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

Moreangels M. Mbizah^{a1}, Damien R. Farine^{b, c, d, e}, Marion Valeix^{a, f, g}, Jane E. Hunt^a, David W. Macdonald^a and Andrew J. Loveridge^a

^aWildlife Conservation Research Unit (WildCRU), Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Tubney, Oxford OX13 5QL, UK.

^bDepartment of Collective Behavior, Max Planck Institute of Animal Behavior, 78457 Konstanz, Germany.

^cCentre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz, Germany.

^dDepartment of Biology, University of Konstanz, 78457 Konstanz, Germany.

^eEdward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK.

^fCNRS, Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Université Claude Bernard Lyon 1, Bât Grégor Mendel, 43 Bd du 11 novembre 1918, 69622 Villeurbanne, France.

^gLTSER France, Zone Atelier “Hwange”, Hwange National Park, Bag 62, Dete, Zimbabwe - CNRS HERD (Hwange Environmental Research Development) program.

Corresponding Author:

¹Moreangels M. Mbizah

Wildlife Conservation Research Unit (WildCRU), Department of Zoology, University

of Oxford, Recanati-Kaplan Centre, Tubney House, Tubney, Oxford OX13 5QL, UK

E-mail: moreangelsm@gmail.com Telephone: +263774517050

Abstract

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

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

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

4. In general, a greater abundance of dispersed smaller prey resulted in prides being consistently divided into subgroups with weaker cohesion among pride members. By contrast, low abundance and aggregated small herds of prey resulted in stronger connections among individuals. We found interesting trade-offs in individual decisions to associate generally (equally across all other members of the pride) when resources are aggregated and rich, and associating more exclusively (in subgroups of preferred associates) when resources are scarce. Further, lions preferentially associated equally across the pride when prey were large, providing some evidence that the composition of hunting parties might be important when prey are more

difficult to catch.

5. Our study provides evidence that ecological factors can shape both global and fine-scale properties of animal social systems, even when species live in seemingly consistently structured societies. Our findings suggest that the decisions by lions in the compromise between having few strong connections and having many weaker connections is strongly determined by ecological conditions. More broadly, our study reveals how fission-fusion dynamics and ecological factors can play out simultaneously across multiple levels of sociality.

Key words

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

Introduction

One important goal in animal ecology is to understand the relationship between environmental factors and animal population abundance, spatial distribution, and social structure (Solomon 1949). Studies across different taxa have demonstrated that resource availability is an important determinant of the broad-scale structure of animal societies, with most of these studies showing that animal group size is generally larger when food resources are more abundant and of a higher quality (see Hanya & Chapman 2013; Macdonald & Johnson 2015 for reviews). In particular Nel, Loutit, Braby and Somers (2013) found that where food patches were rich, fairly clumped and heterogeneous, black-backed jackals (*Canis mesomelas*) group sizes were large and territory sizes small. In group-living animals, interactions among pairs or subgroups of individuals within a group (Hinde 1956; Macdonald, Yamaguchi &

Kerby 2000; Krause & Ruxton 2002), and the outcome of these interactions can be interpreted as a network of social relationships (Whitehead 2008; Farine & Whitehead 2015). The nature, number, and strength of these relationships are complex and can mediate the benefits, such as food sharing, that individuals accrue from living in groups, particularly in times of need (Carter, Farine & Wilkinson 2017). Earlier attempts at understanding the interactions among individuals in a carnivore social structure, using the example of farm cats (*Felis catus*), were analytically unsophisticated. However, they offered some insights into patterns of social structure of group living carnivores (see Macdonald, Apps, Carr & Kerby 1987). Modern tools in ecology and evolution are now allowing us to understand better the patterns of animal social structure (i.e. the patterns in social relationships) at a finer level of social organization (Tanner & Jackson 2012; Farine *et al.* 2015a), including in carnivores (e.g. Ellwood *et al.* 2017). Understanding the processes generating variation in social structure across populations is critical for understanding the effects of sociality (Ilany & Akçay 2016). Yet, there is still only preliminary understanding of how ecological variables shape the fine-scale patterns of animal social structure (He, Maldonado-Chaparro & Farine 2019) and the implications of these on the overall group social structure and stability.

A number of postulates have been put forward to explain social structure in different animal populations, including predation risk for explaining the grouping patterns of females in non-human primates (Sterck, Watts & van Schaik 1997), kinship for shaping spatial layout of group living animals (Hirsch, Stanton & Maldonado 2012), and homophily (individual preferences for associating with like individuals) for shaping which individuals interact most strongly (Farine 2014). Social network

analysis has been instrumental in testing these postulates. At its base, social network analysis quantifies the strength of associations or interactions among each pair of individuals in a social group or population (Whitehead 2009). It allows us to understand complex social and ecological interactions in animal communities (Croft, James & Krause 2008; Farine & Whitehead 2015) by providing metrics that quantify social structure at different levels of organization, i.e. within individuals, groups and populations. Some pioneering studies have used social network analysis to reveal details of the relationship between food availability and patterns of animal social structure. For example, Tanner and Jackson (2012) found that European shore crab (*Carcinus meana*) individuals aggregated into cohesive stable subgroups when resources were clumped. Additionally, Foster *et al.* (2012) showed that when prey were abundant, the killer whale (*Orcinus orca*) population was characterized by a highly interconnected social network. Nevertheless, our understanding of the relationship between resources and social structure remains superficial. How do different aspects of food availability, such as the size and distribution of prey items, affect the finer-scale patterns of associations among individuals, in particular their decisions to form or disband subgroups?

In species that exhibit a form of fission-fusion social organization, the average size of subgroups, the amount of cohesion they show, and even their sexual composition are expected to vary depending mainly on food distribution and mating systems (Symington 1988). One species that has been widely reported as exhibiting within-group fission-fusion dynamics by forming subgroups is the African lion (*Panthera leo*) (Schaller 1972). Individuals within these subgroups form very close associations (Van Orsdol, Hanby & Bygott 1985), and subgroup membership can potentially be

influenced by the attributes of different individual lions, such as their age, sex and reproductive state. For instance, female lions often form highly stable maternity groups that are effective in defending their cubs against infanticidal males from outside the pride and subgroup (Packer, Scheel & Pusey 1990). However, the interactions between individuals within a group are also likely to vary with ecological conditions. Although lions engage in a wide variety of important social activities, such as cooperative hunting (Scheel & Packer 1991), mutual defence of kills (Cooper 1991) and cooperative defence of territory and young (Mosser & Packer 2009), it has been suggested that lion sociality might be influenced by resource availability (Macdonald, Mosser & Gittleman 2010; Mbizah, Valeix, Macdonald & Loveridge 2019). For example, habitat quality was suggested as a major driver of lion social organisation in the Serengeti National Park, Tanzania (Mosser, Fryxell, Eberly & Packer 2009), and the number of prey herds visiting a waterhole determines maximum lion group size in Hwange National Park, Zimbabwe (Valeix, Loveridge & Macdonald 2012). These studies provide evidence that the general structure of lion populations (group size) is linked to overall resource availability (food abundance).

The dynamics of resource availability especially the abundance, richness, type, and distribution of prey might also influence finer-scale lion social structure. For example, when prey are abundant, we expect that there will be less competition for food, meaning that lions will gain fewer benefits from being in larger groups. As a result, they should preferentially remain with close associates. Extensive work on baboons has shown that the strength of close associations can increase fitness (Silk *et al.* 2010; Alberts 2019). When prey are scarce, then we expect lions to associate with a greater 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

in terms of both assemblages and abundance (Chamaillé-Jammes, Charbonnel, Dray, Madzikanda & Fritz 2016). We therefore commonly distinguish three seasons in Hwange National Park: the wet season (November - February), the early dry season (March - June) and the late dry season (July - October). Lion density is estimated at around 3.5 lions/100 km² in the study area (Loveridge *et al.* 2016) and there is a heterogeneous distribution of prey, both spatially and temporally (Chamaillé-Jammes *et al.* 2016).

Lion pride observations

In this study, we used data from seven GPS-collared lions (two adult females and five adult males) from four different prides for the study period 2013 - 2015. Lion prides were located with the help of GPS radio-collars and at times opportunistically. The prides were observed at least five times per month to record the size and composition of their group at that time. When a group was observed, we recorded the pride name, identity of individuals present, as well as their age, sex and reproductive state (whether they had cubs). We also recorded their activities during observations and these included resting, hunting, feeding and walking. All lion individuals are recognizable by whisker patterns that are unique to each individual and natural markings such as scars, muzzle spots and tooth irregularities (Pennycuick & Rudnai 1970). We looked at two aspects of lion group (1) pride (all the individuals within a group) and (2) subgroup (individuals of a pride present at each observation). We recorded all individuals present together as being connected (Whitehead & Dufault 1999; Farine 2015). The GPS collars recorded locations every two hours day and night, and we regularly downloaded this positional data to estimate lion seasonal home range. Only individuals that had collar data with fixes covering the whole

season were included in calculating seasonal home range.

Ecological factors

To measure prey availability, we conducted multi-species spoor (tracks made by animals when they cross the roads) surveys from 2013 to 2015 during the early dry season and the late dry season. Most of the available roads in the study area were used as transects (n = 64 transects) and were between 9 and 55 km long. The 64 selected transects were within areas that lions frequent. When a fresh spoor (less than 24hrs old) was encountered, it was assessed for species and group size by highly skilled and experienced trackers (see S1 Appendix for further details on the spoor survey method). Only spoor from common lion prey species in the area was used in this analysis. Information on prey availability was extracted for each lion home range in each season (See S2 Appendix for further details). From the spoor surveys, we also extracted information on the abundance of hyaenas within lion home ranges and then calculated the ratio of hyaena abundance to lion pride size. We used a vegetation map (Arraut, Loveridge, Chamaillé-Jammes, Valls-Fox & Macdonald submitted) to calculate the percentage of vegetation cover within each lion home range. We re-classed the original seven vegetation classes into two main classes; open vegetation (grassland and bushed grassland) and closed vegetation (bushland, woodland deciduous, mopane scrubland, mopane woodland and woodland evergreen) and calculated the percentage of the closed vegetation within each lion home range.

