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

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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 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 and prey availability (prey abundance, dispersion, herd size and body size) affect within-pride social structure in African lions.
4. We found that individual decisions about associates depended on resource availability with individuals associating equally across all members of the pride when prey herds were scarce, aggregated or large bodied, and associating more exclusively (in subgroups of preferred associates) when prey herds were abundant, dispersed or small bodied. Individuals within lion prides seemed to be buffering against changes in prey availability by modulating their strength and density of connections with conspecifics when prides split into subgroups. The strength and density of connections among individuals within subgroups was greater when prey herds were large and lower when prey herds were dispersed or are large bodied.
5. Our findings suggest that individual lions are making social decisions at both the subgroup level and the pride level, with decisions representing putatively fitness-enhancing strategies. Individuals were typically shifting between having few

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

KEYWORDS

animal social networks, dynamic networks, ecological factors, fission–fusion, heterogeneity, lion, null models, prey availability

1 | 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 group-living animals, within-group interactions and the outcome of these interactions can be interpreted as a network of social relationships (Farine & Whitehead, 2015; Whitehead, 2008). 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*, did not involve complex analysis, however, this 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 better understand the patterns of animal social structure (i.e. the patterns in social relationships) at a finer level of social organisation (see Ellwood et al., 2017; Farine, Firth, et al., 2015; Tanner & Jackson, 2012). Understanding the processes generating variation in social structure across populations is critical for understanding the evolution of sociality (Ilany & Akçay, 2016). Yet, there is still only preliminary understanding of how ecological variables shape the fine-scale patterns of animal social behaviour (He, Maldonado-Chaparro, & Farine, 2019) and the implications of these on the resulting emergent group social structure and stability (Cantor & Farine, 2018).

A number of postulates have been put forward to explain social structure in different animal populations. These include 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, 2008). 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 organisation, that is, 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 crabs *Carcinus maenas* 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 characterised 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?

Species that exhibit a form of fission–fusion social organisation frequently change their group size and composition within the lifetime of members as groups split (fission) or merge (fusion; Couzin & Laidre, 2009). In these species, 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 (Cortes-Avizanda et al., 2011; Sueur et al., 2011; 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). Pride composition is mostly constant, with most changes taking place when new males take over the pride

(Packer & Pusey, 1983). By contrast, subgroup membership within a pride can change continuously. Some individuals can maintain close associations within subgroups, and this tendency for stability can be driven by attributes such as age, sex and reproductive state (Schaller, 1972; Van Orsdol, Hanby, & Bygott, 1985). For instance, female lions often form stable maternity subgroups that are effective in defending their cubs against infanticidal males from outside the pride and subgroup (Packer, Scheel, & Pusey, 1990). Also highly unstable and dynamic subgroups can be formed during hunting, when pride members briefly come together to execute a hunt (Stander, 1992a). However, the interactions between individuals within a pride 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 linked to, or influenced by, resource availability (Macdonald, Mosser, & Gittleman, 2010; Mbizah, Valeix, Macdonald, & Loveridge, 2019).

The dynamics of resource availability; especially the abundance, type, and distribution of prey might also influence finer scale lion social structure and this can have profound behavioural, ecological and evolutionary impacts (Foster et al., 2012; He et al., 2019). For example, when prey is scarce, then we expect lions to associate less with their pride members to reduce competition for food and increase their own food intake (Packer et al., 1990). The benefits that can be gained from associating with pride members might shape the tendency for members of a given pride to remain cohesive or to split into smaller subgroups, which is a much more flexible strategy than adding or removing members from the pride. Social bonds are therefore likely to form the basis of how species such as lions respond socially to ecological processes. We expect to observe a shift back and forth in decisions by individual lions between maintaining fewer but stronger bonds and maintaining more but weaker bonds depending on resource availability. In this study, we combine data on the fine-scale patterns of association among individuals across multiple prides of African lions with data on the prey herds in each pride's territory within Hwange National Park, Zimbabwe. We consider a herd of prey to represent a resource patch available to lions (Carr & Macdonald, 1986), and the abundance, dispersion and type of these patches (see Table S1) as important attributes that can influence the opportunities for social interactions (Tanner & Jackson, 2012).

