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The social network structure of a wild meerkat population: 1. Inter-group interactions

J. A. Drewe · J. R. Madden · G. P. Pearce

Abstract Groups of individuals frequently interact with each other, but typically analysis of such interactions is restricted to isolated dyads. Social network analysis (SNA) provides a method of analysing polyadic interactions and is used to analyse interactions between individuals. We use a population of 12 groups (ca. 250 animals) of wild meerkats (*Suricata suricatta*) to test whether SNA can also be used to describe and elucidate patterns of inter-group interactions. Using data collected over 24 months, we constructed two sets of networks, based on direct encounters between groups and instances of roving males visiting other groups. We analysed replicated networks of each type of interaction to investigate similarities between networks of different social interactions as well as testing their stability over time. The two network types were similar to each other when derived from long-term data, but showed significant differences in structure over shorter timescales where they varied according to seasonal and ecological conditions. Networks for both types of inter-group interaction constructed from data collected over 3 months reliably described long-term (12- and 24-month) patterns of interactions between groups, indicating a stable social structure despite variation in group sizes and sex ratios over time. The centrality of each meerkat group in roving interactions networks was unaffected by the sex ratio of its members, indicating that male meerkats preferentially visit geographically close groups rather than those containing most females. Indeed, the strongest predictors of network structure were spatial factors, suggesting that, in contrast to analyses of intra-group interactions, analyses of inter-group interactions using SNA must take spatial factors into account.

Keywords Social networks · Meerkats · Inter-group encounters · Roving males · Spatial factors

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Introduction

Defined groups of animals can interact with each other in a way analogous to interactions between individuals. Many such interactions are competitive (e.g. McComb et al. 1994; Wilson et al. 2002; Adams and Mesterton-Gibbons 2003; Radford and du Plessis 2004), but groups may also interact via dispersive individuals joining other groups or groups joining together for short periods under ecological pressures. However, most studies of inter-group interactions in wild animals focus on dyadic contests in isolation (e.g. McComb et al. 1994; Radford and du Plessis 2004). In populations containing numerous groups, as in groups containing numerous individuals, interactions are unlikely to occur in isolation or be truly independent (Krause et al. 2007; Wey et al. 2008). Instead, groups (or individuals) are

expected to exhibit polyadic interactions, with any dyadic interaction being strongly influenced by the network of polyadic interactions that each of the participants is engaged in (Whitehead and Dufault 1999). Analysis of networks of interactions between individuals living in defined groups using social network analysis (SNA) is now well established (reviewed by Krause et al. 2007; Wey et al. 2008) but such methods have not been used to analyse interactions between groups within a population

At its simplest, SNA may be used to determine who is connected to whom in a population and by what relationship (e.g. Croft et al. 2004; Lusseau and Newman 2004; Wolf et al. 2007; Ryder et al. 2008). A key benefit of SNA is its ability to go beyond the spatial arrangement of populations to elucidate meaningful social structure that may not be otherwise apparent. Individuals existing in close spatial proximity may not necessarily interact, and conversely, individuals that are seldom close in space may have important links (e.g. through mating, dispersal or disease transmission) which would not be easily quantifiable or even discernable using conventional methods of behavioural observation and analysis. For example, network analysis of social affiliations in a population of 124 bottlenose dolphins (*Tursiops truncatus*) revealed two social units separated by restricted interactions that were not simply an artefact of spatial separation (Lusseau et al. 2006). This supra-spatial element makes network theory a very useful tool for the study of sociality in animal groups and populations (Krause et al. 2007).

The application and interpretation of SNA when applied to individuals has now progressed beyond simple descriptions of network structure, to predict future fate of individuals based on early connectivity (McDonald 2007), predict the effect of removal of key individuals from groups (Flack et al. 2006), understand disease dynamics (Cross et al. 2004) and explain the evolution and maintenance of cooperative behaviours (Thomas et al. 2008). Similar questions may be asked of discrete groups of individuals. However, before this is possible, it is necessary to understand whether networks of interactions between groups can be treated in the same way as interactions between individuals and whether such networks have biological meaning and relevance. Spatial factors may confound interactions between groups in a way that may not apply to individuals. In cases where groups occupy geographically defined areas, they can interact only with groups from neighbouring areas. In contrast, individuals in groups can, in theory, interact with any other individuals within their group, unhindered by spatial factors.

Meerkats (*Suricata suricatta*) are small (<1 kg) southern African desert-adapted mongooses living in social groups of six to 40 animals (Doolan and Macdonald 1996). Groups typically include a dominant female and male as well as a variable number of other individuals of both sexes who assist with pup rearing (Clutton-Brock et al. 1998). Group composition remains stable over time, although as individuals age, males tend to disperse to join or found other groups (Young et al. 2005) whilst non-dominant females are evicted from the group, either permanently or temporarily, by the dominant female (Clutton-Brock et al. 1998). Groups may interact directly or indirectly in several different ways. Most obviously, groups may fight with each other when they encounter each other (Jordan et al. 2007). Groups may also interact indirectly by marking latrine sites or sleeping burrows within their home ranges and sniffing the latrines of other groups when they encounter them (Jordan et al. 2007). Another form of indirect interaction occurs when one group uses the sleeping burrow previously used by another group. Finally, individuals or coalitions of individuals may leave their natal group and join another group for a short period or permanently (Young et al. 2007).