Social networks construction

We used lion pride observational data to construct a social network for each pride in each dry season in each year, with observations ranging from 16 to 66 observations

per season (Table S3). Thus, each social network represented the patterns of associations within a pride over a four-month period. The social networks contained each of the individuals in one pride as nodes and pairwise association indices as edge weights. Because we did not have complete data on observations of all groups simultaneously, we had to convert the number of associations into an association rate (the propensity for individuals to be seen together). To calculate these edge weights, we used the Simple Ratio Index as an estimate of the proportion of time two individuals spent together (Cairns & Schwager 1987; Hoppitt & Farine 2017). The Simple Ratio Index is defined as $x / (y_a + y_b + y_{ab} + x)$, where x is the number of observations of two individuals together, y_a is the number of observations with only individual a , y_b is the number of observations with only individual b , y_{ab} , the number of simultaneous observations of individuals a and b , was not relevant to our study. This ratio ranges from 0 for two individuals never seen in the same subgroup and 1 for two individuals always seen in the same subgroup. Animals that died during a season were not included in that season's network.

Social network analysis

We first used the multiple regression quadratic assignment procedure (MRQAP) to test if the tendency of lions to associate with individuals of the same sex, same age or same reproductive state had an effect on lion social structure. MRQAP tests the matrix equivalent of a linear regression and are widely used for hypothesis testing in networks (Farine 2017). We conducted a separate MRQAP for each pride in each season with association as the dependent matrices and age based homophily, sex based homophily and reproductive state based homophily as the independent variables. The homophily matrices were constructed by assigning similar pairs a value

of 1, while dissimilar pairs received a value of 0. We conducted these tests using the MRQAP function with a custom null model option in ‘asnipe’ package in the statistical software R (Farine 2013). The null model consisted of 10 000 permutations (see below)

To quantify the division of prides into subgroups and the nature of connections within prides and within subgroups, we used three network metrics: modularity, mean weighted degree and network density. Modularity describes the separation of networks into structural communities, or subgroups of individuals that are more connected among themselves than they are to others (Girvan & Newman 2002). Herein, we call these network-based communities “subgroups”. A higher modularity implies that a group tends to break into distinct subgroups with stronger connections between individuals within a subgroup but weaker connection between individual in different subgroups (Newman 2004). Mean weighted degree is defined as the average sum of the weight of edges surrounding each node in a network; it measures the strength of connections among individuals in a group and a high mean weighted degree means most individuals were seen together most of the time. Network density is the ratio of the number of edges (nonzero edges) in the network over the total number of possible edges between all pairs of nodes. A high network density represents greater gregariousness among individuals with individuals being connected to more conspecifics. We represented the resulting subgroup assignments by giving different colours of nodes to each subgroup within a pride using the community detection algorithm (Fig. 1). All network measures were calculated in R using igraph (Csardi & Nepusz 2006).

Hypothesis testing

We first preliminarily tested for the correlation between the four measures of prey availability, and the correlations were generally moderate to low ($-0.59 \leq r \leq 0.62$), still each measure was analysed separately. All analysis were done in the statistical software R (Bates, Mächler, Bolker & Walker 2015) using linear mixed effects regression analysis and the identity link in the lme4 package. We assessed the relationship between the different network metrics (modularity, mean weighted degree and network density for each pride and subgroup network) and (i) the four measures of prey availability, (ii) a measure of interspecific competition (ratio of hyaena abundance to lion pride size), and (iii) a measure of vegetation cover (percentage of closed vegetation). The network metric was the response variable while the above ecological variables that can potentially influence lion social structure were the fixed effects; with lion pride ID included as the random effect. Using the null model procedure described below, we also generated 10 000 randomised versions of each network, and ran the same regression with each of these randomised networks. We then calculated P-values for each fixed effect by calculating the number of coefficients of the regression slopes from the randomised networks that were greater than or equal to the corresponding coefficient of the regression slopes using the observed network, divided by the number of random networks generated and corrected for a two-tailed test (Farine 2017). The regression coefficients were scaled (by subtracting the mean and dividing by the standard deviation) to make the strength of the effect comparable between the pride level and the subgroup level. All analysis were done in R statistical software (R Core Team 2019).

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

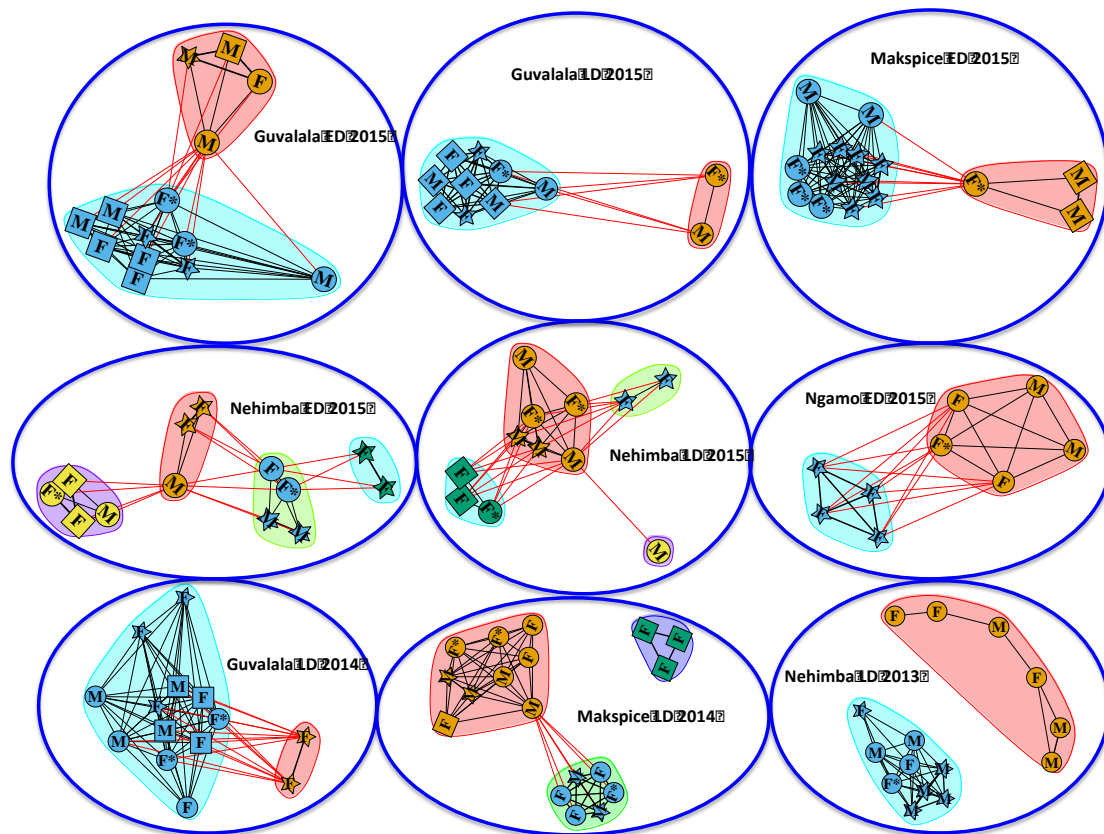


Fig. 1 Subgrouping patterns across a total of four prides, two distinct seasons (early dry season (ED) and late dry season (LD)) and three years (2013 to 2015). Pride identity, season and year are noted in each network. Each node, representing an individual lion, is assigned to a subgroup, which is denoted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

Prey abundance

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

significantly weaker with increasing prey abundance (Fig. 2a.i). However, this was not significant when calculating strength of connections exclusively within subgroups (Fig 2a.ii). Prey abundance had no significant effect on the gregariousness among individuals (how many individuals were connected to, or network density) when measured at the level of pride (Fig. 2.b.i) but an increase in prey abundance decreased the gregariousness among individuals when measured at the level of the subgroups (Fig. 2.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

