Social network structure and personality in captive meerkat, *Suricata suricatta,* populations: assessment, comparison between wild and captive meerkat populations and captive management implications.

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ABSTRACT

Research into the social behaviour of wild animals living in groups has demonstrated the importance of social structure dynamics and their consequences for an individual's fitness. Many aspects of animal behaviour and ecology, including interactions with conspecifics, habitat use and willingness to take risks, can be a reflection of personality. One of the key concerns of captive animal husbandry is the social environment, as it is regularly modified and can shape the social behaviour of the animals in question in different ways. In this thesis I explore how meerkat, *Suricata suricatta*, social dynamics and individual positions may differ between wild and captive groups; I explore personality in the context of social networks and, lastly, I explore how physical and husbandry factors vary across enclosures and how this corresponds to a variation in the social structure of meerkats.

Differences were found between the fifteen groups of captive meerkats when considering association networks based on foraging and resting. Some of these differences could be explained by intrinsic differences between the groups. An individual's position within a network as described by their centrality and closeness measures could be predicted by their age and status, but rarely by their sex. I did not detect consistent patterns of non-random assortment amongst group members based on their sex, age or status.

Groups of wild and captive meerkats differed in various aspects of their social network structure. Such differences may be due to individuals occupying different network positions and the difference in their 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. 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.

Principal component analysis of the four personality traits revealed two personality dimensions, Friendliness and Aggressiveness, across the fifteen groups of meerkats. However, within a subset of my data (five groups), Friendliness was the only measure that robustly captured consistent individual differences across at least one year. A relationship was not found between attributes and personality dimensions due to age, status, and sex. Individuals with high Friendliness scores were more central in networks of foraging competitions. Aggressiveness did not explain an individual's position in any form of interaction. There was no evidence that meerkats preferentially associated with or avoid others based on each of their personality scores.

A relationship was found in the way animals associate with one another in the resting network based on the size and complexity of the enclosure and the type of shelter. Individuals were less likely to associate with others of the same sex or dominance status in enclosures that were larger or more complex. All the six external measures (the size and complexity of the enclosure, the type of barrier and day shelter, environmental enrichment frequency and human contact) influenced how individuals interacted with other group members within grooming, playing and dominance networks. In general, it seems to be that the key features to address in meerkat management in zoos are those of enclosure size and complexity (and perhaps provision of adequate shelters). Providing captive meerkats with more naturalistic and complex enclosures can help to preserve their natural social system.

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DECLARATION

I hereby declare that I am the sole author of this thesis with the advice of my supervisor being provided on drafts of all chapters. This thesis contains four data chapters and three general chapters.

Chapter One

Introduction

General Introduction

Social relationships with social partners and other communities can be defined by the dynamics generated through individuals' optimum strategies (Danchin et al. 2008). The association structure of a group is shaped on multiple levels (McDonald & Pizzari 2015). First, it depends on the individual members' attributes such as sex, status and age (Croft et al. 2008). Second, it depends on the group composition and the relationships between its members, such as the mix of its members (Michelena et al. 2008), social assortativity (Croft et al. 2005), group size (Durrell et al. 2004) and patterns of kinship (Carter et al. 2013). Third, it may be shaped by external ecological processes that include intergroup encounters (Drewe et al. 2009), ectoparasite infection levels (Madden & Clutton-Brock 2009), food availability (Foster et al. 2012), and stimuli from other animals (Hosey et al. 2013).

Much work on social associations and interactions has tended to focus on single groups, which may illustrate only group-specific factors with no comparison of patterns among groups within a single species. Most of the studies in animal social networks focus merely on one relational system that depends on interactions or associations, such as patterns of grooming or instances of co-feeding (Levé et al 2016; Firth et al. 2017), but very few studies utilize them simultaneously and compare them (e.g. King et al. 2011). Furthermore, little attention has been paid to how individual behaviour and captivity conditions influence the more general social structure of captive animal groups (e.g. Kanngiesser et al. 2011; Rose & Croft 2017). Research is necessary on these factors and their effects upon individual and group-level behaviour to reveal more about social behaviour in captive conditions and its potential welfare outcomes. Rose and Croft (2015) highlight the validity and usefulness of SNA application to populations of zoo-housed animals with the purpose of providing insight into how husbandry can alter social structure and the social bonds between individuals in a group. Moreover, Dufour et al. (2011) emphasise the significance of such analyses to understand how social organizations may possibly be disrupted after modification or relocation in group structures.

Meerkats, Suricata suricatta, are group living mammals whose social structure in a wild population is fairly well understood (Drewe et al. 2009; Madden et al. 2009; Madden et al 2011). They are also commonly exhibited in zoos and thus provide a good system in which to explore how social structures in captive animals differ from their wild counterparts and what the causes and consequences of such differences may be for individual welfare.

In this thesis I address these points by asking first how association dynamics work in captive populations of meerkats, where I looked at more subtle social relations in order to extend the understanding of the structure of social networks among meerkat members (Chapter 3). I then ask how social network structure (associations and interactions) may differ in different conditions: wild and captive (Chapter 4). I subsequently ask how other intrinsic factors, such as personality (Chapter 5), and extrinsic factors, such as husbandry and enclosure design (Chapter 6), may influence social network structure.

The following literature review explores relevant information in animal social networks and factors influencing its structure. In section 1.1 the complexity of social organization is reviewed with particular focus on animals held in a confined environment. In section 1.1.1 I describe measures that can be used to characterize animal network structure and introduce two distinct features of social dynamics: interactions and association networks. In section 1.2.1 the potential factors influencing an animal social structure are reviewed, while in section 1.2.2 I concentrate on the role of animal personality in structuring social networks. The importance of measuring animal welfare using social network analysis and personality assessment is reviewed in section 1.3. Information about the behavioural ecology of meerkats is presented in section 1.4.

1.1 Complexity and nature of social dynamics

Substantial research has been done on the group living phenomenon in which animal formation behaviour has been used as a study system (Krause & Ruxton 2002). At present, we are familiar with several definitions and categorizations of group living. For instance, Wilson (1975) defined a group as “a set of organisms belonging to the same species that remain together for any period of time while interacting with one another to a much greater degree than with other conspecific organisms”. A group formation has been characterized by many authors as a familiar social system that takes place in a variety of taxa and which entails a trade-off of cost and benefits (e.g. Majolo et al. 2008; Meldrum & Ruckstuhl 2009; Polizzi et al. 2012). While individuals may benefit from characteristics of group life, such as defence against predation and, increased foraging efficiency (McFarland 1998), there are also some potential costs that they have to live with, for instance, greater risk of contracting diseases and parasites and more competition for food and partners (Alcock 2009).

Various costs and benefits of group living in foraging, grooming and other social behaviours may be taxon-specific; however a number of generalities come into sight, such as the size of the group. Larger groups are assumed to face greater competition within group foraging due to the rapid exploitation of resources or the intrusion of other group members (Grove 2012). When group size increases, grooming time may become more concentrated on fewer members of the group because of the demand for other essential activities such as foraging (Dunbar 1991; Lehmann et al. 2007)

One of the key aspects of group living success, within highly structured societies, is division of labour (Fewell 2010) and cooperation in the care of offspring (Hall & Halliday 1998). Additional individual functions can be nest construction and guarding of colonies (Barnard 2004).

Social context may influence decision making and add circumstantial complexity to sorts of interactions between individuals and which, in turn, may result in regulated estimation of individual relationships or resources (Whitehead 2008). Social relationships will be structured both by cooperation and by competition, and are expected to reveal some degree of coercion or compromise as individuals manipulate interactions and associations with their companions (Pusey & Packer 1997). The complexity and nature of interactions among such individuals living in social groups is highly varied (Manning & Dawkins 2012). Individuals will adopt optimum strategies and generate dynamics that will define their social relationships with social partners and other communities (Danchin et al. 2008).

1.1.1 Social dynamics in captive conditions

Social organization is a complex phenomenon that emerges from patterns of individual dyadic relationships within a population (Manning and Dawkins, 2012). Such organization will be formed by different frequencies and intensities of interactions adapted to the existing ecological circumstances (Whitehead, 2008). In the wild, the structure of the environment acting simultaneously with factors like demography, phenotype, and predation pressure can be crucial in shaping certain properties of the social network such as stability, fidelity and subgroup size (Webster et al., 2013). For instance, seasonal separation and subsequent re-integration of males and females can be the reason for changes in a wild group composition (Whitehead 2008). Additionally, the group variation size is self-regulated through a cost-benefit balance where individuals will leave or join the group depending on the cost or benefits that they face within or apart from the group (Estevez et al. 2007). However, this possibility for self-regulation does not exist in the captive environment. In captivity, the composition of a group is predominantly shaped by the artificial introduction and removal of individuals, which is done for a variety of management reasons such as breeding programs and veterinary care (Hosey 2005; Schel et al. 2013) or prevention of animal overcrowding (Plowman et al. 2005) and aggression (Hinton et al. 2013). These composition alterations are likely to influence the group network function or efficiency and, thus, the group level stability (Wey et al. 2008).

The complex dynamic nature of many animal societies makes it particularly challenging to fulfil the needs of social group-living species. In zoos of high standards, social species are maintained in social groups of appropriate size and composition matching natural conditions (Stroud 2007). However, this is not ubiquitous, and there is room for further improvement in species-appropriate group compositions within captive husbandry protocols and management practices for improved animal welfare (e.g. Hosey 2005; Price & Stoinski 2007; Mattiello et al. 2014). Group size has been regarded as a key feature in influencing and maintaining social groups in captivity successfully. Constraints on group size in captivity are lower because resources are freely available (Price and Stoinsky, 2007). However, it is clear that the management of captive social groups has to be carefully done and constantly monitored, as inappropriately sized groups (Price and Stoinsky, 2007) or sex ratios (Glatston 1997) can have negative consequences on the behaviour, reproduction and welfare of animals. In a study on captive brown bears, *Ursus arctos*, looking at social conflicts in a large number of different locations (various zoological parks) (Mountaudouin & Le Pape 2005), it was found that in groups with no more than two bears housed together, social relationships were more playful and less agonistic. A different study looking at influence of internal factors effects (such as age and sex) on the social behaviour and maintenance of captive groups of gorillas, *Gorilla gorilla gorilla* (Stoinski et al. 2004; Stoinki et al. 2013) found that keeping smaller all-male groups of similar age may decrease the likelihood of escalated aggressions. Correspondingly, Mallapur et al. (2005) suggest in their work on lion-tailed macaques, *Macaca silenus*, that housing males in groups containing a large number of females and young may reduce stress levels because of the higher levels of allogrooming.

The physical environment of captive animals may seem simple (Huntingford 2004) but it is actually multifaceted due to daily management practices and captivity conditions which can play an important role in the change of animal behaviour and welfare. For instance, a small and poorly furnished enclosure may limit possibilities for exploration and foraging behaviour, as well as founding low playing episodes and social interactions with conspecifics (Martín et al. 2016). Buchanan-Smith et al. (2013) have a different view regarding enclosure size; they explain that intra- and interspecific interactions of animals in captivity may be multiplied because they find themselves in closer proximity than in the wild due to space restricted enclosures. Furthermore, Valuska and Mench (2013) state that animal aggression dynamics may intensify as inter-individual distances in small enclosures are reduced because of physical barriers (zoo cages or fences). However, there is some discrepancy in the literature regarding the size of the enclosure and the animals' behaviours. Some authors state that larger enclosures can give animals the freedom to choose whom they associate with and to express their natural fission-fusion social behaviour (e.g. Schel et al. 2013). Other authors have found not enclosure size per se, but rather the quality of the space, to have an effect on animal social behaviours (e.g. Herrelko et al. 2015). Ross et al. (2011a) argue that, while there is a general statement about welfare enhancement by providing more space for captive animals, the quality of space can be as, or even more, important as the quantity of space. They state that animals may be highly selective in the use of their enclosure, highlighting, the importance of the environmental complexity and animal preferences.

1.2. Measuring social structure using Social Network Analysis

Between the 1930s and the 1970s, work on cognitive and social psychology led to research on 'group dynamics'. Subsequently, anthropologists and sociologists worked on Radcliffe-Brown's concept of social structure, where in turn a serious exploration started to look at the 'fabric' and 'web' metaphors of social life (Scott 2000). A step forward on a well-developed methodology of social network analysis occurred during the 1960s, and throughout the 1970s a large amount of specialist applications and technical work suddenly focussed on the metaphor of the social network (Scott 2000).

Network analyses of social systems are applied in humans to study, for instance, disease transmission and information flow (Rowell 1970). Network analysis was used in non-human vertebrate societies during the very beginning of the 21st century, where scientists started to apply it in species such as dolphins, fish and primates (Whitehead 2008). Nowadays, analysis in animal populations investigates a range of topics, such as preferences in group-joining decisions, the impact of social networks on animal collective motion, and roles that individuals play in their social network (Reddon et al. 2011; Bode et al. 2011; Lusseau & Newman 2004), to name a few. Krause et al. (2015) define a social network as “any number of individuals interconnected via social ties between them”.

Social structure results from behavioural interactions between individuals (Rowell 1972) that exist over some period of time (Olsén 1968). Additionally, such individuals compose an inter-individual association network that may vary in strength, type and dynamic. The structure of this social network can be influenced by behaviours present in, for example, foraging, mating, guarding, and within the development and preservation of cooperative activities (Croft et al. 2008).

Network analysis is a valuable tool for studying the interaction among individuals which are dependent on one another’s networks (Hobson 2016) and is applicable to almost any species (Pinter-Wollman et al. 2013). Analysing social networks can be, nonetheless, rather complicated as individuals and their links are non-independent (Croft et al. 2011). Croft et al. (2011) state that an individual’s network strength is not independent from the network strength of other individuals in the group, so this detail requires appropriate consideration when analysing data and relevant null hypotheses.

Social network analysis can be a very useful tool to study animals in captivity where some features of the captive environment help to evade sampling issues and continuous fine-scale interaction data which is difficult to collect in the wild (Clark 2011). Group sizes in captivity are usually smaller and close-range, detailed observations can be achieved more easily over a sustained period (Clark 2011). There is a vast range of social analysis options with captive populations, such as the analysis of shifting dominance hierarchies and triadic interactions (Whitehead 2008). There may be, however, some disadvantages with such populations. For instance, social structures of small populations in unnatural habitats can be strongly influenced by particular individuals and events (Whitehead 2008).

Most of the measures to characterize network structure are node-based measures in which the majority of these are centrality measures that include: outdegree, indegree centrality, betweenness, closeness, clustering coefficient, among others (Krause et al. 2015). In order to characterize an entire social network network-level measures are commonly used, such as density, dyad census, degree distribution/sequence, and correlational analysis of assortativity (Krause et al. 2015). Most of all these measures are used in this thesis.

Essentially, social network analysis assesses the relationships (''edges'' or ''links'') among different individuals (''nodes'') (Croft et al. 2008; Templeton et al. 2011). Two classes of relational data may be considered as the basis for an animal social network. One class can be defined by pair-wise relations based on associations between individuals, which may be considered to be associating when they are in the same social group, roost or nest. A second class can be outlined by edges based on an observed behavioural interaction between individuals, such as competitive or cooperative pair-wise interactions (Croft et al. 2008) (information about analysis and methodology are discussed in more detail in Chapter 2).

Interaction networks are considered to be the fundamental element of social behaviour and can be defined structurally or by consequence (Whitehead 2008). The fitness of individuals within social groups can be shaped by such emergent patterns among individuals that occur dynamically across space and time (Pinter-Wollman et al. 2013). Individuals within a group will normally interact non-randomly, which can be due to multiple behavioural and ecological factors, such as limitations on dispersal and spatio-temporal variation in the distribution of resources (McDonald & Pizzari 2015). Additionally, social interactions may differ in their frequency, duration and type. These may include cooperative, sexual and antagonist interactions, which will depend on factors such as body size, sex, age, parasite load, and the individual's dominance (Croft et al. 2008). For example, grooming, being one of the most common interactions studied within networks due to its importance for reinforcing social bonds, has been found to be correlated with kinship, age, and status, where individuals with a higher social status occupy more central positions in the network (Kanngiesser et al. 2011).

An alternative basis for edges between individuals is their patterns of associations in which their proximity to each other is considered. Carter and colleagues (2009) state that "when individuals form groups non-randomly, defined by a spatiotemporal measure of proximity, the society is said to be structured" and therefore, the individual association patterns can be used to exemplify a species social system. The motivation of maintaining close proximity to group members, considered as an affiliative social behaviour, is related to strengthening group cohesion and founding and preserving preferential relationships (Patison et al. 2010). Zoologists have been measuring the strength of associations between social individuals in which assumptions are made that physical proximity between members of a group signifies social affiliation and that the amount of time together correlates with the strength of affiliation (Bejder et al. 1998). As described by Croft et al. (2008), "social bonds may last for years or just minutes or seconds". Physical proximity between individuals of a group is a requirement for social interactions and the developing and maintenance of relationships (Vonhof et al. 2004). Juveniles, for instance, have to face tremendous challenges such as travelling through complex environments, finding suitable breeding territories and mates, and learning to avoid predators in addition to learning and developing the behaviours necessary for maintaining social relationships with partners and social groups (Templeton et al. 2011; White et al. 2012).

1.2.1. Factors influencing social network structure

Within complex animal societies, different characteristics, such as an individual's age, sex, body size, kinship and the size of the group can influence the type of interaction among individuals. These interactions, in turn, will influence the network structure (Aschwanden et al. 2008; Croft et al. 2008; Whitehead 2008). These factors affecting networks based on interactions may pertain to the attributes of individual group members. For instance, Ross and colleagues (2011) report in their study on a wild meerkat population that differences between individuals in their position within the network of foraging competitions were generally due to the individual's age and mass. Younger and lighter individuals presented a higher indegree centrality (received higher overall rates of foraging competitions) than older and heavier individuals. Kanngiesser et al. (2011) investigated the grooming network of a captive chimpanzee group and found a correlation with age and kinship (especially females) and that central individuals, being the ones with higher social status, played a key role in maintaining the cohesiveness of the network.

Alternatively, networks may be shaped by factors beyond the individual and instead depend on external ecological factors or group-level influences. Variance in group size has been found to influence aggressive interactions in captive groups (Erwin & Erwin 1976; Estevez et al. 2007; Sosnowka-Czajka et al. 2007) that may result in either destructive aggression (Erwin & Erwin 1976) or a modification of dominance relationships which are crucial to the maintenance of group cohesion (Krause et al. 2015).

Similar factors may shape networks based on associations. Studies of the variation of affiliative relationships have found that animals frequently form relationships based on kinship, rank and sex. Individuals may prefer to affiliate with kin, the same sex, and with similarly ranked animals (Weinsten & Capitanio 2008). For instance, farm animals (i.e. cows and sheep) have been shown to form preferential associations where certain individuals seem to prefer the company of a specific member (mostly of individuals of the same age and sex) of the group over other ones (Durrell et al. 2004). Alternatively, a study on sleeping associations and nesting groups in captive chimpanzees showed that males associations were influenced by kin (Lock & Anderson 2013), and a study on captive dolphin calves associations observed factors such as age and individual calf behaviour having a larger influence than others factors such as kin (Levengood & Dudzinski 2016).

External ecological factors such as predation threat can also influence association networks. In a study on proboscis monkeys, *Nasalis larvatus*, Matsuda et al. (2010) showed that on non-flooded days, when predation threat increases from terrestrial predators such as clouded leopards, male groups frequently slept closer to other male groups on the riverside trees. Contrastingly, on flooded days, male groups slept away from other groups in the inland forest, as a result of reduced predation threats.

1.2.2 Additional factors influencing social network structure: specifically personality

It is important to clarify the different terms used in the literature of animal personality research in order to continue with this subject. In general, two main terms (temperament and behavioural syndromes) have been used between different fields: Behavioural ecology, Ethology, Primatology, Psychobiology, Comparative Psychology, among others. ‘Temperament’ is defined as a tendency to react to stressful stimuli that can be identified in early infancy (Weinstein et al. 2008). ‘Behavioural syndromes’ refers to suites of correlated behaviours across different contexts (Sih et al. 2004; Bell 2007). The terminologies of ‘trait’ and ‘dimension’ are also used interchangeably with personality and behavioural terms. A personality/behavioural trait refers to specific traits of individuals that are consistent throughout time and environmental conditions (Réale & Dingemanse 2010) and personality/behavioural 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 behavioural syndromes and temperament, and will use the terminologies personality trait and personality dimension according to their definition.

Personality may be considered as a complex and refined characteristic unique to humans. However, evidence on such individual variation in traits has been recognized to be present in a variety of taxa, ranging from fish to monkeys, to molluscs (Bell 2007). Behavioural ecologists assume that animal behaviours are adaptations that result from long-term selection pressures which have adjusted the individual’s responses to specific situations (Réale et al. 2010). For instance, individuals of many species behave in a characteristic manner; individuals may differ in aggressiveness, risk-taking, exploratory behaviour and general activity in a variety of contexts (Réale & Dingemanse 2010). Studies have shown how activity parameters can be influenced by different personality domains. Bergvall and colleagues (2010), for example, highlight within their study how foraging behaviour in ungulates was affected by boldness where bolder individuals tended to eat novel food. Magnhagen (2007) showed how individuals adjusted their exploratory tendencies to the boldness and exploratory activity of other individuals in the group. New questions in relation to the implications of personality on the ecology of animal populations, mainly their social systems, are increasing due to new discoveries.

At present, two different approaches have been developed in order to assess animal personality in a large range of species: behaviour coding, where animal responses are coded during novelty tests or during observations and assessments under natural conditions, and personality trait ratings, which are subjective ratings of behavioural traits (Korpela 2011, Vazire et al. 2007). The first animal personality ratings were done on primates due to their similarity with humans; personality descriptor adjectives are still taken from human literature (Pederson et al. 2005; Weiss et al. 2012). Research on animal personality focuses on within-species (or intra-species) comparison and cross-species comparison. Levels of personality are compared between members of the same species in within-species comparison, while a common trait to both species is usually considered in cross-species comparisons (Gosling 2001). Gosling (2001) mentions the importance of differentiating both types of variation: within-specie variation can be used to understand individual differences in traits that enable us to ask questions about the selective benefits of those traits, and cross-species variation can be used to explore the origins and adaptational significance of particular traits.

Personality traits are often consolidated into larger dimensions or factors using data reduction techniques such as Factor Analysis (FA) or Principal Component Analysis (PCA). PCA is commonly used in animal behaviour research. Its objective is to keep the most important summary scores by reducing the numbers of measures to a small set. Firstly, correlations between the original variables (personality traits) are calculated; secondly, such correlations result in a new group of linear combinations (principal components) by exposing them to specific transformations; and thirdly, loadings of the original variables on these principal components are calculated which will represent the correlation between these two (Budaev 2010). FA has the same function as PCA, however the approach is different as it uses a mathematical model to achieve a reduction of the variables to dimensions (Widaman 1993; Kline 1994; Jolliffe 2002). More information on these issues can be found in Chapter 2 (section 2.5).

Many aspects of animal behaviour and ecology, including interactions with conspecifics, habitat use, and willingness to take risks, can be a reflection of personality (Schuett & Dall 2009). While numerous studies have investigated personality traits, the maintenance of personality variation within a population and their responsible processes are still not well understood (Cote et al. 2008). Similarly the ecological and evolutionary consequences of personality differences in social contexts remain mostly unknown (Schuett & Dall 2009).

Literature suggests that consistent individual differences captured by a measure of personality can affect an individual's interaction with other members of a social group, as well as the former can be influenced in turn by the social dynamics (Krause et al. 2010; Wolf & Krause 2014). A particular personality type can occupy influential network positions compared to others group members, thus impacting within-group network dynamics (Modlmeier et al. 2014). The frequency and distribution of these interactions within the animal social network can be a consequence of individual personality (Pike et al. 2008). For example, more active individuals (a trait connected to Sociability and Friendliness dimensions; Weiss et al. 2011) may have more encounters with other members of the group than aggressive individuals (Pike et al. 2008).

Similarly, an individual's behavioural type (personality) can act as an important factor in shaping assortativity. For example, some individuals might be more aggressive or bold in different contexts and may avoid (Pike et al. 2008) or associate with individuals with the same characteristics (Croft et al. 2009). Numerous studies have investigated how individuals assess the relative benefits and costs of associating or interacting with others within the group. For instance, the option to associate with a bolder/aggressive individual could influence overall interactions and social composition of a group and also cause a reduction in the group's overall mating (Sih & Watters 2005).

A behavioural trait expressed by the companion can greatly influence the other's behaviour who may decide to adjust his/her behaviour in order to gain individual fitness. Michelena and colleagues (2008) show for example how the influence of a bold individual on social interactions can have important implications for group behaviour and their foraging dynamics in inconsistent environments. They show in their investigation that groups with bold sheep tended to split into subgroups in a way to minimize interference competition in foraging. In a zoo environment, similar findings have been found in chimpanzees (Massen & Koski 2014), where chimpanzees associated with others of similar Sociability dimension. Association dynamics facilitated mutual benefits in cooperative contexts (such as grooming and coalitions) among individuals with a similar personality dimension.

1.3 Animal welfare and the importance of measuring social network and personality in captive animals

The term ‘animal welfare’ was first utilised between the 1960s and 1980s but was not, at that time, defined properly (Broom 2011). The Brambell Report (1965), in which the Five Freedoms outline five basic aspects of animal welfare, had a noteworthy influence in many countries (Broom 2011; Ohl & van der Staay 2012) and lead to the creation of legislation and standards managing farms, livestock husbandry systems, laboratory operations and zoological institutions (Ohl & van der Staay 2012; Whitham & Wielebnowski 2013). After the 1980s the concept of animal welfare was more widely used in science, in legislation and general discussion about the effects of the treatment of animals (Broom 2011). In the 1990s animal welfare was agreed upon as a scientific concept (Broom 2011). Currently, the term animal welfare is defined as ‘the state of an animal as regards its attempts to cope with its environment’ (Hill & Broom 2009). It acknowledges that the subjective state of an animal may differ between individuals and that it may vary over time (Hosey et al. 2013). More simply, welfare may be considered as “the quality of life as perceived by the animal” (Bracke & Hopster 2006). The modern study of animal welfare incorporates evolution, animal behaviour, behavioural ecology, cognitive science, neuroscience and consciousness studies (Dawkins 2006).

Much progress has been made in developing new indices of animal welfare and it has been acknowledged that there is no single measure that can be used by itself (Dawkins 2004). Identifying and constantly improving the most suitable welfare assessment techniques can be essential in order to ensure acceptable standards of welfare in zoos (Maple & Perdue 2013).

Animal welfare assessment usually incorporates physiological indicators (hypothalamic-pituitary-adrenal axis, or HPA, respiratory and heart rates), health indicators (prevalence of disease; Whitham & Wielebnowski 2013), and behavioural measures (expression of behavioural repertoires, development of abnormal behaviours, inability to express specific behaviours; Hosey et al. 2013). Common methods of zoo animal welfare assessment also include consideration of life history and events (fecundity and longevity measures; Hosey et al. 2013), the resource-based approach (measures of the environment and management practices of institutions; Whitham & Wielebnowski 2013) and the cognitive approach (effect of affective state on cognitive processes; Yeates & Main 2008; Mellor 2015).