Our aim in the present study was to investigate the inter-group social structure of a free-living meerkat population through application of SNA to detailed empirical data. We use two common and unambiguous forms of interactions between groups of meerkats to construct networks linking meerkat groups. We examine how these networks persist or vary over time and compare networks of different forms of interactions. We consider how spatial arrangement of meerkat groups affects their position in social networks and ask whether group attributes such as the sex ratio and number of individuals affect inter-group network structure. Finally, we observe how external ecological processes such as variation in rainfall and vegetation growth may affect the structure of inter-group networks.

Materials and methods

Study site and data collection

We studied a population of 12 habituated meerkat groups (ca. 250 animals) in the southern Kalahari Desert, South Africa (26°58′ S, 21°49′ E). Mean group size was 19 meerkats (range 5–43). All members of the population were habituated to close (<1 m) observation by researchers and could be visually individually identified by small marks of hair dye, confirmed when necessary by scanning of subcutaneous microchips. Further details of the study site habitat and population are given in Clutton-Brock et al. (1999). Detailed behavioural observations were made between January 2005 and December 2006. Each group was visited on average for 3 days per week, with observation periods lasting for at least 3 h in the morning (between 0600 and 1300 hours, depending on season) after

the meerkats emerged from their burrows and for at least 1 h before they re-entered their burrow in the evening (between 1600 and 2000 hours).

Descriptions of network types

We collected data on two distinct forms of meerkat inter-group interactions: prospecting males ('rovers') and inter-group encounters. A *rover* event was recorded when a male meerkat left its original social group, either singly or as part of a coalition of males, and actively sought out and approached another group of meerkats in a non-aggressive manner. This usually occurred as males sought breeding opportunities in other groups. Rovers were only recorded if they subsequently returned to their original group, which usually occurred on the same day. An *inter-group encounter* event was recorded when two or more social groups met and interacted in an aggressive manner. This took three main forms, viz. one group chasing another, physical contact and fighting and excavation of burrows to dig out meerkats from another group. Inter-group interactions were recorded ad libitum by a single observer as part of an established data collection protocol. Over the 2-year observation period, we recorded a total of 531 roving events and 270 inter-group encounters.

Network measures analysed

A list of definitions and descriptions of common social network terms used in this paper appears in Table 1; the reader is referred to more detailed texts for fuller explanations of network terminology (e.g. Hanneman and Riddle 2005; Wasserman and Faust 1994). Throughout we use the following terms with specific meaning: *network structure* refers to network-level characteristics of the study population (e.g. density), *network measures* indicates intrinsic network properties calculated from either all or a subset of nodes (e.g. degree centrality) and *attributes* refers to non-network properties of meerkat groups (e.g. group size, sex ratio).

Degree centrality

We present four measures of centrality for rover networks and two for inter-group encounter networks. For the rover data, it was possible to calculate both a group *outdegree* measure (number of episodes of rovers leaving the group) and an *indegree* measure (number of episodes of rovers from other groups visiting the group). Data from inter-group encounters networks are presented simply as *degree*, because inter-group contacts are non-directional (if group A interacts with group B, then group B must by definition interact with group A) and thus, outdegree and indegree in

this instance are identical. For each centrality measure, we present both *weighted* and *unweighted* data.

Distance

We present two measures of distance. The first is the mean distance between pairs of individuals within a network (*average path length*); in social animals, high average path length scores indicate that some individuals only interact with others very indirectly. The second measure, *compactness* (or *distance-based cohesion*), indicates how directly connected the network is (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.

Density

We present two measures of *density*: that relating to the whole network (a 'population'-level measurement) and to the main component (a more local-level measurement). In social animals, a high *density* score indicates that most individuals (or groups) are interacting with the majority of all the other individuals (or groups). Density calculation for weighted networks is sometimes contested (Wey et al. 2008) so we present only values for unweighted networks, although we retain direction in the relationships.

Clustering

We present both *unadjusted* and *adjusted clustering coefficients*, the latter one taking into account network density which is important because clusters are less likely to persist in networks of low density than those of high density (simply because there are fewer ties in the former). Thus, a clustering coefficient that remains high after adjusting for low network density is likely to be significant (Hanneman and Riddle 2005). Clustering coefficients were calculated using unweighted association data.

Data analysis

Social network analysis was performed using UCInet for Windows (Borgatti et al. 2002). A quadratic assignment procedure (QAP) was used to search for correlations between networks. QAP involved computation of Pearson's correlation coefficients for corresponding cells of two data matrices (each matrix coding for one network), followed by random permutation of one matrix and re-computation of Pearson's correlation coefficients. This was repeated 50,000 times in order to calculate the proportion of times that

Table 1 Definitions of social network terms used in this paper

A *node* is the unit of study: usually an animal or group of animals. Nodes are often displayed as circles on network diagrams

An *edge* represents an interaction or association between two or more nodes. Several different relationships can be examined in one network, for example, aggression, mating and grooming may all occur between the same nodes. Edges are also sometimes known as *ties*

A *social network* consists of nodes joined by edges (Fig. 1)

An *unweighted* network indicates presence or absence of interactions only, no matter how frequently these may occur. Such networks therefore indicate who interacts with whom. Unweighted networks are also referred to as *binary networks*

A *weighted* network includes data on frequency of interactions. Such networks therefore indicate not only who interacts with whom, but by how much. The weight of an edge is also known as its *strength*

A *directed* network includes information on the direction of interaction, e.g. who groomed whom, and thus indicates an initiator and a recipient node. Direction is usually indicated using arrows on a network diagram (Fig. 2)

A *component* of a network is a group of connected nodes. If all nodes in a network are linked, such that a path of edges exists between any two nodes, the network has only one component. In networks with two or more components, the largest group of connected nodes is called the *main component*

Degree centrality is a measure of how many direct edges an individual node has with others and indicates a node's prominence (importance) in the network. For directed relationships, *outdegree* is the number of edges that originate from the focal node (e.g. the number of grooming events initiated by the focal animal) whilst *indegree* is the number of edges that are directed towards the focal animal (e.g. the number of grooming events that the focal animal receives)

Distance in a network is often expressed as *average path length*, which is the mean number of edges between pairs of individuals within a network; in social animals, high average path length scores indicate that some individuals only interact with others very indirectly. To compare distance across networks of different size, *compactness* should be used, which inherently controls for the size of the network. The higher the compactness score of a network, the more directly nodes are interacting with others

The *density* of a network is a measure of how many potential edges between nodes are actually present. Density values range from 0 to 1, with high scores indicating 'saturated' networks (all possible ties are present) and low scores indicating 'sparse' networks

The *clustering coefficient* (*C*) of a network describes how 'cliquish' the network is and measures the extent to which two neighbours of a focal animal (or group) 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

coefficients from randomly arranged networks were larger or equal to the observed Pearson's coefficient and thus generate an associated probability value that the relationship between the networks was due to chance.

Results

Network diagrams for inter-group encounters and roving males are presented in Figs. 1 and 2, with network measures summarised in Tables 1 and 2.

What are the structural properties of networks of interactions between meerkat groups?

The weighted rover network showed a positively skewed degree centrality distribution (Fig. 3a): Most groups had low weighted outdegree and indegree scores; a small number had high degree scores. Two groups (Whiskers and Lazuli) appear centralised in the network (Fig. 3b), having far more rovers leave and visit them than any of the other ten meerkat groups. Indeed, the weighted degree centrality scores for both Whiskers and Lazuli were at least 50% greater than for any other group (Table 2). The unweighted rover network was far less skewed, with no group substantially more central than the others (Table 2). Thus, information would be

lost by considering only the presence of roving interactions between groups, rather than the rate of these interactions. Indeed, Whiskers and Lazuli shared a disproportionately high number of ties, almost three times the number of the two next most connected groups (Fig. 1b).

The weighted inter-group encounters network was less skewed than the equivalent rovers network (Table 2) and structurally similar to the unweighted inter-group encounters network (node-level regression test with 30,000 permutations, $r^2 = 0.94$, $p = <0.001$). This suggests that inter-group encounters network degree was more influenced by the number of other groups encountered than by the frequency of interactions with each group encountered.

The structure of both roving and inter-group encounters networks varied with time of year (Table 3). For roving networks, mean degree was higher during July to December than in January to June in both years studied, although the timing of peak degree differed between 2005 (October to December) and 2006 (July to September).

Density of the rovers network was significantly positively correlated with weighted degree (node-level regression test with 30,000 permutations, $r^2 = 0.877$, $p = 0.001$) suggesting that as the number of rovers leaving a group increased, the more groups they visited, rather than simply visiting the same groups more times. Conversely, density of the inter-group encounters network was not significantly
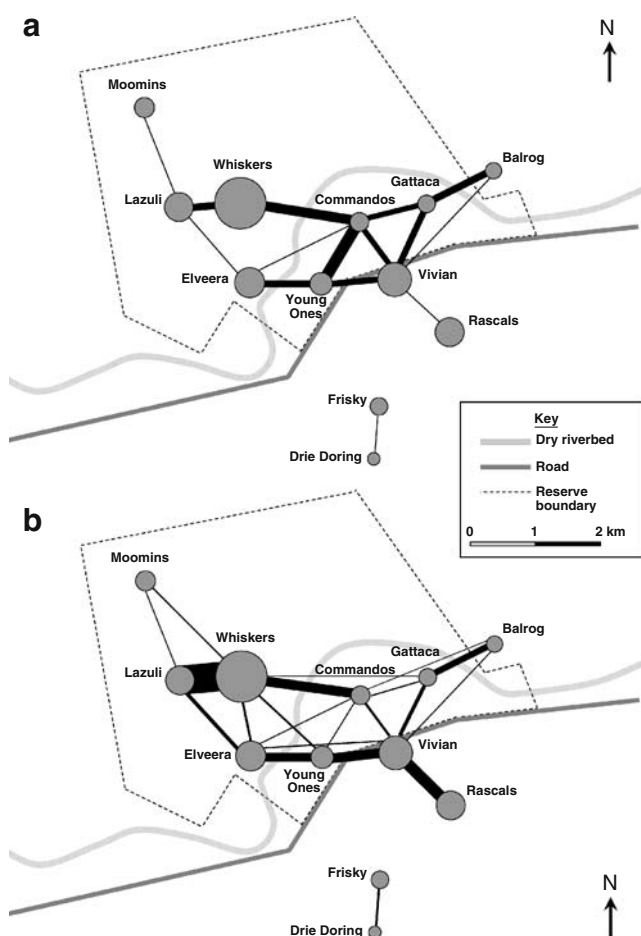
Fig. 1 Map of Kuruman River Reserve showing the geographical locations of the 12 meerkat groups studied. Two social networks are shown: **a** intergroup encounters network and **b** roving males network. The two networks are structurally very similar but the rover network contains more links (edges) between groups (nodes). There are two components to each network: a main component containing ten interlinked nodes and a separate minor component containing two nodes with only one link between them. Node size is proportional to group size. Edge thickness is proportional to number of intergroup interactions. Both networks constructed from 12 months' data (January to December 2005)

correlated with weighted degree (node-level regression test with 30,000 permutations, r^2=0.208, p=0.271), signifying that an increase in inter-group encounter rate was due to more interactions between the same pairs of groups rather than formation of new dyads between different groups.

How stable are network structures over time and across different time intervals?

Network structure was relatively constant across 2005–2006 for both rovers and inter-group encounters (Table 4; Fig. 2). There were two obvious exceptions: The structure of the rover network in October to December 2006 differed from all other time periods examined, and the pattern of inter-group

encounters during April to June 2006 differed from the pattern of inter-group encounters in all other time periods.

Network structure was consistent across timescales. Networks generated from data collected over 3 months were significantly correlated with networks formed from datasets containing 12 and 24 months' data, for both types of interactions (Table 5). Thus, data collected over the relatively short timeframe of 3 months allowed valid extrapolation and conclusions to be drawn for inter-group interactions over longer time periods because inter-group social structure was stable. We therefore used 3-month datasets for remaining analyses, selecting the season for which the number of recorded interactions was largest (i.e. October to December 2005).

How distinct are rover networks from inter-group encounters networks?

Although the specific meerkat groups possessing highest degree centrality differed between networks (Table 2), rovers and inter-group encounter network structures were well correlated (Table 5), particularly over longer timeframes. Networks of rovers constructed from 12 and 24 months of data were structurally similar to inter-group encounter networks that included 12 and 24 months of data. However, shorter-term datasets displayed different structures, with rover networks constructed from 3-month datasets being structurally different to longer-term (12 and 24 months) inter-group encounter networks (Table 5). Similarly, inter-group encounter networks constructed from 3-month datasets were structurally different to longer-term rover networks (Table 5). This suggests that the networks of rovers and inter-group encounters are subtly distinct in the short term, but show similar long-term structural inter-relationships.

How does inter-group network structure relate to physical attributes of meerkat groups?

Group size

Group size was significantly positively related to rover centrality, for both indegree and outdegree (Table 6). Thus, the bigger the group, the more males that left to go roving and to a lesser but still significant degree, the more males that visited from other groups. Inter-group encounters degree centrality was not correlated with group size, indicating that bigger groups were no more likely than smaller groups to be involved in inter-group contacts.

Sex ratio

The proportion of females in a group, which ranged from 0.32 to 0.70, did not relate to a group's degree centrality in
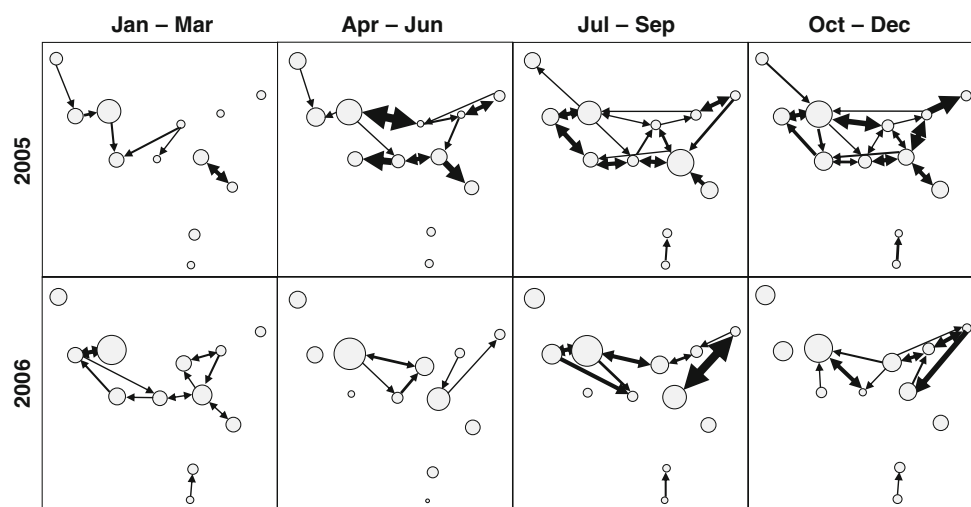
Fig. 2 Seasonal variation in meerkat social network structure. Eight networks showing movements of meerkat rovers between 12 social groups are shown. Whilst network structure (who interacts with whom) remains relatively constant over time, both network density and clustering coefficient vary with season. The network for Jan–Mar 2005 exhibits low density (network density=0.05, indicating only one in 20 possible ties is present) and low clustering (adjusted coefficient= 0, indicating no two groups connected to any other group are themselves connected). The network for Oct–Dec 2005 shows moderate density (network density=0.19) and high clustering (adjusted coefficient=1.51) reflected by many triads present between neighbouring groups. *Arrowheads* indicate direction of movement of roving males. *Arrow size* is proportional to rate of roving episodes. Node size is proportional to group size

either the rovers or inter-group encounters networks (Table 6).