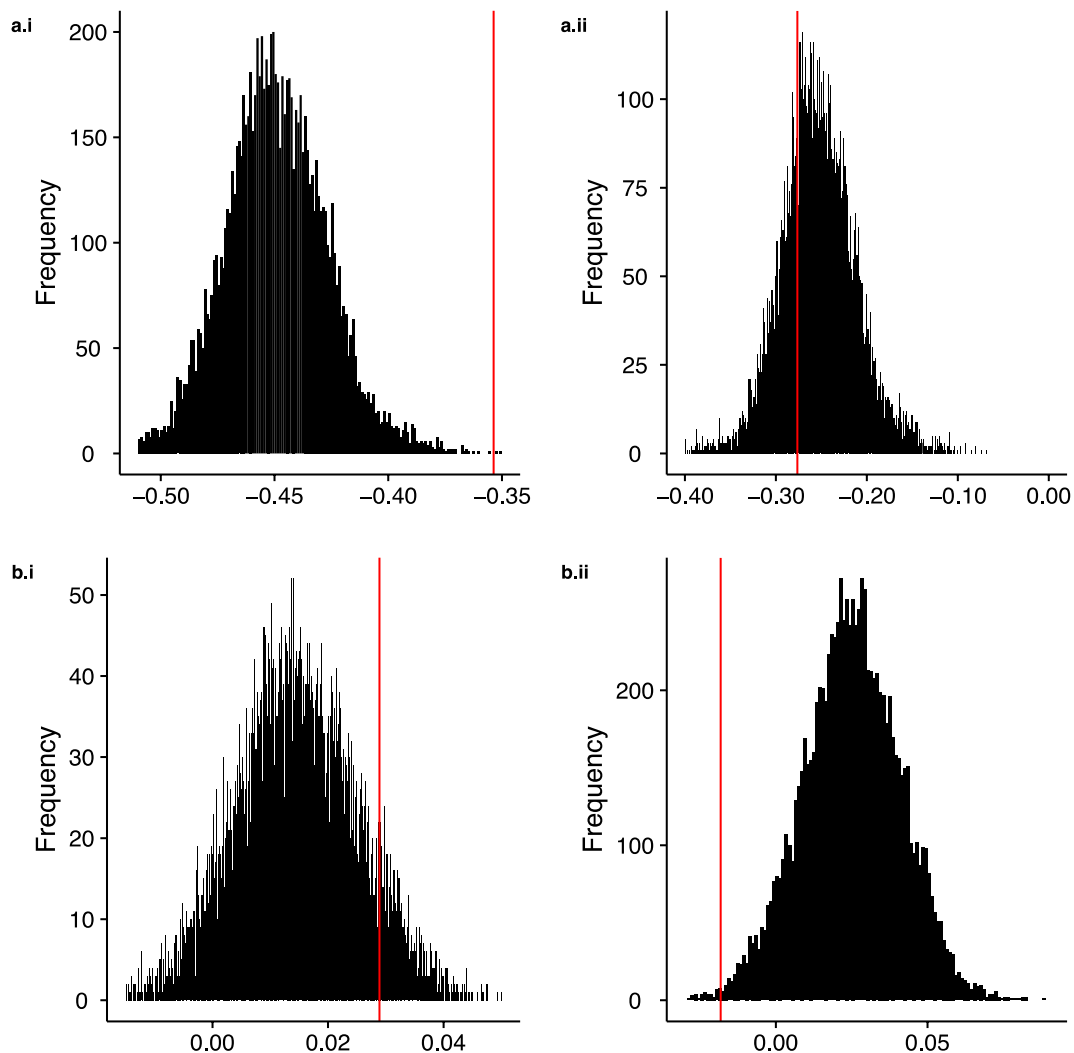


Fig. 2. The relationship between number of prey herds/km (index of prey abundance) and a) mean weighted degree (strength of connections among individuals) within (i)

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

Prey dispersion

The strength of division of prides into subgroups significantly increased (i.e. subgroups became clearer and more consistent, resulting in a higher modularity score) with increase in prey dispersion (Table S4). Prey dispersion had no significant effect on the strength of connections among individuals at the pride level, but significantly increased the strength of connections among members of subgroups (Figs. 3a.i and 3a.ii). Prey dispersion had no significant effect on the gregariousness among individuals when measured at the level of pride (Figs. 3.b.i) but an increase in prey dispersion decreased the gregariousness within subgroups (Figs. 3.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

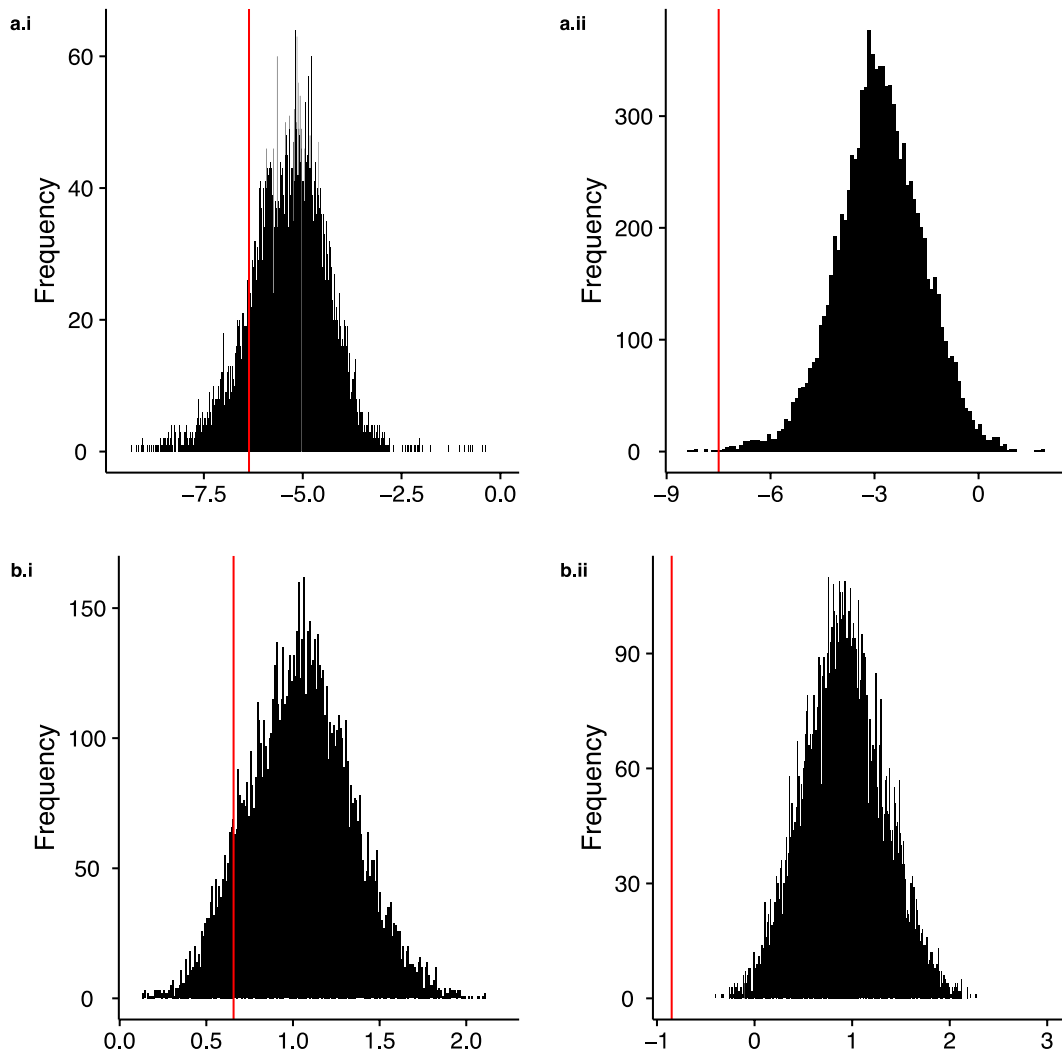
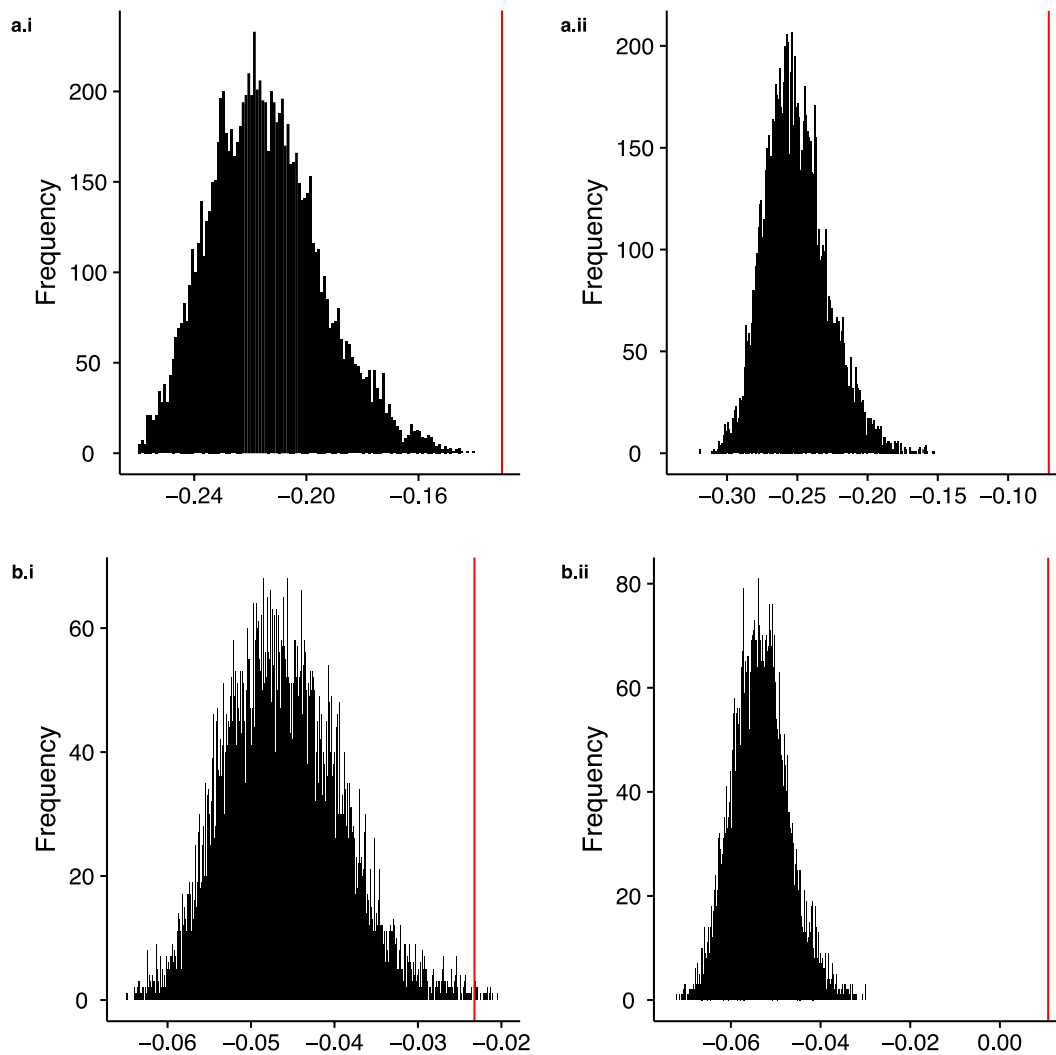