2 | MATERIALS AND METHODS

2.1 | Study area

Hwange National Park covers approximately 15,000 km^2 of semi-arid dystrophic savanna on Kalahari sands, on the north-western border of Zimbabwe. During the wet season (November to February), various waterholes, rivers and pools are rain fed and available to animals, but natural surface water then becomes scarce as the dry season progresses and only pumped waterholes (~50), mostly in the North of the park, maintain water availability. The end of dry season coincides with the lowest quantity and quality of browsing and grazing resources. We therefore commonly distinguish three seasons in Hwange National Park characterised by surface water availability and vegetation quality: the wet season, the early dry season (March–June) and the late dry season (July–October). However, for this study only the early dry and late dry season data was available as the study area is inaccessible during the wet season. Lion density is estimated at around 3.5 lions/100 km^2 in the study area (Loveridge et al., 2016). Differences in vegetation and 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).

2.2 | Lion pride observations

For this study we used data from four different prides between 2013 and 2017 (Mbizah et al., 2020). We located lion prides with the help of GPS radiocollars fitted to two adult females and five adult males, as well as opportunistically during other field work activities. The prides were observed at least five times per month to record their size and composition. Some prides were, however, not observed in some of the months and seasons during the study period. When a pride was observed, we recorded its name, identity of individuals present as well as their age, sex and whether they had cubs. We also recorded their activities during observations, which included resting, hunting, feeding and walking. All lion individuals are recognisable by whisker patterns, natural markings such as scars, muzzle spots and tooth irregularities that are unique to each individual (Pennycuick & Rudnai, 1970). We looked at two aspects of lion pride: (a) pride (all the individuals within a pride) and (b) subgroup (individuals of a pride present at each observation). We recorded all individuals present together as being connected (Farine, 2015; Whitehead & Dufault, 1999). The GPS collars recorded locations every 2 hours day and night, and we regularly downloaded these 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 to avoid underestimation of home-range size.

2.3 | Prey availability

To measure prey availability, we conducted multi-species surveys of tracks made by animals when they cross the roads. Track counts were conducted from 2013 to 2015 during the early dry season and the late dry season. Most of the available roads in the study area (ranging from 9 to 55 km long) were used as transects ($n = 64$ transects). The 64 selected transects were within areas that lions frequent. When a fresh track (<24 hr old) was encountered, it was assessed for species and group size by highly skilled and experienced trackers (see Appendix S1 for further details on the track survey method). Only tracks from common lion prey species in the area were used in this analysis. Information on prey availability measured as; prey abundance, prey dispersion, prey herd size and prey body size, was extracted for each lion home range in each season (see Appendix S2 for further details; Mbizah et al., 2020).

2.4 | Social networks construction

We used lion pride observational data to construct a social network for each pride in each 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 4-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 individuals 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, 2018). The Simple Ratio Index (SRI), which is considered the least-biased estimate of association rates (Hoppitt & Farine, 2018), 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 and y_{ab} is the number of simultaneous observations of individuals a and b when not together, was not relevant to our study because we could not observe two subgroups at the same time. The SRI ranges from 0 for two individuals never seen together to 1 for two individuals always seen together. Animals that died during a season were not included in that season's network to avoid bias.

2.5 | Social networks analysis

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

We then calculated three network metrics to characterise the structure of each pride: modularity, mean weighted degree and network density to quantify the division of prides into subgroups and the nature of connections within prides and within subgroups. We selected these measures a priori with the aim of describing three biological dimensions of the social structure of prides: how strong the connections are (mean weighted degree), how many connections are there (density) and how distributed the connections are across dyads (modularity). First, we calculated modularity to quantify the division of prides into subgroups. Modularity describes the separation of networks into structural communities, or subgroups of individuals that have more connections among themselves than they do with nodes outside of their community (Girvan & Newman, 2002). Herein, we call these network-based communities ‘subgroups’. A higher modularity implies that a pride tends to break into distinct subgroups defined by stronger connections between individuals within a subgroup but weaker connections between individual in different subgroups (Newman, 2004). We then calculated mean weighted degree and network density to quantify the nature of connections within prides and within subgroups. 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 pride or subgroup 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; it measures the density of connections among individuals in a pride or subgroup. A high network density represents a greater overall tendency for different individuals to come into contact with one-another, and is a fundamental property of networks (e.g. it strongly influences spreading processes). We represented the resulting subgroup assignments by giving different colours to nodes from different subgroups detected using greedy optimisation of modularity community detection algorithm (Figure 1). All network measures were calculated in R using IGRAPH (Csardi & Nepusz, 2006).