Less attention has been paid to more complex assays of animal behaviour as additional measures of animal welfare in captivity. These could include individual-centric metrics, such as animal personality (Tetley & O'Hara 2012) or measures describing interactions between individuals typified by social network analysis (Rose & Croft 2015). Some authors encompass the assessment of social interactions within behavioural measures (e.g. Hosey et al. 2013; Maple & Perdue 2013) or as an indirect measure of welfare (e.g. Rees 2015). Social network analysis helps us to identify the different traits of social groups and which network characteristics are important for group success (Wey et al. 2008). Social network analysis has been recognized to have a clear potential in application to zoo animal management (Rose & Croft 2015). Group management in a zoo can be quite a complicated task, as it might involve the addition and/or removal of members of a social group which can sometimes introduce unnecessary aggression (Maple & Perdue 2013). Understanding how social interactions can influence the behaviour of others within their social network can have many potential effects on the welfare of a group (Makagon et al. 2012). Social network analysis, besides of providing an effective strategy to track changes in group social dynamics, can provide a valuable predictor of deleterious aggression and significant instabilities within a group, helping managers to prevent severe outbreaks of aggression and violence before they occur (McCowan et al. 2008). Schel et al. (2013) explains how such analysis can act as a powerful tool to document and advise management decisions of the integration of new individuals or the removal of a specific individual on the social group. Moreover, comparative analysis of social networks and inter-individual distances can be an important tool to understand the different responses of animals to change and can help to predict how social organizations may possibly be disrupted after relocation (Dufour et al. 2011). Analysing the social structure of a group within multiple housing areas, such as indoor and outdoor housing, breeding sites, and enclosure furnishings, will aid enclosure designs with the objective of reducing, for instance, antagonistic encounters and thus maintaining the welfare of the individuals housed in the exhibit (Rose & Croft 2015). Additionally, the use of social network analysis is considered very useful in breeding programmes. Rose and Croft (2015) state that applying such analysis can help to identify animals with strong bonds with others that can be moved together to increase the success of groupings that are made for breeding purposes.

Personality has been shown to be influential in habitat use, interaction with conspecifics (Boon et al. 2008), mating strategies, parental care, cooperative breeding (Réale & Dingemanse 2010) and many aspects of an animal's behaviour and ecology, hence the importance of the research on this subject. Smith and Blumstein (2013) remark on the importance of the study and management of animal personalities in conservation biology because personality variations can be related to the genetic variation of a population. They explain that personality variation preserves higher levels of genetic diversity because of the fluctuating selection pressures. This variation consequently permits populations to adapt to changing environmental conditions and decrease their risk of extinction. The application of personality research in captivity has made substantial contributions to animal management science as a basis for informing decisions about group composition (Tetley & O'Hara 2012) and selecting appropriate enrichment conditions (Freeman & Gosling 2010). Stoinski et al. (2004) point out that given the large range in personality characteristics, it is likely that some personality types may be better suited for some individuals living together than others, which makes personality assessment a significant tool for zoo management decisions. Also, Powell and Gartner (2011) highlight that personality should be taken into account when designing housing environments and husbandry practices and that personality can be used to assess the value of enrichment for each individual. For example, a bold individual should be given more novel items to explore and a shy animal might need more places to hide. Summarily, the study of personality behaviour can be highly applicable to a range of group-living social captive mammals in which a better understanding of individual differences in behaviour may lead to differences in welfare.

1.4 Study system: meerkats, *Suricata suricatta*

Meerkats are cooperatively mongooses living in stable social groups (Bousquet & Manser 2011) of 2 to 50 individuals in the arid regions of southern Africa (Doolan & Macdonald 1996; Clutton-Brock et al. 1999a). Meerkat groups typically consist of a dominant pair, a number of subordinates of both sexes, and one or more immigrant males and pups (Sharpe 2005b; Drewe et al. 2011) The dominant pair contributes 80% of the litters (Griffin et al. 2003), which are reared by a variable number of subordinate helpers (Bousquet & Manser 2011). Individuals that cannot occupy the preferred social role in the group remain as subordinates and specialize in cooperative behaviours to increase their inclusive fitness (Carter et al. 2014). Meerkat are strictly diurnal, by night they shelter in highly structured warren systems. Pups spend around 30 days underground in a breeding burrow, and upon emergence they accompany the group on foraging trips (Bousquet & Manser 2011). Males around 1-2 years old tend to leave their natal group to explore the local area and may successfully immigrate into groups (Jordan 2007), whereas females typically remain in their natal group or are evicted by the dominant female (Kutsukake & Clutton-Brock 2006a). Meerkat group compositions remain relatively stable for years despite intergroup migration by males or fissions (Clutton-Brock et al. 2002; Young et al. 2005). They are characterized by foraging cohesively (Bousquet & Manser 2011) and interacting frequently, mutualistically and antagonistically with other individuals exclusively from within their group (Madden et al. 2009).

Meerkats are included in a large number of zoological parks due to their popularity. They are kept in a variety of group structures and housing conditions. Various features of captive meerkat populations have been studied, such as alarm call behaviour (e.g. Hollén & Manser 2007), physiological stress measures (e.g. Scott et al. 2017), behavioural response to zoo visitors (e.g. Sherwen et al. 2014), and reproductive success (e.g. Newman et al 2016). Previous work on meerkat social behaviour, mainly in wild populations, has looked at individual differences (e.g. sex, age, status, personality and weight) and other attributes (e.g. group size) that can influence behaviours such as mobbing (Graw & Manser 2007), aggression (Hodge et al. 2009), alarm call (Hollén & Manser 2006), scent marking (Jordan 2007), reproductive competition (Clutton-Brock et al. 2006), and cooperative behaviour (Clutton-Brock et al. 2002; English et al. 2010; Carter et al. 2014). Yet, few empirical studies have investigated the factors affecting social dynamics within these animal societies (see Drew et al. 2009; Madden et al. 2009, 2011; Newman et al. 2016).

1.5 Thesis preview

This thesis will investigate how captivity may shape the social structure exhibited by group-living animals, specifically meerkats. In Chapter 2 I describe the methods that were used in the present study, followed by four research chapters: 3, 4, 5 and 6. In Chapter 3 I ask how captivity may influence patterns of association based on foraging and resting. In Chapter 4 I reiterate the work of Madden et al. (2009, 2011) to explore how network structures and individual positions in networks differ between wild and captive groups of meerkats. In Chapter 5 I explore personality in the context of social networks across fifteen captive groups of meerkats. In Chapter 6 I explore how physical and husbandry factors vary across enclosures and how this corresponds to a variation in the social structure of meerkats. And finally, in Chapter 7, I bring the results together and provide a general discussion. By understanding the social structure of a common captive group-living animal and comparing and contrasting it with their social structures observed under natural conditions I explore how the welfare of captive animals may be improved through consideration of their social behaviour.

Chapter Two

General Methods

2.1 Study animals and field sites

Fifteen captive groups of meerkats comprising 113 individuals were studied from September 2011 to September 2013 in Zoological parks in the UK and Mexico: Africam Safari, Bristol Zoo Gardens, Cotswold Wildlife Park, Flamingo Land (two groups), Longleat Safari Park, Morelia Zoo (two groups), Paignton Zoo & Animal Wildlife Park, Paradise Wildlife Park (two groups), Shaldon Wildlife Trust, Shepreth Wildlife Park, Twycross Zoo and West Midland Safari Park. A second period of observations were carried out in five of these Zoological parks: Africam Safari, Bristol, Shaldon, Shepreth and West Midland Safari Park. There are large populations of meerkats in captivity, which provides a good opportunity to take a subsample of these collections to use as study systems.

The selection of all the zoos and parks was done by searching for zoos holding groups that comprise mixed sex/age individuals, that were available for the study and for which the travel expenses were affordable (see table 2.2 for more information about zoo and parks management). Due to the husbandry routines of each zoo and the basic logistics, it was impractical to carry out the observations in all captive meerkat groups around the same seasons and hours as those of the wild meerkat project done by Madden et al. (2009; 2011; Table 2.1). 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. I observed each group for a total of 20 hours over the 4 days of observations. Data were collected on all members of the group. In order to identify them, 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 (Fig 2.1).

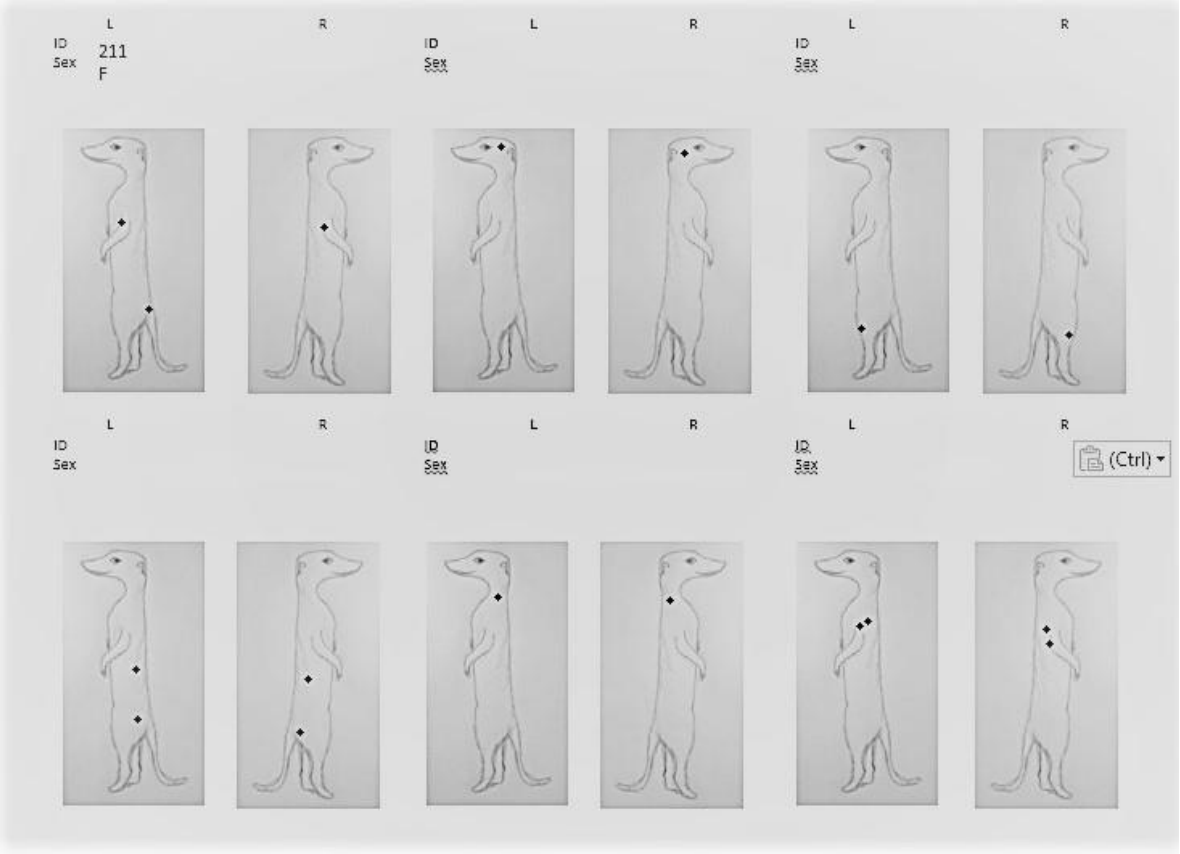
2.2 Individual attributes

Three attributes were considered for all individuals: age, sex, and status. Age of individuals 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 reports. With those for which I had no information on sex, I determined it 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 over other group members with behaviours such as: chin marking, chasing, charging, hip-slamming, 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 & 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 (Clutton-Brock et al. 2008). In captivity, humans actively manage group composition and may sometimes remove individuals competing for dominance so as to reduce conflict between individuals and avoid escalated aggression and injuries. As a result, some of the captive groups did not consist of a typical composition of members seen normally in the wild. That is, some groups were made up of unrelated individuals or formed by just siblings.

2.3 Behavioural, association and interaction measures

Instances of social associations and interactions were collected during scan sampling and continuous focal observations. I collected pilot data in order to construct ethograms and decide on key common behaviours that I was likely to encounter regularly and hence, were worth focusing on (Table 2.3). These behaviours included: grooming, playing, foraging, foraging competitions, resting, and dominance behaviour.

Figure 2.1 Representations of meerkats designed to help individual identification through their naturally distinctive markings or through hair dye marks.



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 back and forth between partners was not considered. When grooming was separated by intervals of more than 1min, a new grooming interaction was defined.

A foraging association was recorded when two individuals foraged in close proximity (within 1m of each other). All these associations were recorded as dyads, not considering how long the individuals foraged close to other individuals. When foraging was separated by intervals of more than 1min, a new foraging association was defined.

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.

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. Events included any individual attacking or intimidating (hip slamming, chin marking, glaring, chasing, charging, pushing aside, threatening, etc.) others individuals competing and/or fighting for dominance.

A resting association was recorded when an individual lay down in a relaxed manner (lazy sitting, high sitting, sunbathing and sleeping) close to other member(s) of the group (when any part of the subject was in contact with a conspecific or within one body-length of a conspecific). Additional patterns of association, such as resting underground or whilst moving together were not measured.

A playing interaction was recorded when an individual acted playful toward another individual. Events included any individual clasping, grappling, mounting, pawing, wrestling, play chasing, etc. Play interactions were differentiated from aggressive ones when individuals maintained a playful context, in other words, when play markers such as role-reversing (individuals roll over regardless of their status or age), self-handicapping (individuals give their partner a competitive advantage), inhibited bites or bouncy and exaggerated movements were present throughout all the interactions.

2.4 Network measures and analytical methods descriptions

Social network analysis has long been used in different sciences; it fundamentally examines the relationships (known as “links”) among different individuals (known as “nodes”; Templeton et al. 2012) (Fig. 2.2). Castles et al. (2014) state that two principal categories have been developed to sample social interactions in animal populations: interaction and association methods.

Table 2.1 Observation protocol for wild meerkat groups by Madden et al. 2009, 2011.

Study site	Observation date	Observation time	Additional information
South of the Kalahari desert, South Africa (26°58'S, 21°49'E)	April 2007 July 2007 Observations were carried out for 3 days.	In the morning after the meerkats emerged from their burrows and at least 1hr before they re-entered their burrows in the evening.	Wild meerkats were habituated to accept close observation (<1m) from observers and were identified via small marks of hair dye.

Interaction methods are recognised to involve techniques based on behavioural interactions or observed physical contact. For example, such networks may be based on actions that one individual performs towards another such as one grooming another, one dominating another, or one giving something to another. In contrast, association methods (proximity) involve connections through spatial proximity or shared resource use. For example, such networks may be based on observations of two (or more) individuals sleeping together, or being at a feeder together. This method is generally used in aquatic animals or undemonstrative animals such as kangaroos, *Macropus giganteus*, because interactions may not be easily observed. Association and interaction techniques should be applied to a population at multiple time periods to gain the best understanding of the animal social environments (Castles et al. 2014).

In captive meerkats, my data on interactions included grooming, dominance, foraging competitions and play. I observed a total of 9,408 social interactions. These comprised 3,564 grooming, 772 dominance, 1,353 foraging competitions, and 3,719 playing interactions. My data on associations included foraging and resting. I observed a total of 14,012 social associations. These comprised 10,052 foraging associations, and 3,960 resting associations (Table 2.4).

Table 2.1 Observation protocol and zoo information.

Zoo (Study site)	**Observation dates**	**Observation times**	**Housing**			**Husbandry**		
			Furnishing	**Exhibition type**	**Feeding manner**	**Enrichment**	**Visitor contact**	**Management type**
Africam	January 2012 **Second observations:** November 2012	08:00/09:00 - 16:00/17:00	Natural setting. Natural tree branches and trunks. Rocks and sand.	Indoor off-show Outdoor visible to visitors.	Food provided indoors.	No	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
Bristol	June, 2012 **Second observations:** April 2013	08:00/09:00 - 16:00/17:00	Natural setting. Artificial and natural trees, trunks, rocks. Sand.	Indoor and outdoor visible to visitors. Public had visual access to the entire enclosure through a glass barrier.	Scattered in the outdoor enclosure on the floor and different furniture structures.	Yes	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
Cotswold	May/June 2012	08:00/09:00 - 16:00/17:00	Tree branches and trunks, artificial and natural rocks, sand.	Indoor off-show Outdoor visible to visitors through a concrete barrier.	Food provided indoors.	No	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
FlamingoG1	November 2012	08:00/09:00 -	Natural setting. Artificial and natural	Indoor and outdoor	Scattered in the outdoor	Yes	No	Animal caretakers enter the enclosure

		16:00/17:00	trees, trunks, rocks. Sand and stones.	visible to visitors. Public had visual access to the entire enclosure through a glass barrier (indoor) and by concrete barriers (outdoor).	enclosure, on the floor and different furniture structures.			(outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
FlamingoG2	November 2012	08:00/09:00 - 16:00/17:00	Artificial and natural trees, trunks, rocks. Sand and stones.	Indoor and outdoor visible to visitors. Public had visual access to the entire enclosure through a glass barrier (indoor) and by a concrete barrier (outdoor).	Scattered in the outdoor enclosure on the floor and different furniture structures.	Yes	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
Longleat	October 2011	08:00/09:00 - 16:00/17:00	Natural setting. Artificial and natural trees, trunks, rocks. Sand and stones.	Indoor and outdoor visible to visitors. Public had visual access to the entire enclosure through a glass barrier and fences. A walking path was present through the enclosure so	Scattered in the outdoor enclosure on the floor and different furniture structures.	Yes	Yes	Contact by visitors for feeding and petting. Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.

				visitors can walk through it.				
MoreliaG1	December 2012	08:00/09:00 - 16:00/17:00	Natural setting. Artificial and natural trees, trunks, rocks. Sand and stones	Indoor off-show. Outdoor visible to visitors through a concrete barrier.	Food provided indoors	No	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
MoreliaG2	December 2012	08:00/09:00 - 16:00/17:00	Natural setting. Artificial and natural trees, trunks, rocks. Sand and stones	Indoor off-show. Outdoor visible to visitors with a low concrete barrier.	Food provided indoors	No	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
Paignton	September 2011	08:00/09:00 - 16:00/17:00	Natural setting. Artificial and natural trees, trunks, rocks. Sand and pond.	Indoor and outdoor visible to visitors. Public had visual access to the entire enclosure through concrete barriers. The shelter (indoor) although out of reach, is visible to visitors.	Scattered in the outdoor enclosure on the floor	Yes	No	Animal caretakers enter the enclosure for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.

PWPG1	September 2011	08:00/09:00 - 16:00/17:00	Artificial trunks and rocks. Sand	Indoor off-show Outdoor visible to visitors through a concrete barrier.	Scattered in the outdoor enclosure on the floor and feeding by hand by caretakers and visitors	Yes	Yes	Contact by visitors for feeding and petting. Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarans when necessary.
PWPG2	September 2011	08:00/09:00 - 16:00/17:00	Artificial trunks and rocks. Sand and woodchips	Group off-display to visitors. Outdoor and part of the indoor enclosure was visible to observer	Scattered in the outdoor enclosure	Yes	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinaries when necessary.
Shaldon	September 2011 **Second observations:** April 2013	08:00/09:00 - 16:00/17:00	Artificial and natural trees, trunks, rocks. Soil	Indoor and outdoor visible to visitors. Public had visual access to the entire enclosure through wood and glass barrier (shelter).	Scattered in the outdoor enclosure	Yes	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding and occasionally they feed them by hand. They were also occasionally fed by visitors. Medical procedures were done by veterinarians when necessary.

Shepreth	July 2012 **Second observations:** July 2013	08:00/09:00 - 16:00/17:00	Artificial and natural trees, trunks, rocks. Sand.	Indoor and outdoor visible to visitors. Small shelter not visible. Public had visual access to the entire enclosure through wood and glass barriers.	Scattered in the indoor and outdoor enclosure	Yes	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
Twycross	March/April 2012	08:00/09:00 - 16:00/17:00	Natural bushes, trunks, rocks and soil.	Indoor and outdoor visible to visitors. Public had visual access to the entire enclosure through concrete (outdoor) and glass barriers.	Scattered in the indoor and outdoor enclosure	Yes	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.
WMSP	March 2012 **Second observations:** August 2013	08:00/09:00 - 16:00/17:00	Natural trunks, rocks and soil. Artificial structures	Indoor and outdoor visible to visitors. Small shelter not visible. Public had visual access to the entire enclosure through concrete (outdoor) and glass barriers.	Food scattered outdoors	No	No	Animal caretakers enter the enclosure (outdoor and indoor) for common husbandry routines such as cleaning and feeding. Medical procedures were done by veterinarians when necessary.

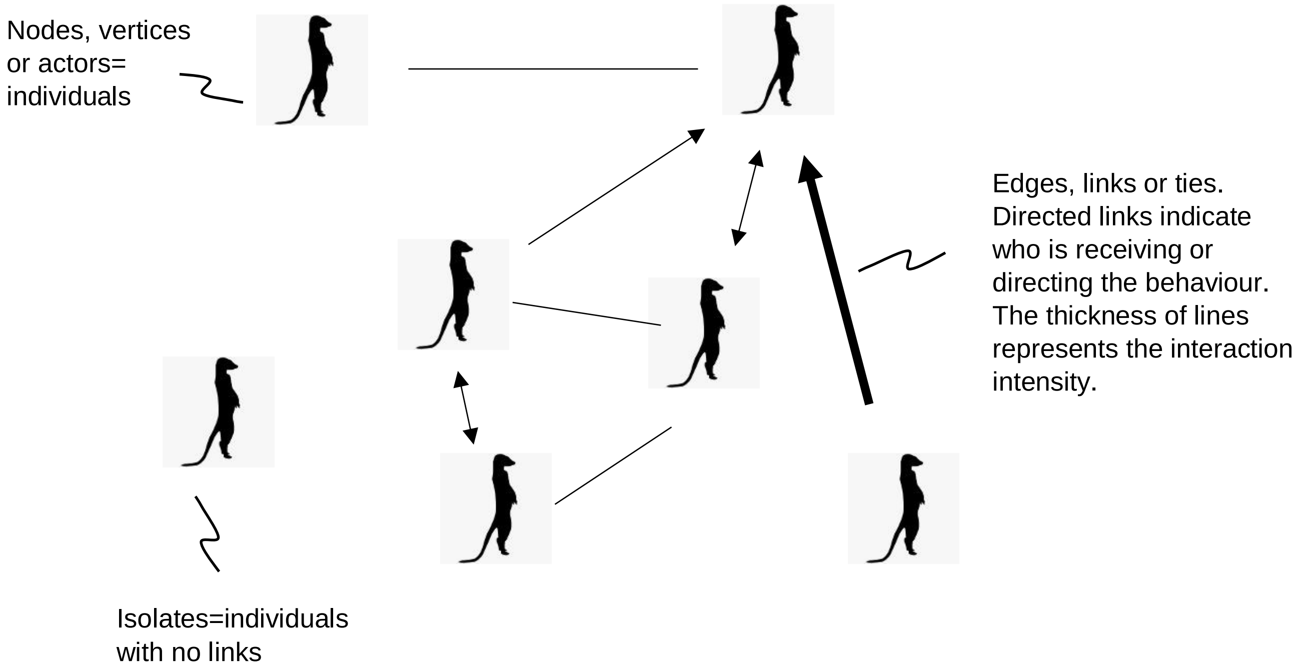
Table 2.3 Ethogram for *Suricata suricatta*

	Behaviour	**Definition**
	Allogrooming	manipulation of the fur of other individuals with the mouth, ears and mouth region with licking and smooth biting.
	Foraging	an animal is moving across the floor, with ducked body and lowered tail, while it is excavating the ground superficially.
	Attacking	biting a subordinate and possibly ultimately chasing 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.
	Hip-slaming	slamming the hip against the side of a subordinate.
	Threatening	an animal is growling while head and tail are lowered.
	Resting	a general, inclusive term for lying in a relaxed manner. It could include: Lazy sitting: the animal sits, with the lower extremities stretched forward, the trunk being folded forward, while the head touches the ground in between the legs. High sitting: the animal sits upright with the lower extremities and backside on the ground, while the upper extremities are bent in front of the body. Sunbathing: posture as high sitting but belly is clearly directed towards the sunlight. This posture enables meerkats to absorb energy in form of solar radiation. Sleeping: the animal stays in one place remaining in a relaxed posture with closed eyes and is not alert to environmental change
	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 holds another one tightly 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.
Wrestling	one animal adopts a submissive posture lying on its back while the other stands on or over it.

The ethogram was developed from a recompilation of several authors: Drewe, et al. 2011; Kutsukake & Clutton-Brock 2008; Santema & Clutton-Brock 2012; Sharpe 2005a, 2005b.

Figure 2.2 Fictitious social network of meerkats describing some representative factors in social network analysis.



Most of the following network descriptions are deliberately copied from Madden et al. (2009, 2011) methods to avoid any misinterpretation (see Table 2.5 for a summary and illustration of the SNA). *Degree centrality* describes the number of direct ties an individual has to others. The more individuals an actor interacts with, the better connected they are and the more central their position in the network. Those with very few interactions with their neighbours will be on the periphery of the network (Croft et al. 2008; Madden et al. 2009). *Outdegree* centrality describes the interactions initiated by the individual (e.g. the overall rate of grooming to other individual). *Indegree* centrality describes the interactions received by an individual (e.g. the overall amount of being groomed by other individual; Whitehead 2008).

High outdegree and *indegree* scores indicate centralised networks, and low scores indicate a more even spread of ties (Madden et al. 2009). For example, an individual with a high outdegree score may be influential in the social network of the group or may have, for example within dominance networks, an established position in the top of the hierarchy. Individuals with a higher indegree score can be considered central as other individuals seek to direct ties to them, or they can be considered as victims, for instance within foraging competitions. Degree centrality can be described as *weighted* and *unweighted* relationships in which the former is a description of the total strength of interactions that an individual is involved with, and the latter is a description of the number of other individuals that an animal 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, that is, individuals may avoid interacting with others of the group. A high compactness score indicates the opposite, that is, that the interaction between individuals is direct, indicating that the network is more solid (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 & Riddle 2005). High scores indicate that all dyadic connections are present and low scores indicate that most of the possible dyadic connections between animals do not exist (Croft et al. 2008).

Table 2.4 Description of the attributes of the fifteen groups and the number of interactions observed in the group.

Group/ Location	Num. of indiv.	Number of females	Number of males	Min age	Max age	Grooming associations	Playing interactions	Foraging associations	Foraging competitions	Resting associations	Dominance interactions
Africam Safari/Mexico	13	4	9	5	10	268	202	812	308	294	107
Bristol Zoo/UK	13	3	10	0.5	7	272	71	714	64	1056	19
Cotswold Wildife Park/UK	10	5	5	0.3	6	220	197	817	101	83	144
Flamingo Park (G1)/UK	8	5	3	1	12	125	241	950	137	69	37
Flamingo Park(G2)/UK	5	2	3	4	6	537	258	1763	183	227	44
Longleat Safari Park/UK	14	9	5	0.7	8.8	420	763	1259	263	277	171
Morelia Zoo (G1)/Mexico	5	2	3	1	3	362	271	365	58	172	24
Morelia Zoo (G2)/Mexico	3	2	1	2	3	187	6	190	13	22	18
Paignton Zoo/UK	3	1	2	0.4	7.5	11	80	250	16	9	8
Paradise Wildlife Park (G1)/UK	4	3	1	2	5	36	16	317	15	156	19
Paradise Wildlife Park (G2)/UK	5	2	3	0.6	6	154	227	370	53	213	12
Shaldon Wildlife Trust/UK	7	4	3	2	5	509	397	708	45	560	1
Shepreth Park/UK	5	3	2	5	10	138	159	286	2	240	75
Twycross Zoo/UK	12	6	6	0.7	10	136	595	769	14	437	27
West Midland Safari Park/UK	6	3	3	0.8	7	189	236	482	81	145	66

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). A high C score means that all neighbours of an individual are themselves linked, meanwhile a low C score means that most of them are not linked to each other (Whitehead 2008). *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 shortest paths between pairs of individuals within the social network. Individuals with high betweenness scores have a big impact on the nature of the social structure (Whitehead 2008). *Closeness centrality* describes how influential an individual is on other group members by being able to reach them via shorter path lengths (Hanneman & Riddle 2005).