Fig. 3 The relationship between nearest neighbour index of prey herds (index of prey dispersion) and a) mean weighted degree (strength of connections among individuals) within (i) prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups.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

Patch richness (mean prey herd size)

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

422 individuals decreased at both the pride- and subgroup-level when prey herd size
 423 increased (Figs. 4a.i; 4a.ii). Increase in prey herd size resulted in significant decrease
 424 in gregariousness among individuals within prides (Fig. 4.b.i), and a significant
 425 increase in gregariousness within subgroups (Fig. 4.b.ii; see Figure S1, Table S4, S5
 426 and S6 for full results).
 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

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

Patch richness (mean prey body size)

The strength of division of prides into subgroups decreased with an increase in mean prey body size, meaning that individuals tended to associate more evenly with all other members of their pride (Table S4). The strength of connections among individuals within prides and subgroups increased significantly with an increase in mean prey body size, with this effect being stronger within subgroups (Figs. 5a.i and 5a.ii). Mean prey body size had no significant effect on gregariousness when measured at the level of pride (Fig. 5.b.i) but an increase in mean prey body size significantly decreased the gregariousness among individuals when measured at the level of the subgroups (Fig. 5.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

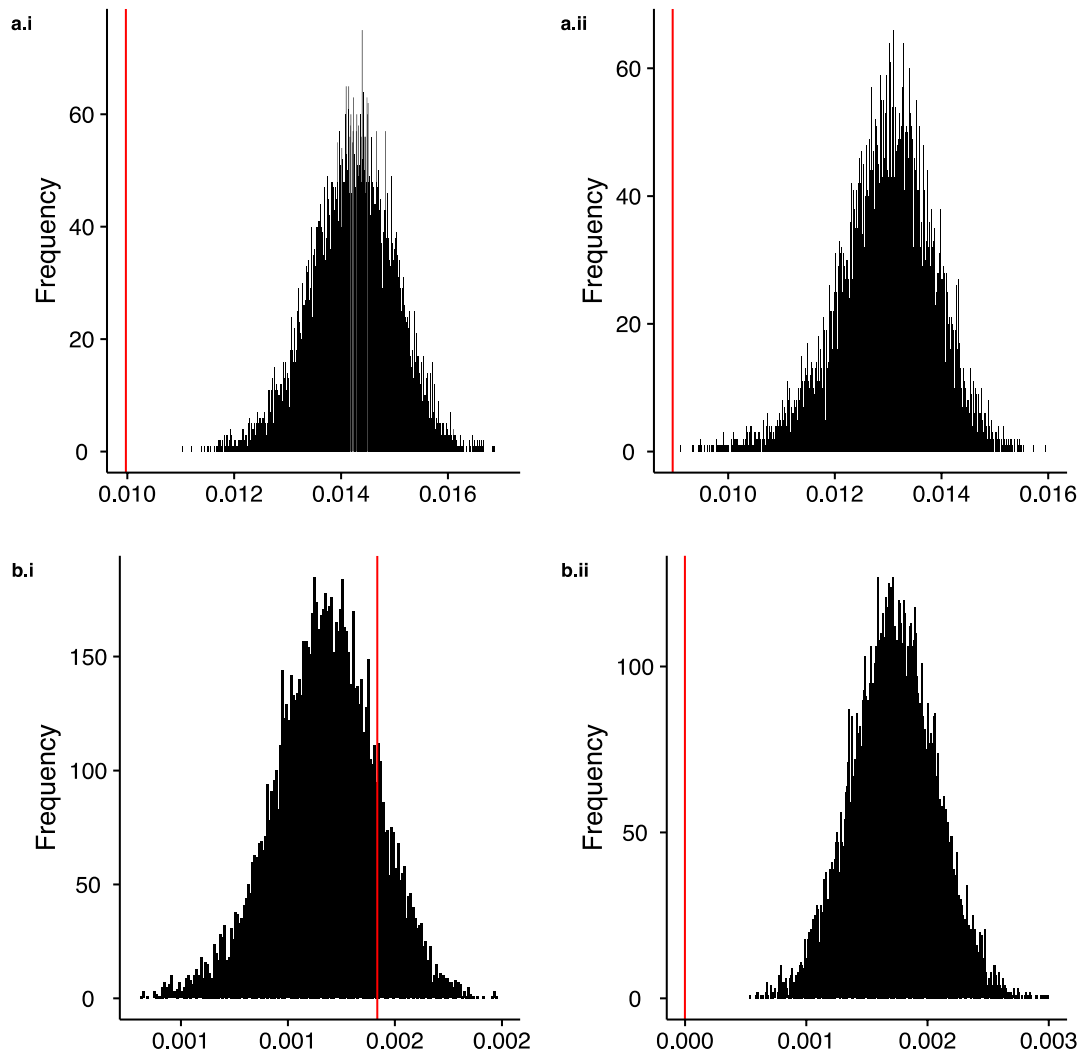
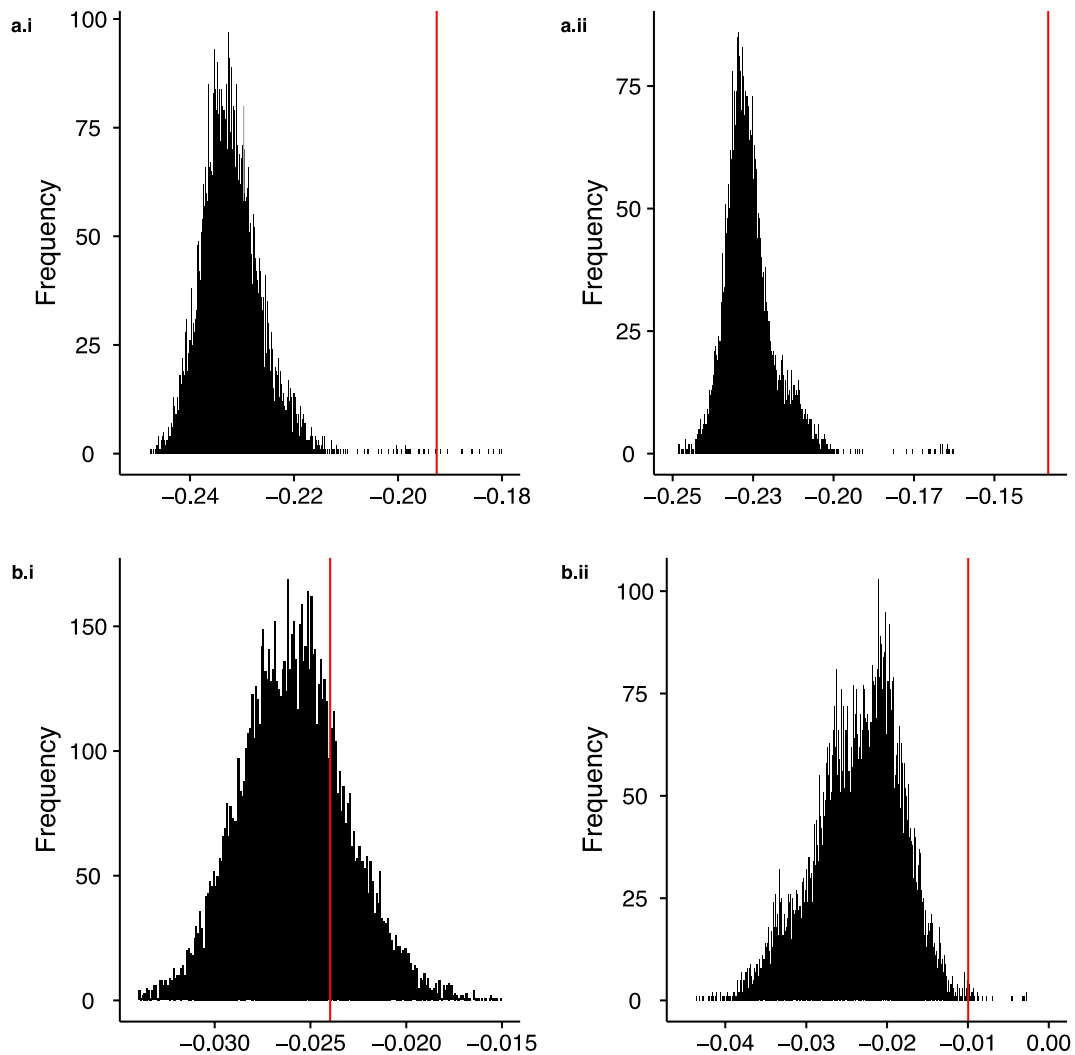


Fig. 5 The relationship between mean prey body size (index of patch richness) and a) mean weighted degree (strength of connections among individuals) within (i) prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups. The distribution of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

Interspecific competition

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

457 decreased, for both pride and subgroups, when interspecific competition increased
 458 (Figs. 6a.i; 6a.ii). Interspecific competition had no significant effect on the
 459 gregariousness within prides (Fig. 6.b.i), but an increase in interspecific competition
 460 significantly decreased the gregariousness among individuals within subgroups (Fig.
 461 6.b.ii; see Figure S1, Table S4, S5 and S6 for full results).



462
 463 **Fig. 6** The relationship between ratio of hyaenas to lions (interspecific competition)
 464 and a) mean weighted degree (strength of connections among individuals) within (i)
 465 prides and (ii) subgroups and b) network density (gregariousness among individuals)
 466 within (i) prides and (ii) subgroups. The distribution of the coefficients of the
 467 regression slope of the random networks (black lines) and the observed network (red

line).

