species surveys of tracks made by  
200 animals when they cross the roads. Track counts were conducted from 2013 to 2015

201 during the early dry season and the late dry season. Most of the available roads in the  
202 study area (ranging from 9 to 55 km long) were used as transects (n = 64 transects).  
203 The 64 selected transects were within areas that lions frequent. When a fresh track (less  
204 than 24hrs old) was encountered, it was assessed for species and group size by highly  
205 skilled and experienced trackers (see S1 Appendix for further details on the track survey  
206 method). Only tracks from common lion prey species in the area were used in this  
207 analysis. Information on prey availability measured as; prey abundance, prey  
208 dispersion, prey herd size and prey body size, was extracted for each lion home range  
209 in each season (See S2 Appendix for further details).

210

#### 211 *Social networks construction*

212 We used lion pride observational data to construct a social network for each pride in  
213 each season in each year, with observations ranging from 16 to 66 observations per  
214 season (Table S3). Thus, each social network represented the patterns of associations  
215 within a pride over a four-month period. The social networks contained each of the  
216 individuals in one pride as nodes and pairwise association indices as edge weights.  
217 Because we did not have complete data on observations of all individuals  
218 simultaneously, we had to convert the number of associations into an association rate  
219 (the propensity for individuals to be seen together). To calculate these edge weights,  
220 we used the Simple Ratio Index as an estimate of the proportion of time two individuals  
221 spent together (Cairns & Schwager, 1987; Hoppitt & Farine, 2018). The Simple Ratio  
222 Index (SRI), which is considered the least-biased estimate of association rates (Hoppitt  
223 & Farine, 2018), is defined as  $x / (y_a + y_b + y_{ab} + x)$ , where  $x$  is the number of  
224 observations of two individuals together,  $y_a$  is the number of observations with only  
225 individual  $a$ ,  $y_b$  is the number of observations with only individual  $b$ , and  $y_{ab}$  is the

226 number of simultaneous observations of individuals *a* and *b* when not together, was not  
227 relevant to our study because we could not observe two subgroups at the same time.  
228 The SRI ranges from 0 for two individuals never seen together to 1 for two individuals  
229 always seen together. Animals that died during a season were not included in that  
230 season's network to avoid bias.

231

### 232 *Social networks analysis*

233 We first used the multiple regression quadratic assignment procedure (MRQAP)  
234 (Krackhardt, 1988) to test if the tendency of lions to associate with individuals of the  
235 same sex, same age or same reproductive state (of adult females) had an effect on lion  
236 social structure. MRQAP tests hypotheses based on matrices, i.e.  $N \times N$  matrices where  
237 elements in row *i* and column *j* represent the relationship between individuals *i* and *j*,  
238 unlike linear models which commonly use a data table with individual-level measures,  
239 i.e. an Individual by Observation (or  $N \times K$ ) data frame (Farine, 2017; Krackhardt,  
240 1988). We conducted a separate MRQAP for each pride in each season with the  
241 association index (measured using the SRI) as the dependent matrices and age-based  
242 homophily, sex-based homophily and reproductive state-based homophily as the  
243 independent variables. The homophily  $N \times N$  matrices were constructed by assigning  
244 the elements in the matrix the value of 1 if the two corresponding individuals had the  
245 same age, sex, or state, and the value of 0 otherwise. We conducted these tests using  
246 the MRQAP function with a custom null model option in 'asnipe' package (Farine,  
247 2013) in the statistical software R. The null model consisted of 10 000 permutations  
248 (see below).

249

250 We then calculated three network metrics to characterise the structure of each pride:

251 modularity, mean weighted degree and network density to quantify the division of  
252 prides into subgroups and the nature of connections within prides and within subgroups.  
253 We selected these measures *a priori* with the aim of describing three biological  
254 dimensions of the social structure of prides: how strong the connections are (mean  
255 weighted degree), how many connections there are (density), and how distributed the  
256 connections are across dyads (modularity). First, we calculated modularity to quantify  
257 the division of prides into subgroups. Modularity describes the separation of networks  
258 into structural communities, or subgroups of individuals that have more connections  
259 among themselves than they do with nodes outside of their community (Girvan &  
260 Newman, 2002). Herein, we call these network-based communities “subgroups”. A  
261 higher modularity implies that a pride tends to break into distinct subgroups defined by  
262 stronger connections between individuals within a subgroup but weaker connections  
263 between individual in different subgroups (Newman, 2004). We then calculated mean  
264 weighted degree and network density to quantify the nature of connections within  
265 prides and within subgroups. Mean weighted degree is defined as the average sum of  
266 the weight of edges surrounding each node in a network; it measures the strength of  
267 connections among individuals in a pride or subgroup and a high mean weighted degree  
268 means most individuals were seen together most of the time. Network density is the  
269 ratio of the number of edges (nonzero edges) in the network over the total number of  
270 possible edges between all pairs of nodes; it measures the density of connections among  
271 individuals in a pride or subgroup. A high network density represents a greater overall  
272 tendency for different individuals to come into contact with one-another, and is a  
273 fundamental property of networks (for example, it strongly influences spreading  
274 processes). We represented the resulting subgroup assignments by giving different  
275 colours to nodes from different subgroups detected using greedy optimization of

276 modularity community detection algorithm (Fig. 1). All network measures were  
277 calculated in R using igraph (Csardi & Nepusz, 2006).