Network measures were calculated using functions in UCINET 6 for Windows (Borgatti et al. 2002). The UCINET software package performs a range of network and other analysis, it can carry out some processing of the raw data into similarity or dissimilarity matrices (Whitehead 2008). UCINET facilitates the manipulation and import of data from Excel, and permits the calculation of quantitative values, which are very useful in comparing and contrasting systems and in evaluating the evolution of a network over time. To visualize the overall social network for each group and their specific links connecting each individual with other individuals, the spring-embedding function in NetDraw (Borgatti 2002) was used.

Weighted and unweighted data were employed to calculate degree centrality and closeness: Network>Centrality>Degree; Network>Centrality>Closeness. While betweenness, distance, density and clustering coefficients were calculated using just unweighted interaction data: Network> Centrality> Freeman betweenness> Node betweenness;Network>Cohesion>Distance;Network>Cohesion>Density;Network> Cohesion>Clustering coefficient.

2.4.1 Network positions of individuals with similar attributes

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: Tools>Testing hypothesis>Node-level>T-test. Differences by individual type were calculated for each group individually then combined using Fisher's method to calculate an overall level of significance. If a variation was present in the relationship 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 & Clutton-Brock 2009; Madden et al. 2011).

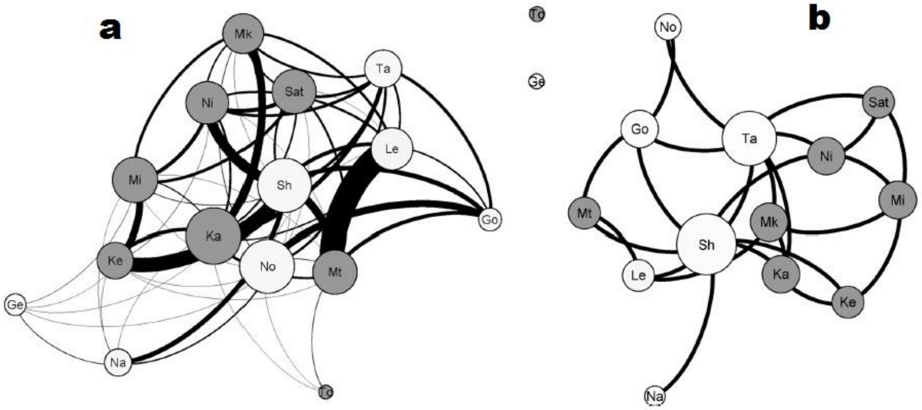
2.4.2 Assortative association of individuals

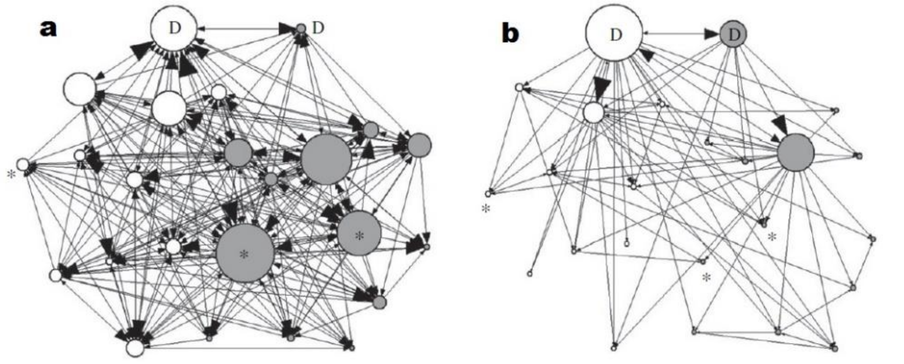
Permutation tests in UCINET were used to calculate the probabilities of individuals' categories associating assortatively. Non-random associations probabilities between individuals based on their sex, status and age were calculated based on unweighted interaction data, using 10,000 permutations: Tools>Testing hypothesis>Mixed dyadic/nodal>Categorical attributes>Join-Count.

2.5 Personality Assessment

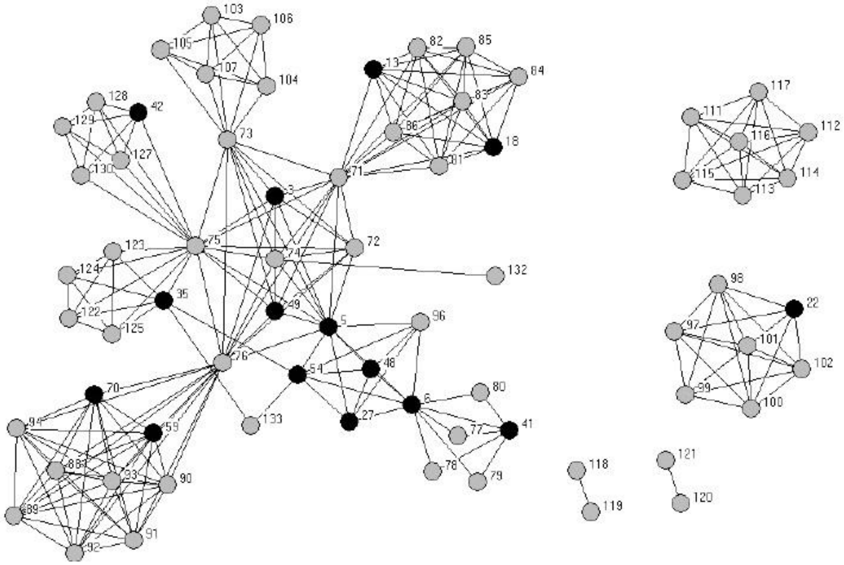
Animal personality can be evaluated by two principal methods: behaviour coding and trait ratings. Coding observable behaviour has been used widely in studies of animal personality and consists of more conventional observations coding detailed behaviours so that the personality of individuals is established (Korpela 2011; Vazire et al. 2007). Studies applying this method may concentrate entirely on natural behaviours (e.g Rouff et al. 2005). One refinement of this method is to consider behaviour under experimental manipulations. For example, researchers may record behavioural responses during specific behavioural tests, presenting novel objects to individuals or placing individuals in novel environments to explore and move in.

Table 2.5 Summary of the different social network analyses used in the present thesis and sample illustrations.

Measure	Meaning	Diagram	Example
Degree centrality	number of direct ties between individuals	 Social network from Levé et al. 2016 Captive population of chimpanzees, *Pan troglodytes*. **a.** weighted social grooming networks. **b.** unweighted social grooming networks (binary). White nodes=wild origine, grey nodes=captive origine. Larger size nodes= higher degrees.	Degree centrality is useful for investigating the transmission of many diseases. It can help to identify which individuals or groups may be more likely to be at risk or being involved in disease transmission, especially when weighted data is calculated in the network centrality (Drewe & Perkins 2015).
weighted	description of the total strength of interactions that an individual is involved in		
unweighted	description of the number of individuals an animal interact with		

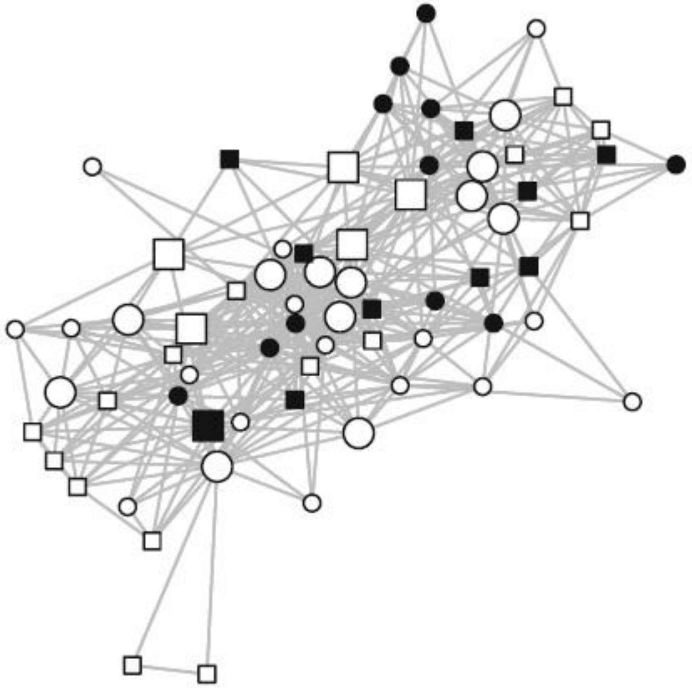
-Outdegree centrality	interactions initiated by the individual	 Social network from Drewe 2010 Wild population of meerkats, *Suricata suricatta*. Grooming (a) and aggressive (b) interactions. Node size- proportional to outdegree centrality, arrowheads size-proportional to indegree centrality. White nodes-females, grey nodes-males,D-dominants, Age-arranged in descending order from top to bottom. Asterisks-individuals tuberculosis test-positive.	In the example of the meerkat network, individuals that received end of aggression (high aggression indegree cenrality) were more likely to become infected (Drewe 2010)
-Indegree centrality	interactions received by the individual		
Distance measure			
L ,average path length	average distance between pairs of individuals within a network		L can be used to predict how quickly disease or information will spread throughout the population. In the network example, the mean path length suggests that any two giraffes can be connected to one to three other giraffes. The disease or

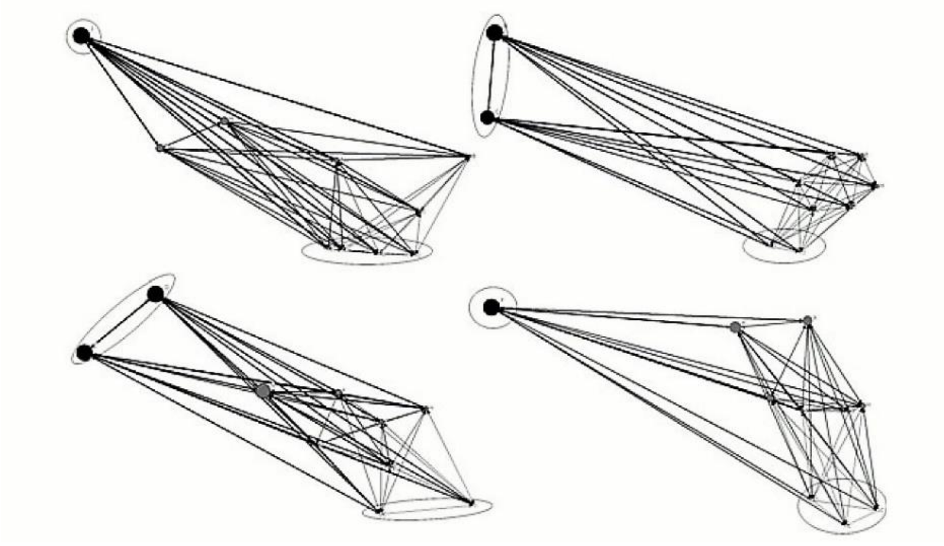
information between individuals with smaller L values will spread more quickly (Shorrocks & Croft 2009).

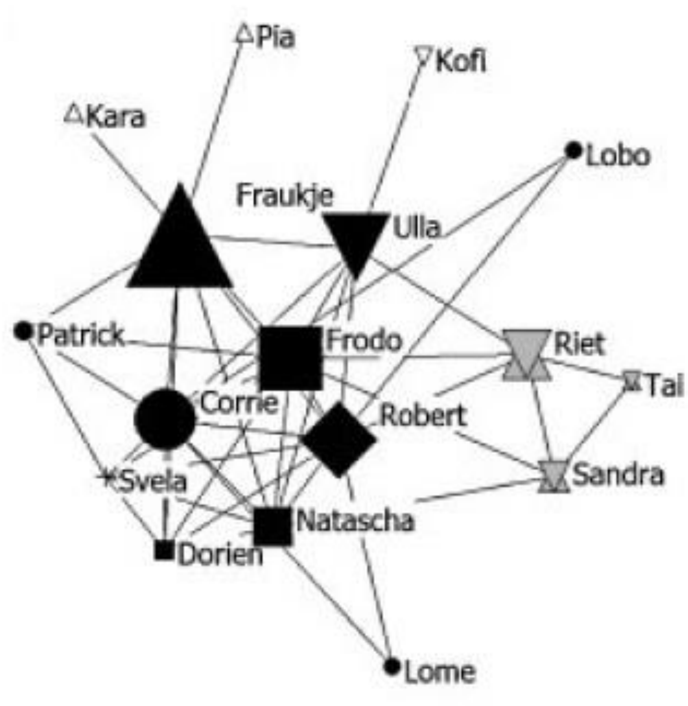


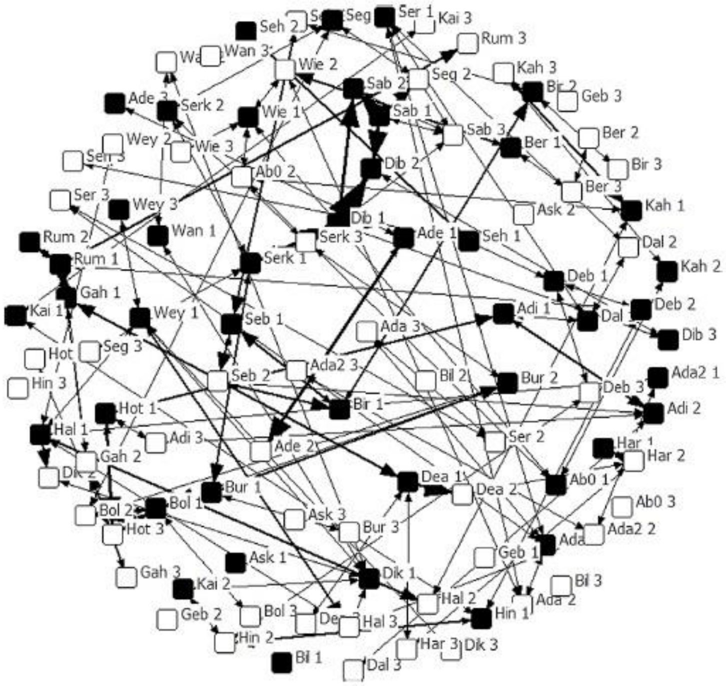
Social network from Shorrocks & Croft 2009

Wild population of reticulated giraffe, *Giraffa camelopardalis reticulata*. Black nodes and grey nodes are individuals first seen in two different years. The links between individuals represent the network of 80 giraffes that were seen in the same group at least once.

Density (D)	proportion of all possible dyadic connections that are actually present in a population	 Social network from VanderWaal et al. 2013 Wild population of ground squirrels. Squares-males; circles-females; large nodes-adults; small nodes-juveniles. Black nodes- infected by a disease during contact period. As the juvenile male's percentage in a group increased, the network became more dense.	The density of a network may give us insight into the speed at which information diffuses among the nodes, and into which individuals have high levels of social constraint (Hanneman and Riddle 2005). In this network example of ground squirrels, from an epidemiological perspective, a network with high density results in more infected individuals (VanderWaal et al. 2013).
Clustering coefficient (C)	measure of the cliquishness of a network		The clustering coefficient helps us to quantify the extent to which neighbours of an

		 Social network from Cañon Jones et al. 2017 Captive population of Atlantic salmon, *Salmo salar*. Black, grey and white colours represent initiators, initiators/receivers and receiver individuals of aggression interactions. Cluster of initiators and receivers are encircled.	individual are themselves neighbours. A high clustering coefficient suggests that individuals are surrounded by partners that are well connected to each other. In this example of an Atlantic salmon network, high clustering coefficients suggest cluster of individuals initiating and receiving aggression within the network (Cañon Jones et al. 2017).
Betweenness centrality	number of shortest paths between pairs of individuals within the social network		The betweenness of a network may give insights into the cohesion network (in this example of the cohesion grooming network) and of which individuals play an important role in maintaining the cohesion of the

		 (Social network from Kanngiesser et al. 2011) Captive population of chimpanzees. The size of the nodes characterize the betweenness centrality of the individual. Similar colours represent individuals belonging to the same subgroup and similar shapes represent individuals belonging to the same matriline. Five individuals (Fraukje, Ulla, Robert, Frodo, Corrie) had the highest betweenness centrality coefficients.	group (Kanngiesser et al. 2011). In captive populations, where all individuals can be part of the network, betweenness may be useful to identify key individuals in parasite infection (Corner et al. 2003
Closeness centrality	describes how influential an individual is on other group members by being able to reach		The closeness centrality measure may be used to evaluate the spread of infectious agents (Opsahl et al.

	them via shorter path lengths	 Social network from Sintayehu et al. 2017 Network of cattle herds. Each node represents a herd. Black nodes represents herds that tested bovine tuberculosis positive.	2010) and to evaluate social transmission of abnormal behaviours in captive groups (Makagon et al. 2012). Such individuals can promote the spread of the behaviour to the entire group due to their social position, a high closeness centrality. (Makagon et al. 2012). In this example, the risk of becoming infected with bTB was correlated with high closeness centrality scores where herds were closely connected to the other herds in the network. That is, herds with a higher closeness score may facilitate an epidemic through a network (Sintayehu et al. 2017)

Typically, researchers then collapse such measures from multiple behaviours and so collect emergent dimensions from their analysis (PCA): extraversion-like behaviours, agonistic behaviours, and bold and cautious behaviours (e.g. Rouff et al. 2005).

Alternatively, researchers may rely on qualitative descriptions of personality made by observers who rate the subjects and are familiar with the animals and refer to published ethograms with species-specific behaviour (Uher & Asendorpf 2008). Principal Components Analysis (PCA) and Factor Analysis (FA), both used in animal behaviour research, aim to reduce a set of variables into a smaller number of latent variables (Budaev 2010). The PCA method used in the present study is most widely used in personality literature; this will make it possible for me to compare results with previous studies.

I used behavioural coding to assess the individuals' personality in their captive condition under unmanipulated circumstances. During the collection of pilot data I conducted focal observations on each individual for the same amount of time to extract rates of each behaviour. Personality traits were derived from published ethograms of species-typical behaviour. Four traits were included: playful, curious, sociable and aggressive. The playful personality trait was recorded when the following behaviours were present: play chasing, play biting, clasping, grappling, mounting, pawing, play object (solitary play) and wrestling. The curious personality trait was recorded when approaching, exploring and foreleg stabbing behaviours were present. The sociable personality trait was recorded when allogrooming, huddling, side by side and touching the snout behaviour were present. The aggressive personality trait was recorded when the following behaviours were present: attacking, biting, charging, chasing, chin marking, glaring, hitting, hip slamming and threatening (see table 5.1, in Chapter 5, for the complete description of behaviours).

I first used Spearman's correlation to explore relationships between the individual scores for each of the four personality traits. I then conducted a PCA with the objective of reducing the number of behavioural variables measured (e.g. Lantová et al. 2010). The scree plot and Kaiser's criterion were used, using this rule, only factors with an eigenvalue of 1.0 or more were retained. Correlations of 0.50 or above were considered relevant. In exploratory analysis, 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; here, the solution of Varimax rotation is presented within the results since it derived more high correlations between components and/or led to loadings on one or more components (Weiss et al. 2017). I wanted to ensure that my measures were robust and so I collected a second set of observations, using the same methodologies, approximately one year later. Five groups of captive meerkats, comprising a total of 36 individuals, were selected for quantifying behavioural repeatability. Spearman's correlation was used to test for relationships between the individual scores for each personality traits during the two periods of observations.

2.6 Validity analysis

My study was primarily exploratory and should be used as an indication of where future studies might concentrate their efforts. Therefore, I conducted multiple analyses on the same data set in order to address multiple hypotheses. This risks rejecting null hypotheses simply because the large number of tests are coupled with an α level usually intended for single analyses. The adjustment of the p-value may reduce the chance of making a type I error for null associations, but it may, however, increment the chance of making a type II error. By reducing the chance of introducing ineffective behaviours (type I error), the chance that effective behaviours are not discovered may increase (type II error; Rothman 1990; Feise 2002). Rothman (1990) cites that "a policy of not making adjustments for multiple comparisons is preferable because it will lead to fewer errors of interpretation when the data under evaluation are not random numbers but actual observations on nature". Therefore, every result in the present thesis should be interpreted with caution and I recommend that future studies set out to explicitly test hypotheses that may arise from my more preliminary findings.

Chapter Three

Association dynamics of meerkat social networks in captive populations

3.1 INTRODUCTION

Within a society, social relationships are typically characterized by interactions between two individuals at a particular time (Deag 1980). These interactions play a key role in the structuring of communities, the establishment of the richness and duration of interaction dynamics (Danchin et al. 2008) and the transfer of information within networks (Pike et al. 2008).

The basis for animal social networks may consider two classes of relational data that represent how animals may be related to each other (Croft et al. 2008). One class can be defined by pair-wise relations based on associations, typically based on spatial proximity between individuals, which may include instances of periods when they occupy the same social group, roost or nest. Such relationships are typically undirected, simply describing that two individuals are in proximity. A second class can be based on an observed behavioural interaction between individuals, for instance, competitive or cooperative pair-wise interactions (Croft et al. 2008). Such relationships may be directed, revealing which individuals initiated an action towards another. This chapter will focus on meerkat social networks based on associations and Chapter 4 will go on to consider meerkat social networks based on interactions. Links between both classes can also provide an indication of the number of interactions among group members (weighted network) or simply depict the fact that the pair interacts, with no description of the interaction strength (unweighted network; Pinter-Wollman et al. 2013).

The structure of associations within a group is shaped by two key internal processes. First, it depends on the attributes of its members, such as kinship (Carter et al. 2013) and an individual's sex, status and age (Aschwanden et al. 2008; Madden et al. 2009). For example, it has been shown that northern long-eared bats, *Myotis septentrionalis*, of all ages prefer to associate more often with younger individuals during roosting as a technique to maintain stronger connections between all members of the group (Patriquin et al. 2010). Contrarily, adult male spider monkeys, *Ateles geoffroyi*, associated preferentially with others of similar ages more than expected by chance when foraging or resting during the day (Ramos-Fernández et al. 2009). Kinship is an important determinant of associations between individuals in some mammals (Möller et al. 2006; Silk et al. 2012) (but see Mitani et al. 2000) For instance, in female bottlenose dolphins, *Tursiops aduncus*, a significant relationship was found between maternal kinship and genetic relatedness with the frequent association of females in the group (Möller et al. 2006). Second, the structure of association within a group depends on the mix of its members, their preference for associating with a specific member of the group (social assortativity), and the group size. For example, in a study on wild guppies, *Poecilia reticulata*, (Griffiths & Magurran 1997) it was revealed that as the group size increased in number the tendency of female guppies to school with familiar fish declined. Durrell et al. (2004) assert that, indeed, preferential associations can be inhibited by a large number of individuals in the group and/or a limited space allowance.

The pattern of associations is also shaped by external processes (Durrell et al. 2004). These may include intergroup encounters (Wilson et al. 2001; Drewe et al. 2009), ectoparasite infection levels (Madden & Clutton-Brock 2009), or food availability (Foster et al. 2012). During intergroup encounters, individuals from neighbouring groups come close to the residents causing mainly aggressive interactions between individuals. Nevertheless, intruder encounters also provide an opportunity for breeders and helpers to gather information and assess neighbouring individuals and groups (Lazaro-Perea 2001). Group structure may considerably influence the form and outcomes of social behaviours such as foraging success, mating, predation risk (Hirsch et al. 2013), the strength and nature of social bonds (Carter et al. 2013), and an individuals' position within an association network may facilitate fitness from such behaviours. Conversely, members may suffer costs in term of fitness, which may be driven by these same organizational patterns due to increased disease and parasite transmission (Sintayehu et al. 2017) or increased local competition for food (Snijders et al. 2017) and mates (Wey et al. 2013). Previous studies on association patterns and environmental variability show how food availability can be very influential in animal social organizations. For instance, in chacma baboons, *Papio hamadryas ursinus*, (Henzi et al. 2009) female spatial association varied depending on the availability of food. Females tended to associate more briefly during food-abundant seasons than in food-scarce seasons where a constant companionship among females was observed. A different result has been observed in killer whales, *Orcinus orca*, where rates of associations grow during high salmon abundance (Parson et al. 2009; Foster et al. 2012).

Meerkats are characterized by foraging cohesively (Bousquet & Manser 2011) and interacting repeatedly and exclusively with other group members (Madden et al. 2009). Intergroup interactions are common when two or more groups come into contact whilst foraging. Additionally, rates and patterns of intergroup interactions vary within and between years, and within group sizes (Drewe et al. 2009). Variation in the network structure of a meerkat group can be influenced by the interaction type of intergroup encounters (Drewe et al. 2009), resulting in inconsistent patterns of interaction and associations between members of meerkat groups.

A natural habitat, where previous data on meerkat associations have been collected, differs greatly from a captive environment, which can often restrict animals from performing natural behaviours. Hosey and colleagues (2013) highlight that social behaviour in captive animals may be quantitatively and qualitatively different from social behaviour in wild animals, and, as a result, the range of animal social structure in confined conditions may overlap to different degrees with that observed in the wild. These are likely to strongly influence patterns of association in zoo collections with animals being either forced to associate at higher than preferred rates, or to associate with individuals who they might naturally avoid. The external processes mentioned previously can apply to a confined milieu in a completely different way. For instance, in a captive environment, availability of food and parasite infections are commonly managed, and intergroup encounters do not occur. A slightly comparable process (where individuals encounter new ones) is that of social group adjustments made by humans where removal and introduction of individuals are part of the zoo husbandry (discussed in Chapter 4 and 6). As novel approaches to welfare assessment and best practice husbandry guidelines are emerging, more work is being done on the importance of exhibit design and the animals' social environment. Accordingly, a large number of studies about the effects of the size and type of the enclosure on social dynamics have been done (Little and Sommer 2002; Marriot & Meyers 2005; Schaffner and Smith 2005; Koene & Ipema 2014; Dufour et al. 2011). For example, in chimpanzees, *Pan troglodytes*, (Clark 2011) a larger and more complex enclosure resulted in more affiliative interactions, preferred spatial associations and a decrease in agonistic interactions. In common squirrel monkeys, *Saimiri sciureus*, (Marriot & Meyers 2005) changes to enclosure design and size resulted in higher inter-individual distances.

Much work on social associations and interactions has tended to collect data from only single groups, which may illustrate only group specific factors rather than permitting comparisons of patterns among groups within single species (but see Beisner et al. 2012; Verme & Iannacone 2012; Webster et al. 2013; Royle et al. 2015). Furthermore, most of the studies on animal social networks focus merely on one relational system that depends on: interactions (e.g. Leinfelder et al. 2001; Schino et al. 2007; Wittemyer and Getz 2007; Ryder et al. 2008; Madden et al. 2009,2011; Edenbrow et al. 2011) or associations (e.g. Knick & Mech, 1980; Myers et al. 1983; Smolker et al. 1992; Christal & Whitehead 2001; Lusseau 2003; Gero et al. 2005; Gursky 2005; Silk et al. 2006; Carter et al. 2009; Génin 2010; Matsuda et al. 2010; Carter et al. 2013; Kilgour et al. 2013; Firth & Sheldon 2015), but very few utilize them simultaneously and compare them (e.g. Hobson et al. 2013). Hobson et al. (2013) state that the implementation of both methods for visualizing, quantifying and testing change patterns in social networks can help to gain a better understanding of social structure alterations over time. They explain that an examination of social interactions at multiple levels can offer a more comprehensive perspective on the drivers and temporal dynamics characteristics in networks, and that a comparison of temporal dynamics across association types can offer a comparative perspective on social change and a more comprehensive standpoint on association types and their fitness consequences.