2.6 | Hypothesis testing

Before testing our hypotheses about the links between prey availability and pride structure, we first tested for the correlation between the four measures of prey availability (prey abundance, dispersion, herd size and body size). Because these correlations were generally moderate to low ($-0.59 \le r \le 0.62$), we included all measures in our model. We then assessed the relationship between the different network metrics (modularity, mean weighted degree and network density for each pride and subgroup network) and the four measures of prey availability using linear mixed effects regression analysis with the identity link in the LME4 package

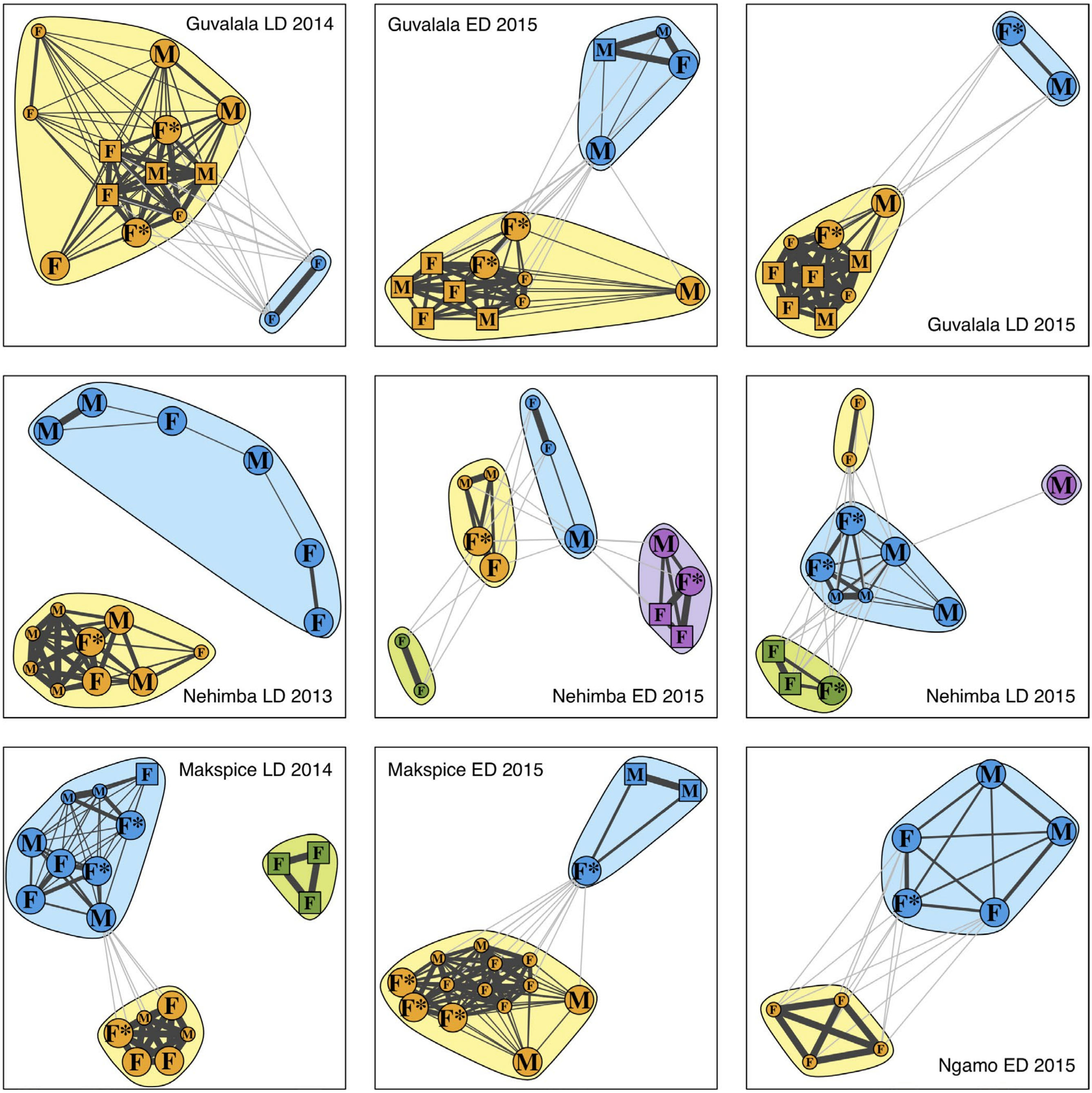

FIGURE 1 Subgrouping patterns in four prides across different seasons. We generated networks for two distinct seasons [early dry season (ED) and late dry season (LD)] and 3 years (2013–2015). Pride identity, season and year are noted in each network. Subgroups were extracted and visualised using greedy optimisation of modularity community detection algorithm and plotting the network with the IGRAPH package (Csardi & Nepusz, 2006) in R. Each coloured polygon represents the social boundaries of one subgroup entity, the members of which are more densely connected among themselves than with the rest of the network. Each node represents an individual lion, with the shape of the node representing age class (large circle = adult, square = sub-adult and small circle = cub), the letter of the node indicates sex (M = male, F = female) and the * indicates the reproductive state (F* = females with cubs). Edge widths (the connections between individuals) are proportional to the association index

(Bates, Mächler, Bolker, & Walker, 2015) in R. The network metric was the response variable while the above measures of prey availability that can potentially influence lion social structure were the fixed effects; with the ID of each lion pride included as the random effect to account for pride-level differences. Using the null model procedure described below, we then generated 10,000 randomised versions of each network, and ran the same regression with each of these randomised networks. We estimated *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 result was significant at $p = 0.05$ if fewer than 2.5% of the random values were greater than the observed value, or if more than 97.5% of the random values were greater than the observed value. All analysis were done in R statistical software (R Core Team, 2020).