Vegetation cover

Vegetation cover had no significant effect on division of prides into subgroups (Table S4). The effect of vegetation cover on the strength of connections among individuals was not significant either within prides or within subgroups (Figs. 7a.i and 7a.ii). An increase in vegetation cover resulted in a significant increase in gregariousness among individuals within subgroups (Figs. 7.b.i, 7.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

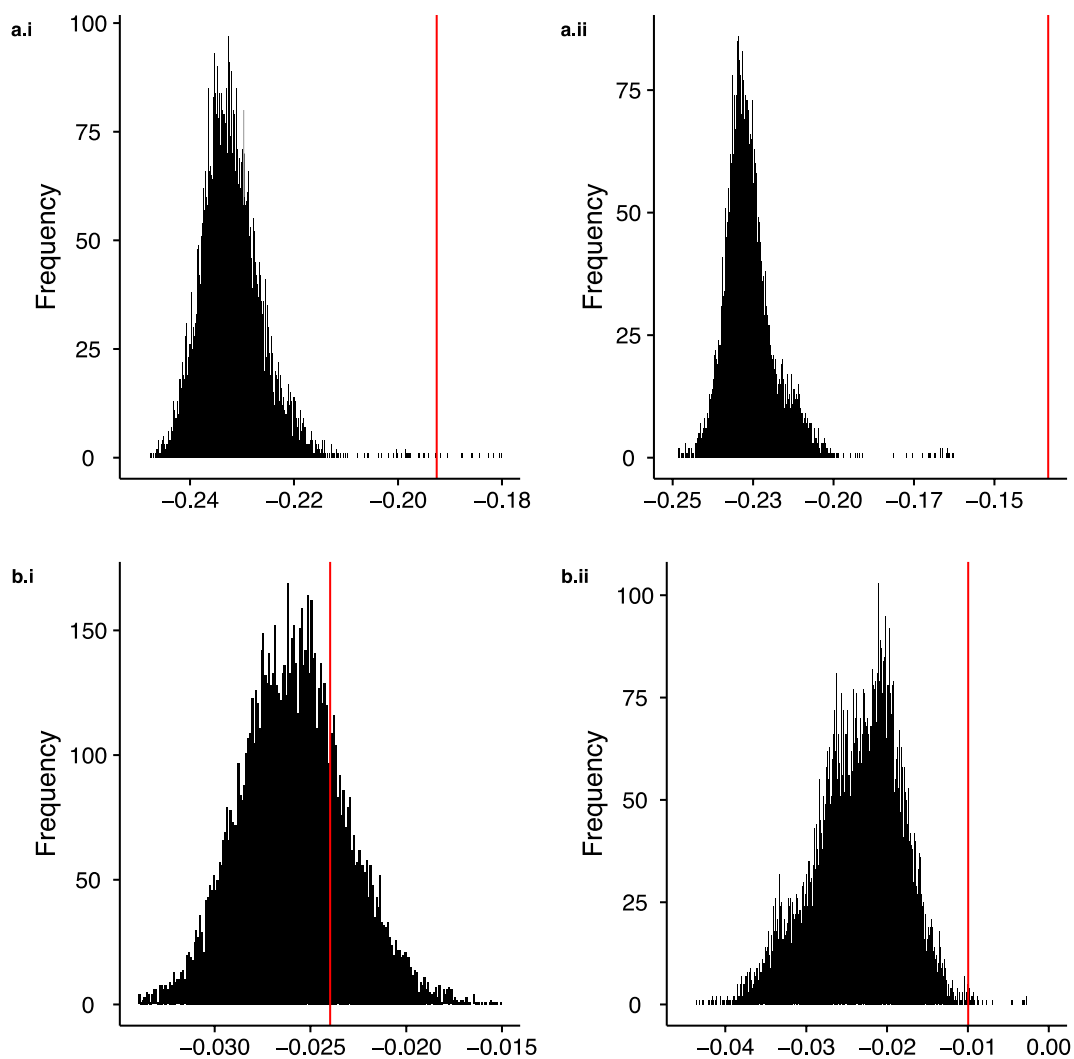


Fig. 7 The relationship between percentage of closed vegetation (vegetation cover) and a) mean weighted degree (strength of connections among individuals) within (i) prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups. The distribution of the coefficients of the regression slope of the random networks (black lines) and the observed network (red line).

Discussion

Our study extends prior studies on the role of ecological factors in determining broad population structure by demonstrating their effects on the fine scale patterns of association among individuals at two scales: within groups and within subgroups. More specifically, our study revealed that an increase in prey abundance, prey dispersion, interspecific competition and a decrease in prey body size resulted in clearer and more consistent subgroups. These ecological factors also affected the strength, total amount, and variability in subgroup membership among individuals within a pride. Our study therefore provides evidence that ecological factors can shape both global and fine-scale properties of animal social systems, even when species live in seemingly consistently structured societies (e.g. with defined and long-lasting territories).

Individuals of similar characteristics often band together to form cliques, for example coalition males in cheetahs (*Acinonyx jubatus*) come together to increase their chances of holding territories (Caro & Collins 1986). Our network analyses captured some fundamental properties of lion behaviour, including the general propensity for lions to associate with individuals of the same sex. In lions, females often come

together to defend their cubs against nomadic males (Packer & Pusey 1983) whereas males form coalition to take over and protect territories (Schaller 1972; Packer 1986). However, overall our results suggest that the effect of individual trait similarity alone explains relatively little of the variance in subgroup composition. One pride did show consistent significant effects, but this is likely to be because this was a highly gregarious pride composed of only adult males and females and their cubs, which was quite unique to this particular pride.

Our key finding is that different axes of resource availability explained patterns of social structure within groups and within subgroups. As the amount of available food increased, prides tended to divide into subgroups. The excess available food might provide individuals with an opportunity to invest more into strengthening bonds with close associates within their subgroups rather than maintaining weaker bonds with all pride members. Research in vampire bats (*Desmodus rotundus*) has highlighted that strongly connected associates are the primary source of help when an individual is going hungry (Carter *et al.* 2017). Subgroups of lions were also more gregarious when food was scarce, capturing their tendency to maximize foraging efficiency by searching in groups (Lachlan, Crooks & Laland 1998). Searching in groups is also useful for sharing information about the resources as shown in other studies that personal information and experience may be used to optimize search pattern and can be useful in locating food patches (Aplin, Farine, Morand-Ferron & Sheldon 2012). These results are in contrary to what Foster *et al.* (2012) discovered for killer whales for which the associations between individuals in a group were stronger and the network highly interconnected when food was abundant.

The dispersion of resources potentially increases searching behaviour (Sogard & Olla 1997; Valeix *et al.* 2010), thus limiting the opportunity for social interactions between individuals at the pride level (Tanner & Jackson 2012). When resources are dispersed across the landscape, prides tended to break into subgroups. We found that this led to prides that were socially fragmented. Persistent separation between subgroups within a pride reduces encounter rates and contacts among individuals across different subgroups, which could have impacts on processes such as mate choice and other social behaviours (Banks, Piggott, Stow & Taylor 2007; Krause, Lusseau & James 2009). Further, weaker associations between subgroups can make the pride less stable (Beisner, Jackson, Cameron & McCowan 2011) and susceptible to other anthropogenic and stochastic influences (Snijders, Blumstein, Stanley & Franks 2017). Recent experiments that involved temporarily splitting colonies of zebra finches found that social instability increased social exclusivity (i.e. subgrouping) and, as a result, decreased the collective performance of colonies in terms of foraging efficiency (Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby & Farine 2018). When resource patches become more aggregated, for example through clustering of prey herds in patches of specific habitats or around waterholes (Valeix *et al.* 2009), lion prides tend to use these resource patches intensively (Valeix *et al.* 2010). This aggregation of prey appears to allow regular associations among pride members, leading to highly connected pride members with little subgrouping within prides. Golden jackals (*Canis aureus*) have also been reported to aggregate around clumped food sources resulting in a larger and more cohesive group (Macdonald 1979).

Prey herd size had no significant effect on the strength of the division of the pride into subgroups, however the overall strength of connections among individuals, within

both prides and subgroups, decreased with increase in the size of prey herds. This result is contrary to what we were expecting since larger prey herds can potentially provide a chance for several predators within a group to make a kill or for more than one individual to be killed from the herd (e.g. Creel & Creel 2002). Our results might instead be interpreted in terms of lion foraging behaviour where both prides and subgroups avoid hunting large prey herds because the increased vigilance by very large groups reduces the attack success rate (Kenward 1978; Cresswell & Quinn 2011) which could make it difficult for lions to hunt successfully, especially buffalos which have been known to mob predators and kill lions (Mangani 1962; Estes 1991). In Serengeti lions have been shown to prefer smaller prey herds over large herds (Scheel 1993).

We further found that the strength of division of prides into subgroups decreased with increase in prey size. Large prey species (rich patches) such as buffalo, zebra, giraffe or juvenile elephant can feed several lions, consequently, competition for prey within the pride is likely to be minimal and individuals can associate frequently outside of their close connections. Essentially, individuals in the pride tended to come together more often (fusion), which could allow them to cooperatively hunt the large sized prey (Scheel & Packer 1991) and increase success of prey capture (but see Caraco & Wolf 1975; Packer *et al.* 1990) while minimizing energetic costs (Carbone, Teacher & Rowcliffe 2007). Similarly, Kruuk (1972), and later Smith, Kolowski, Graham, Dawes and Holekamp (2008), showed that when energy per resource patch is high, hyaenas tend to congregate at such food patches and spend relatively more time with conspecifics than alone. As a result the increased pride-level cohesion when prey is large may also provide a number of other benefits to pride members, including

increased chances of communal defence of cubs (Packer & Pusey 1983) and territorial defence (Grinnell 2002; Mosser & Packer 2009).

The strength of division of prides into subgroups increased with increase in interspecific competition with the hyena. Furthermore, the gregariousness among individuals in both subgroups and prides and the strength of their connections decreased with increase in competition. This was contrary to our expectations of how interspecific competition and predation risk would influence the fine scale animal social structure. We expected cooperation to be higher and connections stronger particularly in areas where there are higher densities of hyaenas as lions might need to defend their kills from hyaenas (Cooper 1991). Perhaps our result is because the cooperative mobbing behaviour by hyenas when they encounter lions (Lehmann *et al.* 2017) has the effect of weakening the bonds between individual lions and reducing gregariousness.

As stalk-and-ambush hunters, vegetation cover has been shown to be an important variable in the foraging behaviour and hunting success of lions (Funston, Mills & Biggs 2001; Hopcraft *et al.* 2005) particularly for male lions (Loarie *et al.* 2013). In our study, gregariousness among individuals within subgroups increased with increase in vegetation cover. As expected of a stalk-and-ambush predator, lions would spend more time and associate more with subgroup members, for a more coordinated hunt in areas of good cover (Stander & Albon 1993; Hopcraft *et al.* 2005) where they have a higher chance to successfully hunt prey like buffalo that are vulnerable to predation in dense bush (Hay, Cross & Funston 2008).

The structure of the pride social networks, and the subgroups therein, captured the trade-offs individuals face between associating generally (equally across the pride) when resources are abundant and easy to find and catch, and associating more exclusively (in subgroups of preferred associates) when resources are scarce or more difficult to come by. Thus, we found seemingly consistent and predictable patterns of ecological factors on different aspects of within-pride social structure. However, the effect of ecological factors on the strength of connections and the frequency of associations among individuals were often more pronounced within subgroups than at the pride-level. Our results therefore suggest that the changes in pride structure under different ecological conditions can be dramatic from the perspective of individuals.

Our findings could be important given that individual lions are highly dependent on their pride mates for survival and reproduction (Packer, Pusey & Eberly 2001). Our results also suggest that increasing pride-level connectance with decreasing prey abundance is likely to arise from re-allocation of social associations from subgroups to other group members. This contrasts with a more traditional view of hierarchical societies in which higher-level organisation (here a pride) emerges from connections among more stable lower levels (here subgroups). Drawing on our knowledge of decision-making, our findings may insinuate that individual lions are making decisions at both the subgroup level and at the pride level.

A number of studies have examined the relationship between ecological factors and group size across a range of species, for example white-throated magpie-jays (*Calocitta formosa*) (Langen & Vehrencamp 1998), river dolphins (Gomez-Salazar, Trujillo & Whitehead 2012) and lions (Mbizah *et al.* 2019). Our findings suggest that

ecological factors can also influence the more complex fine-scale elements of social dynamics within groups. Decisions about sociality are often optimized to maximize individual fitness (Silk 2007; Farine, Montiglio & Spiegel 2015b) and in our study we found that individuals compromise between having few strong connections and having many weaker connections. These patterns mirror recent findings in vampire bats showing that individuals exhibit patterns of social bet-hedging, maintaining both stronger and weaker associations, which are differentially important in times of need (Carter *et al.* 2017). We further show that the trade-off is driven by different axes of variation in the underlying distribution of ecological resources. Our study therefore provides evidence that ecological factors can shape fine-scale properties of animal social systems at different scales, even when species live in structured societies that outwardly appear to be consistent.

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Authors' Contributions

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

References

- Alberts, S.C. (2019) Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology*, **88**, 47-66.
- Aplin, L.M., Farine, D.R., Morand-Ferron, J. & Sheldon, B.C. (2012) Social networks predict patch discovery in a wild population of songbirds. *Proc R Soc Lond [Biol]*, **279**, 4199-4205.
- Arraut, E., Loveridge, A.J., Chamaillé-Jammes, S., Valls-Fox, H. & Macdonald, D.W. (submitted) 2013-14 vegetation structure map of Hwange National Park, Zimbabwe, produced with free satellite images and software. *Koedoe*.
- Banks, S.C., Piggott, M.P., Stow, A.J. & Taylor, A.C. (2007) Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Canadian Journal of Zoology*, **85**, 1065-1079.

679 Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects
680 Models Using lme4. *Journal of Statistical Software*, **67**, 48.

681 Beisner, B.A., Jackson, M.E., Cameron, A.N. & McCowan, B. (2011) Detecting
682 instability in animal social networks: genetic fragmentation is associated with
683 social instability in rhesus macaques. *PLoS ONE*, **6**.

684 Bejder, L., Fletcher, D. & Brager, S. (1998) A method for testing association patterns
685 of social animals. *Animal Behaviour*, **56**, 719-725.

686 Cairns, S.J. & Schwager, S.J. (1987) A comparison of association indices. *Animal*
687 *Behaviour*, **35**, 1454-1469.

688 Caraco, T. & Wolf, L.L. (1975) Ecological determinants of group sizes of foraging
689 lions. *American Naturalist*, **109**, 343-352.

690 Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007) The costs of carnivory. *PLoS*
691 *Biology*, **5**, e22.

692 Caro, T.M. & Collins, D.A. (1986) Male cheetahs of the Serengeti. *National*
693 *Geographic Research*, **2**, 75-86.

694 Carr, G.M. & Macdonald, D.W. (1986) The sociality of solitary foragers: a model
695 based on resource dispersion. *Animal Behaviour*, **34**, 1540-1549.

696 Carter, G.G., Farine, D.R. & Wilkinson, G.S. (2017) Social bet-hedging in vampire
697 bats. *Biology Letters*, **13**.

698 Chamaillé-Jammes, S., Charbonnel, A., Dray, S., Madzikanda, H. & Fritz, H. (2016)
699 Spatial distribution of a large herbivore community at waterholes: an
700 assessment of its stability over years in Hwange National Park, Zimbabwe.
701 *PLoS ONE*, **11**.

702 Cooper, S.M. (1991) Optimal hunting group-size: the need for lions to defend their
703 kills against loss to spotted hyaenas. *African Journal of Ecology*, **29**, 130-136.

704 Creel, S. & Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology, and*
705 *Conservation*. Princeton University Press.

706 Cresswell, W. & Quinn, J.L. (2011) Predicting the optimal prey group size from
707 predator hunting behaviour. *Journal of Animal Ecology*, **80**, 310-319.

708 Croft, D.P., James, R. & Krause, J. (2008) *Exploring Animal Social Networks*.
709 Princeton, Princeton University Press.

710 Croft, D.P., Madden, J.R., Franks, D.W. & James, R. (2011) Hypothesis testing in
711 animal social networks. *Trends in Ecology & Evolution*, **26**, 502-507.

712 Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network
713 research. *InterJournal, Complex Systems*, 1695.

714 Ellwood, S.A., Newman, C., Montgomery, R.A., Nicosia, V., Buesching, C.D.,
715 Markham, A., . . . Macdonald, D.W. (2017) An active-radio-frequency-
716 identification system capable of identifying co-locations and social-structure:
717 Validation with a wild free-ranging animal. *Methods Ecol Evol*, **8**, 1822-1831.

718 Estes, R. (1991) *The Behavior Guide to African Mammals: Including Hoofed*
719 *Mammals, Carnivores, Primates*. University of California Press.

720 Farine, D.R. (2013) Animal social network inference and permutations for ecologists
721 in R using asnipe. *Methods Ecol Evol*, **4**, 1187-1194.

722 Farine, D.R. (2014) Measuring phenotypic assortment in animal social networks:
723 weighted associations are more robust than binary edges. *Animal Behaviour*,
724 **89**, 141-153.

725 Farine, D.R. (2015) Proximity as a proxy for interactions: issues of scale in social
726 network analysis. *Animal Behaviour*, **104**, e1-e5.

727 Farine, D.R. (2017) A guide to null models for animal social network analysis.
728 *Methods Ecol Evol*.

729 Farine, D.R., Firth, J.A., Aplin, L.M., Crates, R.A., Culina, A., Garroway, C.J., . . .
730 Sheldon, B.C. (2015a) The role of social and ecological processes in
731 structuring animal populations: a case study from automated tracking of wild
732 birds. *Roy Soc Open Sci*, **2**.

733 Farine, D.R., Montiglio, P.-O. & Spiegel, O. (2015b) From Individuals to Groups and
734 Back: The Evolutionary Implications of Group Phenotypic Composition.
735 *Trends in Ecology & Evolution*, **30**, 609-621.

736 Farine, D.R. & Whitehead, H. (2015) Constructing, conducting and interpreting
737 animal social network analysis. *Journal of Animal Ecology*, **84**, 1144-1163.

738 Foster, E.A., Franks, D.W., Morrell, L.J., Balcomb, K.C., Parsons, K.M., van
739 Ginneken, A. & Croft, D.P. (2012) Social network correlates of food
740 availability in an endangered population of killer whales, *Orcinus orca*.
741 *Animal Behaviour*, **83**, 731-736.

742 Funston, P.J., Mills, M.G.L. & Biggs, H.C. (2001) Factors affecting the hunting
743 success of male and female lions in the Kruger National Park. *Journal of*
744 *Zoology*, **253**, 419-431.

745 Girvan, M. & Newman, M.E.J. (2002) Community structure in social and biological
746 networks. *Proceedings of the National Academy of Sciences of the United*
747 *States of America*, **99**, 7821-7826.

748 Gomez-Salazar, C., Trujillo, F. & Whitehead, H. (2012) Ecological factors
749 influencing group sizes of river dolphins (*Inia geoffrensis* and *Sotalia*
750 *fluviatilis*). *Marine Mammal Science*, **28**, E124-E142.

751 Grinnell, J. (2002) Modes of cooperation during territorial defense by African lions.
752 *Hum Nature-Int Bios*, **13**, 85-104.

753 Hanya, G. & Chapman, C.A. (2013) Linking feeding ecology and population
 754 abundance: a review of food resource limitation on primates. *Ecological*
 755 *Research*, **28**, 183-190.

756 Hay, C.T., Cross, P.C. & Funston, P.J. (2008) Trade-offs of predation and foraging
 757 explain sexual segregation in African buffalo. *Journal of Animal Ecology*, **77**,
 758 850-858.

759 He, P., Maldonado-Chaparro, A.A. & Farine, D.R. (2019) The role of habitat
 760 configuration in shaping social structure: a gap in studies of animal social
 761 complexity. *Behavioral Ecology and Sociobiology*, **73**, 9.

762 Hinde, A. (1956) The biological significance of the territories of birds. *Ibis*, **98**, 340-
 763 369.

764 Hirsch, B.T., Stanton, M.A. & Maldonado, J.E. (2012) Kinship Shapes Affiliative
 765 Social Networks but Not Aggression in Ring-Tailed Coatis. *PLoS ONE*, **7**,
 766 e37301.

767 Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005) Planning for success: Serengeti
 768 lions seek prey accessibility rather than abundance. *Journal of Animal*
 769 *Ecology*, **74**, 559-566.

770 Hoppitt, W.J.E. & Farine, D.R. (2017) Association indices for quantifying social
 771 relationships: how to deal with missing observations of individuals or groups.
 772 *Animal Behaviour*.

773 Ilany, A. & Akçay, E. (2016) Social inheritance can explain the structure of animal
 774 social networks. *Nat. Commun.*, **7**, 12084.

775 Kenward, R.E. (1978) Hawks and Doves: Factors Affecting Success and Selection in
 776 Goshawk Attacks on Woodpigeons. *Journal of Animal Ecology*, **47**, 449-460.

777 Krause, J., Lusseau, D. & James, R. (2009) Animal social networks: an introduction.
778 *Behavioral Ecology and Sociobiology*, **63**, 967-973.

779 Krause, J. & Ruxton, G.D. (2002) *Living in groups*. Oxford University Press.

780 Kruuk, H. (1972) *The Spotted Hyaena. A Study of Predation and Social Behaviour*.
781 University of Chicago Press, Chicago.

782 Lachlan, R.F., Crooks, L. & Laland, K.N. (1998) Who follows whom? Shoaling
783 preferences and social learning of foraging information in guppies. *Animal*
784 *Behaviour*, **56**, 181-190.

785 Langen, T.A. & Vehrencamp, S.L. (1998) Ecological Factors Affecting Group and
786 Territory Size in White-Throated Magpie-Jays. *The Auk*, **115**, 327-339.

787 Lehmann, K.D.S., Montgomery, T.M., MacLachlan, S.M., Parker, J.M., Spagnuolo,
788 O.S., VandeWetering, K.J., . . . Holekamp, K.E. (2017) Lions, hyenas and
789 mobs (oh my!). *Curr. Zool.*, **63**, 313-322.

790 Loarie, S.R., Tambling, C.J. & Asner, G.P. (2013) Lion hunting behaviour and
791 vegetation structure in an African savanna. *Animal Behaviour*, **85**, 899-906.

792 Loveridge, A.J., Valeix, M., Chapron, G., Davidson, Z., Mtare, G. & Macdonald,
793 D.W. (2016) Conservation of large predator populations: Demographic and
794 spatial responses of African lions to the intensity of trophy hunting. *Biological*
795 *Conservation*, **204**, 247-254.

796 Macdonald, D.W. (1979) The Flexible Social System of the Golden Jackal, *Canis*
797 *aureus*. *Behavioral Ecology and Sociobiology*, **5**, 17-38.

798 Macdonald, D.W., Apps, P.J., Carr, G.M. & Kerby, G. (1987) *Social dynamics,*
799 *nursing conditions and infanticide among farm cats, felis catus*. Paul Parey
800 Scientific Publishers, Berlin and Hamburg, West Germany.

801 Macdonald, D.W. & Johnson, D.D.P. (2015) Patchwork planet: the resource
802 dispersion hypothesis, society, and the ecology of life. *Journal of Zoology*,
803 **295**, 75-107.

804 Macdonald, D.W., Mosser, A. & Gittleman, J.L. (2010) Felid society. *Biology and*
805 *Conservation of Wild Felids* (eds D.W. Macdonald & A.J. Loveridge), pp.
806 125-160. Oxford University Press, Oxford.

807 Macdonald, D.W., Yamaguchi, N. & Kerby, G. (2000) Group-living in the domestic
808 cat: Its sociobiology and epidemiology. *The Domestic cat: the Biology of its*
809 *Behaviour* (eds D.C. Turner & P. Bateson), pp. 95–118. Cambridge University
810 Press, Cambridge

811 Maldonado-Chaparro, A.A., Alarcón-Nieto, G., Klarevas-Irby, J.A. & Farine, D.R.
812 (2018) Experimental disturbances reveal group-level costs of social instability.
813 *Proceedings of the Royal Society B: Biological Sciences*, **285**, 20181577.

814 Mangani, B. (1962) Buffalo kills lion. *African Wildlife*, **12**, 27.

815 Mbizah, M.M., Valeix, M., Macdonald, D.W. & Loveridge, A.J. (2019) Applying the
816 resource dispersion hypothesis to a fission-fusion society: A case study of the
817 African lion (*Panthera leo*). *Ecology and Evolution*.

818 Mosser, A., Fryxell, J.M., Eberly, L. & Packer, C. (2009) Serengeti real estate:
819 density vs. fitness-based indicators of lion habitat quality. *Ecology Letters*, **12**,
820 1050-1060.

821 Mosser, A. & Packer, C. (2009) Group territoriality and the benefits of sociality in the
822 African lion, *Panthera leo*. *Animal Behaviour*, **78**, 359-370.

823 Nel, J.A.J., Loutit, R., Braby, R. & Somers, M. (2013) Resource dispersion, territory
824 size and group size of black-backed jackals on a desert coast. *Acta*
825 *Theriologica*, **58**, 189–197.

826 Newman, M.E.J. (2004) Detecting community structure in networks. *Eur. Phys. J. B*,
827 **38**, 321-330.

828 Packer, C. (1986) The Ecology of Sociality in Felids. *Ecological Aspects of Social*
829 *Evolution: Birds and Mammals* (eds D.I. Rubenstein & R.W. Wrangham), pp.
830 429-452. Princeton University Press, Princeton

831 Packer, C. & Pusey, A.E. (1983) Adaptations of female lions to infanticide by
832 incoming males. *American Naturalist*, **121**, 716-728.

833 Packer, C., Pusey, A.E. & Eberly, L.E. (2001) Egalitarianism in female African lions.
834 *Science*, **293**, 690-693.

835 Packer, C., Scheel, D. & Pusey, A.E. (1990) Why lions form groups - food is not
836 enough. *American Naturalist*, **136**, 1-19.

837 Pennycuick, C.J. & Rudnai, J. (1970) A method of identifying individual lions
838 *Panthera leo* with an analysis of the reliability of identification. *J. Zool.*, **160**,
839 497-508.

840 R Core Team (2019) R: A language and environment for statistical computing. R
841 Foundation for Statistical Computing. Vienna, Austria.

842 Schaller, G.B. (1972) *The Serengeti lion; a study of predator-prey relations*.
843 University of Chicago Press, Chicago.

844 Scheel, D. (1993) Profitability, encounter rates, and prey choice of African lions.
845 *Behavioral Ecology*, **4**, 90-97.

846 Scheel, D. & Packer, C. (1991) Group hunting behavior of lions - A search for
847 cooperation. *Animal Behaviour*, **41**, 697-709.

848 Silk, J.B. (2007) The adaptive value of sociality in mammalian groups. *Philos. Trans.*
849 *Royal Soc. B*, **362**, 539-559.

850 Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R.,
851 . . . Cheney, D.L. (2010) Strong and consistent social bonds enhance the
852 longevity of female baboons. *Current Biology*, **20**, 1359-1361.

853 Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E. & Holekamp, K.E. (2008)
854 Social and ecological determinants of fission-fusion dynamics in the spotted
855 hyaena. *Animal Behaviour*, **76**, 619-636.

856 Snijders, L., Blumstein, D.T., Stanley, C.R. & Franks, D.W. (2017) Animal social
857 network theory can help wildlife conservation. *Trends in Ecology &*
858 *Evolution*, **32**, 567-577.

859 Sogard, S.M. & Olla, B.L. (1997) The influence of hunger and predation risk on
860 group cohesion in a pelagic fish, walleye pollock *Theragra chalcogramma*.
861 *Environmental Biology of Fishes*, **50**, 405-413.

862 Solomon, M.E. (1949) The Natural Control of Animal Populations. *Journal of Animal*
863 *Ecology*, **18**, 1-35.

864 Stander, P.E. & Albon, S.D. (1993) Hunting success of lions in a semi-arid
865 environment. *Symposia of the Zoological Society of London*, **No. 65**, 127–143.

866 Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997) The evolution of female social
867 relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*,
868 **41**, 291-309.

869 Symington, M.M. (1988) Food Competition and Foraging Party Size in the Black
870 Spider Monkey (*Ateles paniscus chamek*). *Behaviour*, **105**, 117-134.

871 Tanner, C.J. & Jackson, A.L. (2012) Social structure emerges via the interaction
872 between local ecology and individual behaviour. *Journal of Animal Ecology*,
873 **81**, 260-267.

- 874 Valeix, M., Loveridge, A.J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F.,
875 Fritz, H. & Macdonald, D.W. (2009) Behavioral adjustments of African
876 herbivores to predation risk by lions: Spatiotemporal variations influence
877 habitat use. *Ecology*, **90**, 23-30.
- 878 Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald,
879 D.W. (2010) How key habitat features influence large terrestrial carnivore
880 movements: waterholes and African lions in a semi-arid savanna of north-
881 western Zimbabwe. *Landscape Ecology*, **25**, 337-351.
- 882 Valeix, M., Loveridge, A.J. & Macdonald, D.W. (2012) Influence of prey dispersion
883 on territory and group size of African lions: a test of the resource dispersion
884 hypothesis. *Ecology*, **93**, 2490-2496.
- 885 Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985) Ecological correlates of lion
886 social organization (*Panthera, leo*). *J. Zool.*, **206**, 97-112.
- 887 Whitehead, H. (2008) *Analyzing Animal Societies: Quantitative Methods for*
888 *Vertebrate Social Analysis* University of Chicago Press.
- 889 Whitehead, H. (2009) SOCPROG programs: analysing animal social structures.
890 *Behavioral Ecology and Sociobiology*, **63**, 765-778.
- 891 Whitehead, H. & Dufault, S. (1999) Techniques for analyzing vertebrate social
892 structure using identified individuals: Review and recommendations. *Adv Stud*
893 *Behav*, **28**, 33-74.

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Supplementary Information Text

S1 Appendix

The spoor survey method

In this study prey availability was assessed using the spoor counting method, which is an indirect method of estimating population abundance. This method assumes that the intensity or frequency of animal signs is correlated to population size (Wilson & Delahay 2001). Spoor counting has been extensively used for estimating carnivore abundance (e.g. Funston *et al.* 2010), and has been found to be reliable for estimating abundance of large herbivores as well (e.g. Silveira, Jacomo & Diniz 2003). Multi-species spoor (animal track) count surveys were conducted from 2013 to 2015 during the early dry season and the late dry season. Roads or routes, termed transects, were divided into short segments, and these formed the units of the survey. Selected transects were driven and spoor were identified with the help of highly skilled and experienced trackers and care was taken to avoid double counting spoor. Vehicles driven at a speed of 10 - 15 km.h⁻¹ served as an observation platform during spoor surveys, with a driver, a recorder and a tracker sitting on a customized seat mounted to the front of a vehicle. Roads were not swept before the surveys and surveys were undertaken once per season for each of the five study sites.

When fresh spoor (less than 24h old) was encountered, it was assessed for species, herd size, age class and sex. The experienced trackers were able to determine if the spoor was fresh by the state and detail of the spoor, the shape and size of the spoor aided in determining the species, its age and sex, while the number of spoors around that area were counted to get the herd size. Only prey species and herd size were used in the analyses and we are confident that our highly skilled and experienced trackers could reliably assess these. Spoor were counted if they crossed transects but subsequent re-crossings were ignored when the trackers judged from the animal's movement patterns that these were apparently made by the same animal. During the surveys, spoor of a range of herbivores and carnivores were identified to the species level, but only spoor from lion prey species were used in this study. Prey species included in the analysis were Burchell's zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), steenbok (*Raphiceros campestris*), common duiker (*Sylvicapra grimmia*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*) and juvenile African elephant (*Loxodonta Africana*) (frequently recorded as prey during drought years in Hwange; Loveridge, Hunt, Murindagomo & Macdonald 2006).

S2 Appendix

Prey availability within lion home ranges

Lion home ranges were defined as the 90% probability contour of location distribution using the fixed kernel density estimator (Powell 2000) and the reference smoothing factor href (Hemson *et al.* 2005). Home range analyses was undertaken using the 'AdehabitatHR' package in the statistical software R (Calenge 2006). We used data from only one GPS collared lion per pride for each of the lion pride seasons. Prey availability data from spoor counts were overlaid on lion home ranges in QGIS (QGIS Development Team 2019) and the road transects that fell within each lion home range were clipped. For each home range and each season, we calculated four measures of prey availability, comprised of an index of prey abundance (number of

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

Figures

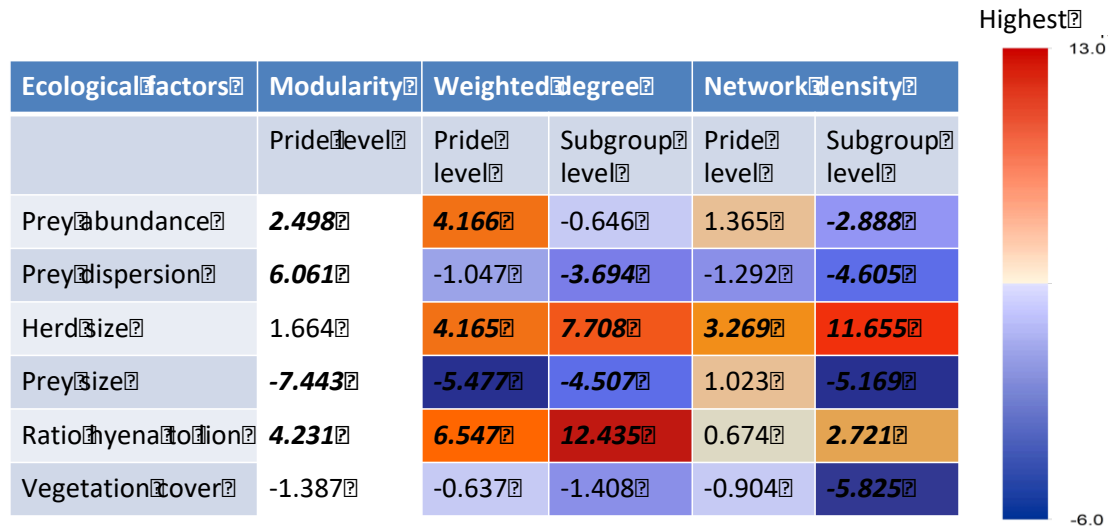


Fig. S1 The scaled coefficients of the relationship between ecological factors and (i) modularity (strength of division of a network into subgroups), (ii) mean weighted degree (strength of connections among individuals) and (iii) network density (gregariousness among individuals). The bold and italics 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.

Supplementary Information Tables

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

Description of Social and Ecological Factors

A. Social Factors

(i) Individual trait similarity

Sex - Grouping patterns of male lions may be influenced by their tendency to form coalitions that cooperate to compete with other coalitions for exclusive access to females (Packer & Pusey 1982). Grouping patterns of female lions is believed to be influenced by the need to protect their young and also maintain a long-term territory (Packer, Scheel & Pusey 1990).

Age - Age specific behaviour can also influence grouping patterns in lions. For example, subadult male lions may disperse from their natal pride and form coalitions with other dispersing subadult males (Van Orsdol 1981).

Reproductive state - In lions, lactating mothers tend to temporarily separate from the rest of the pride to forage and nurse their young (Packer *et al.* 1990).

B. Ecological Factors

(ii) Prey availability

Prey abundance - According to the prey abundance hypothesis, lions would be predicted to prefer areas of higher prey abundance (Hopcraft, Sinclair & Packer 2005), therefore individual lions may aggregate around these areas of high prey abundance

Prey dispersion - A measure of prey dispersion describes the distance lions have to travel to encounter prey or the effort involved in searching for prey. Lions would be expected to aggregate around areas of clustered prey patches, which are easily accessible (Valeix *et al.* 2010).

Prey herd size - A larger herd of prey might be considered a richer patch insofar as, all else being equal, it provides an opportunity for more than one lion to make a kill (in the Serengeti lions were observed sometimes to kill multiple prey when several lions attacked a herd and each captured an animal (Schaller 1972, page 251)) and also provides a higher chance of the lions finding a vulnerable individual within the herd. Larger preys herds are therefore expected to support larger lions groups.

Prey body size - A large bodied prey also might be considered a rich patch insofar as, for example, a single eland or giraffe could readily feed several lions, whereas a single gazelle could not. Availability of large prey would therefore promote large lions groups and strengthen group ties.

(iii) Interspecific competition

Hyaena to lion ratio - It is suggested that competition with hyaenas may impact the grouping patterns and social structure of lions (Cooper 1991). To avoid detection and encounters with hyaenas, lions may form smaller prides and also hunt smaller prey, so that they are less conspicuous (Périket, 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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Table S2. Multiple regression quadratic assignment procedure (MRQAP) results for the effect of individual trait (sex, age and reproductive state (Repro state)) similarity on the connections among lions in a pride in the nine-pride seasons from 2013 to 2015. In bold are the significant P values.

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

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

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

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

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

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

Ecological factors	β	P	Range from	Range to	Mean	SD
<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

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

<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

References

- Calenge, C. (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516-519.
- Cooper, S.M. (1991) Optimal hunting group-size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology*, 29, 130-136.
- Cumming, D.H.M. & Cumming, G.S. (2003) Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia*, 134, 560-568.
- Davidson, Z., Valeix, M., Loveridge, A.J., Hunt, J.E., Johnson, P.J., Madzikanda, H. & Macdonald, D.W. (2012) Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy*, 93, 677-685.
- Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., . . . Ferreira, S.M. (2010) Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, 281, 56-65.
- Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. & Macdonald, D. (2005) Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology*, 74, 455-463.
- Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74, 559-566.
- Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W. (2006) Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *Journal of Zoology*, 270, 523-530.
- Packer, C. & Pusey, A.E. (1982) Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature*, 296, 740.
- Packer, C., Scheel, D. & Pusey, A.E. (1990) Why lions form groups - food is not enough. *American Naturalist*, 136, 1-19.
- Péruquet, S., Fritz, H. & Revilla, E. (2015) The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biol Rev* 90, 1197-1214.
- Powell, R.A. (2000) Animal home ranges and territories and home range estimators. *Research techniques in animal ecology controversies and consequences* (eds L. Boitani & T.K. Fuller), pp. 65-110. Columbia University Press, Columbia
- QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- Schaller, G.B. (1972) *The Serengeti lion; a study of predator-prey relations*. University of Chicago Press, Chicago.
- Silveira, L., Jacomo, A.T.A. & Diniz, J.A.F. (2003) Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation*, 114, 351-355.
- Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald, D.W. (2010) How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337-351.

1220 Van Orsdol, K.G. (1981) Lion predation in Rwenzori National Park, Uganda. Ph.D.
1221 Thesis, University of Cambridge.
1222 Wilson, G.J. & Delahay, R.J. (2001) A review of methods to estimate the abundance
1223 of terrestrial carnivores using field signs and observation. *Wildlife Research*,
1224 28, 151-164.
1225
1226