278

### 279 *Hypothesis testing*

280 Before testing our hypotheses about the links between prey availability and pride  
281 structure, we first tested for the correlation between the four measures of prey  
282 availability (prey abundance, dispersion, herd size and body size). Because these  
283 correlations were generally moderate to low ( $-0.59 \leq r \leq 0.62$ ), we included all measures  
284 in our model. We then assessed the relationship between the different network metrics  
285 (modularity, mean weighted degree and network density for each pride and subgroup  
286 network) and the four measures of prey availability using linear mixed effects  
287 regression analysis with the identity link in the lme4 package (Bates, Mächler, Bolker,  
288 & Walker, 2015) in R. The network metric was the response variable while the above  
289 measures of prey availability that can potentially influence lion social structure were  
290 the fixed effects; with the ID of each lion pride included as the random effect to account  
291 for pride-level differences. Using the null model procedure described below, we then  
292 generated 10 000 randomised versions of each network, and ran the same regression  
293 with each of these randomised networks. We estimated P-values for each fixed effect  
294 by calculating the number of coefficients of the regression slopes from the randomised  
295 networks that were greater than or equal to the corresponding coefficient of the  
296 regression slopes using the observed network, divided by the number of random  
297 networks generated and corrected for a two-tailed test (Farine, 2017). The result was  
298 significant at  $P = 0.05$  if fewer than 2.5% of the random values were greater than the  
299 observed value, or if more than 97.5% of the random values were greater than the  
300 observed value. All analysis were done in R statistical software (R Core Team, 2020).

301

302 *Estimating statistical significance using null models*

303 Social data are typically non-independent (Croft, Madden, Franks, & James, 2011); in  
304 order for one individual to have a connection, it requires another to do so as well. We  
305 used permutation-based null models to estimate the statistical significance in the  
306 relationships between the ecological variables and the connections among individuals  
307 within prides and within subgroups. Permutation tests allowed us to account for  
308 confounding factors that affect estimates of social structure, such as variation in  
309 sampling effort, by randomizing observations in ways that keep these factors constant  
310 while at the same time removing the signal of the social factors that shape the social  
311 network (Farine, 2017; Farine & Whitehead, 2015). We first ran pre-network  
312 permutation test in the ‘asnipe’ package (Farine, 2013) to compare the mean weighted  
313 degree, network density and modularity of the study pride networks to the distribution  
314 of the corresponding measures calculated on randomised versions of the pride  
315 networks. Our pre-network permutations worked by sequentially swapping  
316 observations of pairs of individuals between subgroups in a pride such that individual  
317 A that occurred in subgroup 1 now occurs in subgroup 2, and individual B that occurred  
318 in subgroup 2 now occurs in subgroup 1 (Bejder, Fletcher, & Brager, 1998). This  
319 swapping procedure was repeated once for each iteration of the randomization to  
320 increasingly randomize the observed data. After each swap, the associations (SRI  
321 values) among all individuals were recalculated and the above three network metrics  
322 recalculated. We conducted 10,000 such incremental swaps, thus generating a null  
323 distribution from 10,000 randomised networks and network metrics.

324

325 We then re-ran the same null model procedure but restricted swaps to occur only within  
326 the subgroups that were identified within each pride network, thus evaluating our  
327 hypotheses at a subgroup level (i.e. by controlling for the pride-level social structure).  
328 We calculated the mean weighted degree and network density for each subgroup  
329 network and compared these to the corresponding values calculated from the random  
330 subgroup networks. We report our effects relative to the null distribution. Because the  
331 fitted coefficient values of the model contain multiple other factors (including sampling  
332 variation) that shape the metric, the null distribution will often not be centred on 0  
333 (Farine, 2017). We therefore subtracted the median of the randomised distribution from  
334 both the observed and randomised values, allowing us to interpret the coefficients  
335 relative to chance. This is possible because the distribution of random values is  
336 generated from datasets in which we have kept all aspects of our sampling constant,  
337 meaning that the values in this distribution have the same biases as in the observed  
338 dataset. Removing the median of this distribution removes the average effect of these  
339 non-social factors, allowing us to more directly interpret the effects of the social  
340 decisions that individuals make (see Farine & Whitehead, 2015). Conducting this  
341 analysis allowed us to determine whether individuals are shifting back and forth  
342 between within-subgroup social investment and pride-level social investments.