2.7 | Estimating statistical significance using null models

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

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

3 | RESULTS

In our study, female home ranges ranged from 27.8 to 329.6 km^2 ($M = 224.5$ km^2; $SD = 170.5$ km^2) and male home-range sizes ranged from 121.3 to 498.8 km^2 ($M = 330.9$ km^2, $SD = 159.0$ km^2). However, we found no significant difference between male and female lion home-range sizes (estimate ± SE =106.31 ± 122.39; $t_7 = 0.87$; $p = 0.41$). We first generated a baseline understanding of social structure in each of the four lion prides by testing whether individual traits influenced patterns of associations among individuals in the replicated networks, each representing 4 months of observations in one of two dry seasons (see Section 2). Generally, there was a correlation between the individual trait (age, sex and reproductive state) similarity and the probability that individuals would be observed together (Table S2). In most prides, the adjusted R^2 value of the MRQAP models for the relationship between similarity in individual traits and the association index among individuals within lion prides was generally low (between 0.010 and 0.062), except for Ngamo pride ($R^2 = 0.737$, see Table S2), meaning that the model explains very little of the variation in the association index.

We then tested whether prides exhibited structured patterns of subgrouping. We found that the seasonal networks for each pride could be statistically partitioned into two, three or four subgroups (Table S3; Figure 1). Season itself had no significant effect on the strength of division of a network into subgroups (modularity estimate ± SE = −0.08 ± 0.13; $t_7 = -0.62$; $p = 0.56$). We then tested whether seasonally varying prey availability measures could explain patterns of structure, including subgrouping, in the networks.

3.1 | Effect of prey availability on association patterns within prides

The mean weighted degree, which is the strength of connections among individuals in a pride was greater at high prey abundance (Table 1; Figure 2a.i). Nonetheless, the network density, which is the density of connections among individuals in a pride was not affected by changes in prey abundance (Table 1; Figure 2a.ii). Modularity, which is the strength of division of prides into subgroups was greater at high prey abundance (Table 1; Figure 2a.iii), thus, the subgroups became more distinct from each other, with even weaker associations between subgroups. Prey dispersion had no significant effect on both the strength and the density of connections among individuals within prides (Table 1; Figures 2b.i and 2b.ii). However, the strength of division

TABLE 1 Summary of the relationship between measures of prey availability and network metrics. Mean weighted degree (strength of connections among individuals), network density (the density of connections among individuals) and modularity (strength of division of prides into subgroups), were calculated within prides. Mean weighted degree and network density were also calculated within subgroups. The tables show results of a more positive (+), more negative (−) or a non-significant (.) relationship (relative to chance), between network metrics and prey availability

	Pride level			Subgroups level	
Measures of prey availability	Mean weighted degree	Network density	Modularity	Mean weighted degree	Network density
Prey abundance	+	.	+	.	−
Prey dispersion	.	.	+	−	−
Prey herd size	+	+	.	+	+
Prey body size	−	.	−	−	−

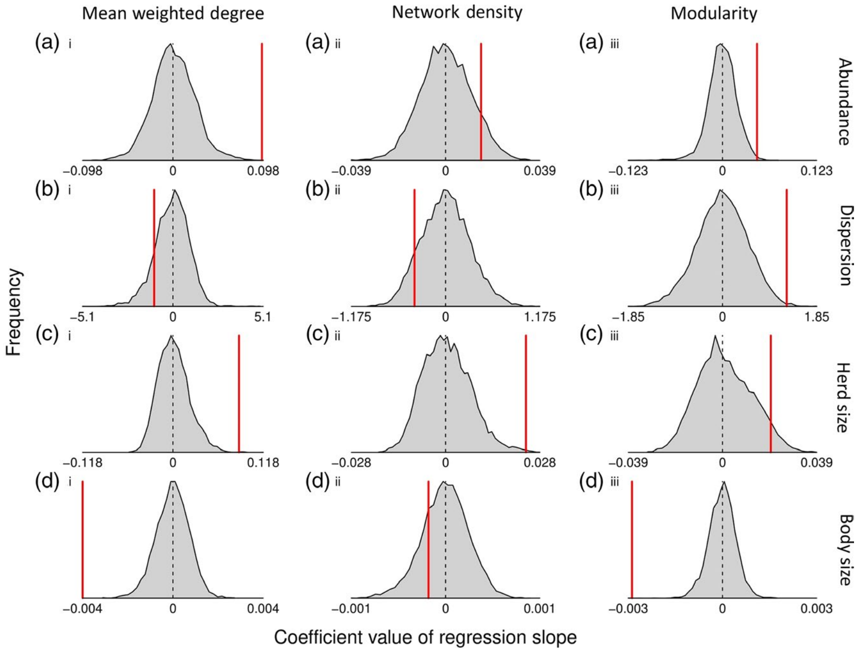

FIGURE 2 Relationship between pride-level social structure and measures of prey availability. The relationship between (a) number of prey herds/km (index of prey abundance), (b) nearest neighbour index of prey herds (index of prey dispersion), (c) mean prey herd size, (d) mean prey body size and (i) mean weighted degree (strength of connections among individuals), (ii) network density (density of connections among individuals) and (iii) modularity (strength of division of prides into subgroups) within prides. Histograms show the distribution of coefficient values from the model applied to the permuted networks, and the red lines show the coefficient value of the regression fitted to the original (observed) data. Significance was calculated by evaluating the observed data relative to the distribution of values calculated from the permuted data. We note that there were strong signals of non-social factors most likely caused by sampling (see Farine, 2017) shaping our original observed effects, meaning that the randomised values were often not centred on 0 (see Figure S1). Thus, we corrected the effects to control for these factors (see Section 2; Farine & Whitehead, 2015)

of prides into subgroups was greater at high prey dispersion (Table 1; Figure 2b.iii), thus, the subgroups became more distinct from each other, with even weaker associations between subgroups when prey was more dispersed across the landscape. The strength and the density of connections among individuals within prides were greater when prey herds were larger (Table 1; Figures 2c.i and 2c.ii). Nonetheless changes in prey herd size had no significant effect on the strength of division of prides into subgroups (Table 1; Figure 2c.iii). The strength of connections among individuals within a pride was lower when prey was large (Table 1; Figure 2d.i), whereas the density of connections among individuals was not affected by changes in prey body size (Table 1; Figure 2d.ii). The strength of division of prides into subgroups was lower when prey body size was large (Table 1; Figure 2d.iii). Individuals within prides tended to associate more evenly with all other members of their pride as prey body size became larger.