Within meerkat studies, less attention has been directed to more subtle social relations such as resting and foraging. The objective of foraging is to meet metabolic requirements in environments that can vary in time and space (Doolan & MacDonald 1996). Foraging behaviour has been determined as the core of community structure (Pyke et al. 1977). Meerkat foraging activity is carried out in tightly cohesive bands and can occupy most of their active period (Doolan & MacDonald 1996). Similarly, meerkats rest or sleep together in groups (Ewer 1963) and may take ‘siestas’ during the day, sometimes retreating into their burrows and emerging from it later to continue foraging or other activities before sunset (Doolan & MacDonald 1996). Sleep precludes energy-producing behaviours and may establish a restriction on energy uptake, such as in foraging (Stuber et al. 2015), hence its importance in the study of sleep patterns in the social behaviour of animals. Moreover, cohesiveness in groups, such as in primates, can be measured by sleeping association frequencies (Dröscher & Kappeler 2013).

Therefore, in order to extend the understanding of social networks structures in meerkats, I looked at the network structure of fifteen captive meerkat groups considering foraging and resting associations. As mentioned earlier, environmental factors can shape the nature and degree of interaction and association. Accordingly it may be expected that such dynamics differ between one population in the wild and another in confinement. Further information on association patterns between individuals in a population and how this relates to sex, age and status can be required to understand patterns of social structure within animal societies (Vonhof et al. 2004). Meerkats offer a system in which social behaviour can be quantified in multiple groups and across multiple behavioural and associative situations. Crucially, meerkats are commonly held in zoos and are also being well studied in the wild. Meerkat groups vary greatly in composition in a natural environment. The number of individuals in one group can vary from 2 to 50 and consist of one dominant female, a number of subordinate females, a number of natal subordinate males and one or more immigrant males (Clutton-Brock et al. 2008). Meerkats are known to be obligately cooperative (Clutton-Brock et al. 2002), to interact frequently with other members of the group (Madden et al. 2009) and to be entirely dependent on social cohesion for their survival (Sharpe 2005a). Additionally, the structure of their intragroup relationships varies due to external, social and individual characteristics (Madden et al. 2009).

The meerkats' natural habitat is highly complex with heavy or low vegetation, dependent on weather (Clutton-Brock et al. 1999b) and food season (Hodge et al. 2009), and with constant intergroup (Drewe et al. 2009) and predator encounters (Clutton-Brock et al. 1999a). In a zoo environment conditions are unnaturally stable with an excess of high quality food, accessible shelter and supplementary heating, and no chance of interactions with competing groups. The present study provides a good opportunity to explore in detail the effects of intrinsic factors, the controlling of extrinsic factors and critically, to determine the influence that housing/husbandry may have on association patterns. In order to achieve that, the following questions were asked: 1) Does the network structure vary depending on group attributes? Wild meerkats in large groups tend to interact with a subset of others rather than trying to uphold interactions with all group members (Drewe et al. 2011). Therefore, I predict that individuals in smaller groups will tend to have denser networks in resting. Similarly, I predict the same type of network in foraging (individuals foraging closely to others in smaller groups than in larger ones) as it is known that animals in larger groups face more food competition: consequently individuals tend to split into several groups (Kazahari & Agetsuma 2010). Group members may choose to forage with partners who most likely show tolerance and disposition to share food patches, (King et al. 2011) and so a mixed-sex (due to the tension between meerkats of the same sex) foraging association and/or associations of equal meerkat status can be expected within the groups. An analogous situation can apply to sleeping associations where individuals may prefer tolerant resting partners. Therefore, diffuse foraging and resting networks can be predicted when groups are female or male skewed. 2) Does an individual's position within an association network correspond to their attributes? In Madden and colleagues' work (2011) on meerkat positions within networks they found that differences between individuals regarding their positions within foraging competition networks were generally due to an individual's age and mass, rather than their sex or status. That is, younger and lighter meerkats received higher overall rates of foraging competition from more partners. This leads me to assume that individuals may choose to associate with individuals that may be prone to compete less during foraging. Therefore, I predict that juvenile meerkats may engage in more associations with meerkats of a similar age; males or females may engage in more associations with the opposite sex; and subordinate meerkats may engage in more associations with others of similar status. On the grounds that individuals would choose to forage with tolerant individuals, individuals may choose to rest with tolerant partners. Therefore, I predict more equal association networks when considering resting behaviour than when considering foraging behaviour. 3) Is meerkat assortativity predicted by sex, age and/or status within foraging and resting networks? Wild meerkat assortativity has been predicted by age, status and sex in grooming and dominance networks (Madden et al. 2011). Wild young meerkats, like other social mammals, receive much of their food from adult helpers who have more experience (Clutton-Brock et al 2001). Therefore, I predict that individuals may have patterns of association in foraging networks based mainly on age (between individuals of dissimilar age).

3.2 METHODS

3.2.1 Behavioural measures, network measures and individual attributes

Fifteen captive groups of meerkats comprising a total of 113 individuals were studied from September 2011 to December 2012 in Zoological parks of UK and Mexico (Table 3.1). Social associations were collected during scan sampling observations every 10 minutes. These 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 forage close to other individuals. When foraging was separated by intervals of more than 1min, a new foraging association was defined. A resting association was recorded when an individual lay down in a relaxed manner (lazy sitting, high sitting, sunbathing; see ethogram in Chapter 2, Table 2.3) close to another member(s) of the group. Additional patterns of association, such as resting underground or whilst 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. In order to construct social networks, a total of 14,012 observed social associations (foraging associations: 10,052, resting associations: 3,960) were used. Three attributes were considered for all individuals: age, sex and status (see Chapter 2 for the complete description of methods).

Table 3.1 Description of the attributes of the fifteen groups and their number of interactions observed in the group.

Group/ Location	Dates of obs.	Num. of indiv.	Number of females	Number of males	Min age	Max age	Foraging associations	Resting associations
Africam Safari/Mexico	Nov, 2012	13	4	9	5	10	812	294
Bristol Zoo/UK	June, 2012	13	3	10	0.5	7	714	1056
Cotswold Wildife Park/UK	May/June, 2012	10	5	5	0.3	6	817	83
Flamingo Park (G1)/UK	Nov, 2011	8	5	3	1	12	950	69
Flamingo Park(G2)/UK	Nov, 2011	5	2	3	4	6	1763	227
Longleat Safari Park/UK	Oct, 2011	14	9	5	0.7	8.8	1259	277
Morelia Zoo (G1)/Mexico	Dec, 2012	5	2	3	1	3	365	172
Morelia Zoo (G2)/Mexico	Dec, 2012	3	2	1	2	3	190	22
Paignton Zoo/UK	Sept, 2011	3	1	2	0.4	7.5	250	9
Paradise Wildlife Park (G1)/UK	Sept, 2011	4	3	1	2	5	317	156
Paradise Wildlife Park (G2)/UK	Sept, 2011	5	2	3	0.6	6	370	213
Shaldon Wildlife Trust/UK	Sept, 2011	7	4	3	2	5	708	560
Shepreth Park/UK	July, 2012	5	3	2	5	10	286	240
Twycross Zoo/UK	March/April, 2012	12	6	6	0.7	10	769	437
West Midland Safari Park/UK	March, 2012	6	3	3	0.8	7	482	145

I analysed 9 network measures for the two forms of associations (foraging and resting). *Degree centrality* (weighted data) which describes the number of other meerkats that came to join them resting or foraging (indegree) and the number of meerkats that join others resting or foraging (outdegree). The average distance between pairs of individuals (*L, average path*) and the direct connection of the individuals within resting or foraging were calculated within distance measure. *Density* describes the proportion of all possible dyadic connections in resting or foraging present in a population. *Clustering coefficient* (unweighted data) quantifies how well connected neighbours are to each other during resting or foraging. *Closeness centrality* is a measure of how connected an individual is to others via short distances in the network. *Betweenness centrality* describes how central an individual is in resting or foraging that may play a particularly important role in maintaining the social cohesion of the group (see Chapter 2, section 2.4 for the complete description). Additionally, I analysed the differences of individuals varying in three attributes, sex, status and age by using degree centrality, cluster coefficient, betweenness and closeness.

Spearman's rank correlation coefficient 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.

3.3 RESULTS

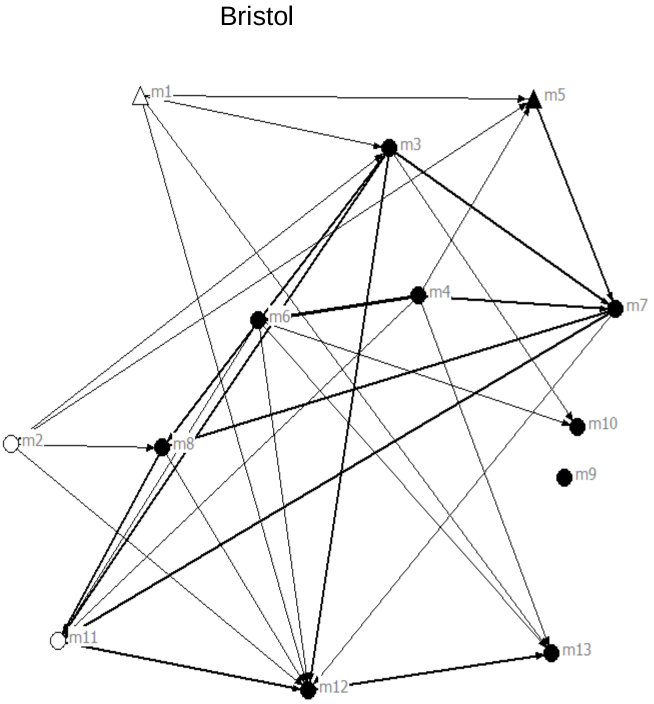
3.3.1 How does group composition influence the structure of associations in groups of captive meerkats?

Substantial differences were found in group structure among the fifteen groups across the two types of associations: foraging and resting (Table 3.2, Fig. 3.1). Some groups such as Paignton and MoreliaG2 had dense and well connected foraging networks where all individuals tended to forage with most others in the group, as indicated by high centrality measures, densities, clustering coefficients and short path lengths. In contrast, other groups, such as Bristol and Shepreth were more diffuse, such that individuals did not forage with a large number of others, as indicated by low centrality measures, densities, clustering coefficients and long path lengths. The proportion of females in a group did not explain variation in foraging networks (Table 3.3)

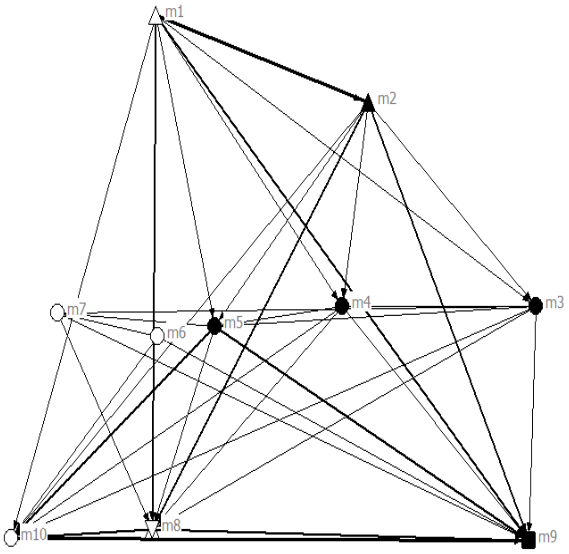
In the same way, groups exhibited different structures in their resting networks. Some groups such as Paignton and Shepreth had a denser resting network and almost half the groups had a moderately compact network, with Shaldon exhibiting the highest score. This variation in resting network was related to both group size and sex ratio. As group size increased in number of individuals and the proportion of females, resting networks became more diffuse with meerkats having a more strict preference for specific individuals in the group. In addition, as the group and females increased in number the average number of ties that an individual takes to connect another individual tended to increase (Fig. 3.2 and 3.3).

Figure 3.1 Examples of network from three captive groups of meerkats, including foraging (a), resting (b) networks. Dense and diffuse networks of different group sizes were chosen. For each network: triangles= dominants, circles=subordinates, white=females, black=males, individuals are approximately arranged by age, with older individuals at the top and younger individuals lower down the diagram, stronger ties are indicated by thicker lines.

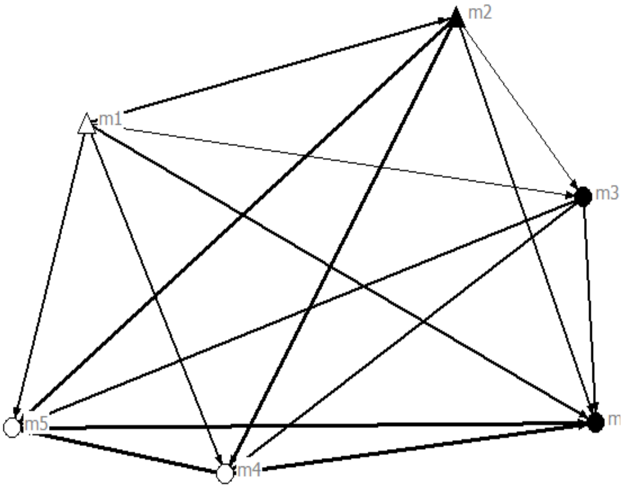
a)



Cotswold

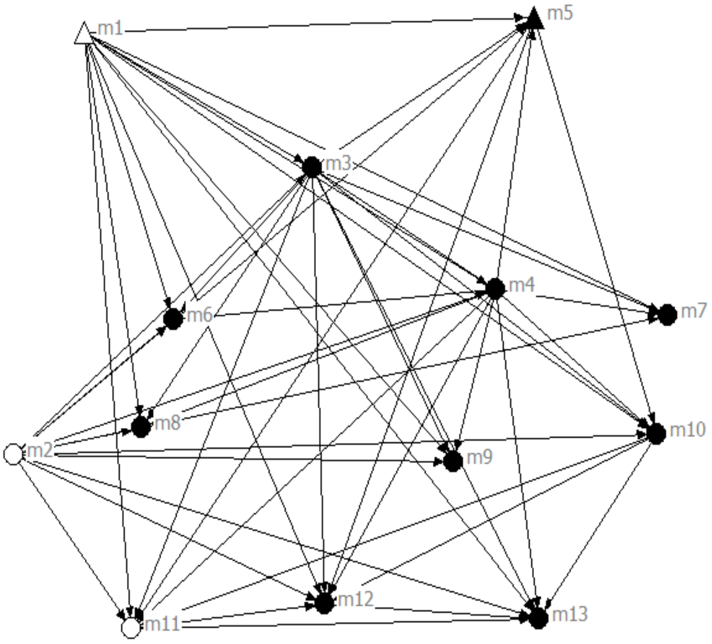


WMSP

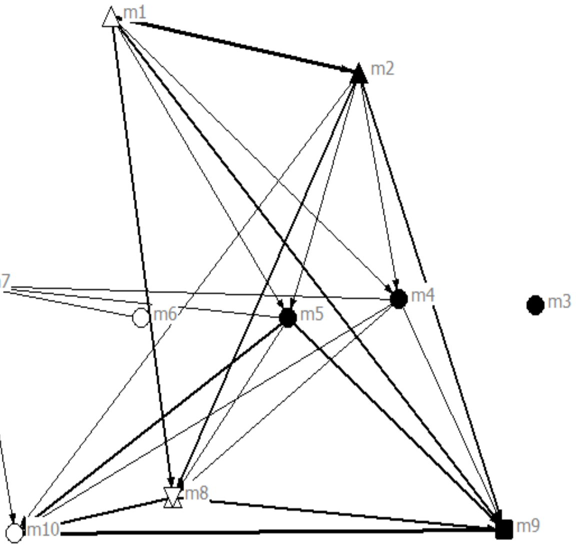


b)

Bristol



Cotswold



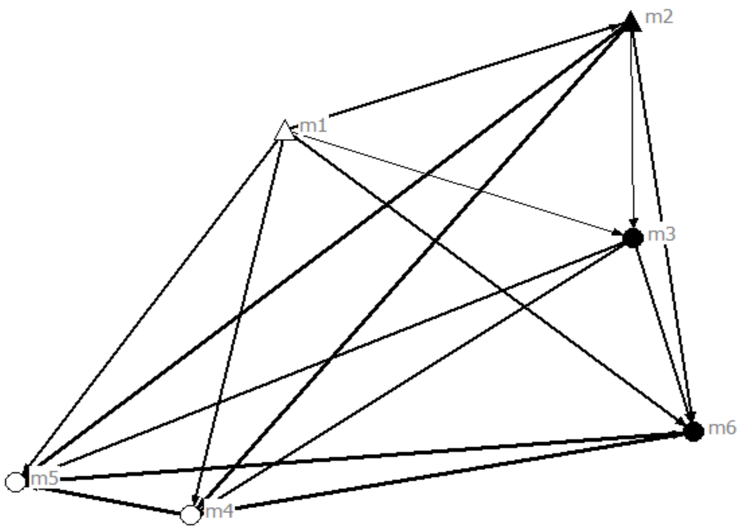

WMSP

Table 3.2 Network measures calculated for fifteen captive groups of meerkats based on two different types of networks.

Group	Network centrality		Distance		Density	Cluster Coefficient
	Weighted data					
	Outdegree	Indegree	L	Compactness	D(SD)	C
FORAGING						
Africam	26.46	20.94	1.25	0.37	0.32(0.46)	0.33
Bristol	11.04	10.22	1.87	0.17	0.11(0.31)	0.18
Cotswold	16.46	31.55	1.21	0.36	0.32(0.46)	0.41
FlamingoG1	37.71	14.85	1.07	0.48	0.46(0.49)	0.47
FlamingoG2	35.53	30.17	1.00	0.50	0.50(0.50)	0.50
Longleat	35.72	35.72	1.00	0.50	0.50(0.50)	0.50
MoreliaG1	25.59	46.42	1.10	0.47	0.45(0.49)	0.45
MoreliaG2	62.00	29.00	1.00	0.50	0.50(0.50)	0.50
Paignton	30.55	57.63	1.00	0.50	0.50(0.50)	0.50
PWPG1	29.63	62.22	1.00	0.50	0.50(0.50)	0.50
PWPG2	33.87	45.96	1.10	0.47	0.50(0.50)	0.45
Shaldon	30.37	43.98	1.00	0.50	0.50(0.50)	0.50
Shepreth	26.38	26.38	1.16	0.27	0.25(0.43)	0.29
Twycross	19.13	29.05	1.00	0.50	0.50(0.50)	0.50
WMSP	38.60	41.60	1.00	0.50	0.50(0.50)	0.50
RESTING						
Africam	21.79	14.85	1.11	0.47	0.44(0.49)	0.44

Bristol	38.67	26.23	1.02	0.32	0.32(0.46)	0.39
Cotswold	16.49	19.86	1.18	0.16	0.07(0.26)	0.38
FlamingoG1	12.38	28.70	1.20	0.24	0.21(0.41)	0.33
FlamingoG2	45.58	48.34	1.00	0.50	0.50(0.50)	0.50
Longleat	29.14	13.95	1.05	0.41	0.40(0.49)	0.48
MoreliaG1	34.15	28.57	1.00	0.50	0.50(0.50)	0.50
MoreliaG2	72.22	63.88	1.00	0.50	0.50(0.50)	0.50
Paignton	30.00	90.00	1.00	0.33	0.33(0.47)	0.00
PWPG1	51.68	42.37	1.00	0.50	0.50(0.50)	0.50
PWPG2	56.85	47.78	1.00	0.50	0.50(0.50)	0.50
Shaldon	54.08	37.67	1.00	0.50	0.83(0.37)	0.50
Shepreth	45.49	70.20	1.00	0.35	0.35(0.47)	0.43
Twycross	25.35	16.49	1.00	0.34	0.34(0.47)	0.55
WMSP	34.76	53.23	1.00	0.50	0.50(0.50)	0.50

3.3.2 Do individuals with similar attributes occupy similar positions within a network of associations?

Across groups, individuals differed in their positions within foraging networks depending on their age and social status. Dominant and juveniles individuals initiated more foraging behaviour with others than subordinates (outdegree), and conversely, subordinates and adults tended to receive more foraging interactions from all group members (indegree; Table 3.4). Similarly, dominants and juveniles exhibited shorter paths to reach the other groups members by foraging behaviour (outcloseness), and subordinates and adults were rapidly connected to other individuals in the group (incloseness).

Individuals differed in their positions within resting networks depending on their age and social status. As with foraging interactions, dominant individuals initiated more resting behaviour than subordinates, and subordinates and adults were engaged more in such behaviour than dominants and juveniles. Dominant and juvenile individuals had shorter paths to reach other group members via resting behaviour and subordinates and adults were rapidly connected to other individual’ resting behaviour.

Figure 3.2 Relationship between weighted centrality indegree measure of resting networks and the size of the group.

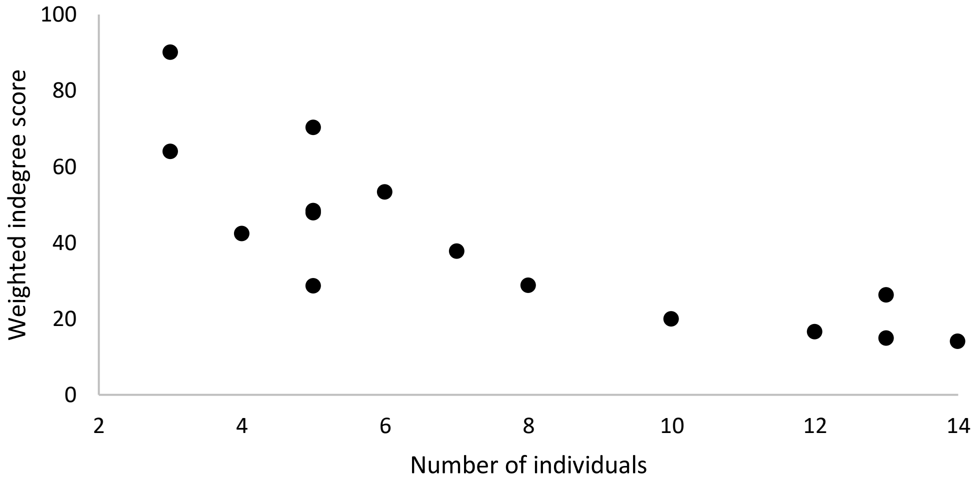
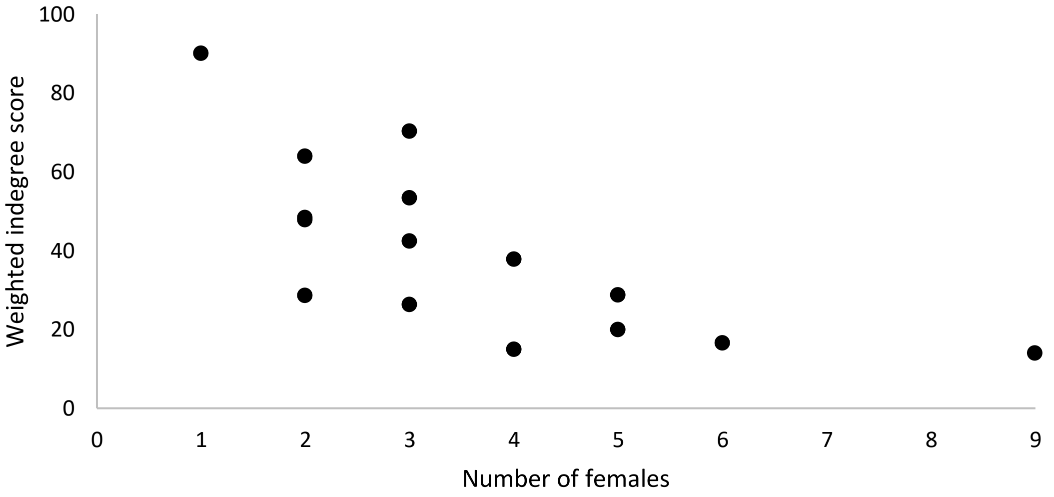


Figure 3.3 Relationship between weighted centrality indegree measure of resting networks and the proportion of females in the group.



3.3.3 Do individuals associate assortatively?

Across all groups, I found no evidence that individuals associated preferentially by sex, status or age (Table 3.5).

Evidence of preferential associations was found in individual groups. There was a weak tendency of resting association depending on an individual's sex. In the Africam group males rested nearer males more than expected (*p*=0.042) and females rested nearer males less than expected (*p*=0.023), while in the Bristol group females rested nearer males more than expected (*p*=0.039). There was no preferential association by status in either foraging or resting in any of the fifteen groups. Patterns of assortativity could be explained by age within foraging and resting behaviours in some groups. In the Cotswold group, pups foraged with adults more than expected (*p*=0.034) and adults foraged with adults less than expected (*p*=0.024). And finally, within resting behaviour, individuals interacted more assortatively in the Cotswold group in which adults tended to rest nearer another adults less than expected (0.015).

3.4 DISCUSSION

Captive meerkat groups did not appear to exhibit uniform association network structures when considering their patterns of resting or foraging. Instead, differences were found between the fifteen groups of captive meerkats when considering association networks based on foraging and resting. Some of these differences could be explained by intrinsic differences between the groups. The weighted centrality measures of resting networks varied with both group size and proportion of females. An individual's position within a network as described by their centrality and closeness measures could be predicted by their age and status, but rarely by their sex. I did not detect consistent patterns of non-random assortment amongst group members based on their sex, age or status.

Table 3.3 Relationship between network measures, group size and proportion of the individuals' sex in foraging and resting networks.

	Foraging				Resting			
	Group size		Proportion of females		Group size		Proportion of females	
	p	r	*p*	r	*p*	r	*p*	r
Network centrality								
Weighted data								
Outdegree	.22	-.33	.49	-.18	**.021**	-.59	**.022**	-.58
Indegree	.054	-.50	.17	-.36	**.000**	-.85	**.001**	-.74
Distance								
L	.16	.37	.78	.07	**.004**	.69	**.014**	.61
Compactness	.25	-.31	.85	-.05	.08	-.45	.09	-.45
Density								
D	.17	-.37	.57	-.15	.13	-.40	.16	-.38
Clustering								
C. Coefficient	.24	-.32	.87	-.04	.58	-.15	.82	-.06

Table 3.4 Differences for network measures of individuals from fifteen groups of meerkats varying in three attributes (sex, status and age) based on foraging and resting associations.