Geographic distance between groups

There was a significant negative correlation between geographic distance between meerkat groups and both types of inter-group interaction studied (Table 6). This is reflected in the finding that geodesic distance (the number of links in the shortest path between two groups) was significantly positively correlated with geographic distance (physical distance between two groups on the ground) for both the rover and inter-group encounter networks (Table 6). Thus, as groups move geographically further away from each other, linkage between groups become progressively more indirect.

Discussion

Networks of interactions between groups of meerkats, based on inter-group encounters and patterns of roving males, can be constructed in a way similar to that used for networks of associations between individual animals. Such networks appeared to be fairly consistent over periods of up to 2 years, but did vary in structure according to time of year and unusual ecological conditions, in ways that were biologically meaningful. Inter-group encounter and rover networks constructed using long-term (multi-year) data were similar to each other, but networks constructed using data from shorter periods (months) differed from each other. Group size was related to a group's position within networks of roving and its network attributes, with large groups being well connected to others. Such a relationship was not seen with networks of inter-group encounters, nor were there relationships with the group's sex ratio. As expected, geographical distance was a strong predictor of both inter-group encounter and roving networks, suggesting that analyses of inter-group interactions using SNA must take into account spatial factors, in contrast to most analyses of intra-group interactions.

Structural properties of inter-group networks

We found network analysis of degree centrality to be a simple technique to facilitate comparisons of different interactions between multiple meerkat groups over time. Degree centrality was useful in identifying the most connected meerkat groups, particularly when weighted data were used. Well-connected groups are likely to be at higher risk of infection with transmissible diseases (Christley et al. 2005) and so measurement of degree centrality offers a way to identify which groups within an at-risk population are more likely to be involved in disease transmission (Corner et al. 2003). Degree centrality usefully differentiated meerkat groups central to the network (Table 2; Fig. 3) into those that were well connected with many other groups (e.g. Vivian) and those that had many connections but shared them with few other groups (e.g. Whiskers; Fig. 1). We suggest degree centrality holds many advantages over

Table 2 Comparison of degree centrality measures for two types of interactions over a 3-month period between 12 groups of meerkats

Group name	Rovers				Intergroup encounters	
	Weighted data		Unweighted data		Weighted degree	Unweighted degree
	Outdegree	Indegree	Outdegree	Indegree		
Whiskers	51	32	4	4	6	2
Vivian	28	16	5	4	9	3
Lazuli	23	45	1	2	4	2
Gattaca	19	4	3	2	8	3
Young Ones	14	11	3	4	11	3
Commandos	8	8	4	3	12	4
Elveera	7	17	2	3	8	2
Drie Doring	4	0	1	0	0	0
Rascals	4	14	1	1	0	0
Moomins	3	0	1	0	0	0
Balrog	0	10	0	1	4	1
Frisky	0	4	0	1	0	0
Total	161	161	25	25	62	20

The most connected meerkat groups (those with the highest degree centrality scores) vary depending on the type of interaction studied and whether weighted or unweighted data are used

other centrality measurements in wild animal network analysis or other situations where data may be incomplete. First, degree centrality is the simplest and most readily measured centrality measurement (Wasserman and Faust 1994). Second, it is far less sensitive to error than, for example, betweenness centrality—a measure of how often a node lies in the shortest path between all other pairs of nodes and thus how much control a node has on flow of information through the network—which can change dramatically if only one or two observations are missing or were wrongly recorded (Krause et al. 2007). Third, degree centrality has been found to be at least as good as other network parameters in predicting flow of information (in this case, risk of infection) when SNA was used to identify high-risk individuals in a simulation study of disease spread (Christley et al. 2005). Unlike commonly used measures of social complexity (e.g. group size, mating system), network analysis does not assume homogeneity of effect on all individuals or groups, resulting in a deeper understanding of social complexity (Wey et al. 2008) that is likely to complement rather than replace relationship-based approaches previously applied to animal behaviour (e.g. Whitehead 1997).

Network structure was best determined through local-level measurements, that is, analysis of the structure of the main component (the largest group of connected nodes) in the network. Variation in the number of nodes in the main component did not preclude meaningful comparisons between networks, since density and adjusted clustering coefficient calculations implicitly included the number of nodes (groups) in the component under study. However, local level measurements were not necessarily representative of the whole network, particularly when based on non-directional ties in a small component. For example, during April to June 2006, only three of the 12 meerkat groups in the intergroup encounters network were interconnected (Table 3). This was reflected in a low network density (0.05) and a low compactness score (0.05), yet cluster coefficients (both absolute and adjusted) were both relatively high (1.00). Thus, not all network measures are necessarily meaningful or applicable to all network types and a degree of caution is required when interpreting network measures, particularly when comparing networks or components of different sizes. Our data show that comparisons of network measures may become unreliable for networks with more than one component.

Stability of networks over time and across different time intervals

Both types of inter-group network were remarkably stable over time, though some between-year differences did occur. The timing of peak degree centrality for rovers differed between 2005 (when most roving occurred in October to December) and 2006 (when most activity occurred between
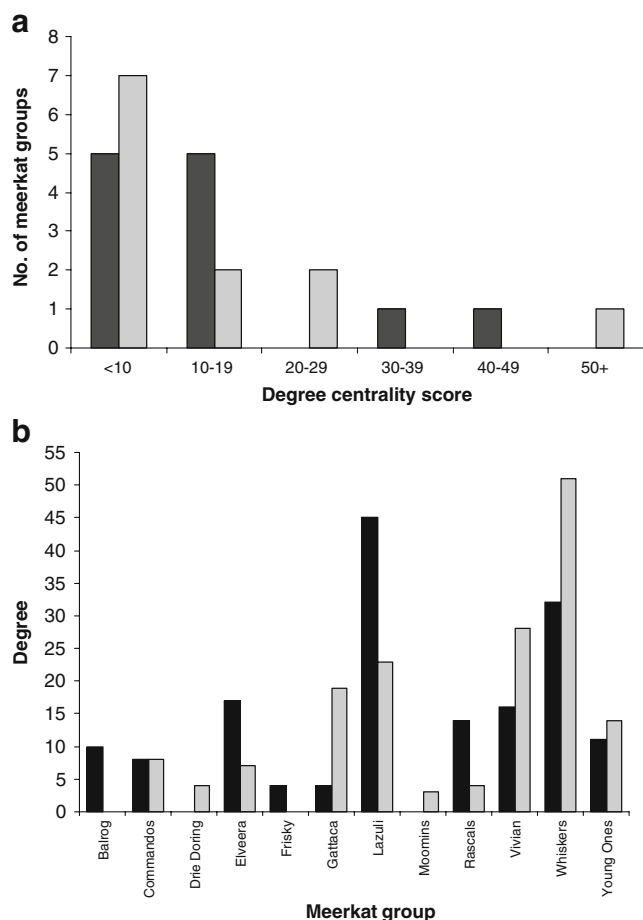
Fig. 3 Summary of network centrality measures for roving meerkats from 12 groups over a 3-month period from October to December 2005. **a** Frequency distribution of weighted degree measures. **b** Comparison of weighted degree centrality measures on a group-by-group basis. Geographically adjacent groups Lazuli and Whiskers show differences in degree centrality for the roving males networks, a feature that may reflect differences in sex ratios of these groups (proportion of female meerkats=0.57 for Lazuli and 0.47 for Whiskers). For both graphs: *dark grey bars* = indegree; *light grey bars* = outdegree

July to September; Table 3). If male roving is driven by availability of fertile females (Young et al. 2007), this suggests that the meerkat breeding season began earlier in 2006 than in 2005. However, fewer than half the number of roving episodes occurred in 2006 (n=164) compared with 2005 (n=367), and there was more roving outside the main breeding season (September to March; Clutton-Brock et al. 1999) in 2005 than there was during it in 2006 (Table 3). This reflects a limitation of social network analysis, particularly of unweighted network diagrams, in that sample size is not always obvious which may lead to erroneous conclusions being drawn.

Whilst the intensity of roving varied by season (Table 4), the structure of the rover networks was very stable over time, and rovers visited the same groups regardless of

season. An exception occurred in October to December 2006, during which the rover network was structurally dissimilar to that of any other season studied (Table 4). A possible explanation is the exceedingly low rainfall during these 3 months, which was 66% below average for the time of year (Fig. 4). Recent rainfall is known to affect meerkat food availability (Barnard 2000); hence, body condition may be poorer following a drought. This may lead to fewer females in breeding condition (Young et al. 2007) and therefore less stimulus for males to go roving, though males that are themselves in poor body condition may continue to rove, if fertile females are available (Young et al. 2005).

Abnormal rainfall patterns may also explain why the inter-group encounters network for April to June 2006 did not resemble inter-group encounters networks computed for most of the other seasons studied (Table 4). Total rainfall during the previous 3 months (January to March 2006) was almost twice the mean for that season (Fig. 4), resulting in massive growth of vegetation such as Kalahari sourgrass (*Schmidtia kalahariensis*) which grows up to 90 cm tall (Clayton et al. 2006). This severely reduced visibility on the ground (Fig. 5) and may have precluded nearby meerkat groups from visually detecting each other, an event which would usually lead to an inter-group encounter (JAD, personal observation). It can thus be seen that analysis of changes in network structure over time may reflect and explain biological phenomena affecting the population of animals under study. This illustrates an advantage of the network approach over conventional methods in that SNA is suited to exploration of biological phenomena that are influenced by indirect relationships better than other measures, such as group size, which do not contain sufficient detail about individual social relationships (Wey et al. 2008).

Similarities between inter-group networks of different social interactions

The high degree of correlation between networks constructed from two different inter-group interactions is in contrast to the lack of similarity between intra-group networks (JRM, JAD and GPP, unpublished data). Such similarity is perhaps surprising because the two inter-group associations studied (inter-group encounters and roving males) are likely to occur for different reasons (Doolan and Macdonald 1996) and suggests inter-group interactions may be driven by ecological or environmental factors, rather than by individual or group attributes. That the inter-group networks were subtly different in the short term (3 months) but such differences decreased over longer timescales (12 to 24 months) illustrates the importance of careful and meaningful definition of data in network analysis in a way that reflects a biologically relevant level of resolution (Wey et al. 2008).

Table 3 Summary of mean network measures by season over 2 years calculated from two social networks, each containing the same 12 groups of meerkats

Social network	Year	Season	Number	Individual node level		Local level					Network level			
				Centrality		Size of main component	Density of main component	Cluster coefficient	Adjusted cluster coefficient			Distance		Density of whole network
				Degree (weighted)	Degree (unweighted)	No. of nodes	Dmc	C	C/Dmc	No. of components		Distance (L)	Compactness	Dn
Rovers (N=531)	2005	Jan–Mar	22	1.83	0.58	6	0.17	0	0	6		1.40	0.06	0.05
		Apr–Jun	56	4.67	1.17	10	0.16	0.14	0.92	3		1.94	1.17	0.11
		Jul–Sep	128	10.67	1.83	10	0.23	0.18	0.78	2		1.82	0.30	0.17
		Oct–Dec	161	13.42	2.08	10	0.26	0.39	1.51	2		1.96	0.35	0.19
	2006	Jan–Mar	29	2.42	1.17	8	0.23	0.33	1.43	4		2.63	0.22	0.11
		Apr–Jun	12	1.00	0.50	3	0.67	0.50	0.75	8		1.33	0.06	0.05
		Jul–Sep	75	6.25	1.08	7	0.29	0.36	1.26	5		2.15	0.16	0.10
		Oct–Dec	48	4.00	1.08	7	0.29	0.47	1.65	5		1.64	0.14	0.10
Intergroup encounters (N=270)	2005	Jan–Mar	20	1.67	1.00	5	0.40	0	0	6		1.69	0.14	0.09
		Apr–Jun	58	4.83	1.83	9	0.28	0.27	0.96	3		2.19	0.32	0.17
		Jul–Sep	20	1.67	0.83	4	0.50	0	0	7		1.56	0.10	0.08
		Oct–Dec	62	5.17	1.67	8	0.36	0.24	0.67	5		1.96	0.27	0.15
	2006	Jan–Mar	24	2.00	1.33	6	0.47	0.53	1.14	6		1.81	0.17	0.12
		Apr–Jun	24	2.00	0.50	3	1.00	1.00	1.00	10		1.00	0.05	0.05
		Jul–Sep	28	2.33	1.00	5	0.40	0	0	6		1.69	0.14	0.09
		Oct–Dec	34	2.83	1.00	5	0.40	0	0	6		1.85	0.14	0.09

Data are presented at three levels of resolution: individual level (each node represents one meerkat group), local level (main network component, i.e. largest coalition of connected groups) and network level (all 12 groups). All data are unweighted except where indicated. Rover networks are illustrated in Fig. 2

Table 4 Stability of networks between seasons: correlations between intergroup networks of 12 meerkat groups over 2 years

		Rovers							Intergroup encounters						
		Apr–Jun 2005	Jul–Sep 2005	Oct–Dec 2005	Jan–Mar 2006	Apr–Jun 2006	Jul–Sep 2006	Oct–Dec 2006	Apr–Jun 2005	Jul–Sep 2005	Oct–Dec 2005	Jan–Mar 2006	Apr–Jun 2006	Jul–Sep 2006	Oct–Dec 2006
Jan–Mar 2005	r	**0.23**	**0.25**	**0.37**	**0.36**	−0.04	0.09	−0.05	**0.49**	**0.61**	0.13	**0.28**	−0.02	0.03	−0.06
	p	**0.04**	**0.03**	**0.02**	**0.02**	0.73	0.10	0.51	**0.01**	**0.01**	0.12	**0.04**	0.81	0.29	0.55
Apr–Jun 2005	r		**0.27**	**0.34**	0.18	**0.31**	0.04	0.06		**0.66**	**0.57**	**0.34**	0.16	0.15	**0.27**
	p		**0.04**	**0.02**	0.06	**0.02**	0.19	0.18		**<0.001**	**<0.001**	**0.04**	0.12	0.18	**0.05**
Jul–Sep 2005	r			**0.89**	**0.70**	0.14	**0.47**	0.06			**0.34**	0.22	0.24	**0.39**	**0.33**
	p			**<0.001**	**<0.001**	0.06	**0.01**	0.18			**0.03**	0.07	0.08	**0.02**	**0.04**
Oct–Dec 2005	r				**0.75**	0.06	**0.47**	0.01				0.26	0.13	0.24	**0.28**
	p				**<0.001**	0.13	**0.01**	0.26				0.06	0.14	0.07	**0.04**
Jan–Mar 2006	r					0.01	**0.43**	0.07					−0.03	0.11	−0.08
	p					0.32	**0.01**	0.15					0.75	0.13	0.44
Apr–Jun 2006	r						**0.31**	0.01						**0.58**	**0.43**
	p						**0.02**	0.24						**0.01**	**0.02**
Jul–Sep 2006	r							0.19							**0.72**
	p							0.06							**<0.001**

Bold values indicate significant relationships ($p < 0.05$)

Effect of group attributes on network structure

Group size

As might be expected, group size was significantly positively related to rover degree centrality; thus, the bigger the group, the more males that went roving and the more males that visited from other groups (perhaps because more mating opportunities were presented by larger recipient groups). Inter-group encounters were found to be as likely to take place between large and small groups as between similarly sized groups because they usually occurred between direct neighbours (Fig. 1). This resulted in a high clustering coefficient during periods of intense interaction wherein many three-way inter-group encounters took place (Fig. 2).

Sex ratio

It is perhaps surprising that the sex ratio of a group had no effect on that group's centrality in the network of roving male movements, because roving is commonly explained as facilitating additional breeding opportunities (Young et al. 2005). The lack of sex ratio effect suggests that additional factors may determine why male meerkats go roving, such as prospecting for other social groups prior to emigration (Doolan and Macdonald 1996).

Table 5 Correlations between intergroup networks for two interaction types between 12 meerkat groups over 3, 12 and 24 months

		Rovers (12 months)	Rovers (24 months)	Intergroup encounters (3 months)	Intergroup encounters (12 months)	Intergroup encounters (24 months)
Rovers (3 months)	r	**0.42**	**0.37**	0.16	0.11	0.08
	p	**0.02**	**0.02**	0.07	0.15	0.19
Rovers (12 months)	r		**0.96**	0.15	**0.56**	**0.54**
	p		**<0.001**	0.08	**<0.001**	**<0.001**
Rovers (24 months)	r			0.18	**0.59**	**0.67**
	p			0.06	**<0.001**	**<0.001**
Intergroup encounters (3 months)	r				**0.60**	**0.42**
	p				**<0.001**	**<0.05**
Intergroup encounters (12 months)	r					**0.86**
	p					**<0.001**

Bold values indicate significant relationships ($p < 0.05$)

Table 6 Relationships between group attributes and network measures for two intergroup social networks

		Group size	Proportion of group that is female	Geographic distance between groups
Intergroup encounters degree	r	0.12	−0.17	**−0.47**
	p	0.74	0.61	**<0.001**
Rovers outdegree	r	**0.79**	−0.19	**−0.37**
	p	**0.01**	0.54	**<0.001**
Rovers indegree	r	**0.69**	0.01	**−0.37**
	p	**0.02**	0.98	**<0.001**
Intergroup encounters geodesic[a]	r	–	–	**0.94**
	p	–	–	**<0.001**
Rovers geodesic[a]	r	–	–	**0.86**
	p	–	–	**<0.001**

Bold values indicate significant relationships ($p<0.05$)

[a] The geodesic distance represents the shortest connection between any two meerkat groups in the network.

Geographic distance between groups

We have shown that geographical distance between meerkat groups plays a large role in dictating the nature and degree of interactions occurring between two or more groups. This is unsurprising for inter-group encounters, many of which appear to be impromptu interactions occurring when two or more groups meet by chance whilst foraging, or if one group comes across a burrow occupied by pups and their babysitters from another group (JAD, personal observation). Network analysis revealed that roving male meerkats preferentially visit nearby groups rather than seeking groups with a higher female sex ratio. This may be because the risks associated with travelling further, into unfamiliar territory, are unacceptably high for solitary roving males (Ross-Gillespie and Griffin 2007) or because the tradeoffs that exist between extraterritorial roving and contributions to offspring care in this cooperative species (Young et al. 2005) limit roving behaviour.
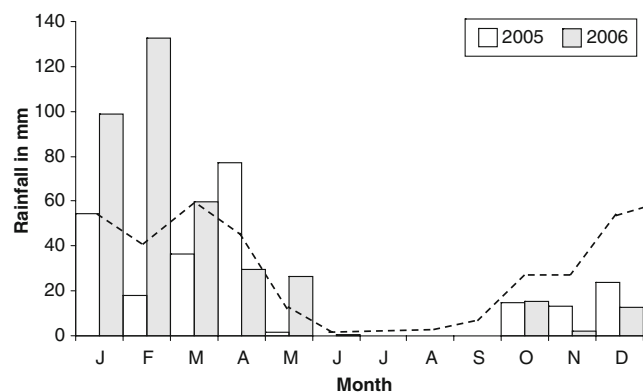
In conclusion, we have shown social network analysis to be a valuable tool for describing and analysing inter-group relationships within a wild meerkat population. This complements and extends the insights into social structure of intra-group interactions determined in the same population (JRM, JAD and GPP, unpublished data). Networks for both rovers and inter-group encounters constructed from data collected over 3 months reliably described long-term patterns of interactions between groups, indicating a stable social structure despite variation in group sizes and sex ratios over time. This suggests that meerkat inter-group networks are robust and may be relatively resistant to the impacts of population fluctuations and may have predictable pathways and patterns of disease transmission or social learning. The analytical methods we describe in the current paper complement existing approaches for the study of

Fig. 4 Monthly rainfall patterns on the study site over the 2-year study period. The *dashed line* indicates mean monthly rainfall over the same area during the preceding 10 years

Fig. 5 Extensive growth of tall Kalahari sourgrass, as shown here, following a period of above-average rainfall in early 2006, severely limited meerkat visibility on the ground and is a possible ecological explanation for reduced rates of inter-group encounters during April–June that year

animal behaviour and offer valuable techniques for comparative analyses of social interactions in different populations and species.

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