3.2 | Effect of prey availability on association patterns within subgroups

Prey abundance had no significant effect on the strength of connections among individuals within subgroups (Table 1; Figure 3a.i),

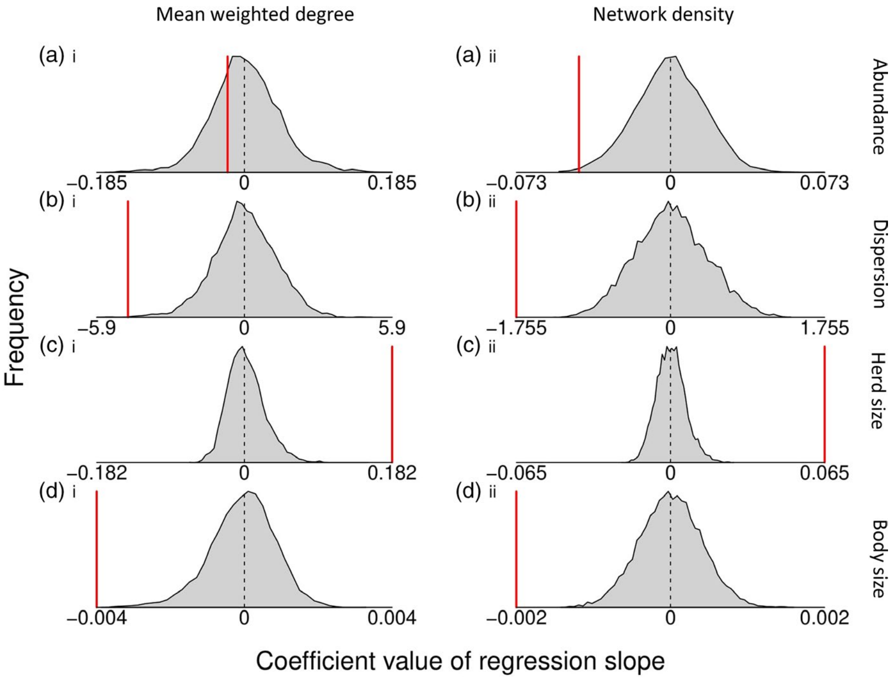

FIGURE 3 Relationship between within-subgroup social connections and measures of prey availability. The relationship between (a) number of prey herds/km (index of prey abundance), (b) nearest neighbour index of prey herds (index of prey dispersion), (c) mean prey herd size, (d) mean prey body size and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

but the density of connections among individuals was lower when prey was abundant (Table 1; Figure 3a.ii), meaning that the individuals within subgroups were not fully connected at high prey abundance. Both the strength and the density of connections among individuals within subgroups were lower when prey herds were more dispersed (Table 1; Figures 3b.i and 3b.ii), meaning that individuals within subgroups are less frequently seen together and come into contact less often when prey is dispersed in the landscape. However, the strength and the density of connections among individuals within subgroups was greater when prey herds were larger (Table 1; Figures 3c.i and 3c.ii). Finally, when prey was larger bodied, the strength and the density of connections among individuals within subgroups became lower (Table 1; Figures 3d.i and 3d.ii).