	Sex						Status					
	K D.Centrality		Betweenness	Closeness		Cluster	K D.Centrality		Betweeness	Closeness		Cluster
	Out	In		Out	In		Out	In		Out	In	
FORAGING												
Africam	0.39	**0.036**	0.69	0.15	0.057	0.80	0.14	0.07	0.22	0.08	0.07	0.68
Bristol	0.54	0.44	0.41	0.09	0.41	-	0.54	0.23	0.55	0.07	0.29	-
Cotswold	0.86	0.61	0.91	0.46	0.72	0.48	**0.022**	0.11	0.56	**0.022**	0.06	0.38
FlamingoG1	0.35	0.12	0.82	0.25	0.22	1.0	0.56	0.78	0.89	0.42	0.39	0.78
FlamingoG2	0.30	0.29	1.0	0.20	0.20	1.0	0.79	0.29	1.0	0.59	0.79	1.0
Longleat	0.46	0.31	1.0	0.15	0.69	1.0	0.07	0.10	1.0	0.054	0.10	1.0
MoreliaG1	1.0	0.79	1.0	0.60	0.80	1.0	0.19	0.19	0.69	0.19	0.20	0.70
MoreliaG2	0.34	0.33	1.0	0.33	0.33	1.0	0.33	0.67	1.0	0.33	0.33	1.0
Paignton	0.33	1.0	1.0	0.33	0.33	1.0	0.33	1.0	1.0	0.33	0.34	1.0
PWPG1	0.49	0.16	1.0	0.75	0.75	1.0	0.33	0.75	1.0	0.16	0.16	1.0
PWPG2	0.29	0.60	0.58	0.49	0.60	0.09	0.40	0.09	0.60	0.10	0.10	0.69
Shaldon	-	-	-	-	-	-	-	-	-	-	-	-
Shepreth	0.50	0.49	1.0	0.40	0.79	0.69	0.50	0.49	0.59	0.40	0.79	0.49
Twycross	0.53	0.80	1.0	0.46	0.45	1.0	0.13	0.06	1.0	0.15	0.058	1.0
WMSP	0.25	0.54	1.0	0.39	0.39	1.0	0.06	0.06	1.0	**0.048**	0.06	1.0
Combined P	0.72	0.42	1.0	0.24	0.59	0.99	**0.037**	**0.039**	0.99	**0.002**	**0.010**	0.99

	Sex						Status					
	K D.Centrality		Betweenness	Closeness		Cluster	K D.Centrality		Betweeness	Closeness		Cluster
	Out	In		Out	In		Out	In		Out	In	
RESTING												
Africam	0.29	**0.020**	0.68	0.13	0.07	0.45	0.07	0.07	0.31	0.07	0.07	0.38
Bristol	0.18	0.32	0.88	0.018	0.11	0.08	0.10	0.22	0.57	0.09	0.19	0.39
Cotswold	0.69	0.62	0.63	0.62	0.71	-	**0.045**	0.39	0.78	0.19	0.44	-
FlamingoG1	0.34	0.36	0.38	0.40	0.35	-	0.96	0.42	0.24	0.66	0.39	-
FlamingoG2	0.20	0.19	1.0	0.20	0.19	1.0	0.89	0.70	1.0	0.60	0.80	1.0
Longleat	0.47	0.22	0.27	0.20	0.44	0.07	**0.045**	0.14	0.93	0.059	0.16	0.37
MoreliaG1	0.80	0.70	1.0	0.60	0.79	1.0	0.20	0.20	1.0	0.19	0.20	1.0
MoreliaG2	0.33	0.33	1.0	0.34	0.33	1.0	0.32	0.33	1.0	0.32	0.33	1.0
Paignton	0.65	0.65	1.0	0.67	0.67	-	0.32	0.33	1.0	0.32	0.32	-
PWPG1	0.74	0.50	1.0	0.75	0.75	1.0	0.16	0.32	1.0	0.17	0.16	1.0
PWPG2	0.49	0.69	1.0	0.50	0.60	1.0	0.10	0.10	1.0	0.10	0.10	1.0
Shaldon	-	-	-	-	-	-	-	-	-	-	-	-
Shepreth	0.40	0.70	1.0	0.40	0.79	0.70	0.40	0.70	1.0	0.39	0.79	0.70
Twycross	0.27	0.73	1.0	0.34	0.64	1.0	**0.017**	0.16	1.0	**0.031**	0.14	-
WMSP	0.39	0.49	1.0	0.40	0.39	1.0	0.06	0.06	1.0	0.06	0.06	1.0
Combined P	0.60	0.45	0.99	0.23	0.58	0.94	**0.002**	0.051	0.99	**0.004**	**0.040**	0.99

	Age					
	K	D.Centrality	Betweeness	Closeness		Cluster
	Out	In		Out	In	
FORAGING						
Africam	-	-	-	-	-	-
Bristol	0.21	**0.018**	0.08	0.057	1.0	0.98
Cotswold	**0.024**	**0.009**	0.45	**0.008**	**0.008**	0.056
FlamingoG1	-	-	-	-	-	-
FlamingoG2	-	-	-	-	-	-
Longleat	0.30	0.21	1.0	0.16	0.65	1.0
MoreliaG1	-	-	-	-	-	-
MoreliaG2	-	-	-	-	-	-
Paignton	0.33	0.33	1.0	0.33	0.33	1.0
PWPG1	-	-	-	-	-	-
PWPG2	0.40	0.09	0.59	0.10	0.09	0.71
Shaldon	-	-	-	-	-	-
Shepreth	-	-	-	-	-	-
Twycross	0.61	0.29	1.0	**0.049**	0.72	1.0
WMSP	0.10	0.051	1.0	0.06	**0.050**	1.0
Combined P	0.06	**0.001**	0.90	**0.000**	**0.043**	0.95
RESTING						
Africam	-	-	-	-	-	-
Bristol	0.19	**0.004**	0.10	0.10	**0.000**	-
Cotswold	0.28	**0.008**	0.12	0.23	**0.007**	-
FlamingoG1	-	-	-	-	-	-
FlamingoG2	-	-	-	-	-	-
Longleat	0.19	0.14	0.58	0.12	0.33	**0.036**
MoreliaG1	-	-	-	-	-	-
MoreliaG2	-	-	-	-	-	-
Paignton	0.33	0.33	1.0	0.33	0.33	-
PWPG1	-	-	-	-	-	-
PWPG2	0.09	0.10	1.0	0.10	0.09	1.0
Shaldon	-	-	-	-	-	-
Shepreth	-	-	-	-	-	-
Twycross	0.48	0.44	1.0	0.54	0.62	0.22
WMSP	0.10	**0.050**	1.0	**0.050**	0.051	1.0
Combined P	0.07	**0.000**	0.76	**0.027**	**0.000**	0.28

Table 3.5 Patterns of association for individuals varying in sex (Female-Female, Female-Male and Male-Male), age (Pup-Pup, Pup-Juvenile, Pup-Adult, Juvenile-Juvenile, Juvenile-Adult, Adult-Adult), and status (Dominant-Dominant, Dominant-Subordinate, Subordinate-Subordinate) attributes in fifteen captive groups of meerkats based on foraging associations and resting associations.

	Foraging						Resting					
	Associate more			Associate less			Associate more			Associate less		
a) Sex associations												
	F-F	F-M	M-M	F-F	F-M	M-M	F-F	F-M	M-M	F-F	F-M	M-M
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	0.900	0.398	1.0	1.0	1.0	0.298	1.0	1.0	1.0	1.0	1.0	1.0
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
Paignton	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.666	1.0	0.666	1.0
Longleat	1.0	1.0	1.0	1.0	1.0	1.0	0.726	0.522	0.415	0.381	0.692	1.0
FlamingoG1	1.0	0.196	0.806	0.180	1.0	1.0	0.855	0.201	0.788	0.341	0.961	0.628
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
Africam	0.857	0.592	0.450	0.377	0.586	0.687	0.504	0.993	**0.042**	1.0	**0.023**	0.984
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
Twycross	1.0	1.0	1.0	1.0	1.0	1.0	0.225	1.0	1.0	1.0	0.455	0.225
Cotswold	0.874	0.389	0.463	0.295	0.849	0.739	0.535	0.438	0.807	0.685	0.839	0.461
Bristol	1.0	0.259	0.773	0.457	0.908	0.369	0.745	**0.039**	0.974	0.685	0.986	0.087
Shepreth	1.0	0.291	1.0	0.597	1.0	0.490	1.0	0.291	0.700	0.291	1.0	1.0
MoreliaG1	0.902	0.400	1.0	1.0	1.0	0.302	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
Combined P	1.0	0.989	1.0	0.999	1.0	0.999	0.999	0.988	0.999	0.999	0.999	0.999
b) Status associations												
	D-D	D-S	S-S	D-D	D-S	S-S	D-D	D-S	S-S	D-D	D-S	S-S
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	0.899	1.0	0.705	1.0	0.604	1.0	1.0	1.0	1.0	1.0	1.0	1.0
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
Paignton	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.335	1.0	0.335	1.0	1.0
Longleat	1.0	1.0	1.0	1.0	1.0	1.0	0.795	0.226	1.0	1.0	1.0	0.226
FlamingoG1	0.927	0.790	0.638	1.0	0.638	0.717	0.428	0.175	0.965	1.0	0.930	0.138
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
Africam												
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
Twycross	1.0	1.0	1.0	1.0	1.0	1.0	0.683	0.683	1.0	1.0	1.0	0.683
Cotswold	0.356	0.446	0.707	1.0	0.707	0.383	0.289	0.604	0.778	1.0	0.647	0.400
Bristol	0.231	0.781	0.490	1.0	0.386	0.626	0.646	0.331	0.722	1.0	0.722	0.331
Shepreth	1.0	1.0	1.0	1.0	1.0	1.0	0.703	0.309	1.0	1.0	1.0	0.309
MoreliaG1	0.898	1.0	0.695	1.0	0.593	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
Combined P	1.0	1.0	1.0	1.0	1.0	1.0	0.999	0.978	1.0	1.0	1.0	0.986

c) Age associations

	Foraging											
	Associate more						Associate less					
	P-P	P-J	P-A	J-J	J-A	A-A	P-P	P-J	P-A	J-J	J-A	A-A
PWPG1												
PWPG2				0.696	1.0	0.900				1.0	0.597	1.0
Shaldon												
Paignton				1.0	1.0	1.0				1.0	1.0	1.0
Longleat				1.0	1.0	1.0				1.0	1.0	1.0
FlamingoG1												
FlamingoG2												
Africam												
WMSP				1.0	1.0	1.0				1.0	1.0	1.0
Twycross				1.0	1.0	1.0				1.0	1.0	1.0
Cotswold	0.334		**0.034**			1.0	1.0		1.0			**0.024**
Bristol				0.121	0.785	0.636				0.976	0.386	0.540
Shepreth												
MoreliaG1												
MoreliaG2												
Combined P				0.959	1.0	0.999				1.0	0.995	0.850
	Resting											
	P-P	P-J	P-A	J-J	J-A	A-A	P-P	P-J	P-A	J-J	J-A	A-A
PWPG1												
PWPG2				1.0	1.0	1.0				1.0	1.0	1.0
Shaldon												
Paignton				1.0	0.333	1.0				1.0	1.0	0.333
Longleat				0.308	0.771	0.735				1.0	0.465	0.298
FlamingoG1												
FlamingoG2												
Africam												
WMSP	1.0	1.0	1.0	1.0	1.0	1.0	0.497	0.90	1.0	0.951	1.0	0.497
Twycross				0.733	1.0	0.776				1.0	0.550	1.0
Cotswold	0.064		0.210			1.0	1.0		0.975			**0.015**
Bristol				0.313	0.799	0.436				1.0	0.311	0.654
Shepreth												
MoreliaG1												
MoreliaG2												
Combined P				0.947	0.994	0.999				1.0	0.955	0.360

3.4.1 Group network structure based on individual associations

There was a variation of network structure measures within the fifteen groups of meerkats. The present results suggest that the exact composition of the group and the attribute mixture of their members may generate different forms of network structure. For instance, within foraging networks, small groups like MoreliaG2 and Paignton had more centralized networks, and larger groups like Bristol and Shepreth had diffuse networks, which could be suggest that internal factors such as group size may have influenced the association dynamics of the studied groups. Groups with fewer individuals have been recognised to be more cohesive than groups with a large number of individuals (Lehmann 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 associate with neighbours at random (Griffith & Magurran 1997) or individuals may choose to interact with a subset of others instead of trying to interact with all their group mates (Drewe et al. 2011). For example, in a study on wild meerkats, Drewe and colleagues (2011) suggested that when group size increased some individuals were limited in the number of interactions in which they could participate and therefore the networks of social interactions became less dense. Group size has an important impact on the foraging dynamics and foraging efficiency of some group members (Grand & Dill 1999; Maniscalco et al. 2001). For instance, in accordance with the present results, a study on sheep, focussing on the effects of group size found that the smallest groups remained cohesive during foraging networks alternating from one patch to another (Michelena et al. 2008). In contrast, as larger groups experience greater (or more) foraging competitions between group members, the group show more dispersion due to the fact that individuals are forced to visit more different patches than they would in smaller groups (Grove 2012). It is unlikely that a single factor can explain this variation in group network structure, whilst intrinsic factors likely shape a network structure extrinsic factors have an important role as well (Grand & Dill 1999). Different adaptive pressures in foraging may vary depending upon the habitat conditions, either in a captive or a wild habitat (discussed in chapter 6). In captivity, where food provision is regular predictable and in excess, competitive foraging is usually unnecessary. However, while foraging behaviour (mostly scratching pattern, defined by Doolan & MacDonald 1996, as ‘excavation with both forepaws together to drag out loose sand before inspecting the spoil’) is frequently shown by captive meerkats, association networks may be shaped differently as the benefits of associating with a specific partner or partners in foraging can be altered.

In small groups, resting associations were more centralised, suggesting that each individual had more associations with other members of the group. Similar relationships between group size and how close animals lie next to one another are seen in other systems (Dröscher & Kappeler 2013). For example, a study on wolves’ sleeping distances, (Knick & Mech, 1980) found that the larger the pack, the shorter and less variable were the sleeping distances. However, variation of resting networks may also be explained through additional factors, such as age. Knick and Mech (1980) discuss within their findings that wolf packs that included pups presented a higher degree of sleeping distance variability and larger sleeping distances because of the expectation of pups having an unstable relationship with adult pack members. This may be an explanation of the low indegree centrality network in resting behaviour in the Cotswold group because they were the only group with pups.

3.4.2 Network positions of individuals with similar attributes

Individual positions in foraging networks differed according to their age and status. Few studies have investigated the relationship between hierarchy positions and network positions in foraging. For instance, a study looking at the effects of both personality and dominance rank on foraging in barnacle geese, *Branta leucopsis* (Kurvers et al. 2010) found that dominance did not have an effect on the proportion of joining other group members, but dominant individuals did have a higher proportion of successful joining than subordinates, which is comparable to the results found in the present study. By investigating individuals’ foraging strategies with respect to their social position in barnacle goose flocks, Stahl et al. (2001) found that subordinate individuals occupied explorative front positions and were the first to find sites with high-quality food or new food patches. Additionally, they noticed that dominant individuals profited from that information when joining them. As such, it is possible that juvenile and dominant (who can monopolize food and foraging holes more easily) meerkats reached and joined subordinates that had already found a good foraging hole, even though the former were the ones initiating more foraging behaviour in the study groups. Meerkats as highly social foraging species depend on their competent foraging abilities for survival and fitness. Conserving time and energy is crucial, their goal would be to find the greatest mass of food with the lowest energy expenditure and the least amount of time spent digging to reduce predation risk (individuals may not be able to dig and scan for predators all at once) and increase their daily weight gain (Thornton 2008). It would be interesting in further research to add visitor count during observations, along with additional species seen as potential predators by meerkats (including objects such as planes, which were observed by the author to be recurrently scanned by meerkats who subsequently hid from them. Such information has been confirmed by several animal keepers and in previous work in meerkats, e.g. Ewer 1963), and information about the meerkats weight gain rates. This, with the purpose of creating a bigger picture of the influence of these factors on foraging association networks in captivity. Association with conspecifics in a situation like predation is generally accepted in many animals as a form of reducing their risk of predation (Grand & Dill 1999) and may influence phenotypic segregation (e.g. sex or body length) at a group level (Croft et al 2008).

In the present results, individual positions in resting networks did not differ according to sex but rather by status and age. Dominant and juveniles meerkats joined more other members of the group in resting behaviour than subordinates and adults. In other mammals, the selection of resting sites can be influenced by territoriality in which animals scent mark in the vicinity of sleeping sites (Génin 2010). Similarly, resting networks may reveal social territoriality where dominant meerkats, which typically have a high rate of scent marking (Carlson et al. 2004; Jordan 2007), have priority to choose a high quality sleeping site and also have the privilege to choose who they want to associate with. Extending such research on scent marking and sleeping sites in different groups of meerkats may give additional insights into dominance relations and sleeping patterns. Age related differences in sleeping sites have been proven to influence spatial arrangements (Zimen 1976; Anderson 1998); however, such information is limited. Association based on age and kinship, has been reported in baboons (e.g. Altmann et al. 1981) or gorillas (e.g. Goodall 1979) as a way for juveniles to get accepted into another sleeping cluster (Anderson 1998) or simply to increase group cohesiveness and consequent protection from predators (Pizzato et al. 2016) or from older group members. The possible thermoregulatory significance of the sleeping association with adults may benefit juveniles when huddling since heat radiation is considered to increase with body surface area (Ueno & Nakamichi 2016); that is, juveniles can benefit from associating with larger-sized, adult individuals.

3.4.3 Assortativity between individuals

The attributes of an individual did not consistently influence how they associated with others group members within foraging networks. Foraging networks only revealed patterns of association based on age. Before reaching maturity, association between young is usually higher in frequency than in adults which is based on their behaviourally specific needs they are less constrained by the mating system and social organization than adults (Gero et al. 2005). However, individuals may prefer to associate with a specific individual who has more experience or who shares the same foraging priorities (Gero et al. 2005). In addition, some individuals may choose to stay closer to conspecifics in foraging activities to be able to make more use of the scrounging tactic (Kazahari & Agetsuma 2010; Kurvers et al. 2010). Young meerkats, like other highly social animals engaging in cooperative breeding, obtain much of their food from adult helpers (Clutton-Brock et al. 2001) and the opportunity to learn feeding behaviour (Thornton & McAuliffe 2006) may clarify the preference observed in the present study of juvenile association with adults.

General patterns in resting associations were not found to be based on age, sex or status. A number of groups presented significant assortative associations, yet, the form of assortativity differed between groups. A mixed-sex association was observed in some groups, other groups showed male-male association instead. Variation in resting associations within groups underscores the social complexity of group formation. Constraints like thermoregulation, predator avoidance, and quality and abundance of sleeping sites can influence sleeping association (Weidt et al. 2004; Génin 2010). For instance, the thermoregulation hypothesis states that sleeping associations should occur more regularly in the cold season (Génin 2010) and the predator avoidance hypothesis states that animals may show sleeping association because predation pressure may be higher in the day time than at night. A previous study on resting associations in African wild dogs, *Lycaon pictus* (McCreery 2000) reported that wild dog associations were based on sex but with variations between the different studied groups. In one of their groups, females and males rested with the opposite sex. In a different group individuals rested next to the same sex at intermediate frequencies and in another group members of the same sex rested together more often. Mixed-sex co-sleeping has been seen as a way of searching for oestrous females at their sleeping sites, and is recognized as a reproductive strategy in some species like squirrels and ungulates (Radespiel 2000). Association among males has been reported in some primates where tolerance and mutual support are gained from establishing and maintaining relationships with specific partners within a group (Van Hooff & Van Schaik 1994). In meerkats, reproductive success is based on status, with the dominant male typically restricting mating access to the dominant female (Spong et al. 2008), which may mean that the mating strategy assumption cannot operate. It is central to emphasize that meerkats sleep in their burrows at night and thus significant data relating to sleeping or resting associations may be missed. Therefore, additional studies of sleeping site types and thermoregulation (with comparisong during different seasons), along with underground cameras may be useful for animals in confinement in order to help us describe and analyse a more precise structure and dynamics of animal resting networks.

In conclusion, the social networks of captive meerkats differed with group size and composition, and differed depending on the type of association being considered. Within such networks, an individual’s position varied depending on their sex, age or status according to what form of association the network was based on, and the identity of their social partner was often non-random. My results suggest that association preferences of individuals are likely to differ, and the factors that drive such preferences may be singular to each member of the group. Extrinsic ecological variation is recognized to underlie differences in social structure across populations (Rubenstein 1994), however little is known of how a social structure is constructed in a confined environment. Understanding and elucidating what factors/attributes influence those inclinations and what roles specific preferred associations play in the social organization of animals in captivity will help us to understand more about the species and enhance group and individual-level fitness in captive environments.

Chapter Four

Does the social network structure of wild meerkat populations differ from that of meerkats in captivity?

4.1 INTRODUCTION

Animal behaviour can be guided by the stimuli of the physical environment surrounding the individual, by their social environment and by the stimuli coming from other animals (McFarland 1999; Davies et al. 2012; Hosey et al. 2013). Additional variables like the animal's age, its reproductive status and its previous experiences may also impact individual behaviour (Brummer et al. 2010). In a wild environment appropriate behavioural responses to a particular circumstance can be shaped by temporal (day-night cycles, lunar cycles, seasons) and spatial variations (different habitats and microhabitats within the animal's home range), and a holistic social environment, including continuous contact with conspecifics and heterospecifics (Hosey et al. 2013). The physical environment in a captive setting differs from a wild one in terms of temperature, humidity, space, substrate, vegetation, light, sound, smell, predators and diseases (Casamitjana 2005). In addition, a different social environment in captivity (whether restricted or unrestricted from conspecifics; Wells 2004; Stroud 2007) and physical surroundings (comprising enclosure type and husbandry schedules; Brummer et al. 2010; Ross et al. 2011a) may also influence the behavioural repertoire of the animals. Thus, it is evident that the behaviour of an individual in a confined environment is likely to be shaped by a number of related situational variables acting together (Hosey 2005).

Most studies 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 & 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). Yet, little attention has been paid to how irregular individual behaviour influences the more general social structure of captive animal groups (e.g. Rose & Croft 2015; Levé et al. 2016).

The social milieu of individuals is represented by their social interactions networks, which can have a big impact on evolutionary and ecological processes at the population level (Fisher et al. 2017). Research into the social behaviour of wild animals living in groups has demonstrated the importance of social structure dynamics and their consequences for an individual's fitness. For example, it has been found that animal social interactions may predict future social status in early life by their connectivity within the social network (McDonald 2007), or that specific social interactions may facilitate or impede the spread of disease within a population (Pinter-Wollman et al. 2013). Individual position within social networks can also have implications for an individual's performance, such as individual mating. For instance, in a free-living population of house finches, *Carpodacus mexicanus*, males with high betweenness centrality had a greater paring success due to their greater social ability (Oh & Badyaev 2010). Despite the fact that little research on social networks has been done in populations of zoo-housed animals (Rose & Croft 2015), the interest in understanding how group social structure is affected by the zoo environment and management is growing.

One of the key concerns of captive animal husbandry is the social environment, as it is regularly modified and can shape the social behaviour of the animals in question in different ways. Individual positions in their social network can change after the addition or removal of individuals (Levé et al. 2016). In the matter of social group adjustments, it has been stated that forced aggregations of individuals can result in aggressive interactions or, in contrast, can establish a friendly relationship (Mattiello et al. 2014). Overcrowding in captive conditions can also affect the stability of a dominance hierarchy in the group and thus, can have an effect on the opportunity for naturalistic social interaction (Grant & Albright 2001). A second concern is the physical environment. A lack of space and diversity in the captive environment due to poor habitat design has been proven to be responsible for the intensity of social interactions (Hediger 1964). Moreover, it has been reported that a spatially unrestricted area results in variations in the physical distances between individuals. That is, animals of a group may choose to avoid others in order to diminish the occurrence of agonistic behaviour (Aschwanden et al. 2008) and as a result, association and interaction dynamics are likely to be transformed. Literature on captive Asiatic wild horses, *Equus przewalskii*, affirms how aggressive and grooming interactions between individuals can increase in a restricted pen, implying that constant close proximity increases the probability of these interactions (Hogan et al. 1988). A captive setting can increase and intensify aggressive interactions between members, which can result in serious physical trauma and reduced psychological wellbeing (McCowan et al. 2008). These findings highlight how within a confined environment several aspects can impact negatively upon social structure, resulting in different patterns of social interactions between group members than would be seen in their wild counterparts. Social dynamics in captivity can differ greatly from those in wild conspecifics given the different ecological constraints on social organization in wild populations, e.g. predation pressure, distribution of resources (food, mates), which are all regulated by their human carers in captive populations (Berger & Stevens 1996). It is likely that much smaller social networks can be generated by captive groups, as group sizes in zoos are usually smaller, than wild groups (Clark 2011). While several studies have focused on animal social networks in the wild, none has directly compared said aspect between captivity and the wild. Meerkats, *Suricata suricatta*, provide an excellent system to compare the social networks of wild and captive groups. Meerkats in the wild are characterized by living in large groups and for being a cooperative species (Clutton-Brock et al. 2008). They interact frequently with each other in a range of ways (Madden et al. 2009), including grooming (placatory) or aggressive dominance assertions (antagonistic; Drewe 2010).

Previous work by Madden and colleagues (2009, 2011) used social network analysis, to explore three different interaction networks (foraging competitions, grooming and dominance interactions) across eight wild groups of meerkats. Relations between internal (social and individual) and external (ecological) factors were considered in their work. They found variations within groups according to interaction type and variations with group attributes, individual attributes and ecological factors. For example, as group size increased, networks became less dense; groups with more established dominant females were more egalitarian in their grooming and foraging competition interactions; younger and lighter individuals received higher overall levels of competitions in foraging.

Differences in the attributes of individuals did not constantly influence association patterns across the different interaction network types. Some individuals' attributes influenced the network position across all groups. In Chapter 3 I focus merely on meerkat social networks based on foraging and resting associations. Differences were found between the fifteen groups in their association networks, which could be explained by intrinsic factors such as group size and age. Additionally, weighted centrality measures of resting networks differed with the composition of the group (by number and sex), and an individual's position within a network could be predicted by status and age.

The present chapter focus solely on interactions, and compares social networks between groups and across different environments to provide insight into potential drivers that shape a group social network in captive environments. In order to do so, I repeated Madden et al. (2009, 2011) work with the fifteen captive groups in order to explore how network structures and individual positions in grooming, foraging competition and dominance networks differed between wild and captive groups of meerkats. Ten network measures were analysed for the three forms of interaction: measures of (indegree and outdegree) degree centrality (unweighted and weighted data), distance, betweenness, closeness, density (average path length and compactness) and cluster coefficient (unweighted data) were calculated for the three different interaction types. Due to the differences between the daily life of captive and wild meerkats (such as social partners/family composition, physical environment, shelter type, cost and benefits) I make the overall prediction that numerous differences will be found in the way meerkats interact with each other in the two environments. Internal factors such as group composition and external factors such as food availability and habitat conditions may lead to different dynamics. For instance, literature confirms that in larger groups, individuals may interact with only a few selected partners (e.g. grooming interactions; Dunbar 1991) and tensions can escalate because of crowding (Dunbar 1991). Such tension may increase the competition for food, and interactions in dominance may increase to maintain stability in social structures. Therefore, I predict that captive groups, which generally comprise fewer individuals than wild groups, may present differences in network measures such as in network centrality which may be characterized by lower scores than the wild groups, where the former may show a more even spread of ties (e.g. in grooming interactions). Average path length may also show lower scores in captive groups than in the wild ones, indicating that individuals interact directly with others in grooming, dominance and foraging competitions. Besides the average path length being influenced by group size, the restriction of space in a zoo enclosure may automatically decrease the average distance between pairs of individuals. A lower clustering coefficient in foraging competition can be shown in captive groups than in wild groups. Competition in foraging may be reduced since animals living in captive conditions are food provisioned and because there are smaller number of animals in captive groups.

