



Does the social network structure of wild animal populations differ from that of animals in captivity?

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ABSTRACT

The social behaviour of wild animals living in groups leads to social networks with structures that produce group-level effects and position individuals within them with differential consequences for an individual's fitness. Social dynamics in captivity can differ greatly from those in wild conspecifics given the different constraints on social organization in wild populations, e.g. group size, predation pressure, distribution of resources (food, mates), which are all regulated by human carers in captive populations. The social networks of animals in zoos is expected to differ from those of free-living conspecifics. While many studies have described the social networks of a wide diversity of wild and captive animals, none has directly compared the networks of multiple groups of a single species both in the wild and in captivity. Meerkats, *Suricata suricatta*, are an excellent species to compare the social networks of wild and captive groups. We replicated the methods of Madden et al. (2009, 2011), who studied eight groups in the wild, in fifteen captive groups. We tested how network structures and individual positions in grooming, foraging competition and dominance networks differed between wild and captive groups. Groups of wild and captive meerkats differed in various aspects of their social network structure. Differences in the network may be due to individuals occupying different network positions and the difference in the number and strength of their connections to other individuals. This distinct way of interacting and associating could be a result of group specific attributes, such as group size, and/or the attributes of the donor and recipient, including sex, status or age. Critically, the differences may be explained by the dissimilar living environment that each encounters.

1. Introduction

Many studies of animals in captivity have investigated the relationship between housing and management conditions and the incidence of undesirable behaviours exhibited by individuals (see Hogan et al., 1988; Clubb and Mason, 2003; Casamitjana, 2005; Mallapur et al., 2005; Stroud, 2007; Ross et al., 2009; Brummer et al., 2010; Cabezas et al., 2013; Shepherdson et al., 2013; Tan et al., 2013; Crast et al., 2014). For social animals, housing and husbandry may have more far reaching consequences, altering not just the behaviour of individuals but also the more general social structure of captive animal groups (e.g. Rose and Croft, 2015; Levé et al., 2016).

The network of social interactions in a group-living species has an impact on evolutionary and ecological processes (Fisher et al., 2017) at the population level (Kurvers et al., 2010), with fitness consequences for

individuals (e.g. McDonald, 2007; Pinter-Wollman et al., 2013; Ellis et al., 2017). There are also indicators that social network structures can have welfare consequences for captive primates (e.g. Flack et al., 2006; McCowan et al., 2008). Such observations have led to the suggestion that a better understanding of social networks may improve individual welfare in captivity (Asher et al., 2009; Cañon Jones et al., 2017). However, it is critical to determine if and how social networks of captive animals differ from those of their wild conspecifics. This is not a minor comparison to make, because it requires an understanding of the representative network for a species which entails studying multiple groups to account for intergroup differences, such as size or environmental conditions. Furthermore, this replication needs to be conducted for both wild and captive groups.

The social network of captive groups is liable to be affected by the husbandry and housing of the animals. For instance, movement of

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individuals between exhibits to facilitate improved breeding success can lead to frequent perturbation of group membership and individual positions in the social network (Levé et al., 2016). Overcrowding in captive conditions, either because of space constraints or poor enclosure design, can affect the stability of a dominance hierarchy and social interactions (Grant and Albright, 2001) and the overall intensity of social interactions (Hediger, 1964). These effects may arise because crowding prevents the avoidance of others in order to reduce agonistic behaviour (Aschwanden et al., 2008) and as a result, association and interaction dynamics are likely to be transformed which can result in serious physical trauma and reduced psychological wellbeing (McCowan et al., 2008). More subtle detrimental effects on individual welfare may arise simply because the social structure either precludes natural patterns of association and interaction, or forced associations inhibit natural behaviours.

While the networks of both free-living animals and those in captivity have been described for a large and diverse set of species, few have investigated for structural properties that are representative of a species by considering multiple groups, and none have explicitly compared the structures of free-living and captive groups of the same species. Meerkats, *Suricata suricatta*, have had their social networks documented in the wild across multiple groups (see Madden et al., 2009; Drewe et al., 2009; Madden et al., 2011), and are commonly held in zoo collections. Meerkats in the wild are characterized by living in large groups and for being a cooperative species (Clutton-Brock et al., 2008). They naturally engage in a wide range of social associations and interactions including allo-grooming, dominance contests and foraging associations (Madden et al., 2009). Therefore, they provide an excellent system to compare the social networks of wild and captive groups.