343

## 344 **Results**

345 In our study, female home ranges ranged from 27.8 to 329.6 km<sup>2</sup> (mean = 224.5 km<sup>2</sup>;  
346 SD = 170.5 km<sup>2</sup>) and male home range sizes ranged from 121.3 to 498.8 km<sup>2</sup> (mean =  
347 330.9 km<sup>2</sup>, SD = 159.0 km<sup>2</sup>). However, we found no significant difference between  
348 male and female lion home range sizes (estimate ± SE = 106.31 ± 122.39;  $t(7) = 0.87$ ;  
349  $p = 0.41$ ). We first generated a baseline understanding of social structure in each of the

350 four lion prides by testing whether individual traits influenced patterns of associations  
351 among individuals in the replicated networks, each representing four months of  
352 observations in one of two dry seasons (see Methods). Generally, there was a  
353 correlation between the individual trait (age, sex and reproductive state) similarity and  
354 the probability that individuals would be observed together (Table S2). In most prides,  
355 the adjusted  $R^2$  value of the MRQAP models for the relationship between similarity in  
356 individual traits and the association index among individuals within lion prides was  
357 generally low (between 0.010 and 0.062), except for Ngamo pride ( $R^2 = 0.737$ , see  
358 Table S2), meaning that the model explains very little of the variation in the association  
359 index.

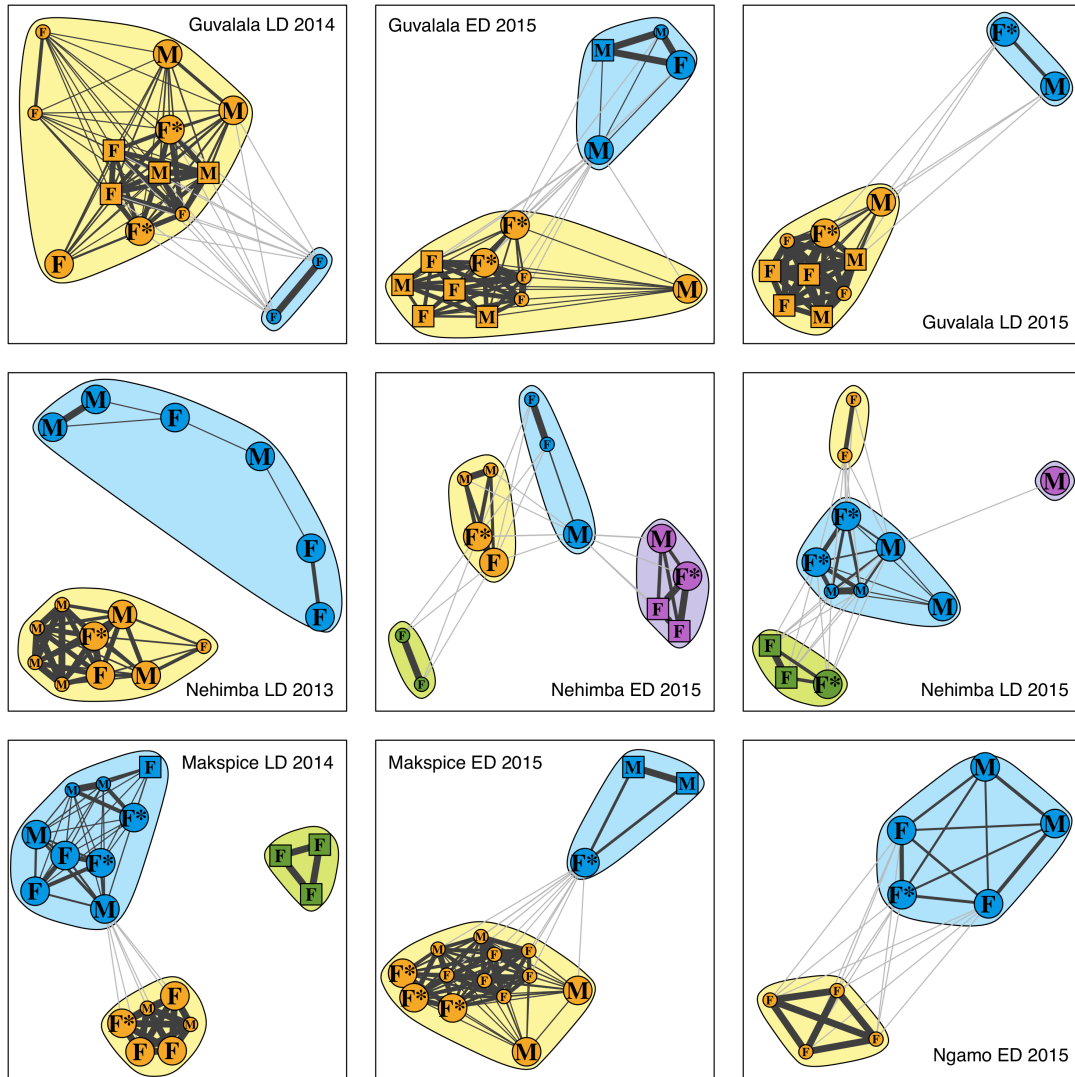
360

361 We then tested whether prides exhibited structured patterns of subgrouping. We found  
362 that the seasonal networks for each pride could be statistically partitioned into two,  
363 three, or four subgroups (Table S3; Fig. 1). Season itself had no significant effect on  
364 the strength of division of a network into subgroups (modularity estimate  $\pm$  SE = -0.08  
365  $\pm$  0.13;  $t(7) = -0.62$ ;  $p = 0.56$ ). We then tested whether seasonally-varying prey  
366 availability measures could explain patterns of structure, including subgrouping, in the  
367 networks.