Network positions in grooming can be expected to be predicted by sex, status and age. Previous research on wild meerkats (Kutsukake & Clutton-Brock 2010) has 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. Higher intrasexual conflict may be observed in males or females in captivity due to the impossibility of dispersal. Therefore, I predict that captive groups will show higher outdegree centrality scores in grooming than wild groups, specifically subordinate individuals (females and males) initiating more grooming than dominant. I can also expect, in groups with young meerkats, that older individuals will initiate more grooming (outdegree centrality) than juveniles as grooming interactions between older and juvenile individuals can be the result of parental care (Kutsukake & Clutton-Brock 2010). Therefore, a quite similar result may be shown between captive and wild groups. It is known that dominant female meerkats are usually more aggressive to other group members, than dominant males (Clutton-Brock et al. 2006). As previously mentioned, higher intrasexual conflict may be expected in captivity due to the space restriction; therefore, differing with Madden et al. (2009) results in dominance network positions, captive females may tend to give higher total rates of dominance than those in wild groups. Here again, as explained in grooming interactions, average path length measures can be expected to differ between both environments. Network positions in foraging competitions in captive groups may be expected to be comparable to wild groups, where differences between individuals in their positions within a network can generally be because of an individual’s age, rather than their status or sex. However, individuals in captive groups may show higher incloseness scores than in wild groups. Individuals in confinement can be rapidly connected and receive more foraging competitions from other group members. Patterns of association in captive groups within grooming networks may be expected to be based on sex, as found in wild groups. However, unlike in wild groups, patterns of association in captive groups may be expected to also be based on status. As clarified before, the impossibility of dispersal may magnify the assertion of dominance in dominant females due to strict intragroup reproductive conflict. An analogous situation may apply in patterns of assortative association in dominance and foraging competitions than in networks of dominance and foraging competitions. A captive individual's dominance association may be expected to be predicted by sex and status, as in in wild groups. And general patterns of assortative association in foraging competitions between captive individuals may be based on their age, differing from wild groups.

4.2 METHODS

4.2.1 Behavioural measures, network measures and individual attributes

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 (see Chapter 2, Table 2.4). Social interactions were collected during scan sampling observations. These compromised: allogrooming interactions, dominance interactions and foraging competitions. In order to construct social networks, a total of 5,689 observed social interactions (grooming: 3,564, dominance: 772, foraging competitions: 1,353) from fifteen captive groups (113 individuals: 54 females, 59 males) were used (Table 4.1). Madden et al (2009; 2011) recorded a total of 2093 allogrooming events, 333 dominance interactions, and 375 foraging competitions (Table 4.2). The three distinct forms of interactions were recorded as described in Madden et al. (2009; see Chapter 2, section 2.3). To compare network structures, I collected network measures and conducted analytical methods identical to those described in Madden et al. (2009; 2011; see Chapter 2, section 2.4 for the complete description) to allow me to compare my findings with those of wild meerkats. I analysed the same 10 network measures as detailed in these papers for the three types of interactions (grooming, dominance and foraging competitions). 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 the three different interaction types. To compare the position of individuals in the network, I analysed the differences between individuals varying in three attributes, sex, status and age by using degree centrality, cluster coefficient, betweenness and closeness.

Table 4.1 Summary of the three types of interactions recorded within the fifteen captive groups of meerkats.

Group	Num. of indiv.	Grooming Interactions	Dominance interactions	Foraging competitions
Africam Safari/Mexico	13	268	107	308
Bristol Zoo/UK	13	272	19	64
Cotswold Wildlife Park/UK	10	220	144	101
Flamingo Park (G1)/UK	8	125	37	137
Flamingo Park(G2)/UK	5	537	44	183
Longleat Safari Park/UK	14	420	171	263
Morelia Zoo (G1)/Mexico	5	362	24	58
Morelia Zoo (G2)/Mexico	3	187	18	13
Paignton Zoo/UK	3	11	8	16
Paradise Wildlife Park (G1)/UK	4	36	19	15
Paradise Wildlife Park (G2)/UK	5	154	12	53
Shaldon Wildlife Trust/UK	7	509	1	45
Shepreth Zoo/UK	5	138	75	2
Twycross /UK	12	136	27	14

West Midland Safari Park/UK	6	189	66	81
Total		3,564	772	1,353

Table 4.2 Summary of the three types of interactions recorded by Madden et al. (2009; 2011) within eight wild groups of meerkats.

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

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: Network>Centrality>Degree; Network>Centrality>Closeness. Betweenness, distance, density and clustering coefficients were calculated using unweighted interaction only: Network>Centrality>Freemanbetweenness>Nodebetweenness;Network>Cohesion>Distance;Network>Cohesion>Density;Network>Cohesion>Clustering coefficient.

I compared network measures and association patterns for the 15 meerkat groups observed in captivity with those from the eight groups observed in the wild (data from Madden et al., 2009; 2011). Network measures were compared using the Wilcoxon Signed Rank Test (SPSS version 20). Friedman tests were used to compare network measures (centrality, distance, compactness, density and clustering coefficient) within the three types of network: grooming, dominance and foraging competitions. Non-parametric tests were used due to the distribution of the data and the small sample sizes (see Chapter 2, section 2.4 for the complete description)

4.3 RESULTS

4.3.1 What is the structure of interaction dynamics for captive groups?

Measures of network structure based on three interactions in captive groups.

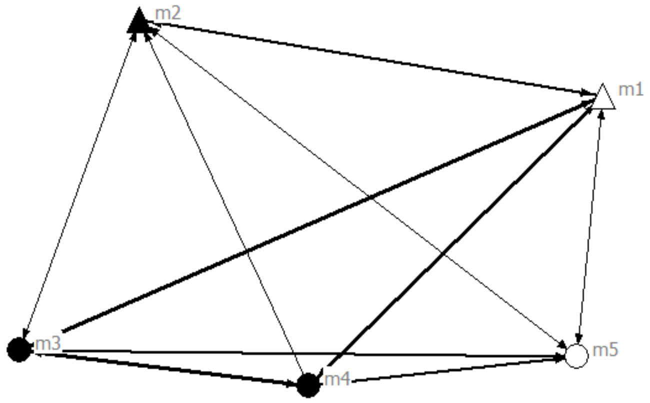
The groups of meerkats observed in captivity differed from each other in the three types of interaction: grooming, dominance and foraging competitions (Table 4.3). For instance, within the unweighted indegree centrality of the grooming network, the Paignton group had a higher centralised network (75.00) than the others, indicating that certain individuals are a target of the grooming interaction. Bristol (18.06) and PWPG2 (18.75) were very diffuse groups in terms of their grooming network. Within outdegree centrality of the same interaction Longleat and Paignton were highly centralised groups (74.56, 75.00), and some groups including FlamingoG1 (12.24) and PWPG2 (18.75) were very diffuse groups. This indicates that in the Longleat and Paignton groups, key individuals initiated most of the grooming interactions. (Fig. 4.1)

Within compactness scores, Shaldon, PWPG1 and Flamingo G2 groups presented a highly compact network in grooming interactions (results of 1.0). Conversely, Longleat (0.43) and Bristol (0.49) groups had lower scores in the grooming network. Within density of dominance interactions, a variation of a highly saturated network (Longleat, 0.51) to a very sparse network (Bristol, 0.01) was observed. Scores for indegree foraging competitions from unweighted data varied between a very centralised group (Paignton, 100.00: in which one individual was the subject of foraging competitions from all other group member) to a very diffuse group (WMSP, 20.00). Within density of foraging competitions, WMSP (0.83) had a highly saturated network, while Twycross (0.08) and Bristol (0.09) had very sparse networks.

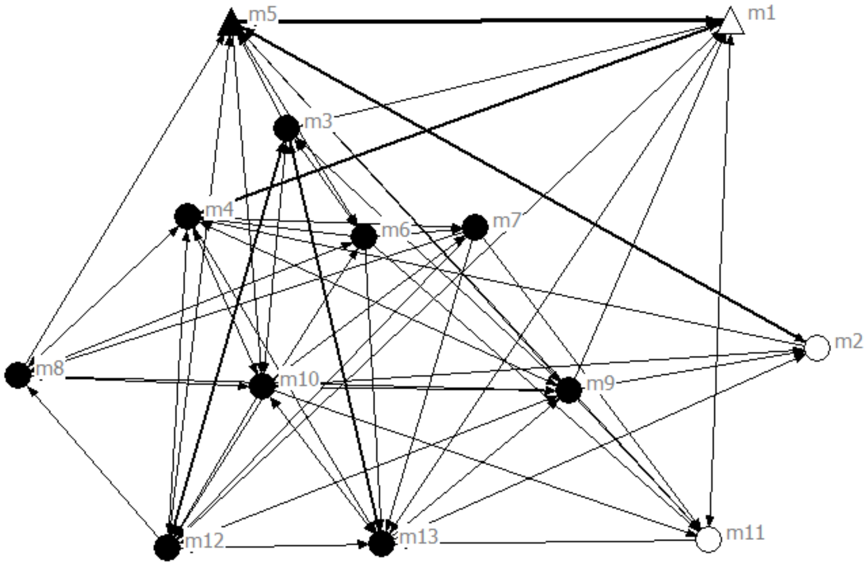
Networks of dominance interactions had higher weighted outdegree scores (Friedman test: df=2, x^2=8.373, *p*=0.015, mean=2.37) than those based on grooming (mean=1.40) and foraging competitions (mean=2.23).

Figure 4.1 Network of grooming from three captive groups of meerkats. PWPG2 and Bristol groups are examples of low centrality scores and Longleat is an example of a group with a high centrality score in grooming networks. For each network: Triangles=dominants, circles=subordinates, white=females, black=males, individuals are approximately arranged by age with older individuals at the top and younger individuals lower down the diagram; stronger ties are indicated by thicker lines.

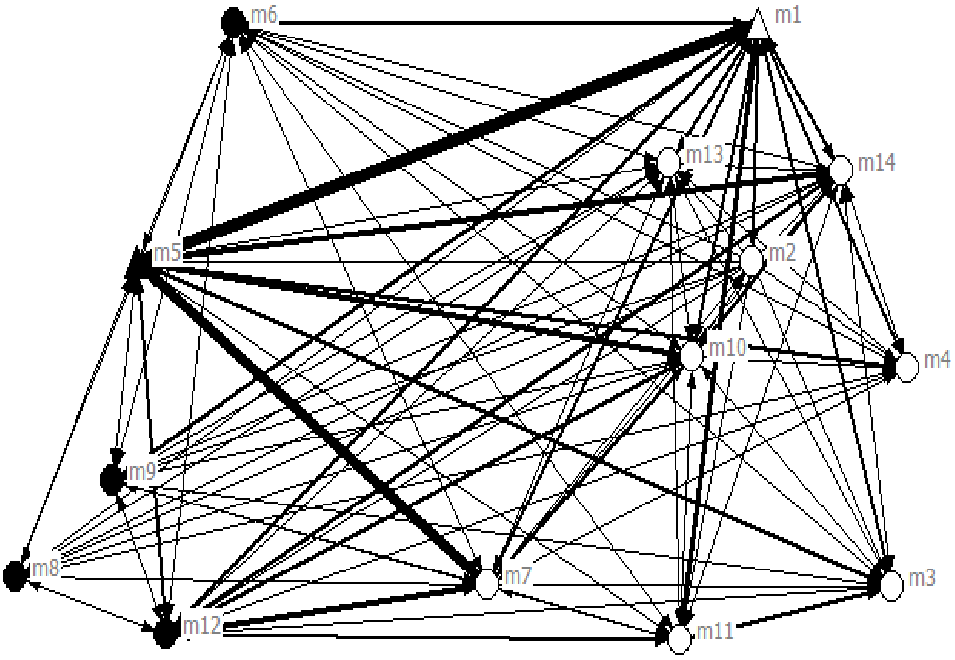
a) PWPG2



b) Bristol



c) Longleat



This suggests that individuals gave a larger amount of dominance events to others. Also, such results indicates that within dominance, a single individual or only a few individuals in the group initiated dominance interactions. This was contrary to grooming and foraging competitions where the number of interaction initiated by the individuals was more even. In contrast, networks of grooming interactions had higher compactness (x^2=14.456, p=0.001, mean=2.73), density (x^2=14.545, p=0.001, mean=2.67) and clustering coefficients scores (x^2=14.517, p=0.001, mean=2.70) compared to networks based on dominance (compactness mean=1.40, density mean=1.33, clustering coefficient mean=1.33) or foraging competitions (compactness mean=1.87, density mean=2.0, clustering coefficient mean=1.97). This indicates that individuals groomed more directly with all other individuals in contrast to dominance and foraging competitions where interactions were sparser (Fig. 4.2). There were no significant differences between the three types of network (grooming, dominance and foraging competitions) within centrality measures of unweighted outdegree data (x^2=3.893, p=0.143), unweighted indegree data (x^2=0.464, p=0.793), weighted indegree data (p=0.538, x^2=1.241) and in distance measures (L) (x^2=1.529, p=0.465).

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Table 4.3 Network measures calculated for fifteen captive groups of meerkats based on three different types of interactions

Group	Network centrality				Distance		Density	Cluster Coefficient
	Unweighted data		Weighted data					
	Outdegree	Indegree	Outdegree	Indegree	L	Compactness	D(SD)	C
GROOMING								
Africam	34.72	43.75	13.48	21.98	1.93	0.59	0.34(0.47)	0.52
Bristol	27.08	18.06	8.27	9.06	1.83	0.49	0.25(0.43)	0.19
Cotswold	41.97	29.63	26.34	20.58	1.65	0.58	0.40(0.48)	0.57
FlamingoG1	12.24	28.57	12.39	15.65	1.69	0.70	0.46(0.49)	0.42
FlamingoG2	0.00	0.00	17.77	17.77	1.00	1.00	1.00(0.00)	1.00
Longleat	74.56	33.14	18.07	18.07	1.76	0.43	0.50(0.50)	0.67
MoreliaG1	0.00	31.25	10.35	38.67	1.25	0.87	0.75(0.43)	0.80
MoreliaG2	25.00	25.00	29.81	21.15	1.16	0.91	0.83(0.37)	0.83
Paignton	75.00	75.00	20.19	17.31	1.00	0.50	0.50(0.50)	0.50
PWPG1	0.00	0.00	29.63	7.41	1.00	1.00	1.00(0.00)	1.00

PWPG2	18.75	18.75	28.12	19.44	1.15	0.92	0.85(0.35)	0.86
Shaldon	0.00	0.00	11.73	9.57	1.00	1.00	1.00(0.00)	1.00
Shepreth	50.00	50.00	21.21	19.32	1.45	0.79	0.60(0.48)	0.68
Twycross	24.79	34.71	15.50	13.02	1.53	0.74	0.50(0.50)	0.61
WMSP	20.00	20.00	26.40	21.60	1.16	0.91	0.83(0.37)	0.80
DOMINANCE								
Africam	70.83	16.67	30.21	13.29	1.30	0.20	0.17(0.38)	0.20
Bristol	15.97	6.94	10.30	7.83	1.40	0.02	0.01(0.13)	0.00
Cotswold	19.75	7.40	11.36	9.48	1.33	0.05	0.04(0.20)	0.00
FlamingoG1	24.49	24.49	21.25	18.37	1.00	0.07	0.07(0.25)	0.50
FlamingoG2	56.25	25.00	44.38	35.00	1.25	0.35	0.30(0.45)	0.00
Longleat	52.66	19.53	47.14	10.32	1.49	0.71	0.51(0.49)	0.59
MoreliaG1	56.25	25.00	63.75	20.00	1.00	0.30	0.30(0.45)	0.00
MoreliaG2	75.00	0.00	64.29	32.14	1.25	0.58	0.50(0.50)	0.00
Paignton	75.00	75.00	65.00	35.00	1.00	0.50	0.50(0.50)	0.50
PWPG1	66.67	66.67	16.67	31.48	1.14	0.54	0.50(0.50)	0.45
PWPG2	62.50	31.25	41.25	16.25	1.16	0.27	0.25(0.43)	0.27
Shaldon	16.67	16.67	16.67	16.67	1.00	0.02	0.02(0.15)	0.01
Shepreth	31.25	62.50	21.96	27.03	1.00	0.25	0.25(0.43)	0.44
Twycross	74.38	14.88	19.52	7.13	1.67	0.23	0.13(0.34)	0.48
WMSP	40.00	40.00	32.00	24.00	1.12	0.50	0.46(0.49)	0.42
FORAGING COMPETITION								
Africam	40.28	22.22	28.24	10.94	1.54	0.57	0.37(0.48)	0.47
Bristol	25.69	25.69	14.29	13.00	1.60	0.13	0.09(0.29)	0.15
Cotswold	25.93	25.93	10.65	9.10	1.73	0.44	0.32(0.46)	0.83
FlamingoG1	55.10	22.45	23.01	18.55	1.53	0.75	0.51(0.49)	0.73
FlamingoG2	18.75	18.75	31.69	24.14	1.15	0.92	0.85(0.35)	0.86
Longleat	52.66	19.53	47.14	10.32	1.49	0.71	0.51(0.49)	0.59
MoreliaG1	25.00	25.00	39.34	19.12	1.31	0.67	0.55(0.49)	0.79
MoreliaG2	75.00	75.00	25.00	70.00	1.00	0.50	0.50(0.50)	0.50
Paignton	100.00	25.00	80.00	35.00	1.00	0.33	0.33(0.47)	0.00
PWPG1	55.56	55.56	58.33	47.22	1.00	0.58	0.58(0.49)	0.58
PWPG2	68.75	37.50	55.11	29.54	1.00	0.45	0.45(0.49)	0.60
Shaldon	22.22	80.56	20.68	42.28	1.18	0.34	0.30(0.46)	0.44
Shepreth	25.00	25.00	25.00	25.00	1.00	0.05	0.25(0.43)	0.10
Twycross	30.58	10.74	14.05	14.05	2.36	0.13	0.08(0.27)	0.00
WMSP	20.00	20.00	22.50	16.50	1.16	0.91	0.83(0.37)	0.85

Network positions of individuals with similar attributes in captive groups.

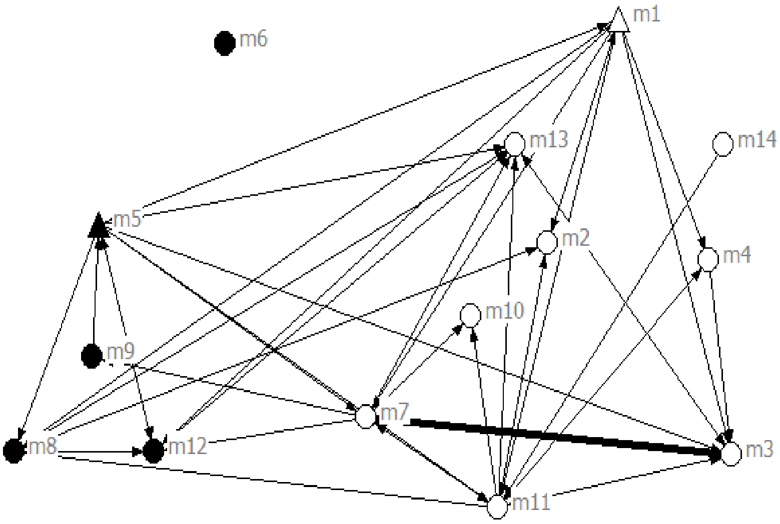
In general, for captive meerkats, an individual's position within a network was predicted by their status and age rather than their sex (Table 4.4). In grooming networks, differences in network position between individuals could not generally be predicted by sex, status or age. However, within individual groups, network positions did differ according to all three attributes. For instance, males initiated more grooming (outdegree) than females in one group (Bristol). Males had shorter paths (outcloseness) to reach the other group members by the use of grooming interactions (Africam, Bristol). Males also had higher density of grooming interactions (clustering coefficient) between group members (Africam). Dominant individuals gave more grooming than subordinates in two groups (Bristol, Cotswold). Adults received more grooming than juveniles in one group (WMSP). Similarly, adults were connected rapidly by the grooming interactions (incloseness) of other individuals of the group (Bristol). And, lastly, adults had a higher density of grooming interactions than juveniles (Cotswold).

In dominance networks, differences between individuals in their position were found mainly in status and age attributes. Dominant individuals tended to give higher total amounts of dominance interactions. Adults received more dominance interactions than juveniles. Also, adults had shortest paths to be reached by other group members via dominance interactions. The sex attribute appeared to have little effect, but in some groups (Bristol, FlamingoG1) males tended to receive higher total rates of dominance. By contrast, in another group (Africam) females were central to dominance interaction networks.

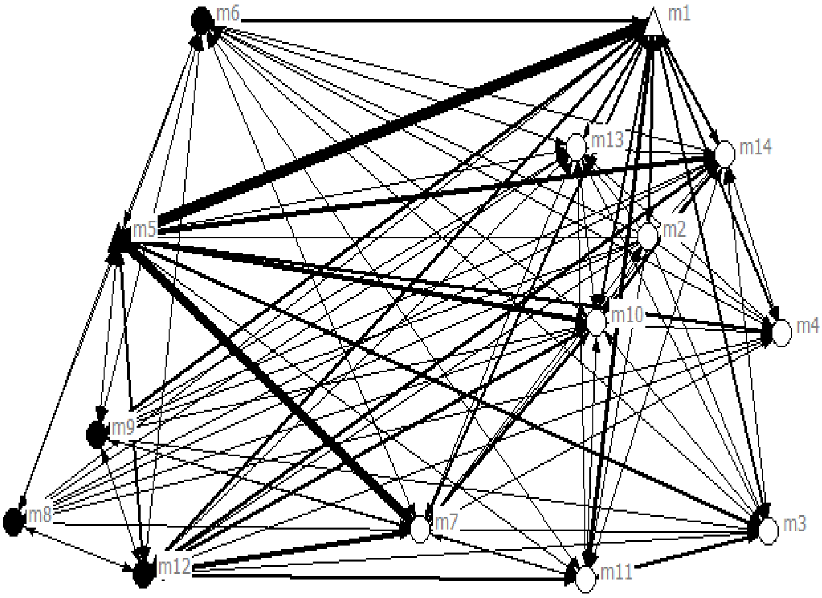
In networks of foraging competition, differences in network position between individuals were mainly due to an individual's age. Juveniles had high incloseness scores which indicates that such individuals could be rapidly connected by the foraging competitions of all group members. Patterns in individual groups showed differences in sex but not in status attributes. Females initiated foraging competitions and they also had shorter paths to reach other individuals of the group by foraging competitions (Cotswold). Conversely, in another group (WMSP), females received more competitions in foraging. Results from two groups (Africam, Bristol) indicated that males could be quickly connected by all other members of the group within foraging competitions.

Figure 4.2 Dominance (a), grooming (b) and foraging competition (c) networks from a captive group of meerkats (Longleat). Dominance networks showed higher outdegree centrality than the other two 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.

a) Dominance network



b) Grooming network



c) Foraging competition network

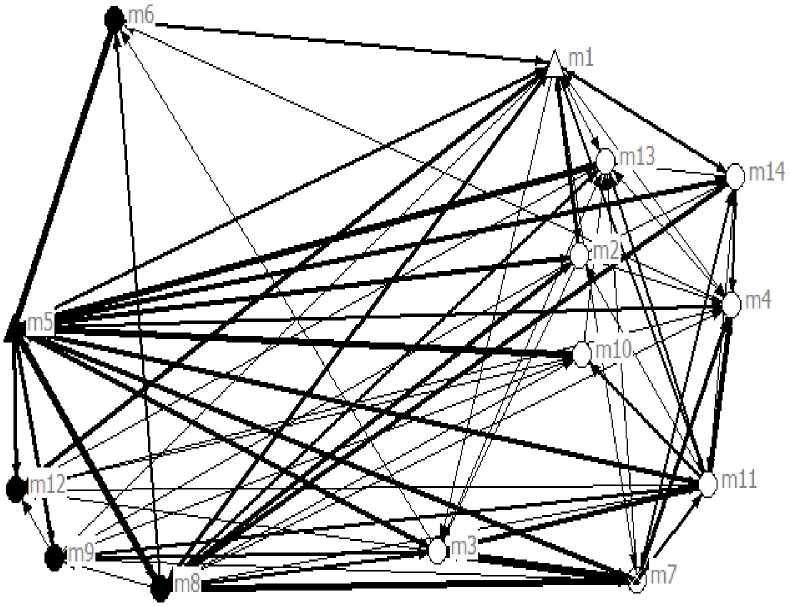


Table 4.4 Differences for network measures of individuals from fifteen captive groups of meerkats varying in three attributes (sex, status and age) based on grooming interactions, dominance interactions and foraging competitions. Significant differences between attribute classes for the group are shown in bold type.

	Sex								Status							
	K	D.Centrality	Kbin		Betweeness	Closeness		Cluster	K	D.Centrality	Kbin		Betweeness	Closeness		Cluster
	Out	In	Out	In		Out	In		Out	In	Out	In		Out	In	
GROOMING																
Africam	0.84	0.60	0.13	0.30	0.28	**0.043**	0.09	**0.004**	0.16	0.07	0.23	0.08	0.23	0.15	0.27	0.23
Bristol	0.19	0.34	**0.048**	0.24	0.94	**0.015**	0.39	0.75	**0.014**	**0.013**	0.71	0.80	0.11	0.50	0.16	0.47
Cotswold	0.91	0.22	0.10	0.26	0.89	0.06	0.059	0.88	**0.046**	0.11	0.10	0.48	0.15	0.14	0.14	**0.042**
FlamingoG1	0.45	0.32	0.60	0.55	0.59	0.53	0.67	0.92	0.14	0.45	0.14	0.67	0.55	0.15	0.66	0.20
FlamingoG2	0.30	0.80	1.0	1.0	1.0	1.0	1.0	0.29	0.90	0.89	1.0	1.0	1.0	1.0	1.0	0.90
Longleat	0.58	0.34	0.61	0.63	0.16	0.80	0.42	0.47	0.22	0.25	0.15	0.41	0.15	0.23	0.30	0.15
MoreliaG1	1.0	1.0	1.0	0.09	1.0	1.0	1.0	0.10	1.0	0.90	1.0	0.90	1.0	0.89	1.0	0.89
MoreliaG2	0.67	1.0	1.0	0.66	1.0	1.0	1.0	0.33	0.68	1.0	0.66	1.0	1.0	1.0	1.0	0.32
Paignton	1.0	0.33	1.0	0.33	1.0	1.0	1.0	1.0	1.0	1.0	0.33	1.0	1.0	1.0	1.0	1.0
PWPG1	0.24	1.0	1.0	1.0	1.0	1.0	1.0	0.49	0.50	0.50	1.0	1.0	1.0	1.0	1.0	0.33
PWPG2	0.50	0.49	1.0	0.89	0.30	1.0	1.0	0.49	0.80	0.19	0.90	0.70	0.90	1.0	0.60	0.79
Shaldon	1.0	1.0	0.61	0.54	1.0	1.0	1.0	0.49	1.0	1.0	0.13	0.14	1.0	1.0	1.0	0.14
Shepreth	0.39	0.89	0.89	1.0	0.09	0.30	1.0	0.40	0.39	0.19	0.30	0.10	0.10	0.79	0.20	0.39
Twycross	0.40	0.59	0.34	0.44	0.83	0.36	0.50	0.39	0.09	0.13	0.09	0.12	0.19	0.08	0.12	0.53
WMSP	0.89	0.50	0.49	0.48	0.39	0.94	0.80	0.80	0.33	0.93	1.0	0.47	0.80	1.0	0.60	0.67
Combined P	0.97	0.99	0.92	0.86	0.99	0.68	0.98	0.41	0.36	0.24	0.47	0.83	0.74	0.95	0.83	0.51
Form of diff.	F>M	M>F	M>F	F>M	F>M	M>F	M>F	M>F	D>S	D>S	D>S	D>S	D>S	D>S	D>S	S>D
DOMINANCE																
Africam	0.052	0.92	0.89	0.53	**0.028**	0.33	0.79	0.65	0.16	1.0	0.08	0.15	0.69	0.15	0.15	0.23
Bristol	0.22	1.0	0.57	**0.004**	0.22	0.42	**0.004**	-	**0.012**	0.29	**0.013**	0.96	1.0	**0.014**	0.70	-
Cotswold	0.45	1.0	0.49	0.41	0.49	0.41	0.07	0.34	**0.044**	0.46	**0.021**	0.45	0.93	**0.025**	0.06	-
FlamingoG1	0.61	**0.036**	0.46	0.54	1.0	0.62	0.38	0.84	1.0	0.63	1.0	0.64	1.0	0.96	0.89	0.06
FlamingoG2	0.49	0.59	0.69	0.50	0.59	0.29	0.90	0.69	1.0	0.19	1.0	0.19	0.41	0.89	0.89	0.29
Longleat	0.39	0.95	0.74	0.76	0.28	0.22	0.14	0.46	0.40	0.79	0.63	0.52	0.42	0.76	0.07	-
MoreliaG1	0.89	0.90	0.60	0.89	1.0	0.90	0.69	1.0	0.10	1.0	0.10	0.10	1.0	0.09	0.09	0.39
MoreliaG2	0.33	1.0	1.0	1.0	1.0	0.66	1.0	1.0	0.33	1.0	0.33	0.33	1.0	0.33	0.33	0.33
Paignton	0.66	1.0	0.67	0.66	1.0	0.67	0.66	0.66	0.33	0.67	0.33	0.33	1.0	0.33	0.33	0.34
PWPG1	0.25	0.49	0.24	0.75	1.0	1.0	0.48	0.74	0.74	0.75	0.17	1.0	1.0	0.17	0.16	0.50
PWPG2	0.40	0.29	0.90	1.0	0.59	0.39	1.0	-	0.09	0.59	0.10	0.29	1.0	0.10	0.20	-
Shaldon	1.0	0.42	0.42	1.0	1.0	1.0	1.0	-	1.0	1.0	1.0	0.85	1.0	0.14	0.86	-
Shepreth	0.30	0.10	0.30	1.0	0.70	0.30	0.89	0.39	0.31	0.30	0.90	0.10	0.59	0.30	0.20	0.69
Twycross	0.91	0.26	0.19	0.85	0.63	0.76	0.37	0.46	0.78	1.0	0.35	0.07	0.53	0.19	1.0	-
WMSP	0.49	0.34	0.39	0.59	1.0	0.44	0.35	0.70	0.06	1.0	0.60	0.64	0.46	0.07	0.06	0.06
Combined P	0.66	0.99	0.92	0.89	0.95	0.94	0.59	0.98	0.10	0.98	**0.044**	0.24	0.99	**0.011**	0.15	0.12
Form of diff.	F>M	M>F	F>M	M>F	F>M	F>M	F>M	F>M	D>S	D>S	**D>S**	S>D	S>D	**D>S**	S>D	S>D

	Sex								Status							
	K	D.Centrality		Kbin	Betweeness	Closeness		Cluster	K	D.Centrality		Kbin	Betweeness	Closeness		Cluster
	Out	In	Out	In		Out	In		Out	In	Out	In		Out	In	
FORAGING COMPETITION																
Africam	0.16	0.18	0.21	0.31	0.86	0.42	**0.013**	**0.003**	0.83	0.38	0.76	0.23	0.31	0.94	0.46	0.39
Bristol	0.79	0.12	0.29	0.85	0.39	0.84	**0.043**	0.057	0.11	0.90	0.38	0.92	1.0	0.25	0.11	0.20
Cotswold	0.13	0.25	**0.047**	0.98	0.06	**0.006**	0.19	0.10	1.0	0.13	0.97	0.10	0.60	0.90	0.52	-
FlamingoG1	0.51	0.69	0.39	0.25	0.25	0.45	0.80	0.25	0.75	0.40	0.14	0.89	0.66	0.15	0.58	0.73
FlamingoG2	0.39	0.69	0.90	0.29	1.0	1.0	1.0	0.70	1.0	0.09	1.0	0.29	1.0	1.0	1.0	0.10
Longleat	0.30	0.47	0.75	0.77	0.49	0.73	0.18	0.54	0.42	0.85	0.45	0.63	0.12	0.50	0.48	0.84
MoreliaG1	0.29	0.60	0.29	0.70	1.0	0.29	0.50	0.90	0.71	0.89	0.71	0.89	0.49	0.29	0.30	0.90
MoreliaG2	1.0	0.33	1.0	1.0	1.0	1.0	0.33	1.0	1.0	1.0	1.0	1.0	0.67	1.0	0.67	1.0
Paignton	0.66	0.66	0.66	0.67	1.0	0.67	1.0	-	0.32	0.33	0.33	0.33	1.0	0.33	1.0	-
PWPG1	0.74	0.50	0.49	0.51	1.0	0.49	1.0	1.0	0.24	0.25	1.0	1.0	1.0	1.0	0.15	0.66
PWPG2	0.29	1.0	0.29	0.19	1.0	0.69	0.89	0.90	0.10	0.29	0.10	0.20	1.0	0.10	1.0	1.0
Shaldon	0.58	0.36	0.20	0.57	1.0	0.57	0.54	0.80	0.14	0.13	0.14	0.14	10	1.0	0.14	0.28
Shepreth	1.0	0.59	1.0	1.0	1.0	1.0	0.59	-	1.0	1.0	1.0	1.0	1.0	1.0	0.59	-
Twycross	0.57	0.97	0.50	**0.037**	0.27	0.78	0.88	-	0.41	0.68	0.49	0.63	0.33	0.40	0.41	-
WMSP	0.74	0.80	0.80	0.50	0.29	0.79	0.80	0.26	0.93	0.53	0.59	0.80	0.93	0.60	0.39	0.93
Combined P	0.75	0.77	0.56	0.76	0.98	0.79	0.43	0.17	0.72	0.58	0.82	0.78	0.99	0.88	0.70	0.85
Form of diff.	F>M	F>M	F>M	F>M	F>M	M>F	M>F	M>F	S>D	S>D	S>D	D>S	D>S	S>D	S>D	S>D

	Age							
	K	D.Centrality	Kbin		Betweeness	Closeness		Cluster
	Out	In	Out	In		Out	In	
GROOMING								
Africam	-	-	-	-	-	-	-	-
Bristol	0.19	0.40	0.88	0.44	0.36	0.31	**0.032**	0.28
Cotswold	0.07	0.20	0.13	0.059	0.80	0.16	0.52	**0.007**
FlamingoG1	-	-	-	-	-	-	-	-
FlamingoG2	-	-	-	-	-	-	-	-
Longleat	0.20	0.72	0.37	0.79	0.82	0.07	0.65	0.06
MoreliaG1	-	-	-	-	-	-	-	-
MoreliaG2	-	-	-	-	-	-	-	-
Paignton	1.0	0.33	0.33	0.33	1.0	1.0	1.0	1.0
PWPG1	-	-			-	-	-	-
PWPG2	0.79	0.19	0.90	0.89	0.90	1.0	1.0	0.80
Shaldon	-	-	-	-	-	-	-	-
Shepreth	-	-	-	-	-	-	-	-
Twycross	0.53	0.51	0.26	0.81	0.90	0.24	0.70	0.26
WMSP	0.45	**0.050**	0.50	0.85	0.15	0.95	0.12	0.85
Combined P	0.51	0.29	0.68	0.82	0.93	0.42	0.44	0.08
Form of diff.	J>A	A>J	J>A	A>J	A>J	J>A	A>J	A>J
DOMINANCE								
Africam	-	-	-	-	-	-	-	-
Bristol	0.58	0.58	0.56	0.58	1.0	0.57	0.42	-
Cotswold	0.73	0.22	0.42	**0.007**	0.18	0.62	0.38	-
FlamingoG1	-	-	-	-	-	-	-	-
FlamingoG2	-	-	-	-	-	-	-	-
Longleat	0.75	0.15	0.58	0.21	0.08	0.78	0.09	0.44
MoreliaG1	-	-	-	-	-	-	-	-
MoreliaG2	-	-	-	-	-	-	-	-
Paignton	0.34	0.66	0.32	0.33	1.0	0.33	0.33	0.33
PWPG1	-	-			-	-	-	-
PWPG2	0.09	0.70	0.10	0.29	1.0	0.09	0.20	-
Shaldon	-	-	-	-	-	-	-	-
Shepreth	-	-	-	-	-	-	-	-
Twycross	0.67	0.60	0.67	0.14	0.09	**0.043**	0.06	0.45
WMSP	0.09	0.10	**0.050**	**0.050**	0.85	0.053	**0.049**	0.29
Combined P	0.53	0.51	0.34	**0.025**	0.62	0.08	**0.029**	0.44
Form of diff.	J>A	A>J	J>A	**A>J**	A>J	J>A	**A>J**	A>J
FORAGING COMPETITION								
Africam	-	-	-	-	-	-	-	-
Bristol	**0.010**	0.09	**0.023**	0.85	0.055	**0.017**	0.59	0.61
Cotswold	0.51	0.051	0.78	0.71	0.41	0.68	**0.005**	0.90
FlamingoG1	-	-	-	-	-	-	-	-
FlamingoG2	-	-	-	-	-	-	-	-
Longleat	0.46	**0.046**	0.46	0.21	0.57	0.63	0.17	0.13
MoreliaG1	-	-	-	-	-	-	-	-
MoreliaG2	-	-	-	-	-	-	-	-
Paignton	0.33	1.0	0.33	1.0	1.0	0.32	1.0	-
PWPG1	-	-	-	-	-	-	-	-
PWPG2	0.09	0.89	0.10	1.0	1.0	1.0	1.0	0.10
Shaldon	-	-	-	-	-	-	-	-
Shepreth	-	-	-	-	-	-	-	-
Twycross	0.58	0.25	0.50	0.19	0.65	0.74	**0.028**	-
WMSP	0.10	0.20	0.20	0.14	0.10	0.95	0.15	0.051
Combined P	0.07	0.10	0.17	0.78	0.43	0.54	**0.024**	0.10
Form of diff.	A>J	A>J	A>J	A>J	A>J	A>J	**J>A**	A>J

Assortative association of individuals within captive groups

Overall, individuals did not associate assortatively by sex, status or age in their grooming interactions (Table 4.5). In one group, groomers did associate according to their sex and status (Twycross, *p*=0.034) with females grooming males more than expected, and dominants grooming subordinates more than expected.

Individuals did not associate assortatively by sex, status and age in their dominance interactions. In one group females did engage in dominance interactions with other females more than expected (Bristol, *p*=0.010).

Individuals did not associate assortatively by sex, status and age in their foraging competition networks. One group did have more competitions than expected between males (Cotswold, *p*=0.026) and in another group, adults competed less than expected with other adults (Bristol, *p*=0.025).

4.3.2 How do interaction networks of captive meerkat groups compare to those of wild meerkat groups?

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. 4.3, Table 4.6). Captive meerkats exhibited more centralised grooming networks, with a higher distribution of groomees (Md=18.07) than those seen in wild meerkats (Md=14.23) (*p*=0.036), and with a less even dissemination of those receiving grooming.

Captive meerkats showed a higher out-degree centrality in their dominance networks (Md=30.21) than wild meerkats (Md=14.29), (*p*=0.026) indicating that a smaller proportion of captive individuals initiated proportionately more dominance events, than in wild populations. Wild meerkats, however, had longer average path length (Md=2.64) than captive meerkats (Md=1.16) (*p*=0.012)*,* which may be because the wild groups were larger than the captive ones.

Table 4.5 Patterns of association for individuals varying in sex (Female-Female, Female-Male and Male-Male), age (Pup-Pup, Pup-Juvenile, Pup-Adult, Juvenile-Juvenile, Juvenile-Adult, Adult-Adult), and status (Dominant-Dominant, Dominant-Subordinate, Subordinate-Subordinate) attributes in fifteen captive groups of meerkats based on grooming interactions, dominance interactions, and foraging competitions.

	Grooming						Dominance						Foraging competitions					
	Associate more			Associate less			Associate more			Associate less			Associate more			Associate less		
c) Sex associations																		
	F-F	F-M	M-M	F-F	F-M	M-M	F-F	F-M	M-M	F-F	F-M	M-M	F-F	F-M	M-M	F-F	F-M	M-M
PWPG1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.500	1.0	0.500	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PWPG2	0.896	0.402	1.0	1.0	1.0	0.298	0.503	1.0	0.499	1.0	0.301	0.899	0.796	1.0	0.501	1.0	0.297	1.0
Shaldon	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.143	0.712	0.431	1.0	0.862	0.661	0.714	0.540	0.862	0.811
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	1.0	1.0	0.665	1.0	0.665	1.0
Longleat	0.466	0.468	0.855	0.642	0.684	0.342	0.645	0.421	0.713	0.485	0.727	0.499	0.640	0.437	0.710	0.494	0.729	0.498
FlamingoG1	0.820	0.683	0.571	0.505	0.635	0.897	0.889	0.434	1.0	0.666	1.0	0.606	0.500	0.838	0.680	0.751	0.462	0.683
FlamingoG2	1.0	1.0	1.0	1.0	1.0	1.0	0.499	1.0	0.607	1.0	0.300	1.0	0.896	1.0	0.698	1.0	0.593	1.0
Africam	0.808	0.963	0.076	0.515	0.057	0.954	0.144	0.272	0.889	0.974	0.843	0.161	0.623	0.959	0.143	0.643	0.092	0.902
WMSP	1.0	0.403	0.798	0.201	1.0	1.0	0.602	1.0	0.600	1.0	0.401	1.0	0.793	1.0	0.800	1.0	0.594	1.0
Twycross	0.953	**0.034**	0.755	0.127	0.998	0.439	0.945	0.400	0.434	0.287	0.851	0.772	0.593	0.479	0.868	0.709	0.802	0.416
Cotswold	0.858	0.902	0.188	0.332	0.404	0.927	0.247	0.789	1.0	0.963	0.593	0.397	1.0	0.877	**0.026**	0.140	0.222	0.983
Bristol	1.0	0.825	0.180	0.291	0.272	0.888	**0.010**	0.707	1.0	1.0	0.685	0.235	0.453	0.699	0.608	0.917	0.532	0.567
Shepreth	1.0	0.103	0.806	0.103	1.0	1.0	0.101	1.0	1.0	1.0	0.101	0.599	1.0	0.602	1.0	0.700	1.0	0.901
MoreliaG1	1.0	.399	0.701	1.0	1.0	1.0	0.600	1.0	0.895	1.0	0.600	1.0	0.701	0.898	0.696	1.0	0.696	0.600
MoreliaG2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.347	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Combined P	1.0	0.922	0.986	0.912	0.998	0.999	0.649	0.997	0.999	1.0	0.972	0.997	0.999	1.0	0.946	0.999	0.958	1.0
d) Status associations																		
	D-D	D-S	S-S	D-D	D-S	S-S	D-D	D-S	S-S	D-D	D-S	S-S	D-D	D-S	S-S	D-D	D-S	S-S
PWPG1	1.0	1.0	1.0	1.0	1.0	1.0	0.829	1.0	0.835	1.0	0.664	1.0	1.0	1.0	1.0	1.0	1.0	1.0
PWPG2	0.902	1.0	0.706	1.0	0.607	1.0	0.497	0.302	1.0	1.0	1.0	0.099	1.0	0.693	0.503	0.196	0.902	1.0
Shaldon	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.706	1.0	0.706	1.0	1.0	0.289	1.0	1.0	1.0	0.289
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	1.0	0.329	1.0	0.329	1.0	1.0
Longleat	0.276	0.156	0.912	1.0	0.902	0.156	0.735	0.859	0.225	1.0	0.195	0.837	0.745	0.858	0.227	1.0	0.198	0.836
FlamingoG1	0.531	0.962	0.353	1.0	0.177	0.962	0.147	0.637	1.0	1.0	0.788	0.323	0.645	0.145	0.966	1.0	0.966	0.145
FlamingoG2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.097	1.0	0.501	1.0	0.097	1.0	0.398	0.701	0.099	1.0	1.0
Africam																		
WMSP	0.936	0.465	1.0	1.0	1.0	0.401	1.0	0.200	0.932	0.132	1.0	0.736	0.937	1.0	0.600	1.0	0.537	1.0
Twycross	0.953	**0.034**	0.755	0.127	0.998	0.439	1.0	0.918	0.385	0.776	0.417	0.945	0.593	0.479	0.868	0.709	0.802	0.416
Cotswold	0.558	0.272	0.883	1.0	0.883	0.251	0.091	0.399	0.956	1.0	0.868	0.198	0.337	0.354	0.979	1.0	0.917	0.268
Bristol	0.358	0.570	0.677	1.0	0.601	0.477	**0.039**	0.197	1.0	1.0	0.879	0.161	1.0	0.973	0.281	0.819	0.281	0.987
Shepreth	0.530	0.123	0.955	1.0	0.939	0.108	1.0	1.0	0.101	0.594	0.101	1.0	1.0	0.777	0.536	0.880	0.566	0.792
MoreliaG1	0.902	1.0	0.699	1.0	0.601	1.0	1.0	0.100	1.0	0.400	1.0	0.100	1.0	0.904	0.400	0.307	0.696	1.0
MoreliaG2	1.0	1.0	1.0	1.0	1.0	1.0	0.664	1.0	1.0	1.0	0.664	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Combined P	0.999	0.864	0.999	1.0	0.999	0.966	0.917	0.810	0.998	0.999	0.993	0.674	1.0	0.969	0.996	0.988	0.999	0.997

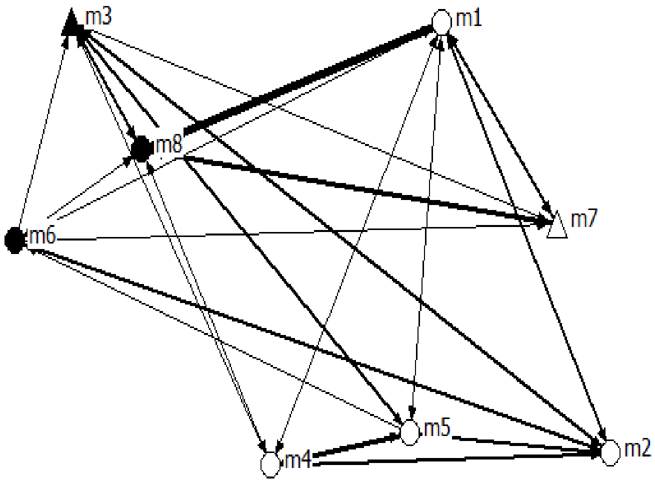
d) Age associations

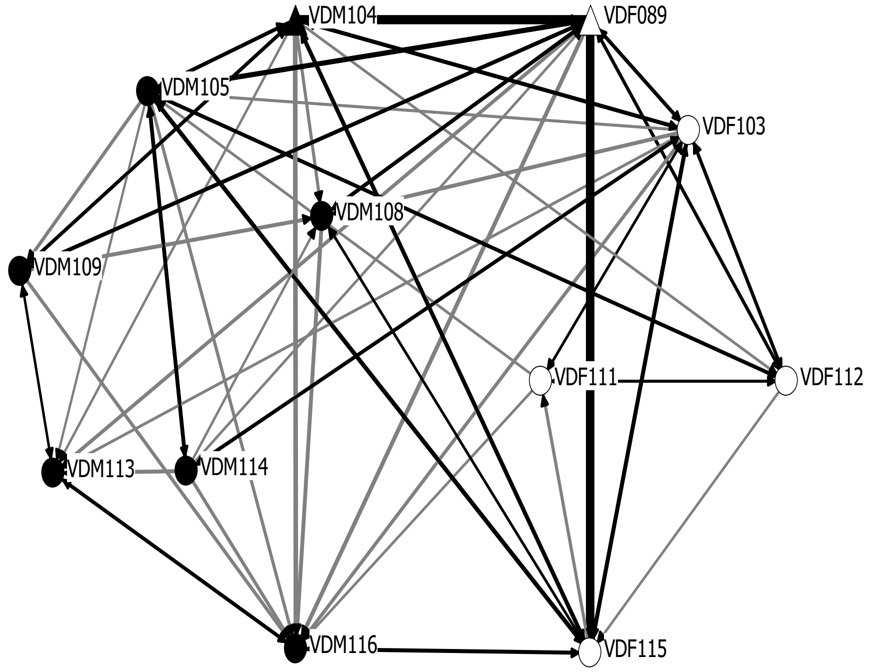
	Grooming											
	Associate more						Associate less					
	P-P	P-J	P-A	J-J	J-A	A-A	P-P	P-J	P-A	J-J	J-A	A-A
PWPG1												
PWPG2				0.699	1.0	0.900				1.0	0.599	1.0
Shaldon												
Paignton				1.0	1.0	1.0				1.0	1.0	1.0
Longleat				0.682	0.945	0.217				0.421	0.150	0.859
FlamingoG1												
FlamingoG2												
Africam												
WMSP				1.0	0.396	0.802				0.197	1.0	1.0
Twycross				0.873	0.618	0.224				0.239	0.607	0.889
Cotswold	0.253		0.567			0.786	1.0		0.655			0.356
Bristol				1.0	0.233	0.730				0.288	0.872	0.419
Shepreth												
MoreliaG1												
MoreliaG2												
Combined P				0.999	0.923	0.898				1.0	0.911	0.993
	Dominance											
	P-P	P-J	P-A	J-J	J-A	A-A	P-P	P-J	P-A	J-J	J-A	A-A
PWPG1												
PWPG2				1.0	0.297	0.504				0.103	1.0	1.0
Shaldon												
Paignton				1.0	1.0	1.0				1.0	1.0	1.0
Longleat				0.101	0.821	0.780				0.979	0.344	0.332
FlamingoG1												
FlamingoG2												
Africam												
WMSP				0.596	0.600	1.0				1.0	0.796	0.399
Twycross				0.236	0.717	0.944				0.949	0.613	0.295
Cotswold	0.243		1.0			0.316	0.973		0.069			0.964
Bristol				1.0	0.701	0.663				0.892	0.673	0.701
Shepreth												
MoreliaG1												
MoreliaG2												
Combined P				0.744	0.950	0.984				0.960	0.975	0.923
	Foraging competitions											
	P-P	P-J	P-A	J-J	J-A	A-A	P-P	P-J	P-A	J-J	J-A	A-A
PWPG1												
PWPG2				0.507	0.702	1.0				1.0	0.899	0.209
Shaldon												
Paignton				1.0	0.338	1.0				1.0	1.0	0.338
Longleat				0.099	0.825	0.785				0.978	0.348	0.329
FlamingoG1												
FlamingoG2												
Africam												
WMSP				0.795	0.403	1.0				1.0	1.0	0.198
Twycross				0.288	0.738	0.886				0.935	0.517	0.412
Cotswold	0.101		1.0			0.123	1.0		**0.041**			0.936
Bristol				**0.011**	0.296	1.0				1.0	0.860	**0.025**
Shepreth												
MoreliaG1												
MoreliaG2												
Combined P				0.117	0.775	0.986				1.0	0.984	0.128

Foraging competitions showed multiple differences between wild and captive meerkats. Captive groups of meerkats exhibited higher centralization. The outdegree centrality total, considering weighted data, was higher in captive meerkats (Md=25.00) than wild ones (Md=10.10) (*p*=0.012), 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. Distance scores showed a higher average path length in wild meerkats (Md=2.38) than in captives meerkats (Md=1.18) (*p*=0.012), which is, again, most likely due to the large size of wild meerkat groups in comparison to captive ones. Conversely, captive meerkats exhibited a higher compactness score (Md=0.50) than wild meerkats (Md=0.29) (*p*=0.036), indicating that the formers had a more solid network of foraging competition, probably due to the size of the captive groups. That is, captive individuals had fewer alternative individuals to target and, therefore, individuals had more direct foraging competition interactions with other individuals, than their wild counterparts. A higher clustering coefficient in foraging competitions was shown in captive meerkats (Md=0.58) in comparison to wild meerkats (Md=0.26) (*p*=0.017) this suggests that captive individuals had a tighter social network where individuals competed in foraging with most (if not all) of their social neighbours.

Figure 4.3 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.

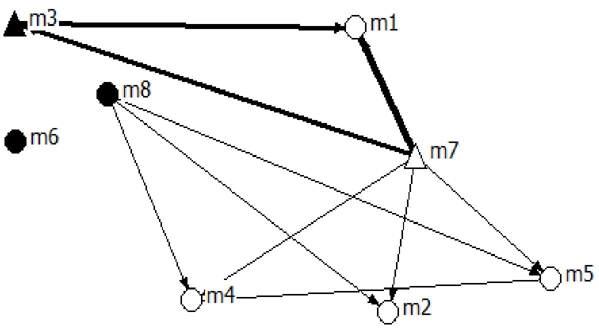
a)


FlamingoG1

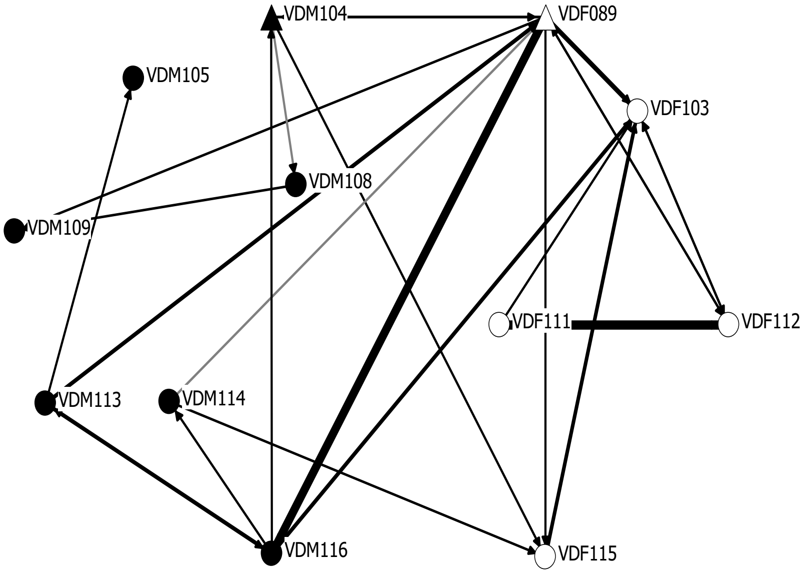

Drie

b)

FlamingoG1

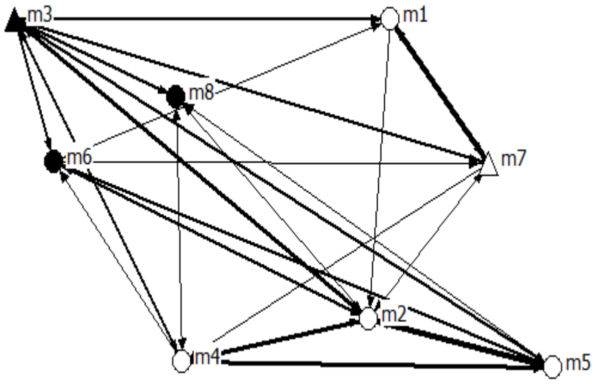


Drie



c)

FlamingoG1



Drie

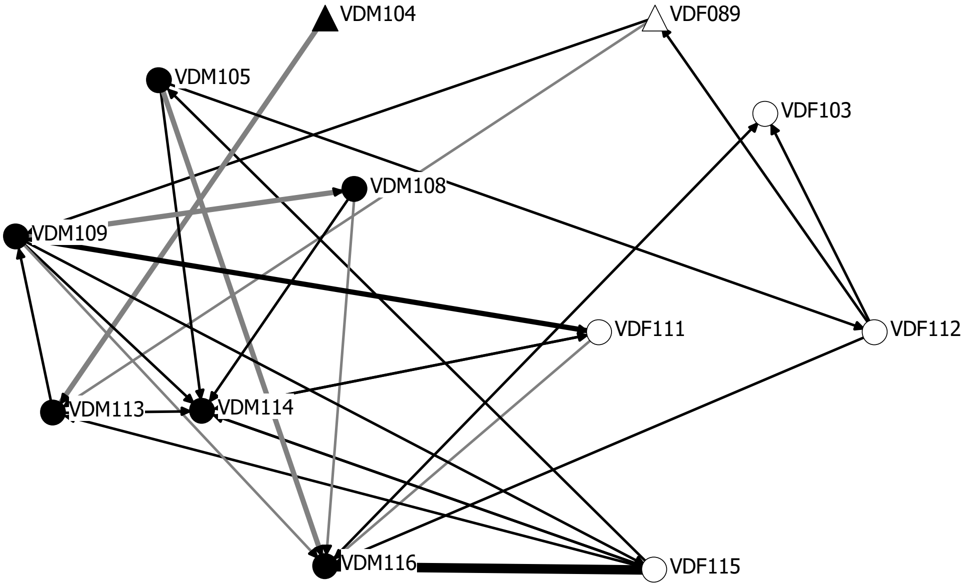


Table 4.6 Comparison of the interaction patterns for meerkat groups in captivity and in the wild based on grooming, dominance interactions and foraging competitions. Significant differences are indicated in bold type.

	Median wild	**Median captive**	**z**	**p**
		GROOMING		
Network Centrality				
Unweighted data				
Outdegree	27.215	24.790	-.420	0.674
Indegree	26.055	28.570	-.280	0.779
Weighted data				
Outdegree	15.180	18.070	-.420	0.674
Indegree	14.235	18.070	-2.100	**0.036**
Distance				
L	1.645	1.250	-.561	0.575
Compactness	0.705	0.790	-.560	0.401
Density				
D	0.455	0.600	-.840	0.401
SD	0.475	0.470	-.423	0.672
Cluster Coefficient				
C	0.525	0.680	-.840	0.401
		DOMINANCE		
Network Centrality				
Unweighted data				
Outdegree	25.000	56.250	-1.540	0.123
Indegree	22.625	24.490	-1.120	0.263
Weighted data				
Outdegree	14.295	30.210	-2.240	**0.025**
Indegree	9.845	18.370	-1.400	0.161
Distance				
L	2.645	1.160	-2.521	**0.012**
Compactness	0.2150	0.270	-.169	0.866
Density				
D	0.455	0.250	-1.820	0.069
SD	0.475	0.430	-1.051	0.293
Cluster Coefficient				
C	0.180	0.270	-.169	0.866
		FORAGING COMPETITION		
Network Centrality				
Unweighted data				
Outdegree	22.035	30.580	-1.820	0.069
Indegree	35.725	25.000	-.890	0.327
Weighted data				
Outdegree	10.105	25.000	-2.521	**0.012**
Indegree	18.605	19.120	-.140	0.889
Distance				
L	2.385	1.180	-2.521	**0.012**
Compactness	0.295	0.500	-2.100	**0.036**
Density				
D	0.115	0.450	-2.103	**0.035**
SD	0.315	0.470	-1.823	0.068
Cluster Coefficient				
C	0.260	0.580	-2.380	**0.017**

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, (Wilcoxon signed rank test Z=2.10, wild N=8, captive N=15, *p*=0.036; Table 4.7), with wild individuals having higher mean betweenness scores. In captive groups, males were more central to networks of grooming than females.

An individual's position within the network of dominance differed between the two conditions in degree centrality measures (Z=2.38, *p*=0.017). Dominants in wild groups of meerkats had a higher indegree centrality in the network than in captive groups. That is, individuals within wild groups received higher total amounts of dominance than individuals within captive groups. Similarly, the two conditions differed in betweenness measures (Z=2.20, *p*=0.028). Wild meerkats had a higher betweenness than captive meerkats; this suggests that wild dominant individuals were more central and consequently more important for controlling social connections within the group by dominance interactions. Also, closeness centrality measures differed between the two conditions (Z=2.24, *p*=0.025). Captive groups of meerkats had a higher incloseness than wild groups of meerkats. This indicates that captive subordinate meerkats had shorter paths to be reached by other group members via dominance interactions.

An individual's position within the network of foraging competitions differed between the two conditions in degree centrality measures (Z=2.36, *p*=0.018), where captive meerkats showed a higher outdegree than wild meerkats. This indicates that females in captive groups initiated higher rates of foraging competitions than in wild groups. Additionally, differences were seen in betweenness centrality (Z=2.20, *p*=0.028) where wild meerkats presented a higher score than captive meerkats. This suggests that subordinates in captive groups were more central to networks of foraging competitions than in wild groups.

Table 4.7 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.

	Median wild	Form of difference	Median captive	Form of difference	z	*p*	Median wild	Form of difference	Median captive	Form of difference	z	*p*
Grooming												
	Sex						**Status**					
K-out	0.33	M>F	0.58	F>M	-1.859	0.063	0.34	D>S	0.39	D>S	-0.420	0.674
K-in	0.41	M>F	0.59	M>F	-1.120	0.263	0.52	D>S	0.45	D>S	-0.280	0.779
Kbin-out	0.21	M>F	0.61	M>F	-1.260	0.208	0.48	D>S	0.33	D>S	0.000	1.0
Kbin-in	0.66	M>F	0.54	F>M	-0.700	0.484	0.86	D>S	0.67	D>S	-1.260	0.208
Betweeness	0.19	M>F	0.89	F>M	-2.100	**0.036**	0.67	D>S	0.80	D>S	-0.700	0.484
Closeness-out	0.18	M>F	0.94	M>F	-1.122	0.262	0.53	D>S	0.89	D>S	-0.140	0.889
Closeness-in	0.62	M>F	1.0	M>F	-0.140	0.889	0.68	D>S	0.60	D>S	-1.352	0.176
Cluster	0.22	F>M	0.49	M>F	-0.560	0.575	0.55	S>D	0.39	S>D	-0.140	0.889
Dominance												
K-out	0.59	M>F	0.45	F>M	-0.560	0.575	0.06	D>S	0.33	D>S	-0.980	0.327
K-in	0.74	M>F	0.59	M>F	-0.840	0.401	0.20	D>S	0.75	D>S	-2.380	**0.017**
Kbin-out	0.51	M>F	0.57	F>M	-1.472	0.141	0.09	D>S	0.33	D>S	-1.35	0.176
Kbin-in	0.65	M>F	0.75	M>F	-0.700	0.484	0.40	D>S	0.33	S>D	-0.140	0.889
Betweeness	0.38	M>F	0.70	F>M	-0.840	0.401	0.10	D>S	1.0	S>D	-2.201	**0.028**
Closeness-out	0.41	F>M	0.44	F>M	-0.280	0.779	0.40	D>S	0.17	D>S	-0.140	0.889
Closeness-in	0.51	M>F	0.66	F>M	0.000	1.0	0.85	S>D	0.20	S>D	-2.240	**0.025**
Cluster	0.25	F>M	0.65	F>M	-0.524	0.600	-	-	-	-	-	-
Foraging competition												
K-out	0.78	F>M	0.57	F>M	-2.366	**0.018**	0.46	D>S	0.71	S>D	-1.153	0.249
K-in	0.35	F>M	0.59	F>M	-0.338	0.735	0.48	S>D	0.40	S>D	-0.314	0.753
Kbin-out	0.76	F>M	0.49	F>M	-1.352	0.176	0.57	D>S	0.59	S>D	-0.507	0.612
Kbin-in	0.39	F>M	0.57	F>M	-0.507	0.612	0.48	S>D	0.63	D>S	-0.085	0.933
Betweeness	0.46	F>M	1.0	F>M	-0.734	0.463	0.10	S>D	1.0	D>S	-2.201	**0.028**
Closeness-out	0.42	M>F	0.69	M>F	-0.314	0.753	0.58	D>S	0.60	S>D	-0.507	0.612
Closeness-in	0.41	F>M	0.59	M>F	-0.169	0.866	0.34	S>D	0.48	S>D	-0.845	0.398
Cluster	0.24	M>F	0.26	M>F	-0.135	0.893	0.14	D>S	0.39	S>D	0.000	1.0

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

Sex and dominance based association in grooming networks was stronger in wild groups than in captive groups, with males associating with other males more strongly in wild groups than in captive groups of meerkats (*p*=0.025; Table 4.8). Dominant individuals in wild groups associated more than expected with other dominant individuals than in the captive ones (*p*=0.018) and, similarly, dominant individuals in wild groups associated more in grooming networks with subordinate individuals than in captive groups (*p*=0.043).

A similar pattern was seen in dominance relationships, with wild groups associating more strongly than captive groups. Dominant individuals interacted with other dominants more frequently in wild groups of meerkats than in captive groups (*p*=0.046). Dominant-subordinate associations were also stronger in wild groups than in captive ones (*p*=0.018).

In networks of foraging competitions, assortment by sex was stronger in wild groups than captive groups. An individual's association in foraging competitions was more significant between male and female meerkats in wild groups than in captive groups (*p*=0.043).

Table 4.8 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**	**z**	***p***
		Grooming		
Sex				
FF	0.86	1.00	-.560	0.575
MF	0.51	0.82	-1.680	0.093
MM	0.46	0.80	-2.243	**0.025**
Status				
DD	0.57	0.92	-2.366	**0.018**
DS	0.61	0.98	-2.028	**0.043**
SS	0.58	0.93	-1.521	0.128
		Dominance		

Sex				
FF	0.37	0.60	-1.400	0.161
MF	0.89	0.78	-1.014	0.310
MM	0.36	0.89	-1.820	0.069
Status				
DD	0.25	0.91	-1.992	**0.046**
DS	0.07	0.74	-2.366	**0.018**
SS	0.97	0.97	-1.461	0.144
Foraging Competition				
Sex				
FF	0.67	0.79	-0.676	0.499
MF	0.48	0.66	-2.028	**0.043**
MM	0.54	0.69	-1.521	0.128
Status				
DD	1.0	1.0	-1.461	0.144
DS	0.63	0.73	-0.338	0.735
SS	0.55	0.78	1.352	0.176

4.4 DISCUSSION

Social network analysis was used to explore three types of social interactions, grooming, dominance and foraging competition, in fifteen captive meerkat groups. A comparison to their wild counterparts in their social network structure was done by repeating Madden and colleagues' work (2009; 2011). Groups of wild and captive meerkats differed in various aspects of their social network structure. Such differences may be due to individuals occupying different network positions and the difference in their 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.

4.4.1 Group network structure based on individual interactions.

Contrasting with my predictions, the grooming networks observed in groups of captive meerkats tended to be more centralised in their grooming indegree than that observed in the wild meerkat groups. To be precise, 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. This unevenness in the grooming network may disrupt the social structure of the group, especially in species where grooming serves to facilitate access to resources. For instance, in tufted capuchin monkeys, *Cebus apella nigritus*, rank-related benefits were attained by reciprocal behavioural interchanges of grooming (Tiddi et al. 2012). Grooming was given in return for tolerance during feeding, a benefit that is granted more easily by higher-ranking females. Similarly, a previous study based on the value of grooming in female primates (Henazi & Barrett 1999) found that individuals traded grooming in a reciprocal manner for the direct benefits of the grooming itself or to trade it for tolerance by more powerful individuals. In addition, such imbalance in grooming networks in the captive group of meerkats may disrupt or distort the direct fitness benefits available to groomees, such as reducing ectoparasite load (Akinyi et al. 2013) or the amelioration of stress (Wittig et al. 2008). The differences in network centrality between wild and captive groups may be a consequence of three co-factors, differing also between the two study environments. First, captive groups tended to be smaller than the wild ones. The captive groups that I studied comprised 3-14 individuals (mean=8.5) whereas the wild groups studied by Madden and colleagues (2009-2011) comprised 9-24 individuals (mean=16.5). Within captive groups, high indegree centralisation scores were observed in two of the smaller groups, MoreliaG1 and G2 (N=5, N=3); however, high indegree centralisation scores were also observed in one of the largest groups, Africam (N=13). In primates, if group size becomes too large, individuals will not have enough time available to maintain an even spread of social relationships and a decrease in group cohesion may occur leading to fragmentation and local centralisation (Lehmann et al. 2007). In the current results, it is not evident that small groups necessarily need to be less egalitarian and more centralised. Clearly, group size alone cannot explain these differences in network structure between the two conditions. Therefore, a second co-factor can be that such patterns in small groups like Shepreth and Paignton were driven by kinship (since individuals in those groups where all direct kin) as pointed out by previous research (Griffiths & Magurran 1997): individuals in smaller groups focus on interactions with kin or with familiar conspecifics. Third, variance in centrality is predicted to vary depending on the group composition, such as sex and age of the individuals. In meerkats, allogrooming interactions tend to predominate between females to reduce conflict between dominants and subordinates (Madden & Clutton-Brock 2009) or to reinforce bonds between females of the same or different status (Kutsukake & Clutton-Brock 2006b). The group at Longleat was comprised of 64% females, which may explain its relatively high indegree grooming centrality, despite its large size. Additionally, patterns of grooming may have been distorted by the presence of pups. The Cotswold group was the only one that contained pups (infants: 0.3 months), which may explain the high grooming centrality. This occurrence of high patterns of grooming interactions has been reported in groups of captive hamadryas baboons, *Papio hamadryas hamadryas*, with infants, which are usually groomed by many different members of the group (Leinfelder et al. 2001). Unfortunately, in the present work, a relation to external factors, such as parasite load or longevity of individuals in the group, cannot be done accurately due to the complexity of obtaining such information in every zoological park.

There was a significant difference between wild and captive groups in the overall rate of dominant events directed towards focal individuals, with captive meerkats having a higher score than wild individuals. Similarly, 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 in both interactions within wild groups than within the captive groups; however, contrasting with my predictions higher clustering coefficients in foraging competition were shown in captive groups. It may be expected that animals living in confinement, where food is continually available, compete much less during feeding or in foraging than their wild counterparts. Yet, 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 & Whiten 1993). Zoo-housed bonobos have demonstrated higher levels of aggressive reactions to food and strong dominance hierarchies (Jaeggi et al. 2010). In fish it has been found that individuals in hatcheries tend to act more aggressively or to dominate their group members more than their counterparts in the wild (Huntingford 2004). Similarly, research on wolves, *Canis lupus*, has shown that the levels of aggression and wounding are more intense in captive wolves than in wild packs (Sands & Creel 2004). The present results and other research results may imply that additional internal factors, like individual behaviour, and external factors, such as zoo management and complexity of enclosure (Price & Stoinski 2007), may perhaps have a powerful effect on dominance interactions (McCowan et al. 2008) and general group social structure (Schulte 2000). Salonen and Peuhkuri (2006) highlight that artificial environment can expose individuals to selection differently than their counterparts in the wild and consequently favour different features to those selected for in nature.

4.4.2 Network positions of individuals with similar attributes.

In contrast to my prediction, individual positions in grooming networks of captive meerkats did not differ according to the attributes of sex, status and age. Network patterns contrasted with the ones seen in groups of wild meerkats where a denser network of grooming was observed. Madden and colleagues explain in their work on wild meerkats (2009) that as group size increased the network tended to change and become less dense, which may suggest that captive groups should have a solid network as the number of individuals in the groups are generally fewer. Grooming interactions develop and maintain social bonds between members in a group (e.g. Feist & McCullough 1976; Muroyama & Sugiyama 1994; Wilkinson 2003; Manning & Dawkins 2012); however, in order for these interactions to continuously occur, group size and sex ratio have also been regarded as essential elements (Lehmann et al. 2007). For instance, cohesion, social relationships and grooming are expected to decrease in very large groups as individuals living in groups of such dimensions have to compromise on their grooming time and consequently their grouping patterns became less stable, which is likely to eventually result in group fission

(Lehmann et al. 2007). Nevertheless, in contrast to wild meerkats (Madden et al. 2009) group size was not related to the grooming networks within the fifteen groups of captive meerkats implying that additional internal factors and/or captivity conditions may be linked to the outcomes. Group composition, in terms of the ratio of females and males in the group during mating season, can have significant effects on allogrooming frequency among individuals (D'Amato et al. 1982; Lin et al. 2008) and the stability of individuals' social relations and their social bonds (Silk et al. 2012). Within my predictions, I expected that captive groups may show higher centrality scores than wild groups, with either subordinate females or males initiating more grooming. In some captive groups, male meerkats did easily connect with others in the group by grooming interactions and, at the same time, males were the ones who gave more grooming. Literature affirms that in wild populations, grooming interactions are more common between females, apparently functioning as part of parental care, placation of dominants by subordinates, and intra-sexual reproductive conflicts (Kutsukake & Clutton-Brock 2006b). One explanation of these differences is that some captive groups were highly skewed with up to 70% being males. A second explanation of this network distribution in grooming is that in groups with a greater number of males, the amount of grooming can occasionally increase as a simple mechanism of tension reduction or as a compensation of a targeted individual helping to restore the incorporation of individuals into the social group (Seyfarth 1980; Harcourt 1979). That is, in species like meerkats, where males in the wild disperse voluntarily because they cannot gain direct reproductive success in their own group, tension may be higher in captive conditions where they cannot disperse, and therefore they may opt to exchange more grooming.

Individual positions in dominance networks of captive meerkats differed mainly according to status and age attributes with dominant and adult meerkats being central within such networks. Captive groups showed similar patterns of outdegree and closeness scores in interaction patterns based on status to those in wild groups, where dominance interactions were mainly hierarchical between dominant and subordinate individuals (Madden et al. 2011). Captive meerkats were more quickly connected by the rest of the group members within the dominance networks than wild meerkats. This finding maybe due to the restricted living area and the group size of captive meerkats. Meerkats in captivity live in conditions where the space is much smaller than the home range of the groups of meerkats studied in the wild, which likely forces individuals into more frequent interactions than occur in the wild. The smaller group size of captive meerkats makes for naturally shorter path lengths between individuals and hence higher closeness scores. Consequently, captive individuals frequently encounter one another and so can easily receive dominance interactions from other members of the group.

Individual positions in foraging competition networks of captive meerkats differed mainly by age and sex, with juvenile and female meerkats scoring highly in measures of incloseness and unweighted outdegree centrality (correspondingly). Juvenile and subordinate individuals in captive groups were more easily reached by other members of the group within foraging competition networks. This matched patterns observed in wild groups (Madden et al. 2011) where younger individuals received higher overall levels of foraging competitions and received competition from more group members. This was probably because smaller individuals were easier targets since they were less able to defend their resources. In a captive environment, this situation may be magnified because young and subordinate individuals have less room to escape competition, and therefore, as expected, a high inclosenness in this interaction was seen in the present groups. As regards sex foraging competitions, females in captive groups initiated more foraging competitions than in wild groups. Similar conditions are observed in females in the wild, such as meerkats (Jordan 2007) and spotted hyenas, *Crocuta crocuta*, (Holekamp et al. 1996), in order to achieve successful reproduction (Stockley & Bro-Jørgensen 2011). 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 & MacDonald 2000); therefore, female meerkats may have the need to fight more for resources. Within status class competition, dominant individuals in wild groups were more important in controlling social connections within the group, by foraging competitions. Madden et al. (2009) found that the duration of dominance tenure was important in the foraging competition networks, and that groups with more established dominant females displaying more egalitarian interactions. Captive populations are frequently disturbed for management reasons. Management of captive groups may disrupt the tenure of a dominant more than it occurs in wild groups and, consequently, a less central network of foraging competition may be found in captive groups, as shown in the present results.

4.4.3 Assortative association of individuals.

There was no general consistency as to how a subject's sex, age or status predicted how they associated with others across the fifteen captive groups in the interaction networks of grooming, dominance and foraging competitions. I 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. Surprisingly, general patterns of association based on status were not found within grooming networks in captive meerkats as expected, or in the groups of wild meerkats. Allogrooming is considered an important activity within social relationships and has been reported to be asymmetrical between subordinate females and dominant females, with the subordinate grooming the dominant more often than vice versa (Kutsukake & Clutton-Brock 2010). Also, it has been shown that grooming interactions between dominant females, offspring and younger subordinates may represent parental care (Kutsukake & Clutton-Brock 2006b). However, additional characteristics may influence grooming displays between social individuals, such as group composition and the existing bonds among individuals. For instance, a study on captive lion-tailed macaques, *Macaca silenus,* found that when males were housed in groups that included large numbers of females and young, they showed higher levels of allogrooming than when males were housed with a small number of females (Mallapur et al. 2005). Furthermore, a study on captive hamadryas baboons, *Papio hamadryas*, documented that, in addition to dominance, 'friendship' can be a very important determinant for the distribution of grooming interactions as it seemed that the captive female baboons built close grooming relationships on mutual trust and loyalty (Leinfelder et al. 2001). Similar results have been found in Japanese macaques, *Macaca fuscata*, where individuals groomed preferentially those individuals that supported them most or, simply, groomed individuals that groomed them most with no covariation of kinship, rank or time spent in proximity (Schino et al. 2007). The captive groups in question are housed in a number of differing compositions; some are formed of purely siblings plus a dominant breeding female, others of 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 & 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 reported in groups in the wild.

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). A single captive group (Bristol) had a significant association between females by dominance interaction. In wild meerkat groups, intrasexual conflict is normally observed as more intense in subordinate and dominant female meerkats than in males, due to reproductive conflicts (Kutsukake & Clutton-Brock 2006a). In natural conditions, the types of agonistic interactions are constrained by the combination of dispersal costs, infanticide for some species, predation pressure and the distribution of critical resources. That is, dominance relationships can be strict, transitive or poorly defined depending on the monopolizable, unvaryingly distributed and nonmonopolizable resources (contest and scramble competition; Wittemyer & Getz 2007). For instance, a study on wild red-legged partridge, *Alectoris rufa*, exemplified how during the spring dispersal of individuals the incidence of agonistic interactions notoriously declined (Green 1983). Meerkats in the wild have the opportunity to join a new group after being constantly harassed and evicted (typically females) or after leaving voluntarily (typically males) (Clutton-Brock, et al. 2002); in captivity they do not have this opportunity. For that reason, captive individuals may avoid any unnecessary continual confrontation to particular individuals to avoid rejection/harassment in a place they cannot escape from, revealing then the low dominance associations between the captive groups.

There were no clear general patterns of association in foraging competitions based on sex, status or age in either the captive or wild groups. It is known that meerkats forage cohesively but with a high level of competition for food (Doolan & 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 & Manser 2011); this may consequently reduce levels of competition in foraging between specific individuals.

In conclusion, the social network structure of captive meerkats generally differed from that of meerkats in the wild. Captive groups presented a rather sparse network of grooming, differing from the dense grooming networks observed in the wild groups. Also, individual network patterns of association in captive groups could not be fully predicted by subject attributes (sex, age and status), contrary to those in wild groups. In general, interaction patterns and social network positions were found mostly in single captive groups. Additionally, there was not a consistent influence of the individual's attributes on association with others in the different interaction networks across all captive groups. Variations in the degree to which members of a group assemble and interact with one another were due to social and non-social factors, such as: group size, group composition, kinship, zoo management and size of the enclosure. 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.

Chapter Five

Personality and social networks: the role of personality in structuring captive meerkats interactions

5.1 INTRODUCTION

Consistent differences in behaviour over time and across contexts have been observed in numerous animals (Hamilton & Ligocki 2012; Riebli et al. 2012; Baugh et al. 2013). Such consistent differences are now commonly described as personalities, also called behavioural syndromes, coping styles, predispositions, individualities, behavioural profiles or behavioural tendencies (Carere & Eens 2005; Sih 2013; Groothuis & Carere 2005; van Oers et al. 2005; Briffa et al. 2008). Differences in behaviour have revealed themselves in exploration, aggressiveness, reactivity, boldness and social tolerance, to mention a few, in both vertebrates and invertebrates (Cote et al. 2008). Ecological and evolutionary causes of such differences have been studied over the last few years where factors such as social niche specialization or social processes (frequency-dependent selection, reputation-building) have been found to be significant in causing the emergence of personality differences within populations (Wolf & Krause 2014). Inter-individual variation in personality differences have demonstrated influence on reproductive success, dispersal, environmental perturbation, divergence in habitat use and resource polymorphism, and interspecific competition and interactions (Webster & Ward 2011).

Even though there is a growing interest in how variations in personality traits are maintained, it is not yet well understood. Such variation is consistent within individuals, and thus individuals will display similar responses across time (MacKay & Haskell 2015). Differences in conditions, such as variation in predation pressure, food availability, and differences in life history strategies are known to maintain personality variation in populations (Boon et al. 2008; Bergvall et al. 2010). Part of this maintenance of variation can be also due to heritable components (MacKay & Haskell 2015) and maternal effects (Réale & Dingemanse 2010). Furthermore, individual variation in behaviour can be present regardless of the age, size and sex of individuals (Carere & Eens 2005; Bell 2007; Réale et al. 2007). One exploratory factor for persistent variation in personality that has received less attention is the social environment that an individual finds itself in.

Bell et al. (2009) explains that in humans, consistency in behaviour increases with age where younger people behave less consistently than older ones and that a possible reason for this could be experience accumulated from the environment and consolidated identity or reputation. It is likely that the same trend applies to animals. For instance, a study on adult pigtailed macaques, *Macaca nemestrina* (Sussman et al. 2014), found that adult personality changed with life experience and age; individuals throughout adulthood showed a decrease in cautiousness and an increase in aggressiveness. They highlight that their results were consistent with specific age-related change patterns observed in humans. The decrease in cautiousness is analogous to the decrease in neuroticism in humans as they mature and the increase in aggressiveness may be analogous to the commonly recognized increase in social dominance with age. In relation to genetic factors, seen as an additional cause for the maintenance of the behavioural variation, Réale and Dingemanse (2010) affirm that two mechanisms are considered: pleiotropy and linkage disequilibrium. The first involves one gene that is responsible for the expression of two different traits; the second involves a gene that is responsible for the expression of one trait that is situated on the chromosome near a gene involved in the expression of another trait. A study looking at genetic influences in response to novel objects and personality dimensions in papio baboons, genus *Papio* (Johnson et al. 2015), found significant heritability for several behaviours expressed by the individuals such as aggressive and affiliative behaviour.

Animal populations face constant selection pressure on the individuals' fitness where socially essential behaviours can vary in relation to individuals' personality and, inversely, personality-dependent behaviour can vary reliant on its social context (Snijders et al. 2014). