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The social network structure of a wild meerkat population: 2. Intragroup interactions

Joah R. Madden · Julian A. Drewe · Gareth P. Pearce · Tim H. Clutton-Brock

Abstract Knowledge of the structure of networks of social interactions is important for understanding the evolution of cooperation, transmission of disease, and patterns of social learning, yet little is known of how environmental, ecological, or behavioural factors relate to such structures within groups. We observed grooming, dominance, and foraging competition interactions in eight groups of wild meerkats (*Suricata suricatta*) and constructed interaction networks for each behaviour. We investigated relationships between networks for different social interactions and explored how group attributes (size and sex ratio), individual attributes (tenure of dominants), and ecological factors (ectoparasite load) are related to variation in network structure. Network structures varied within a group according to interaction type. Further, network structure varied predictably with group attributes, individual attributes, and ecological factors. Networks became less dense as group size increased suggesting that individuals were limited in their number of partners. Groups with more established dominant females were more egalitarian in their grooming and foraging competition interactions, but more despotic in their dominance interactions. The distribution of individuals receiving grooming became more skewed at higher parasite loads, but more equitable at low parasite loads. We conclude that the pattern of interactions between members of meerkat groups is not consistent between groups but instead depends on general attributes of the group, the influence of specific individuals within the group, and ecological factors acting on group members. We suggest that the variation observed in interaction patterns between members of meerkat groups may have fitness consequences both for individual group members and the group itself.

Keywords Social networks · Meerkats · Grooming · Dominance · Intragroup interactions

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Introduction

The networks of interactions between individuals are especially relevant to studies of animals living in social groups, where an individual's interactions with others are unlikely to be independent of the behaviours of others (Hinde 1983; Wasserman and Faust 1994; Croft et al. 2005; Krause et al. 2007; Wey et al. 2008). The network structure of interactions within groups or populations has implications for the evolution of cooperation, transmission of

disease, and patterns of social learning (Nakamura 2006; Krause et al. 2007; Wey et al. 2008; Godfrey et al. 2009). Construction and analysis of such networks is now well developed (see Newman 2003 or Croft et al. 2008 for reviews), and commercial software exists that permits a range of analyses (Borgatti et al. 2002). However, little is known of the ecological or behavioural factors that relate to the structure of social networks, and the external or internal factors that influence the development and final structure of the network, either between or within species.

The social structure of groups may be an emergent property, arising as a consequence of certain ecological, population, or behavioural attributes that are specific to the species, individual group, or members within each group (Lusseau and Newman 2004). It is possible to examine what factors contribute to the emergence of network structural properties by either comparing the networks of several groups that differ in the specific factors or perturbing factors within single groups and observing changes in network structure. Previous work quantifying network structure has typically been restricted to observations of single groups (e.g., dolphins *Tursiops truncatus* Lusseau and Newman 2004; Lusseau et al. 2006; sticklebacks *Gasterosteus aculeatus* Croft et al. 2005; guppies *Poecilia reticulata* Croft et al. 2004; killer whales *Orcinus orca* Guimarães et al. 2007; pigtailed macaques *Macaca nemestrina* Flack et al. 2006; Columbian ground squirrels *Spermophilus columbianus* Manno 2008; long-tailed manakins *Chiroxiphia linearis* McDonald 2007; and wire-tailed manakins *Pipra filicauda* Ryder et al. 2008). Two studies have compared the networks of single groups of different species (Croft et al. 2005; Sundaresan et al. 2007). Three studies have compared measures of network structure in more than one group from a single species (guppies Croft et al. 2005; Thomas et al. 2008; rhesus macaques *Macaca mulatta* McCowan et al. 2008), but in these cases, the groups were formed artificially, with individuals being enclosed with others, under the control of the observers. One study looked at multiple natural groups of the same species (buffalo *Syncerus caffer* Cross et al. 2005) but concluded that these groups were very unstable with frequent fission and fusion events, and so, treated these groups as part of a single population. Only one study has looked at variation between natural groups (ants *Ropalidia marginata* Naug 2009) and concluded that groups were similar in their network structures. Perturbation of artificial groups has been used to ask whether group composition alters network structure. In a single group of pigtailed macaques, the presence of key, policing, individuals facilitated larger, more integrated and more diverse networks (Flack et al. 2006). Removal of randomly chosen individual ants from a series of groups increased network density (Naug 2009). Conversely, experimentally altering

patterns of cooperation and defection by individual guppies in 15 artificially created groups, engaged in predator inspection, had no effect on the network structure of guppy groups (Thomas et al. 2008).

Much previous work on quantifying social networks has relied on association data between individuals, either simply observing individuals together (e.g., Lusseau and Newman 2004; Lusseau et al. 2006; Guimarães et al. 2007; Sundaresan et al. 2007; Ramos-Fernández et al. 2009) or inferring association when individuals are observed within specified distances of each other (e.g., Croft et al. 2005; Wolf et al. 2007; Thomas et al. 2008). Fewer studies have utilised specific forms of behavioural interactions. Such interactions may include contact sitting, proximity, social play, displacement, subordination, grooming, contact aggression, or "amicable interactions" (Flack et al. 2006; McCowan et al. 2008; Manno 2008). Of those studies that have considered behavioural interactions, some have used only a single measure of interaction (e.g., Manno 2008), whilst others have considered several different forms of interaction within the same population (Flack et al. 2006; McCowan et al. 2008). However, no study has examined how networks based on different forms of behavioural interactions relate to each other within a single group. We predict that networks within a single group will differ depending on the form of interaction between group members that is being investigated.

Meerkats *Suricata suricatta* provide an excellent model system for studies of factors determining social network structures. They live in clearly defined groups of three to 50 individuals in the arid regions of southern Africa (Doolan and Macdonald 1999). Each group consists of a pair of dominant adults that contribute to the majority of the reproductive output of the group, and numerous subordinate adults, juveniles, and pups of both sexes (Griffin et al. 2003). Females typically remain in their natal group, competing more strongly for a dominant position as they age (Clutton-Brock et al. 2006); whereas, males tend to leave their natal group at around 2 years and join a new group where they compete for a dominant position (Young et al. 2005). Consequently, meerkat groups comprise individuals of different age, sex, status, and relatedness to each other. Individual meerkats interact frequently with other individuals within their group. Such interactions can take several very different forms: allogrooming and dominance assertions typically occur when the group is close together at a burrow entrance; whereas, foraging competitions typically occur when the group is away from the burrow and engaged in foraging. Allogrooming involves removal of ectoparasites and maintenance of fur (Kutsukake and Clutton-Brock 2006). Dominance interactions can occur between any group members and are not restricted to the breeding dominant pair (Madden and

Clutton-Brock 2009). They can include vocal signals as well as contact aggression, escalating to include violent attacks (Kutsukake and Clutton-Brock 2006). Foraging competitions focus on access to specific food items or holes in which other individuals are digging (JRM, personal observation). Thus, networks linking individual meerkats can be based on each of these three forms of interactions.

Several attributes of meerkat groups might explain variation in how individuals interact with each other, and so, relate to the structure of interaction networks. First, and most simply, network structure may relate to the size of the group. If individuals only interact with a certain number of individuals, or can only interact with a maximum number of individuals, then we predict that as group size increases, networks should become less dense and that the mean distance between individuals in a network will increase (see also Wasserman and Faust 1994). Second, the network structure may vary depending on group composition. One obvious dimension in which composition can vary is in the ratio of males to females. Previous studies indicate that individual meerkats interact assortatively according to sex, with respect to pup feeding, grooming of dominant individuals, and competition over resources (Brotherton et al. 2001; Kutsukake and Clutton-Brock 2006; Hodge et al. 2007). These studies refer to dyadic interactions, but these should be considered within the context of the group's interactions as a whole, accounting for the fact that, for example, one pup may interact with several helpers, who in turn each interact with several pups. Therefore, we predict that as groups become less biassed in their sex ratio, networks become less centralised. As numbers of males increase, the overall distribution of aggressive interactions initiated by the dominant female will decrease, as she is less aggressive to males in the group (Kutsukake and Clutton-Brock 2008). Third, network structure may depend on the behaviour of certain key individuals (e.g., Flack et al. 2006). In meerkat groups, such key individuals could well be the dominant individuals. Groups in which the position of dominant individuals has been clearly established for a long period of time may differ in their network measures from those in which dominance is less well established or more dynamic (McCowan et al. 2008). Long-serving dominant individuals are likely to be better established than those who have just assumed dominance. Therefore, we predict that in groups with long-established dominant females, networks of aggression are more centralised as she concentrates her aggressive acts towards a subset of the females, and other subordinate females initiate fewer aggressive acts themselves. Finally, network structure may vary with some external environmental factor. One example of an environmental factor that may be expected to influence behavioural interactions in meerkats is ectoparasite load, impacting on grooming behaviours.

Therefore, we predict that groups with high mean ectoparasite loads would be expected to exhibit less centralised grooming networks, as grooming serves a hygienic function in which all individuals benefit from reciprocal grooming, as opposed to uninfected groups in which grooming may serve a more social role, mediating social conflict (Kutsukake and Clutton-Brock 2006, Madden and Clutton-Brock 2009).

In order to understand variation in the structure of interactions between members of social group, we look at the network structures of eight groups of meerkats, considering three different forms of intragroup interaction: grooming, dominance interactions, and foraging competitions. We ask (a) how network structures for each form of interaction vary between groups; (b) how networks of different forms of interaction relate to each other within groups; and (c) whether network structures are a general property of that species or driven by ecological or social factors. In so doing, we extend the use of social network analysis in studies of animal behaviour to search for population-wide patterns of network structure by considering several groups and explain variance in network structure between groups in ecological terms.

Materials and methods

Data collection

Study site and population

We studied a population of habituated meerkats in the south of the Kalahari desert, South Africa (26°58′S, 21°49′E). Further details of the site and population are given in Clutton-Brock et al. (1998). All members of the population were habituated to accept close observation (<1 m) from people and could be individually identified via small marks of hair dye. The behaviour of 136 individuals from eight groups was observed between April 2007 and July 2007. Groups were observed by three to four observers for 3 days, with observation periods lasting for at least 3 h in the morning after the meerkats emerged from their burrows and for at least 1 h before they re-entered their burrow in the evening. This gave us an average of 838 ± 77 min observations per group over the 3 days.

Behavioural measures

We collected data on three distinct forms of interactions: allogrooming, dominance interactions, and foraging competitions. An *allogrooming* event was recorded when one individual groomed another. When three or more animals were grooming together in a huddle, we recorded all

interactions as dyads, entering only one record per dyad in the same huddle, regardless of how long the animals groomed or how many times each animal switched back and forth between partners. A separate grooming event was considered to have started if the animals resumed grooming after a pause (during which there was no grooming at all) of more than 1 min. A *dominance* interaction was recorded when initiated by one individual acting in an aggressive manner towards another individual, resulting in competitive interactions between group members, which were not caused by food, access to foraging holes, or social foraging partners (Kutsukake and Clutton-Brock 2006). Events included dominant females or males intimidating or attacking subordinates and animals competing or fighting for dominance. Events also included smaller acts of aggression between any individuals (e.g., chin marking, crouching, glares, and hip slams) and competition which typically involves rubbing noses or hip slamming whilst sunning or when in social situations at the mouth of a bolt hole. A *foraging competition* was recorded when an individual approached a food item or hole owner to <50 cm, prompting a defensive action by the original owner. These actions involved growling vocalisations, moving the body to block approach, pushing body against the other individual, charging at the other individual, or biting the other individual.

Rates of behaviours were calculated as events/minute of observation at the group. We recorded a total of 2,093 allogrooming events, 333 dominance interactions, and 375 foraging competitions (Table 1). During the observation period, all groups contained no pups (individuals <3 months), and no female was pregnant, determined by our observing no births to group members in the subsequent 90 days.

Non-behavioural measures

Group size was recorded on each day of observations (mean=17, range=9–24). All individuals were present in the group every day. Sex ratio was calculated as the percentage of males in the group (mean=53%, range=40–

76%). Meerkats can be sexed visually. The duration of dominance tenure was calculated to within an accuracy of 1–4 days, by independent observers recording antagonistic interactions and marking behaviour of individuals (Clutton-Brock et al. 2001; mean female=775 days, range=168–1,277 days; mean male=533 days, range=59–1,280 days). Parasite load was estimated by counting ectoparasites (Madden and Clutton-Brock 2009; mean=0.76 parasites/individual, range=0.10–1.94 parasites/individual). Observers used binoculars to scan meerkats as they emerged from their sleeping burrows and stood on their hind legs to sun themselves. One observer examined the dorsal side of the meerkat whilst a second observer simultaneously examined the ventral side. We scanned the fur of 112 individuals from six groups for the mornings during the initial 3-day observation period. Ticks (Ixodidae) and fleas (Siphonaptera) were both counted. Many ectoparasites will be hidden in the fur, but a count of visible ectoparasites provided an unbiased index of load.

Analytical methods

Calculations of measures of network structure were conducted using UCInet (Borgatti et al. 2002). Comparisons of network structures across groups and tests of relationship between measures of network structures and group attributes were conducted using SPSS version 13. Non-parametric tests were used given the small sample sizes and distribution of the data. Relationships between different network types within a group and between networks constructed over different time scales were tested using the quadratic assignment procedure correlation in UCInet, using 10,000 permutations. When searching for general patterns of relationship across all eight groups, we calculated the relationships independently for each group then used Fisher's method to combine probabilities from each group to calculate an overall level of significance (Sokal and Rohlf 1994). If the direction of relationship varied between groups, we calculated the strongest overall relationship, and for those groups with an opposing

Table 1 Summary of three types of interactions recorded within eight meerkat groups over 3 days of study

Group name	Group size	Grooming interactions	Dominance interactions	Foraging competitions
Commandos	24	258	54	66
Drie Doring	12	232	44	34
Elveera	15	144	37	112
Frisky	10	86	16	26
Lazuli	24	365	53	59
Moomins	23	258	43	28
Rascals	19	517	67	45
Young Ones	9	233	19	5
Total		2,093	333	375

relationship, we reversed the sign of their natural log transformed P value, effectively subtracting their contribution from the combined χ^2 statistic and then calculated the final combined P value.

Descriptions of network structure

Degree centrality

Degree centrality is a measure of how many direct ties an individual has with others. The more individuals a focal animal interacts with, the more central that they are, and the higher the measure. For directed relationships, *outdegree* is the number of ties that originate from the focal animal (e.g., the number of grooming events initiated by the focal animal), whilst *indegree* is the number of ties that are directed at the focal animal (e.g., the number of grooming events that the focal animal receives). For weighted relationships, the number or rate of interactions (e.g., grooming events) between a pair of animals determine the strength of the tie. Individuals that interact more frequently are tied more strongly. For unweighted relationships, the occurrence of any interaction between a pair of individuals during the study period determines the presence of a tie. Individuals that interact are tied together, regardless of the strength of their ties.

We present the network centralisation for the group network as a whole, correcting for the size of the group to describe how evenly distributed instances of initiating and receiving interactions are within the group. This is a proportional measure, compared with a theoretical 'star' network in which a central individual is connected to all others (Hanneman and Riddle 2005), but each other is only connected to the central individual. High *outdegree* or *indegree* scores indicate centralised networks, dependent on a few key individuals either initiating most of the interactions (*outdegree*) or being the target of the interactions (*indegree*), with low scores indicating a more even spread of ties. In social animals, high scores indicate networks with a skewed distribution of interactions, with specific individuals playing an important role, and may be indicative of a strong dominance or other social structure. High *outdegree* scores suggest that there may be a particularly despotic or generous individual, while high *indegree* scores suggest a victimised or preferred individual within the group. Centralities were calculated using the centrality > degree function in UCInet.

Distance

We present two measures of distance. The first is the average distance between pairs of individuals within a network (*average path length*, L). In social animals, high L

scores indicate that some individuals only interact with others very indirectly. This may be explained by some individuals avoiding contact with others, either due to lack of shared interests or active avoidance of persecution/harassment. Of course, this is to an extent dependent on the total number of individuals within the network. Therefore, a low *compactness* score provides a size corrected measure of this. *Compactness* is a measure of how directly connected individuals in the network are (controlling for the size of the network) with higher scores indicating that the network is more compact, that is, individuals interacting more directly with all other individuals. For both measures, we present data from unweighted networks, but we retain direction in the relationships, such that it may be easy to move from individual A to C via B, if A grooms B who grooms C, but the reverse direction C to A is only possible via a more circuitous route involving other individuals in the network, if C does not groom B, or B does not groom A. L and *compactness* were calculated using the cohesion > distance function in UCInet.

Density

The *density* (D) of a network is a measure of how many potential ties between individuals are actually present. This is expressed as a percentage, with high scores indicating 'saturated' networks (all possible ties are present) and low scores indicating 'sparse' networks. Density calculation for weighted networks is controversial (Wey et al. 2008), so we only present values for unweighted networks, although we retain direction in the relationships. This means that there are two possible ties between each pair of individuals (e.g., A grooms B, B grooms A). In social animals, a high D score indicates that all individuals are interacting with the majority of all the other individuals. This may be likely in groups with a weaker social structure, more egalitarian groups, or groups in social flux, for example, if all or many individuals are competing for dominance after loss of an existing dominant. *Density* values were calculated using the cohesion > density function in UCInet.

Clustering

The *clustering coefficient* (C) of a network describes how 'cliquish' the network is and measures the extent to which two neighbours of a focal are themselves neighbours. A mean value can be calculated for the network as a whole. High C scores indicate that on average, focal individuals are surrounded by other individuals that are well connected to each other. However, C should be compared to D, for in networks with high densities overall, all individuals will be surrounded by well-connected individ-

uals (Hanneman and Riddle 2005). Clustering coefficients are presented for directed, unweighted (association) data. In social animals, cliquishness may be explained by active associations between individuals based on phenotypic or genotypic similarity (Croft et al. 2005). C was calculated using the cohesion > clustering coefficient function in UCInet.

Results

Measures of network structure

Groups differed in all of their measures of network structure (Table 2, Fig. 1), but some general trends could be observed.

Grooming networks (Fig. 1a) exhibited higher weighted outdegree scores compared to weighted indegree scores, but this was not significant (Wilcoxon signed ranks test $Z=$ 1.86, $N=8$, $P=0.063$; Table 2). When outdegree scores exceed indegree scores, the distribution of groomers can be described as more centralised than the distribution of groomees, with certain individuals initiating a disproportionate share of the grooming, with the distribution of those receiving grooming being more even. Such a trend was not seen when we considered unweighted ties ($Z=1.21$, $N=8$, $P=0.225$; Table 2). Unweighted ties produced more centralised networks for both in- and outdegrees than weighted ties (outdegree: $Z=2.52$, $N=8$, $P=0.012$; indegree: $Z=2.38$, $N=8$, $P=0.017$), indicating that considering only the presence of an interaction between individuals, rather than the rate of the interactions, made the group more skewed in its structure.

Dominance networks (Fig. 1b) typically exhibited no consistent difference in outdegree and indegree centrality scores, either considering weighted or unweighted ties (unweighted: $Z=0.73$, $N=8$, $P=0.46$; weighted: $Z=1.40$, $N=8$, $P=0.16$). This suggests that in meerkat groups, generally, the distribution of individuals initiating dominance interactions was similar to that of individuals receiving dominance interactions. However, this does not mean that the specific individuals who engaged in initiating dominance interactions were the same as those who received dominance interactions. It may be that one group of individuals engaged in a disproportionate share of initiating dominance interactions, whilst another group received a disproportionate share of dominance interactions. As was seen with grooming data, use of unweighted ties produced a more centralised network, both in terms of outdegree and indegree (outdegree: $Z=2.52$, $N=8$, $P=$ 0.012; indegree: $Z=2.52$, $N=8$, $P=0.012$), indicating that when the existence of any interaction between individuals was considered, rather than the rate of the interactions

occurring between them, then the group was more skewed in its structure.

Networks of foraging competition typically showed a pattern opposite to that of grooming networks (Fig. 1c). Both weighted and unweighted data produced more centralised networks of receiving foraging competitions than they do of initiating such competitions (unweighted: $Z=1.992$, $N=8$, $P=0.046$; weighted: $Z=2.20$, $N=8$, $P=0.028$). This indicates that individuals are more even in the distribution of foraging competitions that they initiate, compared to the distribution of those receiving such competitions. Put simply, certain individuals were targeted for more frequent harassment in foraging competitions. As was seen with both grooming and dominance data, use of unweighted ties produced a more centralised network, both in terms of outdegree and indegree (outdegree: $Z=2.37$, $N=8$, $P=0.018$; indegree: $Z=2.37$, $N=8$, $P=0.018$).

Despite these general patterns in measures of centrality across groups, we also saw substantial differences between groups in all three types of network (Table 2). For example, the centrality scores for indegree foraging competitions from unweighted data varied from the highly centralised group Elveera (63.27) to the very diffuse Moomins (8.88). In even the most uniform set of measures (unweighted outdegree foraging competitions), the highest score was twice that of the lowest. In the least uniform set of measures (unweighted indegree foraging competitions), the highest score was over seven times that of the lowest.

We found substantial differences between groups for non-centrality measures, replicating the differences that we found for centrality measures (Table 2). Average path lengths exhibited a difference between groups of up to 2.4 times between the highest and lowest scoring group (for dominance networks), while compactness measures varied by up to 7.8 times (foraging competition networks), and density measures varied by up to 4.9 times (foraging competition networks). In even the most uniform set of measures (grooming compactness), the highest score was 1.8 times that of the lowest.

Distance measures (L) were typically higher for dominance and foraging competition networks than for grooming networks (Friedman test: eight groups, $\chi_r^2 = 12.00$, $P= 0.002$). However, the corresponding compactness and density scores and clustering coefficients for these networks were higher for grooming networks than the dominance or foraging competitions (compactness: $\chi_r^2 = 13.07$, $P=0.001$; density: $\chi_r^2 = 11.40$, $P=0.003$; clustering coefficients: $\chi_r^2 = 9.75$, $P=0.008$). These differences may be because we recorded almost four times as many grooming interactions as either foraging competitions or dominance interactions. However, such differences in observed interactions did not

Table 2 Summary of the network measures calculated for eight groups of meerkats, considering three different types of interactions

Group ID	Network centrality				Distance		Density	Cluster Coefficient
	Unweighted data		Weighted data					
	Outdegree	Indegree	Outdegree	Indegree	L	Compactness	D (SD)	C
Grooming								
CD	20.42	24.95	14.12	14.12	2.22	0.52	0.20 (0.40)	0.23
D	41.32	41.32	19.42	15.17	1.55	0.75	0.53 (0.50)	0.59
E	36.22	28.57	13.39	14.35	1.81	0.66	0.38 (0.48)	0.47
F	27.16	27.16	23.63	14.82	1.52	0.76	0.53 (0.50)	0.58
L	32.89	23.82	16.11	7.94	2.09	0.52	0.21 (0.40)	0.32
MM	27.27	17.77	8.35	6.45	1.74	0.65	0.33 (0.47)	0.39
RR	25.62	31.48	15.02	13.07	1.35	0.82	0.65 (0.48)	0.68
Y	15.63	15.63	15.34	16.62	1.14	0.93	0.86 (0.35)	0.88
Dominance								
CD	61.06	11.15	14.60	3.26	3.24	0.20	0.07 (0.25)	0.15
D	37.19	27.27	13.77	12.12	2.39	0.42	0.21 (0.40)	0.32
E	22.45	45.40	9.01	24.32	3.01	0.36	0.15 (0.35)	0.16
F	22.22	34.56	13.99	9.88	1.83	0.19	0.13 (0.34)	0.28
L	14.75	14.75	5.80	7.31	2.82	0.18	0.08 (0.27)	0.03
MM	25.00	20.25	16.94	9.81	2.47	0.17	0.08 (0.27)	0.20
RR	50.31	15.12	25.62	6.56	3.80	0.31	0.14 (0.34)	0.27
Y	25.00	25.00	16.56	10.94	1.59	0.23	0.15 (0.36)	0.00
Foraging competitions								
CD	20.61	38.75	9.36	15.03	2.36	0.27	0.11 (0.31)	0.25
D	27.27	37.19	10.33	17.77	2.41	0.42	0.21 (0.40)	0.27
E	25.00	63.27	10.42	22.45	1.95	0.63	0.34 (0.47)	0.45
F	23.46	48.15	9.88	22.22	2.02	0.43	0.23 (0.42)	0.22
L	26.47	26.47	8.44	9.96	3.07	0.28	0.09 (0.29)	0.18
MM	13.64	8.88	6.72	6.72	2.68	0.10	0.05 (0.22)	0.00
RR	16.67	34.26	13.58	19.44	2.70	0.31	0.12 (0.32)	0.30
Y	20.31	20.31	20.31	20.31	1.29	0.08	0.07 (0.25)	0.27

All measures are based on directed data. Weighted network centrality measures use weighted data. All other measures use unweighted data. Standard deviations (SD) are given for density measures

drive differences in the density-corrected clustering measure (D/C, six groups, $\chi_r^2 = 2.33$, $P=0.31$).

How independent are network measures of each other?

There was no clear pattern of relationships between any of the measures of network structures across all three network types (Table 3). For grooming networks, there were no significant relationships between any of the six pairings of centrality measures (weighted and unweighted, indegree and outdegree) or between the 16 pairings of centrality and non-centrality measures (distance, compactness, density, and clustering coefficients), but all six pairings of non-centrality measures were related to each other (Table 3). By contrast, in networks of foraging competitions, 5/16

relationships between centrality and non-centrality measures were significant, as were 1/6 pairings of centrality and 1/6 pairings of non-centrality measures (Table 3). Dominance networks appeared intermediate in their pattern of significant relationships. Only 2/16 relationships between centrality and non-centrality measures were significant, along with 1/6 pairings of centrality and 1/6 pairings of non-centrality measures (Table 3). Different measures of network structure were generally independent of each other, and so we considered each measure separately.

How independent are network types of each other?

We found no overall correlations between the structures of the three network types (grooming, dominance, and
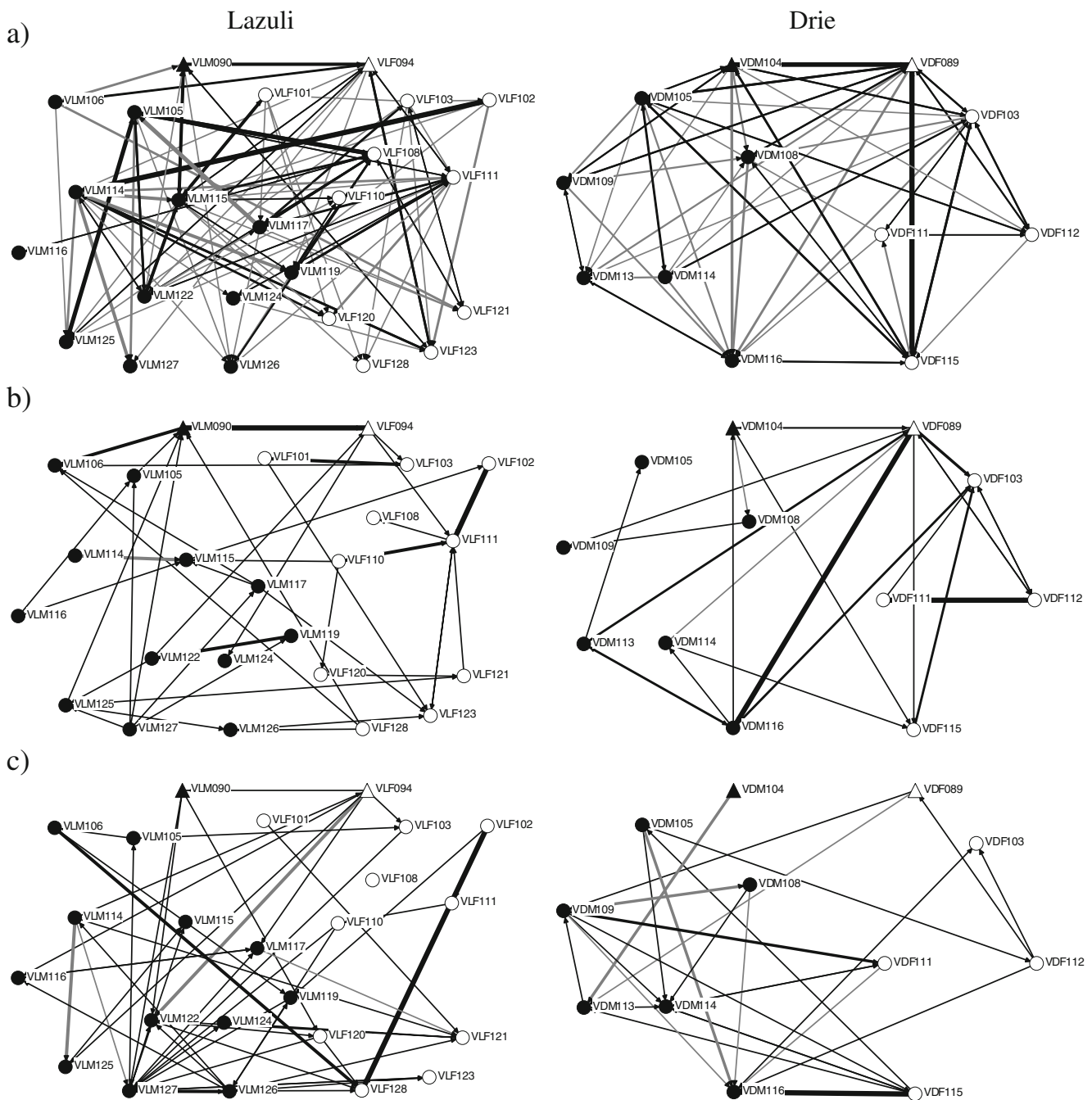
Fig. 1 Examples of networks from two groups: Lazuli, a large group, and Drie, a small group. Networks include (**a**) grooming, (**b**) dominance, and (**c**) foraging competitions. For each network: dominants=*triangles*, subordinates=*circles*; males=*black*, females=*white*; individuals are approximately arranged in age, with older individuals at the top of each diagram, with younger individuals (generally with higher identification numbers) lower down the diagram. Networks are based on weighted data (rates of interactions), with stronger ties (higher rates of interactions) indicated by *thicker ties*. Reciprocated ties are shown in *black* and unreciprocated ties in *grey*

foraging competitions), either when considering weighted or unweighted data (Table 4). Within certain groups, there were a few cases of networks being correlated (Table 4). However, in one case, the significant relationship was in the opposite direction to the mean relationship calculated for all eight groups. Therefore, no general relationships can be described, and we concluded that the three types of interactions are generally independent of each other and can be considered separately.

Table 3 Correlations between network measures calculated for three types of interaction network

		Unweighted indegree	Weighted outdegree	Weighted indegree	L	Compactness	D	C
Grooming								
Unweighted outdegree	r	0.52	0.10	−0.12	0.33	−0.34	−0.24	−0.19
	p	0.18	0.82	0.78	0.42	0.42	0.57	0.65
Unweighted indegree	r		0.26	0.17	−0.02	0.13	0.16	0.19
	p		0.53	0.69	0.96	0.76	0.71	0.65
Weighted outdegree	r			0.52	−0.33	0.32	0.35	0.33
	p			0.18	0.42	0.43	0.40	0.42
Weighted indegree	r				−0.50	0.62	0.61	0.62
	p				0.21	0.10	0.11	0.10
L	r					−0.97	−0.97	−0.95
	p					<0.001	<0.001	<0.001
Compactness	r						0.99	0.97
	p						<0.001	<0.001
D	r							0.99
	p							<0.001
Dominance								
Unweighted outdegree	r	−0.40	0.61	−0.38	0.42	0.38	−0.01	0.17
	p	0.33	0.11	0.35	0.30	0.35	0.98	0.69
Unweighted indegree	r		−0.26	0.90	−0.48	0.43	0.71	0.40
	p		0.53	<0.001	0.23	0.29	0.05	0.32
Weighted outdegree	r			−0.40	0.12	−0.12	−0.12	0.10
	p			0.32	0.78	0.78	0.78	0.82
Weighted indegree	r				−0.55	0.50	0.81	0.19
	p				0.16	0.21	0.02	0.65
L	r					0.12	−0.36	0.00
	p					0.78	0.38	1.00
Compactness	r						0.81	0.31
	p						0.02	0.46
D	r							0.31
	p							0.45
Foraging competitions								
Unweighted outdegree	r	0.50	−0.02	0.19	0.00	0.57	0.60	0.16
	p	0.21	0.96	0.65	1.00	0.14	0.12	0.71
Unweighted indegree	r		0.19	0.67	−0.38	0.83	0.98	0.49
	p		0.65	0.07	0.35	0.01	<0.001	0.22
Weighted outdegree	r			0.74	−0.52	0.14	0.24	0.85
	p			0.04	0.18	0.74	0.57	0.01
Weighted indegree	r				−0.71	0.60	0.69	0.72
	p				0.05	0.12	0.06	0.04
L	r					−0.07	−0.36	−0.41
	p					0.87	0.39	0.32
Compactness	r						0.90	0.44
	p						<0.001	0.27
D	r							0.53
	p							0.18

For all tests, $N=8$. Values in italic indicate significant relationships ($p<0.05$). L=average path length. D=density. C=clustering coefficient

Table 4 Correlations (Pearson's and Jaccard coefficients) between the three networks constructed from both weighted and unweighted data

Meerkat group ID:	CD	D	E	F	L	MM	RR	Y	
Weighted data									
p values									Combined *p* values
Groom/dominance	0.14	0.16	0.11	0.11	0.24	0.49	*0.04*	0.34	0.38
Groom/Fcomp	0.32	0.46	*0.02*	0.25	0.25	0.41	0.05	*0.02*	0.99
Dominance/Fcomp	0.32	0.19	0.42	0.34	*0.02*	0.20	*0.02*	n/a	0.31
Pearson's coefficients (r)									Mean *r*
Groom/dominance	−0.05	0.09	0.10	0.13	0.03	0.00	*0.13*	−0.06	0.05
Groom/Fcomp	0.02	−0.02	*−0.15*	−0.09	−0.03	0.00	0.11	*0.29*	0.02
Dominance/Fcomp	0.02	−0.08	−0.03	0.01	*0.10*	0.02	*0.14*	n/a	0.03
Unweighted data									
p values									Combined *p* values
Groom/dominance	0.98	0.05	0.36	0.71	0.96	0.82	*0.04*	0.83	0.47
Groom/Fcomp	0.61	0.48	0.87	0.15	0.96	0.67	0.17	0.49	0.72
Dominance/Fcomp	0.56	0.70	0.76	0.82	0.10	0.34	0.08	0.58	0.47
Jaccard coefficients (J)									Mean *J*
Groom/dominance	0.02	0.22	0.13	0.11	0.03	0.06	*0.16*	0.14	0.11
Groom/Fcomp	0.07	0.18	0.18	0.25	0.04	0.04	0.13	0.08	0.12
Dominance/Fcomp	0.04	0.10	0.10	0.07	0.08	0.05	0.12	0.07	0.08

Values in italic indicate significant relationships (*p*<0.05). Fcomp=foraging competitions

How do measures of network structure relate to group attributes?

Group size

The only consistent relationship between group size and any measure of network structure, across all three network types, was the predicted one with average path length, which was positively related to group size (Table 5 and Fig. 2). As groups got larger, the average numbers of ties taken for one individual to connect with another individual tended to increase. However, we observed several relationships between group size and network structures that were specific to interaction type. In grooming networks, compactness and density both decreased as group size increased, indicating that larger groups became generally sparser. Even correcting for group size, groups became less compact, and a lower proportion of possible interactions between individuals were realised. These results were supported by the negative relationship between group size and weighted indegree (Table 5). As group size increased, the distribution of grooming becomes less centralised. In dominance and foraging competition networks, there were far fewer relationships between group size and measures of network structure. As in grooming networks, dominance network density decreased as group size increased. Networks of foraging competitions exhibited decreased levels of weighted indegree centrality as group size increased, matching the pattern seen in grooming networks.

Sex ratio

We found no significant relationships between any measure of network structure and the proportion of males in a group for any of the three network types (Table 5).

Duration of male and female dominance tenure

The tenure of the dominant male and female meerkats was related to the network outdegree centrality measures across all three network types (Table 5, Fig. 3). The direction of the relationship differed according to network type. For grooming networks, there was a significant negative relationship between female tenure and outdegree centrality when considering weighted data. A similar relationship was seen in networks of foraging competitions when considering unweighted data. This relationship, in networks of foraging competitions, also applied to the tenure of the dominant male (when considering unweighted data). An opposite, positive relationship was observed in networks of dominance interactions (when considering weighted data).

Mean parasite load

Groups with heavier parasite loads tended to exhibit higher densities of grooming associations (Table 5). Individuals were likely to groom proportionately more individuals within the group when parasite loads were high. The indegree centrality measure (considering unweighted data)

Table 5 Relationships between network measures and group attributes for each of the three network types

			Group size	Proportion of males	Female dominance tenure	Male dominance tenure	Mean parasite load
Grooming							
Clustering	C/D	r	−0.63	0.23	0.45	0.25	0.44
		p	0.10	0.59	0.27	0.55	0.32
Distance	L	r	*0.76*	−0.47	−0.33	−0.45	−0.67
		p	*0.03*	0.24	0.42	0.26	0.10
	Compactness	r	*−0.79*	0.43	0.32	0.40	0.69
		p	*0.02*	0.29	0.44	0.33	0.09
Density	D	r	*−0.78*	0.42	0.25	0.34	*0.75*
		p	*0.02*	0.31	0.54	0.41	*0.05*
Unweighted data	Outdegree	r	−0.02	0.06	−0.43	−0.43	0.50
		p	0.97	0.89	0.28	0.29	0.25
	Indegree	r	−0.19	0.19	−0.38	*−0.71*	*0.89*
		p	0.65	0.65	0.35	*0.05*	*0.01*
Weighted data	Outdegree	r	−0.61	−0.27	*−0.70*	−0.52	0.36
		p	0.11	0.52	*0.05*	0.18	0.43
	Indegree	r	*−0.76*	−0.19	−0.28	−0.38	0.43
		p	*0.03*	0.66	0.49	0.35	0.34
Dominance							
Clustering	C/D	r	0.33	0.02	−0.56	−0.22	−0.10
		p	0.47	0.97	0.19	0.62	0.84
Distance	L	r	0.66	0.38	0.15	−0.32	0.21
		p	0.07	0.36	0.73	0.44	0.65
	Compactness	r	−0.39	0.33	−0.16	−0.43	*0.78*
		p	0.34	0.42	0.70	0.28	*0.04*
Density	D	r	*−0.82*	0.25	−0.17	−0.19	*0.80*
		p	*0.01*	0.55	0.69	0.66	*0.03*
Unweighted data	Outdegree	r	0.28	0.17	0.29	−0.38	0.25
		p	0.51	0.69	0.49	0.35	0.59
	Indegree	r	−0.66	−0.36	−0.32	0.03	0.01
		p	0.07	0.38	0.44	0.94	0.98
Weighted data	Outdegree	r	−0.08	0.61	*0.74*	0.35	0.41
		p	0.84	0.11	*0.04*	0.39	0.36
	Indegree	r	−0.43	−0.16	−0.19	0.08	0.04
		p	0.28	0.71	0.64	0.86	0.93
Foraging competitions							
Clustering	C/D	r	−0.10	−0.71	−0.62	−0.56	−0.41
		p	0.84	0.07	0.14	0.19	0.42
Distance	L	r	*0.78*	0.33	0.01	−0.19	0.10
		p	*0.02*	0.43	0.97	0.65	0.84
	Compactness	r	−0.24	−0.29	−0.61	−0.59	0.27
		p	0.56	0.49	0.11	0.12	0.57
Density	D	r	−0.31	−0.51	−0.56	−0.57	0.05
		p	0.46	0.19	0.15	0.14	0.92
Unweighted data	Outdegree	r	−0.32	−0.36	*−0.94*	*−0.74*	0.24
		p	0.44	0.37	*<0.001*	*0.03*	0.61
	Indegree	r	−0.32	−0.42	−0.61	−0.60	0.11
		p	0.45	0.30	0.11	0.12	0.81

Table 5 (continued)

			Group size	Proportion of males	Female dominance tenure	Male dominance tenure	Mean parasite load
Weighted data	Outdegree	r	−0.60	0.29	0.14	0.21	0.71
		p	0.11	0.48	0.74	0.62	0.07
	Indegree	r	−0.77	−0.14	−0.34	−0.28	0.38
		p	0.02	0.74	0.41	0.50	0.40

Values in italic indicate significant relationships ($p < 0.05$)

also increased with higher parasite load (Fig. 4). Mean parasite load was also positively correlated with network compactness and density in dominance networks (Table 5).

Discussion

Meerkat groups varied in a suite of measures of network structure, both when comparing different forms of interaction within a single group and when comparing the same forms of interactions between different groups. Even when considering a single form of interaction within a single group, the measures of network structure differed depending on whether the interaction was a simple association (unweighted) or a valued interaction (weighted) in which the amount of interactions between a pair was considered. These measures of network structure provide group and interaction-specific values which are the result of the contributory behaviour of the group members and not simply the sum of each individual's attributes. Therefore, groups themselves gain quantifiable attributes (measures of network structure) as a result of the behaviour of their members. Such measures of network structure are not general to the species as a whole, but rather are variable, depending on the exact composition of their membership and the mix of attributes of each of their members. Most

previous studies of network measures have studied only a single group (Lusseau and Newman 2004; Croft et al. 2004, 2005; Lusseau et al. 2006; Flack et al. 2006; Guimarães et al. 2007; Manno 2008, but see Croft et al. 2005; Thomas et al. 2008; McCowan et al. 2008). Our results suggest that such studies risk drawing species-wide conclusions based on single groups whose behaviour and social structure may be determined by group-specific ecological, environmental, or historical factors. General patterns of measures of network structure may only be discernible after studying many groups, to allow for a consideration of such potentially confounding factors. Although we accept that eight groups (as studied here) may still be too few to allow truly valid species-wide conclusions, multiple group study designs should be pursued where possible.

How independent are network types of each other?

Network types were independent of each other, emphasising that different measures of interactions between individuals will produce different forms of networks. This contrasts with networks of two different intergroup interactions, which were found to be highly correlated within the same population of meerkats to that studied here (Drewe et al. 2009). Previous studies have generally
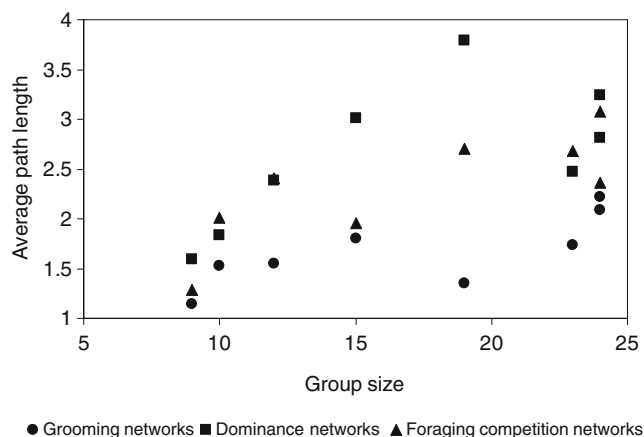
Fig. 2 Relationships between average path length and group size for each of the three network types. $N = 8$ groups
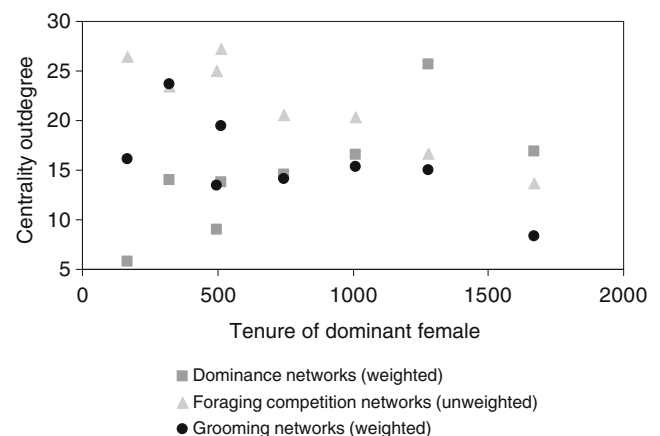
Fig. 3 Relationships between the tenure of the dominant female (days) and centrality outdegree measures for each of the three network types. $N = 8$ groups
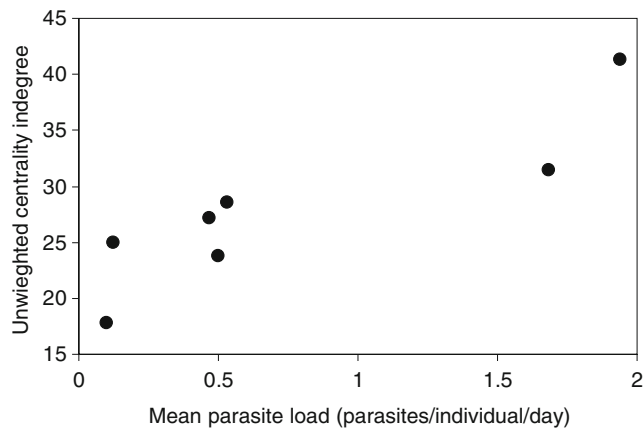
Fig. 4 Relationship between mean parasite loads observed on group members and the group's unweighted grooming centrality indegree measure. $N=7$ groups

considered only a single form of interaction (e.g., Lusseau and Newman 2004; Croft et al. 2005; Lusseau et al. 2006; Guimarães et al. 2007; Manno 2008; Thomas et al. 2008, but see Flack et al. 2006; McCowan et al. 2008). Our results suggest that such an approach should be treated with caution, and we suggest that the interaction type on which networks are based should have a meaningful link to the question being asked of the network analysis. This may especially apply to networks based on associations, which have not considered the context in which the association is recorded. Our results demonstrate that even subtle differences in interaction form have strong influences on network structures. For example, both dominance interactions and foraging competitions are typified by physical aggression between individual meerkats, and casual observation of interactions between individuals regardless of their context may suggest that the two are equivalent, but in the case of foraging competitions, aggression is for a food resource; whereas, in dominance interactions, no such tangible resource is present. Although networks based on these two different forms of aggression were related to each other in two groups (Lazuli and Rascals), there was no general pattern of relationship between networks of dominance interactions and foraging competitions across all eight groups.

How do measures of network structure relate to group attributes?

One set of explanations for variation in network structure between groups is related to group-specific attributes. Such relationships are likely to be species-specific, and the related factors that we find here may not apply in other species. Most simply, measures of network structure changed with group size. Networks tended to become less dense as group size increased suggesting that individuals

were limited in the number of interactions that they could have within a group (We are aware that it is also possible that observers may have been limited in the number of interactions that they could record, but we believe that we recorded the vast majority of interactions, even in the largest groups, due to the very open habitat where we observed the groups, and the automated recording methods that we used). This finding has important implications for models explaining the evolution of reciprocity in structured populations that depend on individuals having restricted interactions with other group members (Nakamura 2006). The decrease in grooming centrality observed with increasing group size suggests that favoured individuals within the group (perhaps dominant individuals) were not as strongly targeted by groomers when in large groups. This may be simply an issue of access, with dominant's demands for a limited amount of grooming being rapidly satisfied within a large group, allowing remaining opportunities for grooming to be distributed more evenly among non-dominant group members. A similar pattern was seen in networks of foraging competitions such that as groups grew larger, there was less skew in who was subjected to foraging competitions. In larger groups, there were fewer "scapegoats", suggesting that poor quality individuals may do relatively better in larger groups, as conflict over access to resources is spread more widely across the group.

Sex ratio is a product of the composition of the group and may provide a factor that relates to measures of network structure. Previous work suggests that in meerkats, sexes differ in their behaviours (Brotherton et al. 2001; Kutsukake and Clutton-Brock 2006; Hodge et al. 2007), and so, we expected that different ratios of group members may explain differing measures of network structure, specifically that as groups become less female biassed, grooming and aggression networks would become less centralised. However, the ratio of the sexes within a group did not relate to any measures of network structure.

It is expected that the most influential members of meerkat groups are the dominant breeding pair who control opportunities for reproductive output (Clutton-Brock et al. 2001). Therefore, we predicted that in groups with long-established dominant females, networks of aggression would be more centralised with the dominant female acting aggressively towards a subset of females, with other subordinate females initiating fewer aggressive acts themselves. Our data supported this prediction. The tenure of dominant females appears to be important for network structure, with groups with more established dominant females becoming more egalitarian in their grooming and foraging competition interactions, but more despotic in their dominance interactions. For grooming networks, the negative relationship indicated that the longer a female had been dominant, the less skewed was the distribution of rates

of initiating grooming. This suggests that early in a female's tenure, some individuals groom others at a disproportionate rate, but this excessive grooming by certain individuals declines as the female's dominance becomes more established. It is likely that these active groomers may be subordinate females, grooming to placate a new dominant female (Kutsukake and Clutton-Brock 2006). A similar relationship was seen in networks of foraging competitions indicating that the longer that the female had been dominant, the less skewed were the distribution of foraging competition pairings within the group. A female early in her dominance tenure may be competing strongly for resources, either to enhance her own condition or to suppress the condition of potential competitors (Clutton-Brock et al. 2006). This relationship, in networks of foraging competitions, also applied to the tenure of the dominant male (when considering unweighted data—the number of foraging competition dyads occurring within the group). An opposite, positive relationship was observed in networks of dominance interactions (when considering weighted data—the frequency of different dyadic dominance interactions occurring in the group), indicating that the longer that a female had held tenure, the more skewed were the distribution of rates of dominance interactions. Therefore, as a female's tenure progresses, specific individuals within the group disproportionately increase their initiation of dominance against others.

Variation in network structures was also explained by external, ecological factors. For example, parasite load was related to grooming networks, as expected, with groups suffering heavier parasite loads exhibiting higher densities of grooming associations. Further, individuals groomed proportionately more individuals within the group when parasite loads were high. Groups with high parasite loads also had higher indegree centrality measures, indicating that the distribution of individuals receiving grooming became more skewed at higher mean parasite loads; whereas, when parasite loads were low, individuals were groomed more equitably. This is perhaps surprising, since at low levels of ectoparasite infection, grooming may be expected to serve more of a social than hygienic role, with subordinate adults specifically targeting dominant individuals in order to reduce the chances of receiving aggression from them (Kutsukake and Clutton-Brock 2006; Madden and Clutton-Brock 2009). Mean parasite load was also positively correlated with network compactness and density in dominance networks. As in grooming networks, individuals in groups with high parasite loads were likely to initiate dominance interactions against proportionately more individuals within the group, and the network of dominance interactions became more compact as parasite load increased. Of course, the parasites may not cause changes in the network structure, but instead be consequences of them,

with dense, centralised networks facilitating efficient transmission of ectoparasites.

Causes and consequences of variation in intragroup network structure

Our results demonstrate that groups of meerkats vary in the structure of their intragroup relationships, and that such variation can be linked to external (ecological) and internal (social and individual) characteristics. The structure of a group's network of intragroup interactions may be driven from three directions. First, network structure may be an emergent property (Lusseau 2003), shaped by the exact composition of their members and dependent on specific attributes of those members, such as individual's sex, status, or age. The removal of key individual's from networks can significantly change their structure (e.g., Lusseau and Newman 2004; Flack et al. 2006). We have demonstrated that intergroup variation is related to group attributes, including group size and tenure of dominants, and so, can be considered an emergent property, dependent on the presence and behaviour of individuals. Second, network structure could be determined by external, ecological factors, such as predation threat (Thomas et al. 2008) or disease (Cross et al. 2005). We show that network structure varies between groups with ectoparasite load. Under such circumstances, we expect that network structures and group dynamics will vary within and between populations, such that even if group compositions were identical in terms of numbers and classes of individuals, the structure of group interactions is likely to differ. Third, networks of groups that are themselves connected to other groups by interactions may be shaped by the intergroup interactions within the population (see also Radford 2008). We examine intergroup interactions in this population of meerkats in a companion paper (Drewe et al. 2009). It is likely that there will be a complex interplay between these three factors, making it hard to describe a species-specific network structure. We conclude that groups vary in the structure of interactions between members, and this variation makes ecological sense. It would be interesting to investigate whether particular structures have fitness consequences for individuals making up the group, whether individuals can adaptively determine, modify, or stabilise a group's structure, and whether a group's structure can persist over time despite a change in the group's constituent members.

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