368

369

370



371

372 **Fig. 1. Subgrouping patterns in four prides across different seasons.** We generated  
 373 networks for two distinct seasons (early dry season (ED) and late dry season (LD)) and  
 374 three years (2013 to 2015). Pride identity, season and year are noted in each network.  
 375 Subgroups were extracted and visualized using greedy optimization of modularity  
 376 community detection algorithm and plotting the network with the igraph package  
 377 (Csardi & Nepusz, 2006) in R. Each coloured polygon represents the social boundaries  
 378 of one subgroup entity, the members of which are more densely connected among  
 379 themselves than with the rest of the network. Each node represents an individual lion,  
 380 with the shape of the node representing age class (large circle = adult, square = sub-  
 381 adult and small circle = cub), the letter of the node indicates sex (M = male, F = female)

382 and the \* indicates the reproductive state (F\* = females with cubs). Edge widths (the  
383 connections between individuals) are proportional to the association index.

384

#### 385 *Effect of prey availability on association patterns within prides*

386 The mean weighted degree, which is the strength of connections among individuals in  
387 a pride was greater at high prey abundance (Table 1; Fig 2a.i). Nonetheless, the network  
388 density, which is the density of connections among individuals in a pride was not  
389 affected by changes in prey abundance (Table 1; Fig 2a.ii). Modularity, which is the  
390 strength of division of prides into subgroups was greater at high prey abundance (Table  
391 1; Fig 2a.iii), thus, the subgroups became more distinct from each other, with even  
392 weaker associations between subgroups. Prey dispersion had no significant effect on  
393 both the strength and the density of connections among individuals within prides (Table  
394 1; Fig 2b.i; Fig 2b.ii). However, the strength of division of prides into subgroups was  
395 greater at high prey dispersion (Table 1; Fig 2b.iii), thus, the subgroups became more  
396 distinct from each other, with even weaker associations between subgroups when prey  
397 was more dispersed across the landscape. The strength and the density of connections  
398 among individuals within prides was greater when prey herds were larger (Table 1; Fig  
399 2c.i; Fig 2c.ii). Nonetheless changes in prey herd size had no significant effect on the  
400 strength of division of prides into subgroups (Table 1; Fig 2c.iii). The strength of  
401 connections among individuals within a pride was lower when prey was large (Table  
402 1; Fig 2d.i), whereas the density of connections among individuals was not affected by  
403 changes in prey body size (Table 1; Fig 2d.ii). The strength of division of prides into  
404 subgroups was lower when prey body size was large (Table 1; Fig 2d.iii). Individuals  
405 within prides tended to associate more evenly with all other members of their pride as  
406 prey body size became larger.

407

408 **Table 1. Summary of the relationship between measures of prey availability and**

409 **network metrics.** Mean weighted degree (strength of connections among individuals),

410 network density (the density of connections among individuals) and modularity

411 (strength of division of prides into subgroups), were calculated within prides. Mean

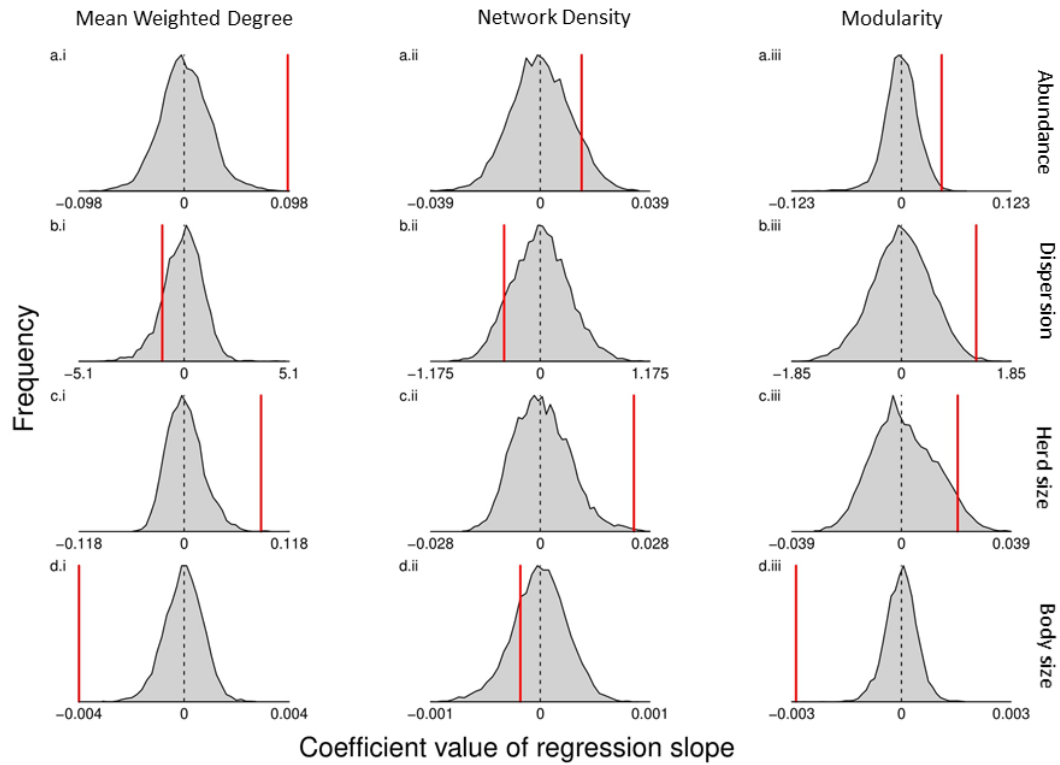
412 weighted degree and network density were also calculated within subgroups. The tables

413 show results of a more positive (+), more negative (-) or a non-significant (.)

