



How consistently do personality attributes relate to an individual's position within a social network: a comparison across groups of captive meerkats

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Abstract

The social network structure of a group arises from the patterns of association of its constituent members, which in turn originates from behaviors and preferences of those individuals. Consequently, an individual's position in their social environment is commonly related to their own attributes. However, most studies that report such relationships are limited to single or very small numbers of groups. I consider one set of attributes suggested to influence network structure, namely personality type, and observed 15 groups of captive meerkats *Suricata suricatta*. Thus, I could assess whether the relationship between individual attributes and patterns of association and network position persisted across groups. Principal component analysis of behavior, within the 15 groups, revealed two personality dimensions: friendliness and aggressiveness. For a subset of five groups, only friendliness was consistent over 1 year. I found little evidence that they were universally good predictors of social network structure or individual positions within networks. Individuals with high friendliness scores were more central in networks of foraging competitions. There was no evidence that meerkats preferentially associated with or avoid others based on each of their personality scores. Alternatively, and contrary to much-published work, it may not be possible to generalize relationships between individual attributes and network position or overall network structure. This may be because social environments emerge from a complex interplay between individual attributes and social interactions, and thus, the role of these elements along with the physical environment in which they live in shaping network structures and personality is challenging to disentangle.

Significance statement

Animal personalities and animal social network structures are increasingly recognized as significant components in animal behavior and welfare. Here, I explore personality in the context of social networks in different captive groups of meerkats. These types of studies are uncommon probably because collecting detailed interaction data from multiple known individuals in multiple groups is time-consuming and because groups are often highly variable in composition and ecological context. When I did consider the social networks and individual attributes of members of 15 groups, I found little evidence that an individual's personality scores consistently explained either their network position or patterns of association across all groups. Individuals in the wild, with different personality profiles, may adjust their network assortment to balance their costs and benefits and shift their environmental pressures. In a captive environment, such characteristics can vary and therefore social associations may be expressed differently from their wild counterparts.

Keywords Personality · Social network analysis · Captivity · Management · Behavior

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Introduction

An individual's position within their social environment may be best described by their patterns of relationships with others and quantified using metrics that emerge from the social network in that group (Krause et al. 2007; Wilson et al. 2013). This network, and consequently the position of an individual within it, may emerge from the individual preferences for association or avoidance exhibited by its constituent members (Weinstein and Capitanio 2008; Firth et al. 2018; Harten et al. 2018). These preferences are expected to be related to other attributes of the individual, such as the individual personality. In general, two main terms are used in the literature of animal personality: one "temperament," which is defined as a tendency to react to stressful stimuli that can be identified in early infancy (Weinstein et al. 2008) and two, "behavioral syndromes" which refers to suites of correlated behaviors across different contexts (Sih et al. 2004; Bell 2007). The terminologies of "trait" and "dimension" are also used interchangeably with personality and behavioral terms. A personality/behavioral trait refers to specific traits of individuals that are consistent throughout time and environmental conditions (Réale and Dingemanse 2010) and personality/behavioral dimensions can describe multiple correlation traits across species (Eckardt et al. 2014). Henceforth, I will use the term of personality (which is commonly used in both humans and animals) to refer to behavioral syndromes and temperament and will use the terminologies personality trait and personality dimension according to their definition.

Researchers often report that the attributes of an individual predict or relate to that individual's position within a social network (Pike et al. 2008; Croft et al. 2009; Krause et al. 2010). For instance, a study investigating whether individual differences in exploration behavior of great tits, *Parus major*, can be related to social network position (Snijders et al. 2014) found that slower exploring males had less central social network positions; in other words, slower males had the fewest unique contacts. Social network position has also been related to the survival probability in killer whales where male individuals well connected to others (high social centrality) have a significantly lower mortality risk (Ellis et al. 2017). Moreover, social association in animal groups may be driven by the behavioral type of individuals (Wilson and Krause 2015). For instance, a study on three-spined sticklebacks, *Gasterosteus aculeatus* (Pike et al. 2008) tested how personality between individuals, specifically bold and shy, affected the frequency and distribution of their interactions within a network. They found that networks constituted of entirely shy individuals tended to form long-lasting associations with one or two other individuals, resulting in highly non-uniform interaction distribution. In contrast, networks comprising bold individuals were characterized by low interaction frequency and uniform distribution. Croft et al. (2009) demonstrated that wild

guppies, *Poecilia reticulata*, of similar attributes (behavioral trait of predator inspection) were more likely to be associated across strong network ties. A more recent study on social networks in great tits, *Parus major* (Johnson et al. 2017), investigated whether exploratory personality trait is related to the social structure of a wild great tit population during the breeding season. Their findings showed that males were positively assorted by behavioral phenotype and were more likely to breed closer to other males of similar personality. Certainly, there is a growing body of evidence about how social interactions and social positions in a network have a strong influence on the development of group members' behavioral traits (Hunt et al. 2018).

With the exception of studies of fish (e.g., Croft et al. 2005; Dey et al. 2013; Gaffney and Webster 2018), relationships between individual attributes and network position are typically based on observations of a single or small number of groups or populations (but see McCowan et al. 2008; Madden et al. 2009; Dey and Quinn 2014). Replication at the group level enables researchers to make statistical inferences by comparing network measures between contexts (Croft et al. 2008). An alternative approach has been to look for consistency in these relationships between individual attributes and network positions within a group across multiple time periods. However, results from such studies are mixed (e.g., Jacoby et al. 2014; Blaszczyk 2018; Smith et al. 2018). For instance, in wild vervet monkeys, *Chlorocebus pygerrhus*, specific social network positions were repeatable in diverse environmental conditions in mixed sex and males only samples, and some other positions were not at all consistent regardless of the individuals' sex (Blaszczyk 2018). Conversely, in Californian ground squirrels, *Otospermophilus beecheyi*, network positions of individuals were generally consistent across years and between ecological contexts (Smith et al. 2018). In meerkats *Suricata suricatta*, networks based on grooming and foraging competitions varied according to the duration of tenure of the dominant female and the level of ectoparasite infestation (Madden et al. 2009). This makes it hard to be confident that such relationships are general properties of that species/system or instead are merely spurious associations that arise by chance or because of circumstances specific to the particular group of study. Such confidence in the general applicability of the relationship is necessary if we are to understand how social networks emerge from the composition of their constituent members, if we want to predict how perturbation of the group composition or broader environment may alter network structure, or if we wish to understand how selection may act on individuals mediated by their network position.

I asked whether there was a consistent relationship between an individual's attributes, specifically a measure of their personality, and their patterns of association and/or position within a social network. To achieve this, I used a model system,

meerkats, which naturally show non-random patterns of association that elicit network structures that may be based on grooming, dominance, or foraging competition interactions (Madden et al. 2009, 2011). The structure of these networks and the position of an individual within them have fitness consequences in terms of susceptibility to disease spread (Drewe 2009). Meerkats are characterized as being highly social and cooperative mongooses that live in groups of up to fifty individuals, with a dominant female and male being the primary reproducers (Griffin et al. 2003; Carlson et al. 2004; Clutton-Brock et al. 2008). Individuals exhibit consistent individual differences in cooperative behavior (English et al. 2010; Carter et al. 2014), indicating that they might be classed as possessing distinct personality types. I use the term personality in this study to refer to an immediate variable that summarizes several other, related, behaviors. I used principal component analysis to reduce the dimensionality of the data set and to look for correlations among variables and new uncorrelated component variables (Carere et al. 2015). This method consolidates the behavioral traits obtained into broader dimensions or factors that can be used quantitatively to compare individuals, populations, and even species (Watters and Powell 2011). The social structure of wild meerkat groups and individuals' positions within it is susceptible to environmental and life history factors (Madden et al. 2009, 2011) including the tenure of the dominant female, the level of ectoparasitism, and the size of the group. I attempted to reduce this variation so that I could better understand the fundamental relationship between personality and social position. Consistent individual variation in behavior and the social dynamic of individuals are progressively acknowledged for their influence on the social group success (Sih 2013), yet the implications are not fully understood. Particular individuals exhibiting a behavioral phenotype can have a large effect on the rest of the group, and vice versa, a specific social structure can influence the behavioral composition of the group and, consequently, how the group operates (Hunt et al. 2018).

In the present study, I studied groups of meerkats held in zoo collections (more information of the study can be found in Pacheco 2017) for which variance in group size was reduced (most of the groups comprised between 7 and 14 individuals), ectoparasites were controlled by husbandry and effects of breeding seasonality were excluded. Captive meerkats appear insensitive to the intensity of visitors (Sherwen et al. 2014, but see evidence that fecal glucocorticoid levels, indicative of stress, rose with higher visitor numbers Scott et al. 2017) suggesting that they commonly perform their species-specific behavioral repertoire. Therefore, I expect that despite these differences in housing and living conditions, the range and expression of individuals' personalities may match those seen in the wild (Herborn et al. 2010).

First, I confirmed that my variable summarizing behavior, specifically personality, was robust and repeatable across time

(Uher and Asendorpf 2008). I achieved this by surveying a subset of the study groups during two periods, 1 year apart and testing whether an individual's personality score in 1 year matched that in the second year. Second, I tested whether the personality measures differed according to their sex, age, and status. This was essential because meerkat interactions, and thus their network position, can be predicted by an individual's age, sex, and status (Madden et al. 2009, 2011). Finally, and critically, I tested whether an individual's personality was consistently influential across multiple groups in determining the social environment of individuals. I took two approaches. First, I tested whether individuals sharing similar network positions also exhibited similar personality types. Second, I investigated how personality scores affected the likelihood of associations between individuals.

Methods

Data collection

Fifteen captive groups of meerkats comprising a total of 113 individuals (54 females, 59 males, Table 1) were studied from September 2011–August 2013 in zoological parks in the UK and Mexico (see Table S1 in the Electronic Supplementary Information for zoo and management information). All observations were undertaken during the opening hours of zoos/parks (8:00–9:00 to 16:00–17:00) and from behind the fence, matching normal visitor behavior, to avoid influencing meerkats' behavior. Each group was observed for a total of 20 h over the 4 days of observations. I returned to a subset of five zoos (Africam, Bristol, Shaldon Park, Shepreth Park, and WMSP) between November 2012 and August 2013 in order to confirm the reliability of my measures. I selected zoos holding groups that comprised mixed sex/age individuals and that were available for the study. I collected data on all members of the group. 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 were not able to be marked. It was not possible to record data blind because my study involved observations of focal animals with obvious attributes in the field.

Individual attributes

Three attributes were considered for all individuals: age, sex, and status. The age of individuals was taken from the taxon reports provided by 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). Individuals' sex was determined either from the

Table 1 Mean values of the social interactions (grooming, dominance, and foraging competitions) from the fifteen captive groups

Group	Grooming interactions	Dominance interactions	Foraging competitions
Africam	1.71	0.68	1.97
Bristol	1.74	0.12	0.41
Cotswold	2.44	1.6	1.12
Flamingo G1	2.23	0.66	2.44
Flamingo G2	26.85	2.2	9.15
Longleat	2.30	0.93	1.44
Morelia G1	18.1	1.2	2.9
Morelia G2	31.16	2.3	2.1
Paignton	18.5	1.3	2.6
PWP G1	3.0	1.5	1.25
PWP G2	7.7	0.6	2.65
Shaldon	12.11	0.02	1.07
Shepreth	6.9	3.75	0.1
Twycross	1.03	0.20	0.10
WMSP	6.3	2.2	2.7

taxon report or 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 at a higher rate over other group members with behaviors such as chin marking, chasing, charging, hip slamming, and biting (Madden et al. 2011). Subordinate individuals were identified when responding to these behaviors and/or the mere presence of a dominant, by adopting postures such as crouching 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 behaviors occur at much lower rates than in dominants (Kutsukake and Clutton-Brock 2006).

Behavioral, interaction, and association measures

I collected pilot data in order to construct ethograms and decide on key common interaction and association behaviors that I was likely to encounter regularly and hence were worth focusing on. Social interaction data, based on behavioral exchanges between pairs of individuals, were collected during scan sampling observations. These interactions, described as directed relationships, comprised 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 dyads. How long the individuals groomed or how many times the meerkats exchanged grooming bouts 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. A dominance interaction was recorded when an individual acted dominant over another individual and when the interaction was not provoked by food, access to foraging holes, or social foraging

partners. Dominance interactions included any individual attacking or intimidating (hip slamming, chin marking, glaring, chasing, charging, pushing aside, threatening, etc.) other individuals competing and/or fighting for dominance. A foraging competition was recorded when an individual approached food or a hole owner, provoking action of defense by the original property owner. Meerkats foraging in holes, especially for large prey, may be displaced by competitors. Actions such as growling vocalizations, 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. I recorded a total of 5689 social interactions (grooming, 3564; dominance, 772; foraging competitions, 1353; Table 1).

Social association data, based on proximity measures, were collected during scan sampling observations every 10 min. These associations, described as undirected relationships, comprised foraging and resting. A foraging association was recorded when two or more individuals foraged close to one another (the subjects are within one body length of each other) and all these associations were recorded as dyads; I did not consider how long the individuals foraged close to other individuals. When foraging was separated by intervals of more than 1 min, a new foraging association was defined. A resting association was recorded when an individual laid down in a relaxed manner (lazy sitting, high sitting, sunbathing) close to other member(s) of the group. Additional patterns of association, such as resting underground or while moving together were not measured. Every time an animal was resting and was joined by another individual, the joiner and the joined were designated. A similar designation was done when foraging. For this, the joined need to be foraging in one place, so the joiner could be easily singled out. I recorded a total of 14,012 social associations (foraging associations, 10,052; resting associations, 3960).

Personality measures

I collected measures of four behavioral traits during continuous recording sampling using all occurrence sampling (Martin and Bateson 2007) in order to record various types of social interactions (Freeman and Gosling 2010): playful, curious, sociable, and aggressive. This allowed me to describe personality in meerkats in their captive condition under unmanipulated circumstances. Several training trials of behavioral data collection were carried out to recognize and record relevant behavior; this was conducted by a single observer (the author). Personality traits were derived from the species behavioral repertoire from published ethograms which were used to code the behavioral data (Weinstein et al. 2008) and were derived independently from the social network data as different values were considered. The ethogram used was developed from a compilation of several authors: Sharpe (2005a, b); Kutsukake and Clutton-Brock et al. (2008); Drewe et al. (2011); Santema and Clutton-Brock (2012). An instance of playfulness was recorded if at least one of the following behaviors was present: play chasing, play biting, clasping, grappling, mounting, pawing, play object (solitary play), and wrestling. An instance of curiousness was recorded if at least one of the following behaviors was present: approach, exploring, and foreleg stabbing behaviors. An instance of sociability was recorded if at least one of the following behaviors were present: allogrooming, huddling, side by side, and touching the snout behavior. An instance of aggressiveness was recorded if at least one of the following behaviors was present: attack, bite, charge, chase, chin mark, glare, hit, hip slam, and threaten (Table 2).

Relationships between individual scores for each personality trait were explored using Spearman's correlations. Subsequently, a principal component analysis (PCA) was performed using the four personality measures for each meerkat and each personality trait, with the objective of reducing the number of behavioral variables measured (e.g., Lantová et al. 2010). The scree plot and Kaiser's criterion were used, such that only factors with an eigenvalue of 1.0 or more were retained. A correlation of 0.50 or above was considered as relevant. Both varimax rotation and promax rotation were performed to maximize the variance of the PCA scores within the principal components (e.g., Lantová et al. 2010; Morton et al. 2013). The results of both rotations were very similar, so I only present the solution of varimax rotation within the results. Linear mixed models were used to identify differences among the individuals' attributes (sex, age, and status). I wanted to ensure that the measures of personality were robust and this is usually indicated by them being repeatable both across contexts and over time. I assessed repeatability across contexts by testing correlations between different types of behavior recorded

within the same sampling period and within the 15 groups. I assessed repeatability across time by returning to five groups for a second sampling period approximately 1 year after the original sampling. This allowed me to compare the same behaviors of 36 individuals over two recording periods. Originally, there were 42 meerkats within the five groups; however, after 1 year, there were changes in the composition of the groups. I only included the same individuals present at both times, and I excluded any new meerkat added to the groups. I used mean values and included group identity (ID) as a random factor in the analyses to account for multiple sampling among group members and for pseudo-replication. I ran a separate PCA for each year's data for the five replicated group data. I then used Pearson's correlation, a common correlational technique frequently used in personality research (Ozer 2009) and for multivariate data that assumes independent observations (Bakdash and Marusich 2017), to test for relationships between the individual scores for each personality trait over the two recording periods.

Network measures and analytical methods

My networks were based on directly observed relations and thus, I could use randomization tests with a permutation of node labels to test hypotheses (Croft et al. 2011). Ten network measures for the five forms of interactions and associations were analyzed. Measures of degree (indegree, outdegree) centrality (unweighted and weighted data), distance, density (average path length and compactness), cluster coefficient (unweighted data), closeness centrality, and betweenness centrality were calculated for every group. I then explored how individuals differed in their network positions (described using degree centrality, cluster coefficient, betweenness, and closeness) according to their attributes: sex, status, and age. The probabilities of differences in network measures between types of individuals (differing in sex, status, and age) were calculated using permuted *t* tests based on 10,000 permutations within UCInet (Madden et al. 2009, 2011). Finally, I tested patterns of association based on individual attributes. Permutation tests in UCInet were used to calculate the probabilities of individuals' categories interacting assortatively. I calculated personality attribute-based differences in network associations for each group individually, then combined them using Fisher's method to calculate an overall level of significance. For groups with a negative relationship, the sign of their natural log-transformed *p* value was reversed subtracting then their contribution from the combined χ^2 statistic and, then, 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 redistribute the node attributes in the network (Whitehead 2008), rely on the assumption that the

Table 2 Ethogram for *Suricata suricatta* and personality category

Category	State behavior	Definition
Playful	Play chasing	Running in pursuit of/from another animal
	Play biting	Inhibited bites directed towards a companion's head or neck, trunk, legs, or tail
	Clasping	One animal hold tightly another one with the arms
	Grappling	Both animals stand bipedally, clasping to push one another over
	Mounting	One animal supports its fore body on its companion's back while clasping the other's sides, between the ribcage and groin
	Pawing	A foreleg is extended towards a companion
	Play object (solitary play)	An animal touches an object or scratches it for a prolonged period
	Wrestling	One animal adopts a submissive posture lying on its back while the other stands on or over it
Curious	Exploring	To investigate the environment, possibly incorporating manipulation of parts of the environment
	Foreleg stabbing	Using a stiff foreleg to poke an object
Sociable	Allogrooming	Manipulation of the fur of other individuals with the mouth, ears, and mouth region with licking and smooth biting
	Huddling	Gathering involving mutual bodily contact between two or more animals
	Side by side	Two animals are accompanying each other with raised tails, while their sides might touch
Aggressive	Touching the snout	An animal is giving another one short touch with the snout
	Attacking	Biting a subordinate and may ultimately chase subordinate off
	Biting	When an animal uses its teeth to pierce another animal
	Charging	Running directly at the subordinate
	Chasing	Running in pursuit of another animal, posture, and vocalizations are the same as threatening.
	Chin marking	Rubbing the chin on a subordinate or shaking its head over the animal in a gesture simulating chin marking
	Glaring	Crouching down low and fixes subordinate with an unwavering stare
	Hip slamming	Slamming the hip against the side of a subordinate
Hitting	Swatting a subordinate with one paw	
Threatening	An animal is growling while head and tail are lowered	

observed network is a solid representation of the exact network (Croft et al. 2011). The Friedman test was used to compare between measures of network and group attributes and Spearman's rho test was used to explore potential relationships among group attributes and the group network structure. Non-parametric tests were used due to the distribution of the data and the small sample sizes.

I tested whether, across all 15 groups, particular relationships or differences were significant by applying a Fisher's combined probability test in which I considered whether the overall p value was < 0.05 . In total, I conducted more than 80 such tests (two personality measures \times eight network measures \times four network types and two personality measures \times six association combinations \times two association types; Table 8). This meant that I expected to find > 3 significant relationships by chance. Because this was an exploratory study, I did not adjust accepted p values as would be normal if hypothesis testing, but instead I was prepared to treat small numbers of significant relationships or differences with skepticism.

Results

Obtaining personality measures to summarize an individual's behavior

I extracted two robust measures of individual personality across the fifteen groups (first sampling period). There was a significant positive correlation between rates of playful, curious, and sociable behaviors, but a negative correlation between rates of playful and aggressive behaviors. Rates of curious behavior were weakly and positively correlated to rates of sociable and aggressive behaviors, and rates of sociable behaviors were negatively correlated to aggressive behaviors ($R = 0.18$; Table 3). The principal component analysis identified two primary factors with an eigenvalue greater than 1 and which together explained $\sim 60\%$ of the total variance (Table 4). The first component (accounting for 33.7% of variance) had positive loadings with playful, curious, and sociable behaviors. Therefore, an individual with a high PC1 score

Table 3 Correlation matrix of individual personality traits' scores

Personality measures	Playful	Curious	Sociable	Aggressive
Playful	1.0			
Curious	0.168	1.0		
Sociable	0.145	0.187	1.0	
Aggressive	-0.026	0.040	-0.062	1.0

exhibited lots of playful, curious, and sociable behavior, and I used this PC as a measure of “friendliness.” The second component (accounting for 26.3% of variance) had a positive loading with aggressive behavior and a negative loading with sociable and playful behavior. Therefore, an individual with a high PC2 score was aggressive, unsociable, and non-playful, and thus, I used this PC as a measure of “aggressiveness.”

Is an individual's personality measure consistent across time?

When I restricted the analysis to just the 36 individuals from the five groups that I visited twice, I was only able to extract a single component during the first set of observations (from September 2011 to July 2012), with an eigenvalue greater than 1 and which explained 42.7% of the total variance (Table 5). Component 1 had positive loadings with playful and sociable behavior and so could be considered similar to PC1 above, summarizing “friendliness.” In the second set of observations (from November 2012 to August 2013), I identified two primary factors with eigenvalues greater than 1 and which together explained 67.1% of the total variance (F1, 40.35%; F2, 26.69%) (Table 6). The first component (explaining 40.4% of variance) had positive loadings with playful, curious, and sociable behaviors. The second component (explaining 26.7% of variance) had a positive loading with aggressive behavior and a negative loading with sociable and playful behavior. Therefore, the first component could be considered to reflect “friendliness” and the second component reflect “aggressiveness.” I used the first component extracted (aka “friendliness”) in each set of observations because I extracted a component corresponding to friendliness in both the first and second set of

Table 4 Factor loadings from principal components analysis conducted on the data from all 15 groups collected on a single visit to each site. Factor loadings of 0.50 or above are marked in italics

	Component	
	Friendliness	Aggressiveness
Playful	<i>0.567</i>	-0.501
Curious	<i>0.634</i>	0.263
Sociable	<i>0.775</i>	-0.054
Aggressive	0.124	<i>0.859</i>

Table 5 Factor loadings from principal components analysis conducted on the data collected during the first visit to a subset of five groups that were revisited 1 year later. Factor loadings of 0.50 or above are marked in italics

	Component
	Friendliness
Playful	<i>0.559</i>
Curious	0.378
Sociable	<i>0.525</i>
Aggressive	-0.242

observation of the five groups; I consider this to be the stronger descriptor of personality and the one that I could use to test for consistency in these five groups of meerkats. An individual's “friendliness” score in the first set of observations was positively correlated to their score around 1 year later ($r = 0.675$, $N = 36$, $p < 0.001$, Figs. 1, 2).

How do an individual's personality dimensions relate to their sex, age, and status?

An individual's personality score in either friendliness or aggressiveness did not correspond to their sex, age, or status. There were no consistent relationships between an individual's personality score and their sex, age, or status across the 15 groups (Table 7).

Do an individual's personality measures consistently predict their network positions across fifteen groups?

An individual's personality score in friendliness consistently corresponded to some, but not all, aspects of their social network position. An individual's position within a social network based on dominance or grooming was not consistently related to their measure of friendliness, while their position within a social network based on foraging competitions did. Friendly individuals within foraging competition networks were surrounded by others well connected to each other (higher clustering coefficient) across groups (Table 8).

Table 6 Factor loadings from principal components analysis conducted on the data collected during the second visit to a subset of five groups that had been previously visited 1 year earlier. Factor loadings of 0.50 or above are marked in italics

	Component	
	1	2
Playful	<i>0.611</i>	-0.607
Curious	<i>0.709</i>	0.062
Sociable	<i>0.742</i>	-0.044
Aggressive	0.111	<i>0.933</i>

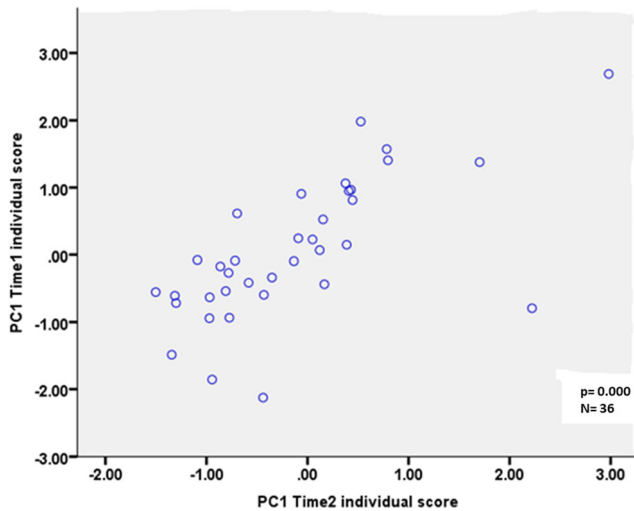


Fig. 1 Correlation between personality traits measured in two different times in five groups: PC1, “friendliness”

Looking at patterns within individual groups, differences were seen in one group (Longleat) where non-friendly individuals initiated higher rates of dominance interactions (weighted and unweighted data) than friendly individuals. Friendly meerkats also acted as central individuals within a dominance and were well connected to the other group members. Within foraging competitions, non-friendly individuals initiated higher rates (weighted and unweighted data) and had shorter paths (outcloseness) to reach the other group members by the same interactions. Lastly, in the same group (Longleat), friendly individuals were focal in playing networks. The lack of consistency in these relationships across most of the groups suggests a strong influence of the group-specific environment on

the relationship between individual social position and personality or other attributes.

There was no consistent correspondence between personality and network position when considering measures of aggressiveness. Differences were found in only one group (Twycross) where aggressive individuals had shorter paths to reach the other group members by dominance interactions and were rapidly connected by grooming interactions to other individuals of the group.

Do an individual’s personality measures consistently predict their patterns of assortment across fifteen groups?

There were no general patterns of non-random assortment predicted by either friendliness or aggressiveness in the fifteen groups (Table 9).

Discussion

Meerkat personality type could be summarized by two variables that I considered to indicate friendliness and aggressiveness, across the fifteen groups of meerkats. For a subset of these groups, I found that an individual’s measure of friendliness was consistent across two periods separated by ~ 1 year. These personality measures were not well related to an individual’s sex, status, or age, suggesting that they could influence patterns of social interactions independently from these factors that have already shown to predict network position and association preferences. However, I found little evidence

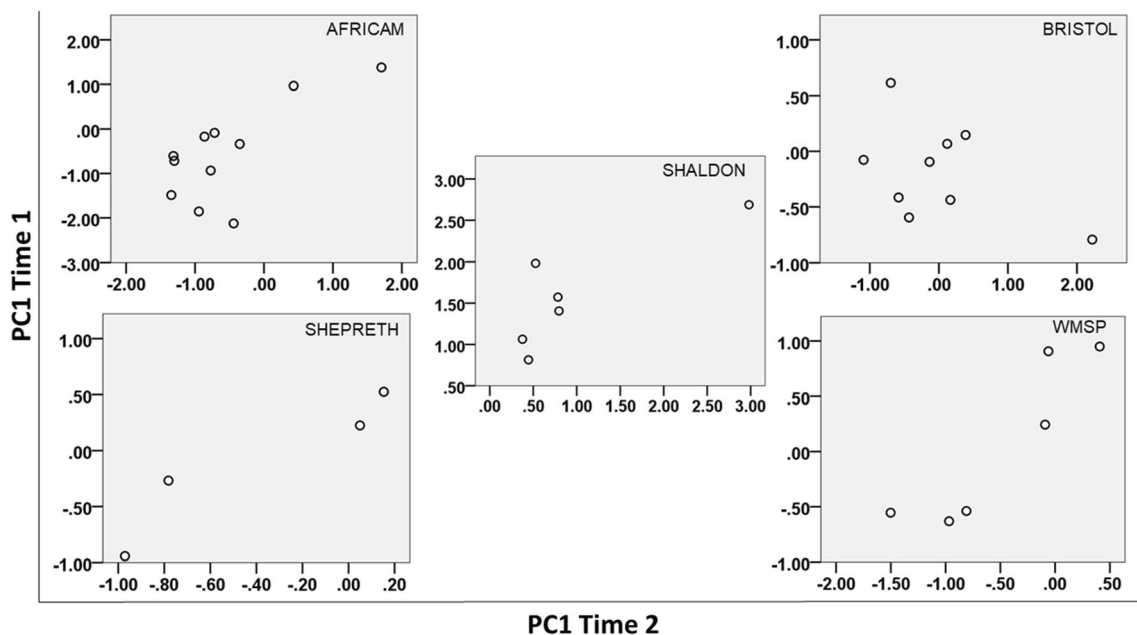


Fig. 2 Scatter plot representing the dispersion of personality traits in time 1 and 2. The five groups are presented here individually: Africam, Bristol, Shaldon, Shepreth, and WMSP. PC1, “friendliness”

Table 7 Relationship between personality dimensions and individual attributes of the fifteen captive groups of meerkats. *F*, female; *M*, male; *P*, pup; *J*, juvenile; *A*, adult; *D*, dominant; *S*, subordinate

	Friendliness				Aggressiveness			
	df	<i>F</i>	<i>P</i>	Mean	df	<i>F</i>	<i>P</i>	Mean
Sex differences	1	0.838	0.371	<i>F</i> : 0.018 <i>M</i> : -0.146	1	0.820	0.383	<i>F</i> : -0.164 <i>M</i> : 0.055
Age differences	2	0.280	0.756	<i>P</i> : 0.793 <i>J</i> : -0.368 <i>A</i> : -0.077	2	0.468	0.630	<i>P</i> : -0.493 <i>J</i> : 0.370 <i>A</i> : -0.092
Status differences	1	0.222	0.639	<i>D</i> : -0.021 <i>S</i> : -0.112	1	0.002	0.961	<i>D</i> : -0.087 <i>S</i> : -0.071

that an individual's personality scores consistently explained either their network position or patterns of association across all groups. The only robust relationship was that between an individual's friendliness and their clustering coefficient on networks based on foraging competitions. This was not an intuitive finding, suggesting that the social partners of friendly individuals (in this specific case, those who they compete within foraging situations) are themselves more cliquish and thus more likely to also compete among themselves. Generally, small individuals (young) or individuals lower in the hierarchy and which can be more playful, curious, or sociable can be poorer competitors in foraging and can be central individuals in foraging competitions. As Madden et al. (2011) clarify, subordinate individuals are typically smaller/lighter and so are easier targets, less able to defend their resources from bigger/heavier individuals. Competition for food resources is a crucial function in shaping the structure of ecological communities (Jeglinski et al. 2013). The extent of such competition varies with the abilities of the ecological context and the distribution in time and space of the resources (Ward et al. 2006).

I was able to summarize rates of 22 different behaviors using just two components. The first component had positive loadings from a series of playful, curious, and sociable behaviors and therefore, I described it as being an indication of the friendliness of the individual. This dimension has similarities with the dimension of sociability in rhesus macaques (Freeman and Gosling 2010; Weiss et al. 2011; Robinson et al. 2018), and in chimpanzees, *Pan troglodytes* (Freeman and Gosling 2010; Koski 2011; Altschul et al. 2018), in golden snub-nosed monkeys, *Rhinopithecus roxellana* (Jin et al. 2013), and the dimension of openness in mountain gorillas, *Gorilla beringei beringei* (Eckardt et al. 2014), in rhesus macaques (Altschul et al. 2016), and in Bolivian squirrel monkey, *Saimiri boliviensis* (Wilson et al. 2018). These dimensions tend to be associated with the traits of playful, curious, and sociable. The second components had positive loadings from aggressive behavior and therefore, I described it as being an indication of the aggressiveness of the individual. This dimension shared similarities with the dimension described

as proactive in rats (de Boer et al. 2003) and fish (Mesquita et al. 2016; Baker et al. 2018), dominance in rhesus macaques (Weiss et al. 2011), and confidence in rhesus macaques and chimpanzees (Freeman and Gosling 2010), and in sea lions, *Zalophus californianus* (Ciardelli et al. 2017), which tend to be associated with the trait of aggressiveness. It is not clear how well my personality measures correspond to those we might expect to see in wild, free-living meerkats. Although the personality of wild and captive animals of the same species are reported to be similar (Herborn et al. 2010), McCowan et al. (2014) argue that the pressures imposed by captivity (along with genetic drift processes) are likely to affect the frequency and characteristics of personality traits. Captive animals experience different environmental conditions to their counterparts in the wild, which may have an impact on their behavior (Morgan and Tromborg 2007). Consequently, captive individuals may be favored by characteristics dissimilar to those selected for in nature (Einum and Fleming 2001; Salonen and Peuhkuri 2006).

Our measure of an individual's friendliness in 1 year was strongly related to the same measure collected around a year later. Repeatability is widely acknowledged as the main criterion for animal personality (Wuerz and Krüger 2015), whether this phenomenon is explained from a genetic standpoint or not (Fisher et al. 2018). Even though repeatability in traits is commonly revealed, particular changes over time can also be expected. Changes in personality may occur with an individual's maturation (Svartberg 2005). Differences in personality axes and their evolution may diverge in juveniles and adults as selection pressures act differently on each of them (Wuerz and Krüger 2015). This may occur due to the shift in hormonal levels during sexual maturation (Bell 2004). In my study, the five groups that were observed over a year were mainly formed by adults that had no obvious life changes during that time and simply got older, which may be one reason for the repeatability I detected. Brust et al. (2015) provide insight as to how behavior is expected to be most repeatable in adulthood. In addition, my focal meerkats remained living in the same stable captive environments over that year and changes in the group composition were minimal. Perhaps, keystone

Table 8 Differences for network measures of individuals from fifteen groups of meerkats varying in two personality dimensions (friendliness and aggressiveness) based on foraging competitions, grooming, and dominance interactions; the Shaldon group was excluded due to the small number of personality scores in the SN. Significant ($p < 0.05$) relationships are marked in italics. *F*, friendly; *NF*, non-friendly; *A*, aggressive; *NA*, non-aggressive; *K*, degree centrality based on weighted data, *K*_{bin} degree centrality based on unweighted data

	Friendliness						Aggressiveness						Cluster						
	K. D. Centrality Kbin			Betweenness			Closeness			K. D. Centrality Kbin				Betweenness			Closeness		
	Out	In	In	Out	In	In	Out	In	In	Out	In	In		Out	In	In	Out	In	In
Dominance																			
African	0.840	0.249	0.922	0.221	0.419	0.161	0.491	0.245	0.693	0.707	0.693	0.712	0.691	0.701	0.538				
Bristol	1.0	0.904	1.0	1.0	1.0	0.396	0.606		0.100	0.796	0.101	1.0	0.107	0.104	0.304				
Cotswold									0.622	0.587	0.802	0.820	1.0	0.620	0.765				
FlamingoG1									0.404	0.399	0.395	0.608	0.800	0.407	0.401	1.0			
FlamingoG2	0.401	0.305	0.496	0.500	0.399	0.796	0.711	1.0											
Longleat	<i>0.012</i>	<i>0.057</i>	<i>0.024</i>	0.292	0.158	0.647	0.458	<i>0.004</i>											
MoreliaG1									0.399	0.494	0.702	0.698	1.0	0.697	0.698	1.0			
MoreliaG2													0.657						
Paignton																			
PWPG1	0.757	1.0	0.751	1.0	1.0	0.499	0.756	1.0	0.500	0.294	0.610	0.704	1.0	0.602	0.500				
PWPG2									0.197	0.397	0.595	0.407	1.0	0.605	0.587				
Shepreth									0.086	0.856	0.079	0.762	0.267	0.025	0.094	0.485			
Twycross									0.169	0.333	0.164	0.330	0.336	0.170	0.166	0.673			
WMSP	0.668	0.392	0.542	0.532	0.198	0.525	0.402	0.935	0.189	0.833	0.389	0.977	0.937	0.247	0.490	0.972			
Combined P	0.415	0.371	0.699	0.882	0.571	0.629	0.932	0.173	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>			
Form of diff.	<i>NF > F</i>	<i>NF > F</i>	<i>NF > F</i>	<i>F > NF</i>	<i>NF > F</i>	<i>F > NF</i>	<i>F > NF</i>	<i>F > NF</i>	<i>A > NA</i>	<i>NA > A</i>	<i>A > NA</i>	<i>NA > A</i>	<i>NA > A</i>	<i>NA > A</i>	<i>A > NA</i>	<i>NA > A</i>	<i>NA > A</i>	<i>NA > A</i>	<i>NA > A</i>
Foraging competitions																			
African	0.812	0.381	0.785	0.365	0.334	0.594	0.666	0.899	0.832	0.295	0.822	0.915	0.056	0.707	0.439				
Bristol									0.095	0.904	0.199	0.106	0.898	0.491	0.598				
Cotswold	0.599	0.691	0.507	0.603	0.698	0.492	0.697		0.491	0.687	0.689	0.255	0.381	0.560	0.806	0.447			
FlamingoG1									0.790	0.197	0.303	1.0	0.402	1.0	1.0	1.0			
FlamingoG2	0.304	0.899	0.599	0.598	0.301	1.0	1.0	0.904											
Longleat	<i>0.011</i>	<i>0.057</i>	<i>0.022</i>	0.298	0.850	<i>0.016</i>	0.279	<i>0.004</i>	0.401	0.101	0.896	1.0	0.294	0.401	0.198	0.298			
MoreliaG1													1.0						
MoreliaG2																			
Paignton																			
PWPG1	0.751	0.503	0.756	0.501	1.0	0.747	0.499	1.0	0.505	0.804	0.697	0.500	1.0	0.700	0.698	0.497			
PWPG2									0.206	0.801	0.202	1.0	1.0	0.199	0.799				
Shepreth																			

Table 8 (continued)

	Friendliness						Aggressiveness						Cluster						
	K D. Centrality Kbin			Betweenness			Closeness			K D. Centrality Kbin				Betweenness			Closeness		
	Out	In	In	Out	In	In	Out	In	In	Out	In	In		Out	In	In	Out	In	In
Twycross							0.255	0.908	0.219	0.207	0.954	0.344	0.359						
WMSP	0.538	0.869	0.802	0.794	0.604	0.430	1.0	0.660	1.0	0.674	0.340	1.0	0.635	0.831					
Combined P	0.260	0.592	0.646	0.723	0.880	0.030	0.588	0.783	0.733	0.807	0.807	0.886	0.915	0.831					
Form of diff.	NF > F	NF > F	NF > F	NF > F	F > NF	F > NF	A > NA	NA > A	A > NA	A > NA	NA > A	A > NA	NA > A	NA > A	NA > A	NA > A	NA > A	NA > A	
Grooming																			
African	0.572	0.161	0.314	0.317	0.260	0.490	0.550	0.778	0.555	0.950	0.779	0.488	0.652	0.612					
Bristol							0.296	0.498	0.396	0.906	0.497	0.396	0.694						
Cotswold	0.502	0.504	0.702	0.499	0.207		0.457	0.715	0.767	0.644	0.429	0.647	0.347	0.498					
FlamingoG1							0.809	0.805	1.0	1.0	1.0	1.0	1.0	1.0					
FlamingoG2	0.392	0.697	1.0	1.0	1.0	1.0	0.792	0.598	1.0	0.603	0.402	1.0	1.0	0.701					
Longleaf	0.175	0.848	0.380	0.699	0.784	0.347													
MoreliaG1							0.196	0.304	0.102	0.305	0.096	0.400	0.402	1.0					
MoreliaG2							0.199	0.207	0.208	0.402	0.201	0.201	0.595	1.0					
Paighton							0.072	0.034	0.146	0.099	0.138	0.141	0.064	0.135					
PWPG1	1.0	0.254	1.0	1.0	1.0	1.0	0.821	0.662	0.839	0.663	0.661	0.664	0.739	0.301					
PWPG2							0.440	0.512	0.629	0.855	0.528	0.664	0.739	0.891					
Shepreth							A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	A > NA	
Twycross																			
WMSP	0.725	0.470	0.338	0.199	0.671	0.663	0.877	0.335	0.877	0.335	0.980	0.877	0.335	0.980					
Combined P	0.612	0.587	0.891	0.789	0.848	0.980	F > NF	F > NF	F > NF	F > NF	NF > F	F > NF	F > NF	0.891					
Form of diff.	NF > F	F > NF	NF > F	F > NF	F > NF	NF > F	F > NF	F > NF	F > NF	F > NF	NF > F	F > NF	F > NF	0.891	A > NA	A > NA	A > NA	A > NA	

Table 9 Patterns of association for individuals varying in the two personality dimensions in the fifteen groups: *F*, friendly; *A*, aggressive; *NF*, non-friendly; *NA*, non-aggressive

	Associate more			Associate less			Associate more			Associate less		
	Resting						Foraging					
Friendliness												
	F-F	F-NF	NF-NF	F-F	F-NF	NF-NF	F-F	F-NF	NF-NF	F-F	F-NF	NF-NF
Africam	0.598	0.857	0.500	0.657	0.392	1.0	0.584	0.424	0.858	0.564	0.727	0.365
Bristol												
Cotswold	1.0	1.0	0.099	1.0	0.099	1.0	1.0	0.693	0.405	1.0	0.405	0.693
FlamingoG1												
FlamingoG2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Longleat	0.763	0.620	0.810	0.620	0.763	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MoreliaG1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MoreliaG2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Paignton	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PWPG1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PWPG2												
Shaldon	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Shepreth	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Twycross												
WMSP	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Combined P	1.0	1.0	0.99	1.0	0.998	1.0	1.0	0.999	0.999	1.0	0.999	0.999
Aggressiveness												
	A-A	A-NA	NA-NA	A-A	A-NA	NA-NA	A-A	A-NA	NA-NA	A-A	A-NA	NA-NA
Africam												
Bristol	0.607	0.497	0.619	0.512	0.644	0.621	0.789	0.486	0.398	0.396	0.710	0.851
Cotswold	0.599	0.496	1.0	0.496	0.599	1.0	0.496	0.599	1.0	0.599	0.496	1.0
FlamingoG1	0.859	0.194	0.783	0.340	0.964	0.622	1.0	0.193	0.808	0.175	1.0	1.0
FlamingoG2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Longleat												
MoreliaG1	1.0	1.0	1.0	1.0	1.0	1.0	0.898	1.0	0.702	1.0	0.601	1.0
MoreliaG2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Paignton	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PWPG1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PWPG2	1.0	1.0	1.0	1.0	1.0	1.0	0.695	0.404	1.0	1.0	1.0	0.099
Shaldon	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Shepreth	0.796	0.796	1.0	0.796	0.796	1.0	0.800	0.803	1.0	0.803	0.800	1.0
Twycross	0.852	0.852	0.684	0.684	0.684	0.852	1.0	1.0	1.0	1.0	1.0	1.0
WMSP	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Combined P	0.999	0.999	1.0	0.999	0.999	1.0	1.0	0.999	0.999	0.999	0.999	0.999

individuals (as defined by Sih and Watters 2005) within the five groups, with a particular behavioral type, were central in shaping overall dynamics in the group and thus affecting individual personality expression. Furthermore, the maintenance of an individual personality can also be a consequence of the group living per se, where individuals must specialize in specified social roles to avoid social conflict (social niche specialization hypothesis; Carter et al. 2014). Differences in

conditions, such as variation in predation pressure, food availability, and differences in life history strategies may cause personality variation in wild populations (Boon et al. 2008; Bergvall et al. 2010). Conditions which rarely change and are fairly predictable, such as those found within a zoo environment, may favor higher levels of repeatability than unpredictable and fluctuating conditions commonly encountered in wild populations (but see Bell et al. 2009).

Notwithstanding the fact that repeatability of friendliness was found in some groups over a long interval between observations, I found little correspondence between an individual's personality and their attributes, such as age. This was perhaps surprising. Friendliness included measures of play and young animals commonly exhibit play behavior (Bekoff and Allen 1998; Bekoff and Byers 1998; Burghardt 2005; Kuczaj and Eskelinen 2014). Play between adults has been found in species like birds, canids, rodents, primates, and ungulates (Mancini and Palagi 2009); nonetheless, in wild meerkats, the social play has been observed more frequently between young than adults (Sharpe 2005b). Nevertheless, a captive environment may transform such a pattern; two possible explanations are considered. First, animals under human control are not impinged by important selection pressures such as obtaining food or escape predation and, as a result, may have more time available and additional energy to exhibit behaviors that are considered as a luxury in the wild. Play behavior can be performed by individuals only when their immediate needs are met so that their welfare is not compromised (Held and Spinka 2011). Thus, parallel levels of play behavior in adult and juvenile meerkats might be expected in the captive groups I studied. Second, several functions of play behavior have been suggested, including regulating energy, developing skills (motor and social skills), assessing risk, increasing cardiovascular fitness, and coping with stressful situations (Sharpe 2005b) or alternatively, it has been suggested that it has no function beyond bringing pleasure (Palagi et al. 2016) or being autotelic, regardless of its adaptiveness or function (Burghardt 2005). Despite captive environments meeting basic physiological and survival needs, they can still produce stressful situations (Held and Spinka 2011), such as an escalated intrasexual conflict caused by individuals being deprived of the opportunity to disperse. Play can contribute to general stress resilience (Tacconi and Palagi 2009) and reduce aggression between group members (Soderquist and Serena 2000). Therefore, play, regardless of an individual's age, possibly helps to cope with the constant hostility of others, such as dominant and/or aggressive individuals in a confined, captive, environment.

Aggressiveness was also surprisingly unrelated to age, sex, and status. In wild meerkats, females are reported to be more aggressive than males due to their intense intragroup reproductive conflict (Jordan 2007); however, captive conditions may result in atypical group compositions with female eviction and/or male emigration being prevented. This condition may lead to increased familiarity and bonding (between males and between females) (Koski 2011) or females may choose to modulate aggression (as reproductive and food benefits are rather controlled in a captive environment) to avoid unnecessary injuries and increase fitness (Bell et al. 2013). Thus, the aggressive personality in wild female meerkats may not be seen only in captive females but in both sexes. The absence

of a relationship between aggressiveness and age may be explained by (artificial) food availability. Hodge et al. (2009) suggest that food availability can be an important factor in aggression for juvenile wild meerkats that tend to be more aggressive to littermates when the amount of food available is low (during low rainfall). Meerkats in captivity are usually provided with food ad lib and in excess which might explain the absence of a relationship between age and aggression.

An individual's personality was not a consistent predictor of their network position or pattern of association across multiple groups. Therefore, it is hard to support the assumption that group social structures predictably emerge from the personality attributes of their constituent members. Perhaps the social environment can have a more meaningful effect on personality, via facilitation, and enhance its expression or restrict it, via conformity (King et al. 2015). Across all 15 groups, I found only a single relationship that was consistent as indicated by a significant combined probability test. This contrasts with patterns in wild meerkats in which, across eight natural groups, several attributes explained an individual's association patterns or network position within particular forms of networks (Madden et al. 2011). For example, there was negative assortativity by age and mass in grooming networks and negative assortativity by status in dominance networks. High-status individuals exhibited higher levels of dominance interactions and were aggressive to more different individuals than subordinates in dominance networks and in these networks, heavier individuals received higher levels of aggression. This absence of predictable patterns in my current study may arise because I was considering more abstract attributes, namely a meerkat's personality. However, other work has revealed that, at least in single or small numbers of groups, an individual's personality can be a good predictor of their social behavior and emergent network measures (Pike et al. 2008; Pruitt et al. 2010; Aplin et al. 2013; Snijders et al. 2014; Best et al. 2015; Walton and Toth 2016). I also found that, in certain individual groups of captive meerkats, there were significant relationships between personality and network measures. For example, in the group at Longleat (Table 7), I detected several significant relationships between personality measures and network positions in dominance and foraging competitions, while in the Twycross group, I detected such relationships in grooming networks. However, these patterns were not replicated across all the other groups, and therefore, it remains unclear whether previously published studies linking personality to network measures in single/few groups are unusual aberrances, perhaps arising due to publication bias for positive results or truly indicating relationships present in those species. My work suggests that researchers should consider multiple groups and either demonstrate that groups differ each other along various important functional axes (Jandt et al. 2014) or demonstrate consistent patterns of relationships across groups. This may help explain why patterns of

relationships are present or absent from particular units. Further work on how management factors (i.e., husbandry procedures and enclosure type) impact social group dynamics through individual personality will help us to understand the mechanisms sustaining the patterns of social dynamics in captivity.

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Data availability The datasets generated or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The author declares that there is no conflict of interest.

Ethical approval Ethics approval was not required for this study. The study was reviewed and accepted 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.

Ethical statement This study was merely observational and was non-invasive, with data collection occurring during normal zoo opening hours so meerkats experienced no additional disturbance.

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