In wild meerkats, across eight studied groups (see Madden et al., 2009, 2011), network structures varied within a group according to the interaction type considering (grooming, dominance contests, foraging contests). Network structure within an interaction type varied with group attributes, the attributes of individual group members and due to ecological factors. We replicated the methods used by Madden et al. (2009, 2011) to explore three different interaction networks (foraging competitions, grooming and dominance interactions, see definitions in the methods section) across fifteen captive groups of meerkats and compared them to those networks observed in wild meerkats. Several factors can lead to different network structures between wild and captive meerkats. For instance, competition in foraging in captive conditions can be reduced since food is provisioned and because there are smaller number of animals in captive groups. Additionally, in larger groups (usually wild groups), individuals may interact with only a few selected partners (e.g. grooming interactions) and, in closed spaces, tensions can escalate because of crowding (Dunbar, 1991). Hence, our first prediction was that captive groups, which generally comprise fewer individuals than wild groups and are in a confined space, can present differences in grooming, dominance and foraging competition within the different network measures. Particularly network centrality, which can be characterized by individuals with lower scores (indicating a more even spread of ties, e.g. in grooming interactions) in captive groups than individuals in wild groups. Density of a network can show higher scores in captive groups indicating that almost all (if not all) individuals are interacting with the majority of all other members of the group. Average path length can also show lower scores in captive groups than in the wild ones, indicating that individuals interact directly with others. Our second prediction was that network positions and patterns of association in grooming and dominance networks can match those seen in wild meerkats and be predicted by sex, status and age, but will differ in individual's network position scores. Previous research on wild meerkats (Kutsukake and Clutton-Brock, 2010) found that the grooming exchange between dominant and subordinate females, with subordinates grooming the dominant female more often, happens more frequently because of intrasexual conflict. However, higher intrasexual conflict may be observed in males or females in captivity due to the inability to disperse.

Therefore, we expect that captive groups will show higher outdegree centrality scores in grooming than wild groups, specifically with subordinate individuals (females and males) initiating more grooming than dominants. If higher intrasexual conflict arises in captivity due to the space restriction, we expect that captive females may give higher total rates of dominance than those in wild groups, as dominant female meerkats are usually more aggressive to other group members than dominant males (Clutton-Brock et al., 2006). Our third prediction was that patterns of association in captive groups can be also expected to be based on their individual attributes, nonetheless, the assortative association of captive individuals based on sex can be expected to differ from wild groups as a consequence of the intrasexual conflict and their inability to disperse.

A better understanding of the general similarities and differences between the networks of social interactions in wild and captive meerkats will inform us of hidden potential effects of captivity on group-living animals, and alert us to possible detrimental impacts on their welfare. Therefore, we first described the network structure of captive meerkat groups and the positions of classes of individuals within them, and then compared these structures and positions with those from previously reported networks of wild meerkats.

2. Methods

2.1. Data collection

Fifteen captive groups of meerkats comprising a total 113 individuals were studied from September 2011–December 2012 in Zoological parks in the UK and Mexico (Table 1; see the appendix for the enclosure and management description). The selection of all zoos and parks was conducted by searching for groups of meerkats that contained a mixture of sexes and ages. Observations were undertaken during the opening hours of zoos/parks (8:00–9:00 to 16:00–17:00) and all were undertaken from behind the fence, as visitors do, so as to avoid any alteration in their standard behaviour. We observed each group for a total of 20 h over the 4 days of observations. Data were collected through scan sampling on all members of the group, this was done only by one observer and using written records. In order to identify them and to avoid the possibility of pseudo replication, subjects were marked with hair dye (Garnier Nutrisse Crème 01 Liquorice) or vet spray on the tail and body. Naturally distinctive body markings were considered when individuals could not be marked.

2.2. Individual attributes

Three attributes were considered for all individuals: age, sex, and status. Age was taken from the taxon reports coming from each Zoological park. Individuals were assigned an age class: infants 0–3 months, juveniles: 3–12 months and adults over 12 months (Clutton-Brock et al., 1998). Most individuals' sex was known via the taxon report. For those with no information provided, sex was determined by observing their external genitalia. Status (dominant and subordinate position) was defined by observations of dominance interactions within the group. Dominant individuals were identified when they asserted their dominance in a higher rate than others individuals over other group members with behaviours such as: chin marking, chasing, charging, hip-slaming, and biting (Madden et al., 2011). Subordinate individuals were identified when responding to these behaviours and/or the mere presence of a dominant, by adopting postures such as crouching, grovelling and rolling over onto their backs, as seen in the wild (Kutsukake and Clutton-Brock, 2008). It is important to highlight that while subordinate females are aggressive to each other, such behaviours occur at much lower rates than in dominants. The mass of individuals was not considered as the present study was aimed at being as non-invasive as possible.

Table 1
Description of the attributes of the fifteen groups and their number of interactions observed in the group.

Group/Location	Num. of indiv.	Number of females	Number of males	Min age	Max age	Grooming interactions	Foraging competitions	Dominance interactions
Africam Safari/Mexico	13	4	9	5	10	268	308	107
Bristol Zoo/UK	13	3	10	0.5	7	272	64	19
Cotswold Wildlife Park/UK	10	5	5	0.3	6	220	101	144
Flamingo Park (G1)/UK	8	5	3	1	12	125	137	37
Flamingo Park(G2)/UK	5	2	3	4	6	537	183	44
Longleat Safari Park/UK	14	9	5	0.7	8.8	420	263	171
Morelia Zoo (G1)/Mexico	5	2	3	1	3	362	58	24
Morelia Zoo (G2)/Mexico	3	2	1	2	3	187	13	18
Paignton Zoo/UK	3	1	2	0.4	7.5	11	16	8
Paradise Wildlife Park (G1)/UK	4	3	1	2	5	36	15	19
Paradise Wildlife Park (G2)/UK	5	2	3	0.6	6	154	53	12
Shaldon Wildlife Trust/UK	7	4	3	2	5	509	45	1
Shepreth Park/UK	5	3	2	5	10	138	2	75
Twycross Zoo/UK	12	6	6	0.7	10	136	14	27
West Midland Safari Park/UK	6	3	3	0.8	7	189	81	66

2.3. Behavioural and network measures

Social interaction data, based on behavioural exchanges between pairs of individuals, were collected during scan sampling observations. We replicated the methods of Madden et al., 2009, 2011 and recorded allogrooming interactions, dominance interactions and foraging competitions. A grooming interaction was recorded when two or more individuals groomed each other, and all these interactions were recorded as directed network relations. How long the individuals groomed or how many times the meerkats exchanged back and forth between partners was not considered. When grooming was separated by intervals of more than 1 min, a new grooming interaction was defined (Madden and Clutton-Brock, 2009). A dominance interaction was recorded when an individual acted dominant over another individual and when the interaction was not caused by food, access to foraging holes, or social foraging partners. Dominant events included any individual attacking or intimidating other individuals competing and/or fighting for dominance. A foraging competition was recorded when an individual approached food or a hole owner, provoking an action of defence by the original property owner. Meerkats foraging in holes, especially for large prey, may be displaced by competitors. Actions such as growling vocalisations, moving the body against the competitor, pushing their body/slamming their hip against the competitor, biting and /or charging at the other individual were included. Interactions were weighted by considering the total number of occurrences recorded. Interactions were directed, with the initiator and recipient of each grooming, dominance or foraging event being noted. Some network measures cannot be reliably calculated using weighted data, so we converted weighted to unweighted data by considering any interaction between two individuals to constitute an edge with value of 1.

We recorded a total of 5,689 social interactions (grooming: 3,564, dominance: 772, foraging competitions: 1,353) from fifteen captive groups (113 individuals: 54 females, 59 males; Table 1). Madden et al.

(2009, 2011) recorded a total of 2093 allogrooming events, 333 dominance interactions, and 375 foraging competitions (Table 2). To compare network structures, we collected the same 10 network measures and conducted analytical methods identical to those described in Madden et al. (2009, 2011) to allow us to compare the findings of captive meerkats with those of wild meerkats. Measures of degree (indegree, outdegree) centrality (unweighted and weighted data), distance (average path length and compactness), density, cluster coefficient (unweighted data), closeness centrality and betweenness centrality were calculated for the three different interaction types. Degree centrality can be described as *weighted* and *unweighted* relationships in which the former is a description of total strength of interactions that an individual is involved with, and the latter is a description of the number of other individuals that an individual interacts with (Madden et al., 2011). Two measures of distance were calculated: the average distance between pairs of individuals within a network (L, average path length) and the direct connection of the individuals in the network (compactness). A high L score indicates that the interaction between individuals is indirect, a high compactness score indicates the opposite, the interaction between individuals is direct (Madden et al., 2009). The density (D) of a network is the proportion of all possible dyadic connections that are actually present in a population (Hanneman and Riddle, 2005). Clustering coefficient (C) is a measure of the cliquishness of a network and describes the solidity of interactions among the associates of a focal individual (Madden et al., 2011). Closeness centrality describes how influential an individual is on other group members by being able to reach them via shorter path lengths (Hanneman and Riddle, 2005). Betweenness centrality is the measure of how much control an individual would have over the flow of an element across the network and describes the number of shorter paths between pairs of individuals within the social network (Whitehead, 2008). To explore how individuals differed in their network position according to their attributes, we used degree centrality, cluster coefficient, betweenness and

Table 2
Description of the attributes of the eight wild groups and their number of interactions observed in the group.

Group	Num. of indiv.	Number of females	Number of males	Min age	Max age	Grooming interactions	Foraging competitions	Dominance interactions
Commandos	14	4	10	0.5	3.6	258	66	54
Drie	12	5	7	0.3	3.5	232	34	44
Elveera	15	8	7	0.3	4.3	144	112	37
Frisky	10	6	4	0.6	2.6	86	26	16
Lazuli	24	11	13	0.3	3.5	365	59	53
Moomins	23	10	13	1.0	7.7	258	28	43
Rascals	19	5	14	0.8	4.6	517	45	67
Young Ones	9	4	5	1.1	8.2	233	5	19

closeness.

2.4. Analytical methods

Network measures were calculated using functions in UCINET 6 for Windows (Borgatti et al., 2002). Weighted and unweighted data were employed to calculate degree centrality and closeness. Betweenness, distance, density and clustering coefficients were calculated using unweighted interactions only. Non-random associations probabilities between individuals based on their sex and status were calculated based on unweighted interaction data, using 10,000 permutations. To visualize the overall social network for each group and their specific links connecting each individual with other individuals, we used the spring-embedding function in NetDraw (Borgatti et al., 2002).

We conducted hypothesis testing accounting for the non-independence of network data by using permutation tests. The probabilities of differences in network measures occurring between types of individuals (differing in sex, status and age) were calculated using permuted t-tests (dialog: tools > testing hypothesis > node-level > T-test) and based on 10,000 permutations. We calculated attribute-based differences in network positions for each group individually, then combined them using Fisher’s method to calculate an overall level of significance. If a variation was present in the relationship (between network measures and individual attributes) direction between groups, the strongest total relationship was calculated. For groups with a negative relationship, the sign of their natural log-transformed *P* value was reversed, subtracting then their contribution from the combined X^2 statistic and, finally, the final combined *P* value was calculated (for further information see: Madden and Clutton-Brock, 2009; Madden et al., 2011). Node-based randomizations (generated in UCINET), which re-distribute the node attributes in the network (Whitehead, 2008), rely on the assumption that the observed network is a solid representation of the exact network (Croft et al., 2011). We did not apply any corrections for these multiple tests when considering just captive groups because we are presenting descriptive statistics rather than testing hypothesis. Consequently, any significant results observed in single groups should be treated with caution but could form the basis for further targeted testing.

Network measures (centrality, distance, compactness, density and clustering coefficient) within the three network types of wild and captive groups were compared using linear mixed models. We adjusted the values with Bonferroni for multiple comparisons to reduce the risk of type I errors as an effect of performing multiple tests and a binomial error as structure to account for the proportional nature of the data. We used the mean value of each zoo to prevent a strong influence from the larger groups of meerkats, and we used group as a random effect. We chose the larger captive groups and reduced the number of groups to 8 (the same number of wild groups) in order to do the comparisons. All analyses were conducted in SPSS v24.

2.5. Ethics statement

The study was reviewed and approved by research committees at each participating zoo and park, and was supported by the British and Irish Association of Zoos and Aquariums (BIAZA) Research Group. The study was non-invasive.

3. Results

3.1. Comparison of interaction networks between captive and wild groups of meerkats

The interaction networks of meerkats observed in the wild differed to some degree from those observed in captivity in the three different types of interactions (Fig. 1, Table 3).

Wild meerkats, had longer average path length than captive meerkats within dominance ($F = 24.95, df = 14, p < 0.001$) and foraging competition networks ($F = 9.75, p < 0.007$), which can be for the reason that the wild groups were larger than the captive ones. Similarly, wild meerkats presented a higher saturated network than captive meerkats in dominance ($F = 7.16, p < 0.018$) and foraging competition networks ($F = 5.73, p < 0.031$), representing a greater interaction of wild individuals with the majority of all other members of the group than captive individuals.

Captive groups of meerkats exhibited higher centralization in foraging competitions. The outdegree centrality total, was higher in

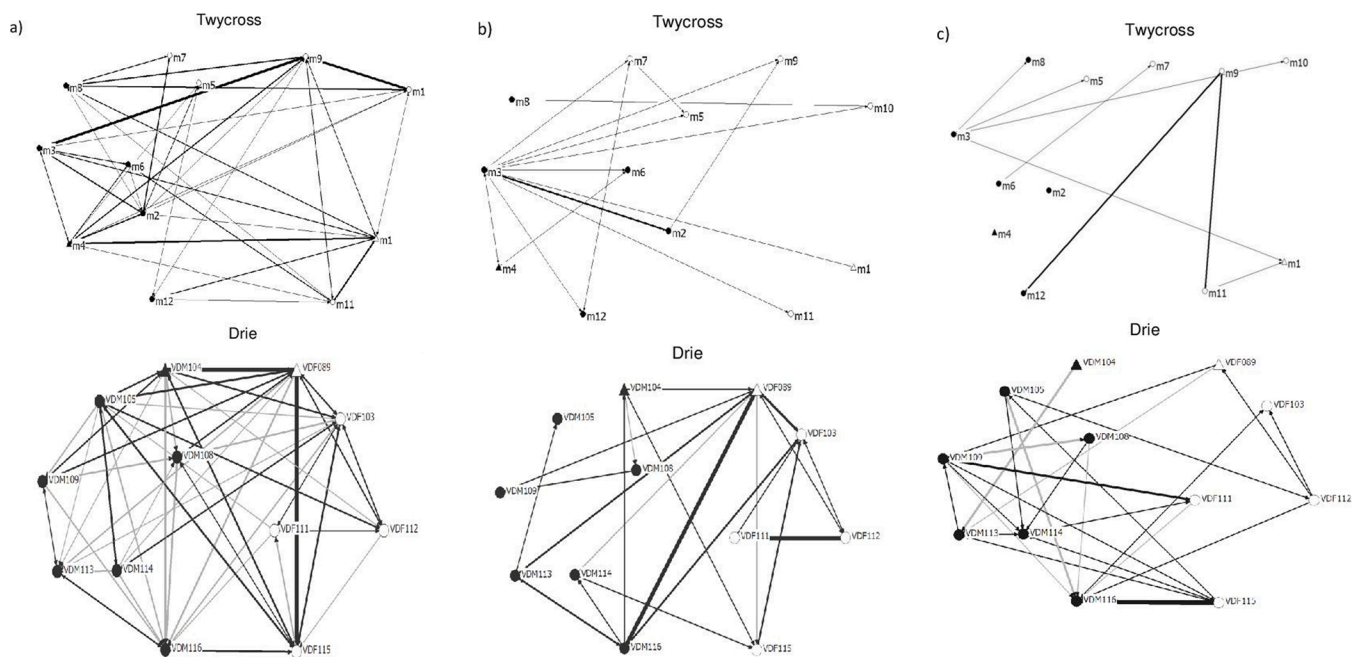


Fig. 1. Examples of networks from a representative captive and wild group, including grooming (a), dominance (b) and foraging competitions (c) networks. For each network: triangles = dominants, circles = subordinates, white = females, black = males, individuals are approximately arranged in age, with older individuals at the top and younger individuals lower down the diagram, stronger ties are indicated by thicker lines. FlamingoG1=captive group, Drie = wild group.

Table 3

Comparison of the interaction patterns for meerkat groups in captivity and in the wild based on grooming, dominance interactions and foraging competitions. Significant differences are indicated in bold type.

	Median wild	Median captive	F	p
GROOMING				
Network Centrality				
<i>Unweighted data</i>				
Outdegree	28.30	29.42	0.017	0.897
Indegree	26.33	25.98	0.004	0.949
<i>Weighted data</i>				
Outdegree	15.67	16.52	0.089	0.770
Indegree	12.81	16.19	2.252	0.156
Distance				
L	1.677	1.568	0.396	0.539
Compactness	0.701	0.680	0.060	0.809
Density				
D	0.461	0.535	0.377	0.549
Cluster Coefficient				
C	0.517	0.597	0.498	0.492
DOMINANCE				
Network Centrality				
<i>Unweighted data</i>				
Outdegree	32.24	39.34	0.482	0.499
Indegree	24.18	18.32	1.133	0.305
<i>Weighted data</i>				
Outdegree	14.53	23.55	3.489	0.083
Indegree	10.52	13.38	0.889	0.362
Distance				
L	2.643	1.288	24.95	0.000
Compactness	0.257	0.225	0.115	0.739
Density				
D	0.461	0.176	7.160	0.018
Cluster Coefficient				
C	0.176	0.275	1.022	0.329
FORAGING COMPETITION				
Network Centrality				
<i>Unweighted data</i>				
Outdegree	21.67	34.00	5.819	0.030
Indegree	34.66	28.39	0.421	0.527
<i>Weighted data</i>				
Outdegree	11.13	22.57	7.009	0.019
Indegree	16.73	16.84	0.001	0.981
Distance				
L	2.310	1.573	9.752	0.007
Compactness	0.315	0.497	2.301	0.152
Density				
D	0.152	0.376	5.734	0.031
Cluster Coefficient				
C	0.242	0.507	5.041	0.041

captive meerkats than wild ones ($F = 5.81$, $p < 0.030$ unweighted; $F = 7.0$, $p < 0.019$ weighted), indicating that the formers had a more centralised network of initiating foraging competitions than receiving, specifically, the interaction rate of foraging competitions was more frequently targeted to certain individuals in captive meerkats. A higher clustering coefficient in foraging competitions was shown in captive meerkats in comparison to wild meerkats ($F = 5.04$, $p < 0.041$) this suggests that captive individuals had a tighter social network where individuals competed in foraging with most (if not all) of their social neighbours.

3.2. Comparison of network positions between captive and wild groups of meerkats with specific attributes (sex and status)

An individual's position within a grooming network differed between captive and wild groups, with captive individuals having higher centrality ($F = 5.81$, $df = 14$, $p < 0.030$; Table 4. The attribute of age was excluded due to the small number of individuals' score in the social network) and higher betweenness scores ($F = 4.64$, $p < 0.049$) in the sex attribute, than wild individuals. In captive groups, males were more

central to networks of grooming than females. Meanwhile, within status attribute, wild individuals obtained higher scores in centrality ($F = 16.80$, $p < 0.001$) and closeness ($F = 6.34$, $p = 0.025$) than captive individuals.

An individual's position within the network of dominance differed between the two conditions, within status attribute, in degree centrality ($F = 8.49$, $p < 0.011$) and betweenness ($F = 6.85$, $p < 0.020$) measures. Dominants in captive groups of meerkats had a higher indegree centrality in the network than in wild groups. That is, subordinate individuals within captive groups received higher total amounts of dominance than subordinate individuals within wild groups. Captive meerkats had a higher betweenness than wild meerkats; this suggests that captive dominant individuals were more central and consequently more important for controlling social connections within the group by dominance interactions.

An individual's position within the network of foraging competitions differed between the two conditions in degree centrality measure ($F = 5.06$, $df = 13$, $p < 0.042$), where wild meerkats showed a higher outdegree than captive meerkats. This indicates that females in wild groups initiated higher rates of foraging competitions than in wild groups.

3.3. Comparison of association assortment between captive and wild groups of meerkats

Sex and dominance-based association in grooming networks was stronger in captive groups than in wild groups, with males associating with other males more strongly in captive groups than in wild groups of meerkats ($F = 5.90$, $df = 14$, $p < 0.029$; Table 5). Dominant individuals in captive groups associated more than expected with other dominant and subordinate individuals than in the wild ones ($F = 5.54$, $p < 0.034$, $F = 11.22$, $p < 0.005$ respectively) during grooming.

A similar pattern was seen in dominance relationships where association between male individuals was predominantly found in captive groups than in wild groups ($F = 6.63$, $p < 0.022$). Dominant-subordinate associations were also stronger in captive groups than in wild ones ($F = 10.81$, $p < 0.005$).

In networks of foraging competitions, assortment by sex was stronger in captive groups than wild groups. An individual's association in foraging competitions was more significant between male and female meerkats ($F = 13.32$, $df = 13$, $p < 0.003$).

4. Discussion

Groups of wild and captive meerkats differed in their overall network structures in the positions that individuals occupied within them and in the patterns of associations between individuals with particular attributes. These differences were inconsistent across three common forms of social interactions: grooming and dominance interactions, and foraging competitions. Some of these differences are likely due to the differences in sizes between wild and captive groups. However, other differences may arise because of the housing and/or husbandry of the captive meerkats.

4.1. Group network structure based on individual interactions

Captive meerkats had a more highly skewed grooming distribution with a small number of individuals being recipients to a large number of grooming interactions; in contrast the distribution of grooming events within the wild groups was more egalitarian. The differences between the two conditions, wild and captive, were minimum and non-significant within the network of grooming. In spite of captive groups being smaller than the wild ones, it was not evident that small groups necessarily needed to be less egalitarian and more centralised when grooming. The captive groups that we selected for this project comprised 6–14 individuals (mean = 10.3) whereas the wild groups studied by Madden et al. (2009; 2011) comprised 9–24 individuals

Table 4

Comparison of the network positions of individuals in captive and wild groups, with specific attributes (sex and status) based on grooming, dominance interactions and foraging competitions. Significant differences are indicated in bold type. K degree centrality is based on weighted data and Kbin degree centrality is based on un-weighted data.

	Median wild	Form of difference	Median captive	Form of difference	F	p	Median wild	Form of difference	Median captive	Form of difference	F	p
Grooming												
	Sex						Status					
K-out	0.32	M > F	0.65	F > M	5.816	0.030	0.40	D > S	0.25	D > S	0.838	0.375
K-in	0.41	M > F	0.48	M > F	0.378	0.549	0.48	D > S	0.36	D > S	0.490	0.495
Kbin-out	0.32	M > F	0.36	M > F	0.077	0.786	0.49	D > S	0.31	D > S	1.134	0.305
Kbin-in	0.62	M > F	0.43	F > M	2.377	0.145	0.84	D > S	0.39	D > S	16.807	0.001
Betweenness	0.30	M > F	0.63	F > M	4.649	0.049	0.64	D > S	0.39	D > S	2.267	0.154
Closeness-out	0.33	M > F	0.46	M > F	0.508	0.488	0.45	D > S	0.40	D > S	0.085	0.775
Closeness-in	0.57	M > F	0.49	M > F	0.325	0.578	0.73	D > S	0.40	D > S	6.342	0.025
Cluster	0.35	F > M	0.58	M > F	1.917	0.188	0.53	S > D	0.30	S > D	2.751	0.119
Dominance												
K-out	0.52	M > F	0.51	F > M	0.002	0.968	0.14	D > S	0.43	D > S	2.882	0.112
K-in	0.64	M > F	0.61	M > F	0.020	0.890	0.34	D > S	0.77	D > S	8.497	0.011
Kbin-out	0.51	M > F	0.51	F > M	0.003	0.955	0.31	D > S	0.30	D > S	3.188	0.096
Kbin-in	0.63	M > F	0.58	M > F	0.083	0.778	0.48	D > S	0.53	S > D	0.107	0.749
Betweenness	0.43	M > F	0.58	F > M	0.629	0.441	0.33	D > S	0.75	S > D	6.853	0.020
Closeness-out	0.45	F > M	0.52	F > M	0.277	0.607	0.34	D > S	0.28	D > S	0.144	0.710
Closeness-in	0.51	M > F	0.38	F > M	0.610	0.448	0.80	S > D	0.47	S > D	4.239	0.059
Cluster	0.38	F > M	0.43	F > M	0.075	0.789	-	-	-	-	-	-
Foraging competition												
K-out	0.75	F > M	0.47	F > M	5.061	0.042	0.44	D > S	0.57	S > D	0.529	0.480
K-in	0.48	F > M	0.48	F > M	0.000	1.0	0.53	S > D	0.50	S > D	0.059	0.812
Kbin-out	0.61	F > M	0.39	F > M	2.061	0.175	0.56	D > S	0.49	S > D	0.174	0.684
Kbin-in	0.49	F > M	0.53	F > M	0.061	0.809	0.55	S > D	0.54	D > S	0.003	0.959
Betweenness	0.46	F > M	0.45	F > M	0.003	0.956	0.48	S > D	0.61	D > S	0.649	0.435
Closeness-out	0.55	M > F	0.57	M > F	0.017	0.900	0.50	D > S	0.59	S > D	0.364	0.557
Closeness-in	0.36	F > M	0.43	M > F	0.155	0.700	0.41	S > D	0.38	S > D	0.035	0.855
Cluster	0.25	M > F	0.25	M > F	0.001	0.975	0.16	D > S	0.42	S > D	1.342	0.276

Table 5

Comparison of the association patterns for meerkat groups in captivity and in the wild varying in two attributes (sex and status) based on grooming, dominance interactions and foraging competitions.

	Median wild	Median captive	F	p
Grooming				
Sex				
FF	0.710	0.964	3.776	0.072
MF	0.498	0.788	3.553	0.080
MM	0.455	0.806	5.905	0.029
Status				
DD	0.560	0.836	5.541	0.034
DS	0.595	0.941	11.25	0.005
SS	0.595	0.804	4.036	0.064
Dominance				
Sex				
FF	0.403	0.750	3.972	0.066
MF	0.857	0.748	0.925	0.353
MM	0.386	0.817	6.635	0.022
Status				
DD	0.315	0.647	3.802	0.072
DS	0.137	0.654	10.81	0.005
SS	0.958	0.942	0.126	0.728
Foraging Competition				
Sex				
FF	0.634	0.789	1.074	0.319
MF	0.512	0.887	13.32	0.003
MM	0.500	0.733	3.220	0.096
Status				
DD	0.710	0.955	2.966	0.109
DS	0.614	0.666	0.080	0.782
SS	0.493	0.768	2.580	0.132

(mean = 16.5). Groups with fewer individuals have been recognised to be more cohesive than groups with a large number of individuals (Lehman et al., 2007; Herbert-Read et al., 2013). Even though the number of potential interactions with group members increases as the group size increase, individuals may choose to interact with a subset of others instead of trying to interact with all their group mates (Drew et al., 2011). Clearly, group size alone cannot explain these differences in network structure between the two conditions, while intrinsic factors likely shape a network structure extrinsic factors have an important role as well (Grand and Dill, 1999). For instance, in a study investigating the effects of enclosure on the behaviour of captive coyotes (Brummer et al., 2010), grooming was found to increase in spatially restricted environments. In other studies (e.g. on marmosets, *Callithrix jacchus jacchus*; Kitchen and Martin, 1996), it was observed that an increase of allogrooming occurred after a decrease of stress due to the enrichment with the enclosure. Thus, perhaps because meerkats are inclined to repeatedly groom particular members of the group in order to gain tolerance in critical circumstances, a quite diffuse network may be perceived in a more relaxed environment; that is, in a spacious, multifaceted and sheltered environment. Furthermore, if a better environment helps reduce their stress levels, the extra energy may be used to distribute quota of grooming across all members of the group. In captive meerkats, circumstances such as the invasion of extra group males are not possible, unlike in the wild, but individuals may still opt for exchanging grooming interactions due to the benefits that valuable relationships may bring. Meerkats in captivity still face an intense intrasexual conflict and may interact in frequent grooming relationships since it is a technique to reduce beta-endorphin concentrations, which reduce stress (Keverne et al., 1989). Grooming interactions in different animal species have been reported to contribute to positive reactions, improving their

welfare, and that specific companions can also buffer stress factors and have the same positive result (Buchanan-Smith et al., 2013).

There was a significant difference between wild and captive groups in the overall rate of dominance events in density and distance, with wild meerkats having higher rates than captive meerkats. This suggests that captive individuals had more indirect dominant interactions with few individuals, which can be explained by active avoidance of any aggressive or dominant behaviour. A higher rate of competition in foraging was observed in captive groups than in the wild groups of meerkats. As expected, average path length was higher within wild groups than within the captive groups, higher clustering coefficients were shown in captive groups. In captivity, where food is continually available, individuals may compete less during foraging than their wild counterparts. However, individuals in confinement usually have fewer alternative individuals to target and, therefore, individuals can have a more direct foraging competition interactions with other individuals. Competition for food plays a fundamental role in the social organization of group-living animals in which individual foraging success is, to a certain extent, regulated by dominance relationships (Barton and Whiten, 1993). Zoo-housed bonobos have demonstrated higher levels of aggressive reactions to food and strong dominance hierarchies (Jaeggi et al., 2010). Our results and other research with similar results may imply that additional internal factors, like individual behaviour, and external factors, such as zoo management and complexity of enclosure (Price and Stoinski, 2007), may distort dominance interactions (McCowan et al., 2008) and general group social structure (Schulte, 2000).

4.2. Network positions of individuals with similar attributes

Individual positions in grooming networks of meerkats differed between the two conditions, according to sex and status attributes, with captive females initiating higher rates of grooming than males. In addition, captive subordinates received less amount of grooming than wild subordinates, and captive males played a more important role than females in maintaining the cohesion of the group through grooming.

Individual positions in dominance networks of captive meerkats differed mainly according to status attributes with dominant meerkats being central within such networks. Status drove similar patterns of outdegree scores in dominance networks in a similar manner to that seen in wild groups, where dominance interactions were mainly hierarchical between dominant and subordinate individuals (Madden et al., 2011). However, captive subordinates show a higher amount of dominance from dominant individuals. This finding maybe due to the restricted living area and the comparatively small group size of captive meerkats which likely forces individuals into more frequent interactions than occur in the wild. Females in captive groups initiated more foraging competitions than in wild groups. Similar conditions are observed in females in the wild (Jordan, 2007). However, in a captive environment, where territories are practically restricted by space, competition for food can be higher in order to divide the available food patches and maximize their own foraging efficiency (Gibeault and MacDonald, 2000); therefore, female meerkats may fight more for resources.

4.3. Assortative association of individuals

There was no general consistency as to how a subject's sex or status predicted how they associated with others across the fifteen captive groups in the interaction networks of grooming, dominance and foraging competitions. We found no evidence that, across captive groups, individuals disproportionately avoided or interacted with each other according to their sex, status or age. This contrasted with individual network patterns of association in groups of wild meerkats in which grooming networks were based on age (see Madden et al., 2011). Our captive groups were housed in a number of differing compositions; some were formed of purely siblings plus a dominant breeding female, others comprised a mix of related/unrelated individuals of

approximately the same age and no dominant pair. Wild meerkat groups on the other hand are relatively stable group compositions that consist of a typical pair of dominant adults, numerous subordinate adults, juveniles and pups of both sexes (Clutton-Brock et al., 2002). In captivity, populations require human intervention to optimize their genetic management and maximize their chances of survival (Spielman and Frankham, 1992), as well as to avoid aggression/injuries between members of a group (Hinton et al., 2013) or prevent overcrowding (Plowman et al., 2005). The constant removal and introduction of individuals could alter long-term/close individual relationships and consequently the network pattern of grooming associations in groups. A combination of these variations in group formations and the management of captive individuals may be an explanation of why there was, in general, very low assortativity in grooming interactions in the three attributes across the captive groups, compared with patterns of assortativity (individuals that are more likely to interact with others similar to themselves; Whitehead, 2008) reported in groups in the wild. Concerning the results of wild-captive comparison patterns of associations during grooming, males, dominants, and dominant-subordinate individuals showed a higher tendency of association in captive individuals.

There were no clear general patterns of association in dominance based on sex, status or age in the captive groups in contrast to the patterns observed in wild groups (Madden et al., 2011). Similarly, there were no general association patterns in foraging competitions, corresponding with the results of wild meerkat groups. Wild meerkats forage cohesively but with a high level of competition for food (Doolan and Macdonald, 1997). Nevertheless, the combination of individual attributes and social and environmental circumstances seems to trigger unpredictable associations in foraging competitions between the different members of the captive groups. Furthermore, individuals may occasionally forego foraging benefits in order to avoid the costs of being isolated from the group since group cohesion is vital for species like meerkats (Bousquet and Manser, 2011); this may consequently reduce levels of competition in foraging between specific individuals. Within the wild versus captive condition, a clearer pattern of association in captivity between individuals with different ranks (in dominance) and dissimilar sex (in foraging competition) was shown. That is, conflict, in captivity, appears to be especially strong between subordinates and dominants individuals in dominance interactions, and between males and females when competing for food. As mentioned before, competition for food resources is a crucial factor in shaping the structure of groups (Jeglinski et al., 2013) and the extent of competition varies with the abilities of the foragers, the context and the distribution in time and space of resources (Ward et al., 2006). Meerkats are known to have a stable hierarchy and dominant interactions are not exclusive of the dominant pair (Madden and Clutton-Brock, 2009). Such dominant display can occur when near a burrow entrance, when approaching preferred individuals (such as helpers), or when disputing for food. In a captive setting where food can be obtained from visitors (which frequently happened during the observations) due to inadequate barriers, animals can exhibit more dominance assertions when contesting for the immediate benefit.

In conclusion, the social network structure of captive meerkats measured for three separate sets of interactions (grooming, dominance, foraging competitions) generally differed from that of meerkats in the wild. This work does not generalize the results beyond the particular groups of meerkats studied here. Nonetheless, the results show how the social interaction of captive meerkats may vary from their wild counterparts and that such variation in the degree to which members of the group interact with one another could be due social and non-social factors. Particularly, the current results suggest that a meerkat social network in captive conditions can be less consistent than in their wild environment in the way they associate with one another, and in the manner they occupy particular positions in the network. Animals in a captive environment, where factors such as predation protection,

availability of food and shelter are already met, may perceive the benefits to be gained from interacting and/or associating with specific group members differently and consequently the social network structure may diverge from their counterparts in the wild. Further work on how different social networks are represented by multiple forms of social connections in dissimilar settings can provide valuable insights on the nature of animal interaction dynamics. Practically, this can serve as an indication that animals in captivity may be behaving in ways subtly different from those of their wild conspecifics, which could prompt efforts to improve housing and husbandry in order to better match the natural social behaviour of a group-living animal.

ORCID iD authorship contribution statement

Xareni P. Pacheco: Conceptualization, Investigation, Methodology,

Appendix A

Classification and description of the enclosure types and management.

	Description
a) Enclosure size	1=small (15 m ² –40 m ²) 2=medium (41 m ² –75 m ²) 3=large (76 m ² –160 m ²) 4= very large (161 m ² –240 m ²)
e) Enclosure complexity	1=low: only concrete, walls, sand, branches, trunks 2=medium: concrete, sand, vegetation and basic furniture like tree branches/tree trunks and rocks 3=high: concrete, sand, vegetation, trees, basic and complex (natural or unnatural) furniture structures (multiple den sites and, rocks, trunks, hills)
h) Enclosure barrier type	1=inadequate: no barrier or good protection measure from public, where animals can be easily disturbed and even get food by visitors 2=acceptable: good protection measure from public but still with possibilities of some disturbance 3=good: very suitable barrier made from transparent material where visitors can appreciate with clarity the animals and the animals can be protected from any disturbance by humans
k) Enclosure shelter type	1 = none 2=available: appropriate for only few individuals 3=available and suitable for all group members with more than one entrance.
n) Environmental enrichment	1 = none 2=occasionally: any type of enrichment such as feeding devices, scattered food, novel objects and sensory stimuli no more than twice a month 3=frequent: same type of enrichment as above but provided at least every three days a week.
q) Human contact	Includes contact by animal caretakers and visitors 1=minor: contact by animal caretakers for habitual husbandry such as enclosure cleaning, change of enclosure furnishing, medical procedures. 2=regular: contact by animal caretakers as above, plus regular petting by caretakers 3=frequent: contact by animal caretakers as above, plus contact by visitors (feeding and petting)

Appendix B. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2021.104446>.

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