414 relationship (relative to chance), between network metrics and prey availability.

<i>Measures of Prey availability</i>	<b><i>PRIDE LEVEL</i></b>			<b><i>SUBGROUPS LEVEL</i></b>	
	<i>Mean Weighted Degree</i>	<i>Network Density</i>	<i>Modularity</i>	<i>Mean Weighted Degree</i>	<i>Network Density</i>
Prey Abundance	+	.	+	.	-
Prey dispersion	.	.	+	-	-
Prey herd size	+	+	.	+	+
Prey body size	-	.	-	-	-

415



416

417 **Fig. 2. Relationship between pride-level social structure and measures of prey**

418 **availability.** The relationship between (a) number of prey herds/km (index of prey

419 abundance), (b) nearest neighbour index of prey herds (index of prey dispersion), (c)

420 mean prey herd size, (d) mean prey body size and (i) mean weighted degree (strength

421 of connections among individuals), (ii) network density (density of connections among

422 individuals) and (iii) modularity (strength of division of prides into subgroups) within

423 prides. Histograms show the distribution of coefficient values from the model applied

424 to the permuted networks, and the red lines show the coefficient value of the regression

425 fitted to the original (observed) data. Significance was calculated by evaluating the

426 observed data relative to the distribution of values calculated from the permuted data.

427 We note that there were strong signals of non-social factors most likely caused by

428 sampling (see Farine, 2017) shaping our original observed effects, meaning that the

429 randomised values were often not centered on 0 (see Supplemental Fig S1). Thus, we

430 corrected the effects to control for these factors (see methods; Farine & Whitehead,

431 2015).

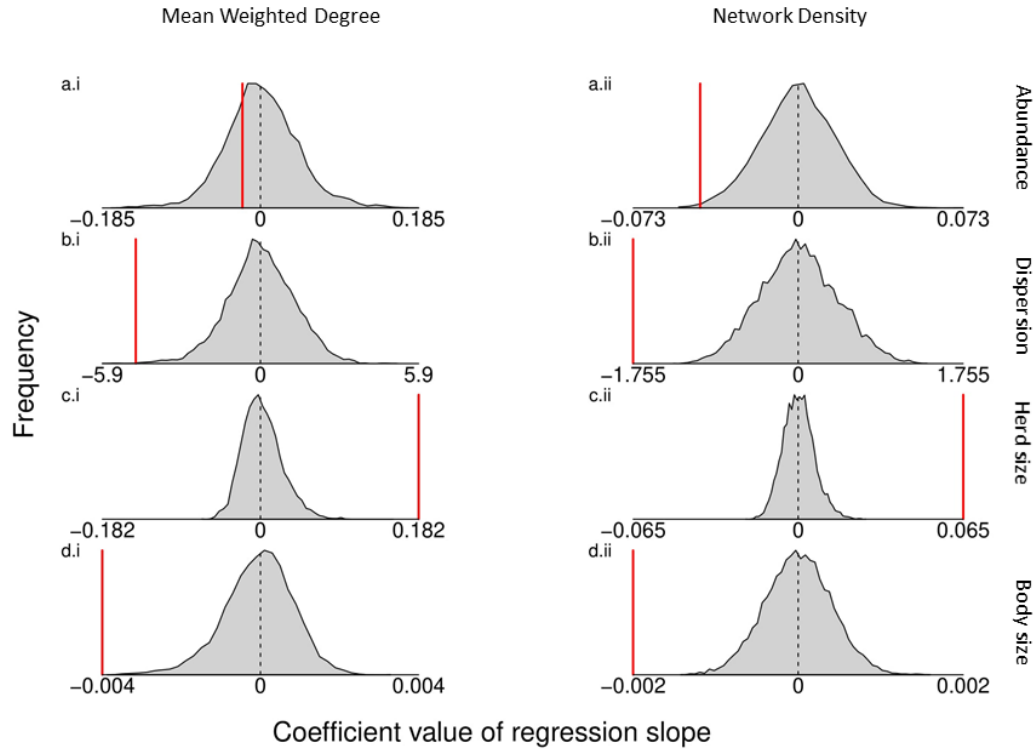
432

433 *Effect of prey availability on association patterns within subgroups*

434 Prey abundance had no significant effect on the strength of connections among  
435 individuals within subgroups (Table 1; Fig 3a.i), but the density of connections among  
436 individuals was lower when prey was abundant (Table 1; Fig 3a.ii), meaning that the  
437 individuals within subgroups were not fully connected at high prey abundance. Both  
438 the strength and the density of connections among individuals within subgroups were  
439 lower when prey herds were more dispersed (Table 1; Fig 3b.i; Fig 3b.ii), meaning that  
440 individuals within subgroups are less frequently seen together and come into contact  
441 less often when prey is dispersed in the landscape. However, the strength and the  
442 density of connections among individuals within subgroups was greater when prey  
443 herds were larger (Table 1; Fig 3c.i; Fig 3c.ii). Finally, when prey was larger bodied,  
444 the strength and the density of connections among individuals within subgroups became  
445 lower (Table 1; Fig 3d.i; Fig 3d.ii).

446

447



448

449 **Fig. 3. Relationship between within-subgroup social connections and measures of**  
 450 **prey availability.** The relationship between (a) number of prey herds/km (index of prey  
 451 abundance), (b) nearest neighbour index of prey herds (index of prey dispersion), (c)  
 452 mean prey herd size, (d) mean prey body size, and (i) mean weighted degree (strength  
 453 of connections among individuals) and (ii) network density (density of connections  
 454 among individuals) within subgroups. Plots are following the same design as Fig. 2.  
 455 See (Supplemental Fig S2) for randomised values not centered on 0.

456

### 457 Discussion

458 Our study extends prior research on the role of ecological factors in determining broad  
 459 population structure by demonstrating several ways in which measures of prey  
 460 availability affect the fine scale patterns of association among individuals. Further, we  
 461 demonstrate that these effects can take place at two scales: within prides and within  
 462 subgroups. Lion prides, characterized by frequent changes in subgroup composition

463 (i.e. fissioning and fusioning), can potentially show rapid responses to changing  
464 ecological conditions (Kotze, Keith, Winterbach, Winterbach, & Marshal, 2018). Our  
465 results suggest that these responses to prey availability might take place via the fine-  
466 scale associations among individuals. More specifically, our study reveals that the  
467 abundance of prey, the dispersion of prey within the landscape and the body size of  
468 available prey have strong effects on the division of prides into subgroups (pride  
469 fission; measured here by modularity) and can potentially shape the stability of lion  
470 prides. We found that the connections among individuals within a pride remained  
471 strong when prides split into subgroups as prey became more abundant within the  
472 pride's home range. This indicates that perhaps the existence of subgroups within prides  
473 acts to maintain connections (not let them erode as much as they would at random)  
474 when resources are plentiful. It has long been suggested that the fission-fusion  
475 dynamics of social animals allows them to adapt to prevailing social and ecological  
476 conditions (see Aureli et al., 2008; Kotze et al., 2018). Our study therefore provides  
477 evidence that prey availability can shape both global and fine-scale properties of animal  
478 social systems, even when species live in seemingly consistently structured societies  
479 (e.g. with defined and long-lasting territories).

480

#### 481 *Individual trait similarity*

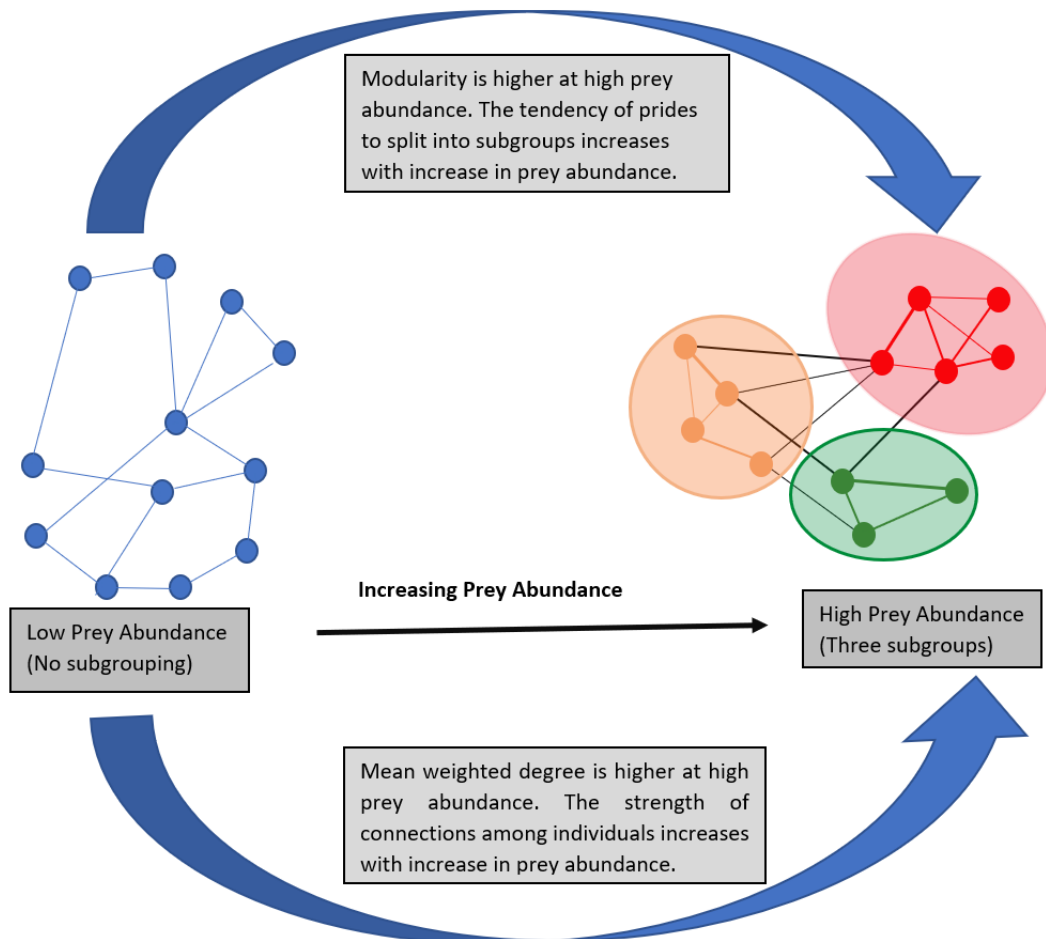
482 Our network analyses captured some fundamental properties of lion behaviour,  
483 including the general propensity for lions to associate with individuals of the same sex  
484 or of the same reproductive state. In lions, females often come together to defend their  
485 cubs against nomadic males (Packer & Pusey, 1983) whereas males form coalitions to  
486 take over and protect territories (Packer, 1986; Schaller, 1972). However, overall our  
487 results suggest that the effect of individual trait similarity alone explains relatively little

488 of the variance in subgroup composition in lion prides. One pride did show consistent  
489 significant effects, but this is likely to be because this pride was composed of only adult  
490 males and females and their cubs, a composition unique to this particular pride.

491

#### 492 *Prey abundance*

493 Our study exposed the flexibility of lion pride structure in the face of environmental  
494 changes and how decisions by individual lions to join or leave subgroups can be  
495 influenced by prey availability.



496

497 **Fig 4. Effect of prey abundance on association patterns within a pride.** An  
498 illustration showing how a pride of 12 individuals can break into subgroups of 3, 4 and  
499 5 individuals at high prey abundances, and that the individuals within and across  
500 subgroups maintain strong connections with other pride mates at high prey abundance.

501

502 Prey abundance has been shown to have a huge impact on lion sociality. For instance,  
503 Packer et al. (1990) found the ideal group size for food consumption when prey was  
504 scarce to be either solitary or groups of five to six female lions. When prey was scarce,  
505 prides had to choose to either become solitary or remain in large groups (that can kill  
506 large prey such as buffalo), and when prey becomes abundant the prides can then break  
507 up into small and medium sized groups. This strategy is adopted to maximize feeding  
508 efficiency (Packer et al., 1990). Our study further shows that prides have a greater  
509 tendency to break into subgroups at high prey abundances, but when they do so,  
510 individuals within the pride maintain strong connections with other pride mates and this  
511 is important for maintaining the stability of prides (Fig 4). Because individuals across  
512 subgroups maintain strong bonds with pride mates, the density of connections among  
513 individuals within these subgroups was therefore reduced at high prey abundance.

514

#### 515 *Prey dispersion*

516 Our results also showed that when prey is more dispersed in the landscape, it reduces  
517 the frequency with which lion prides encounter prey and this leads to lion prides  
518 breaking into more distinct subgroups. Further, we found that individuals within the  
519 subgroups maintain weaker connections and lower density of connections when prey is  
520 more dispersed. The splitting of lion prides into subgroups and the maintenance of poor  
521 connections within these subgroups when prey is hard to come by might be a strategy  
522 to reduce competition and increase searching efficiency (Fryxell, Mosser, Sinclair, &  
523 Packer, 2007; Packer et al., 1990). Since the dispersion of resources increases searching  
524 behaviour (Sogard & Olla, 1997; Valeix et al., 2010), this can potentially limit the  
525 opportunity for social interactions between individuals within prides and subgroups

526 (Tanner & Jackson, 2012). The dispersion of prey herds emerged also as an important  
527 factor in shaping lion home range size (Mbizah et al., 2019).

528

#### 529 *Prey herd size*

530 The strength and the density of connections among individuals within both prides and  
531 subgroups was greater when prey herds were larger, but changes in the size of prey  
532 herds had no effect on the splitting of prides into subgroups. Larger herds potentially  
533 provide a chance for several predators within a group to make a kill or for more than  
534 one individual to be killed from the herd (Creel & Creel, 2002; Schaller, 1972) and  
535 lions have been shown to prefer large prey herds (Hayward & Kerley, 2005).  
536 Nevertheless, the increased vigilance of large prey herds (Hamilton, 1971; Kenward,  
537 1978) makes hunting large herds challenging for lions. Fryxell et al. (2007) found that  
538 group formation by wildebeest reduced lion kill rates by 90% and the strong bonds  
539 within prides and subgroups would be important for co-operation in hunting these large  
540 prey herds, especially when the prey are difficult to capture (e.g. buffalo) (Scheel &  
541 Packer, 1991). Coordination is key during lion hunts (Stander, 1992b) and the strong  
542 coordination that might arise from the strong connections among individuals can  
543 increase chances of prey capture.

544

#### 545 *Prey body size*

546 Although the connections among individuals within prides were weaker when prey was  
547 large, the tendency for prides to break into subgroups was however lower and as a  
548 result, individuals within prides associated more evenly with all other members of their  
549 pride. Large prey species such as buffalo, zebra, giraffe or juvenile elephant are  
550 sharable patches (sensu Macdonald & Johnson, 2015) and can feed several lions and

551 are often preferred (Hayward & Kerley, 2005); consequently, competition for prey  
552 within the pride is likely to be minimal and individuals can associate frequently outside  
553 of their close connections. In the Serengeti, Scheel and Packer (1991) found  
554 cooperation to be common during hunts on larger and more difficult prey. Essentially,  
555 individuals in the pride would come together more often (fusion), which could allow  
556 them to cooperatively hunt the large sized prey (Scheel & Packer, 1991; Stander,  
557 1992a) and increase success of prey location and capture (but see Caraco & Wolf, 1975;  
558 Packer et al., 1990; Stander & Albon, 1993) while minimizing energetic costs (Carbone,  
559 Teacher, & Rowcliffe, 2007). On the other hand, the strength and the density of  
560 connections among individuals within subgroups was lower when prey was large  
561 bodied. This is because the chances for small groups to successfully hunt and capture  
562 large prey are low and it might not be efficient for the small groups to attempt to hunt  
563 large prey (Stander & Albon, 1993).

564

565 Drawing on our knowledge of decision-making, our findings imply that individual lions  
566 are making social decisions at both the subgroup level and the pride level. Such  
567 decisions about sociality are often optimized to maximize individual fitness (Farine,  
568 Montiglio, & Spiegel, 2015; Silk, 2007). We found that the finer-scale social structure  
569 of lions responds to changes in ecological conditions and this is centered around  
570 decisions about reducing competition, increasing chances of prey capture and  
571 maximizing feeding efficiency. These patterns mirror recent findings in vampire bats  
572 showing that individuals exhibit patterns of social bet-hedging, maintaining both  
573 stronger and weaker associations, which are differentially important in times of need  
574 (Carter et al., 2017). The maintenance of connections within prides and subgroups in  
575 the face of ecological change suggests that the fission-fusion nature of lion prides might

576 be essential for the long-term maintenance of social connections even when short-term  
577 conditions do not allow them. Nevertheless, the persistent separation between  
578 subgroups within a pride can reduce the encounter rates and contacts among individuals  
579 across different subgroups, which can have impacts on processes such as mate choice  
580 and other social behaviours (Banks, Piggott, Stow, & Taylor, 2007; Krause, Lusseau,  
581 & James, 2009). Further, some of the weaker associations across subgroups can make  
582 the pride less stable (Beisner, Jackson, Cameron, & McCowan, 2011) and susceptible  
583 to other anthropogenic and stochastic influences (Snijders, Blumstein, Stanley, &  
584 Franks, 2017). At the interface between social affiliations and ecological constraints,  
585 the marginal costs and benefits of lion groupings are moderated by various sociological  
586 pay-offs to given group sizes, for example in the contexts of survival and reproduction  
587 (Packer, Pusey, & Eberly, 2001). Our study therefore provides evidence that prey  
588 availability can shape fine-scale properties of animal social systems and at different  
589 scales, with implications for, and far beyond an understanding of lion society.

590

## 591 **Acknowledgments**

592 We thank the Zimbabwe Research Council and the Director of Zimbabwe Parks and  
593 Wildlife Management Authority (ZPWMA) for permission to undertake this research  
594 and the assistance of ZPWMA staff during field data collection specifically Lovelater  
595 Sebele and Trust Dube. We also thank the Hwange Lion Project field staff for assistance  
596 with data collection particularly Lowani Mpofu. MMM is grateful to Jon Cummings,  
597 C.V Starr Foundation and the Cecil Fund for supporting studentship costs. Research  
598 was supported by Darwin Initiative for Biodiversity Grants, Mitsubishi Fund for  
599 Europe and Africa, R.G Frankenberg, Boesak and Kruger, Rufford Maurice Laing,  
600 SATIB Trust, Eppley, Panthera, Robertson and Recanati-Kaplan Foundations and Riv

601 and Joan Winant. DRF was funded by the Max Planck Society and the European  
602 Research Council (ERC) under the European Union's Horizon 2020 research and  
603 innovation programme (grant agreement No. 850859), and received additional funding  
604 from the Daimler und Benz Stiftung (32-03/16 awarded to DRF), a DFG (grant FA  
605 1420/4-1 awarded to DRF), and the DFG Centre of Excellence 2117 "Centre for the  
606 Advanced Study of Collective Behaviour" (ID: 422037984). An International Program  
607 for Scientific Cooperation (PICS) grant from the CNRS and a Santander travel grant  
608 from Lady Margaret Hall College, University of Oxford, facilitated this collaborative  
609 work. We thank all the anonymous reviewers who made very useful comments to  
610 improve the quality of this manuscript.

611

#### 612 **Authors' Contributions**

613 M.M.M., D.R.F., M.V., J.E.H., D.W.M., A.J.L. conceived the ideas and designed the  
614 methodology; M.M.M. collected the data; M.M.M and D.R.F analysed the data;  
615 M.M.M. led the writing of the manuscript. All authors contributed critically to the drafts  
616 and gave final approval for publication.

617

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