4 | DISCUSSION

Our study extends prior research on the role of ecological factors in determining broad population structure by demonstrating several ways in which measures of prey availability affect the fine-scale patterns of association among individuals. Furthermore, we demonstrate that these effects can take place at two scales: within prides and within subgroups. Lion prides, characterised by frequent changes in subgroup composition (i.e. fissioning and fusioning), can potentially show rapid responses to changing ecological conditions (Kotze, Keith, Winterbach, Winterbach, & Marshal, 2018). Our results suggest that these responses to prey availability might take place via the fine-scale associations among individuals. More specifically, our study reveals that the abundance of prey, the dispersion of prey within the landscape and the body size of available prey have strong effects on the division of prides into subgroups (pride fission; measured here by modularity) and can potentially shape the stability of lion prides. We found that the connections among individuals within a pride remained strong when prides split into subgroups as prey became more abundant within the pride's home range. This indicates that perhaps the existence of subgroups within prides acts to maintain connections (not let them erode as much as they would at random) when resources are plentiful. It has long been suggested that the fission–fusion dynamics of social animals allows them to adapt to prevailing social and ecological conditions (see Aureli et al., 2008; Kotze et al., 2018). Our study therefore provides evidence that prey availability 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).

4.1 | Individual trait similarity

Our network analyses captured some fundamental properties of lion behaviour, including the general propensity for lions to associate with individuals of the same sex or of the same reproductive state. In lions, females often come together to defend their cubs against nomadic males (Packer & Pusey, 1983), whereas males form coalitions to take over and protect territories (Packer, 1986; Schaller, 1972). However, overall our results suggest that the effect of individual trait similarity alone explains relatively little of the variance in subgroup composition in lion prides. One pride did show consistent significant effects, but this is likely to be because this pride was composed of only adult males and females and their cubs, a composition unique to this particular pride.

4.2 | Prey abundance

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

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

4.3 | Prey dispersion

Our results also showed that when prey is more dispersed in the landscape, it reduces the frequency with which lion prides encounter prey and this leads to lion prides breaking into more distinct subgroups. Furthermore, we found that individuals within the subgroups maintain weaker connections and lower density of connections when prey is more dispersed. The splitting of lion prides into subgroups and the maintenance of poor connections within these subgroups when prey is hard to come by might be a strategy to reduce competition and increase searching efficiency (Fryxell, Mosser, Sinclair, & Packer, 2007; Packer et al., 1990). Since the dispersion of resources increases searching behaviour (Sogard & Olla, 1997; Valeix et al., 2010), this can potentially limit the opportunity for social interactions between individuals within prides and subgroups (Tanner & Jackson, 2012). The dispersion of prey herds emerged also as an important factor in shaping lion home-range size (Mbizah et al., 2019).

4.4 | Prey herd size

The strength and the density of connections among individuals within both prides and subgroups were greater when prey herds were larger, but changes in the size of prey herds had no effect on the splitting of prides into subgroups. Larger herds 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 (Creel & Creel, 2002; Schaller, 1972) and lions have been shown to prefer large prey herds (Hayward & Kerley, 2005). Nevertheless, the increased vigilance of large prey herds (Hamilton, 1971; Kenward, 1978) makes hunting large herds challenging for lions. Fryxell et al. (2007) found that group formation by wildebeest reduced lion kill rates by 90% and the strong bonds within prides and subgroups would be important for co-operation in hunting these large prey herds, especially when

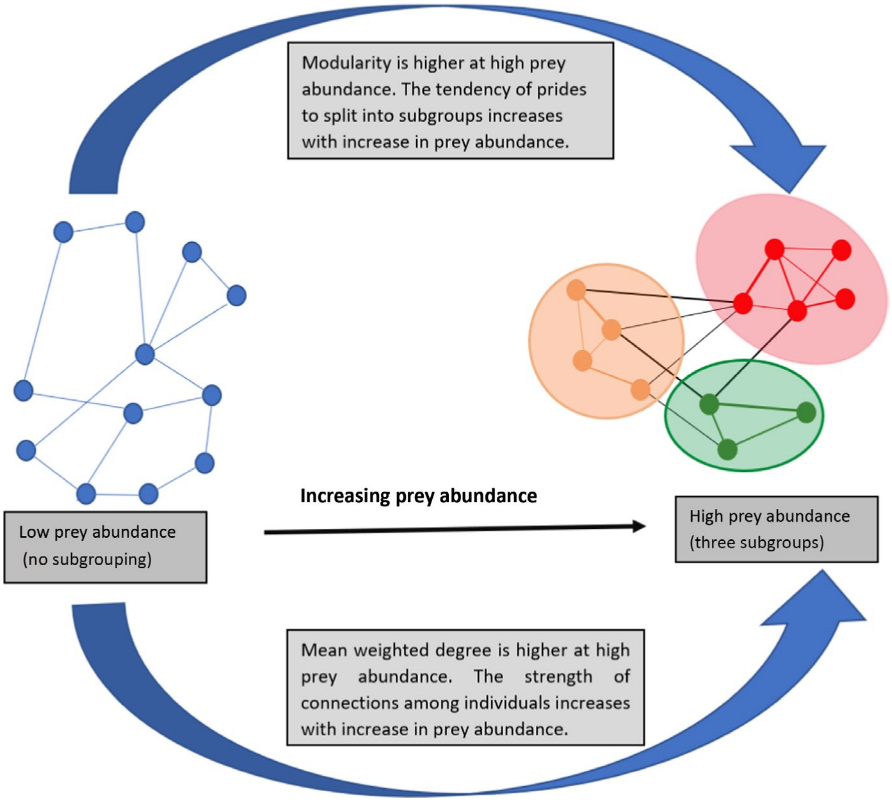

FIGURE 4 Effect of prey abundance on association patterns within a pride. An illustration showing how a pride of 12 individuals can break into subgroups of 3, 4 and 5 individuals at high prey abundances, and that the individuals within and across subgroups maintain strong connections with other pride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

the prey are difficult to capture (e.g. buffalo; Scheel & Packer, 1991). Coordination is key during lion hunts (Stander, 1992b) and the strong coordination that might arise from the strong connections among individuals can increase chances of prey capture.

4.5 | Prey body size

Although the connections among individuals within prides were weaker when prey was large, the tendency for prides to break into subgroups was, however, lower and as a result, individuals within prides associated more evenly with all other members of their pride. Large prey species such as buffalo, zebra, giraffe or juvenile elephant are sharable patches (sensu Macdonald & Johnson, 2015) and can feed several lions and are often preferred (Hayward & Kerley, 2005); consequently, competition for prey within the pride is likely to be minimal and individuals can associate frequently outside their close connections. In the Serengeti, Scheel and Packer (1991) found cooperation to be common during hunts on larger and more difficult prey. Essentially, individuals in the pride would come together more often (fusion), which could allow them to cooperatively hunt the large sized prey (Scheel & Packer, 1991; Stander, 1992a) and increase success of prey location and capture (but see Caraco & Wolf, 1975; Packer et al., 1990; Stander & Albon, 1993) while minimising energetic costs (Carbone, Teacher, & Rowcliffe, 2007). On the other hand, the strength and the density of connections among individuals within subgroups was lower when prey was large bodied. This is because the chances for small groups to successfully hunt and capture large prey are low and it might not be efficient for the small groups to attempt to hunt large prey (Stander & Albon, 1993).

Drawing on our knowledge of decision-making, our findings imply that individual lions are making social decisions at both the subgroup level and the pride level. Such decisions about sociality are often optimised to maximise individual fitness (Farine, Montiglio, & Spiegel, 2015; Silk, 2007). We found that the finer scale social structure of lions responds to changes in ecological conditions and this is centred around decisions about reducing competition, increasing chances of prey capture and maximising feeding efficiency. 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). The maintenance of connections within prides and subgroups in the face of ecological change suggests that the fission–fusion nature of lion prides might be essential for the long-term maintenance of social connections even when short-term conditions do not allow them. Nevertheless, the persistent separation between subgroups within a pride can reduce the encounter rates and contacts among individuals across different subgroups, which can have impacts on processes such as mate choice and other social behaviours (Banks, Piggott, Stow, & Taylor, 2007; Krause, Lusseau, & James, 2009). Furthermore, some of the weaker associations across 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). At the interface between social affiliations and ecological constraints, the marginal costs and benefits of lion groupings are moderated by various sociological pay-offs to given group sizes, for example, in the contexts of survival and reproduction (Packer, Pusey, & Eberly, 2001). Our study therefore provides evidence that prey availability can shape fine-scale properties of animal social systems and at different scales, with implications for, and far beyond an understanding of the lion society.

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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.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository https://doi.org/10.5061/dryad.v15dv41tm (Mbizah et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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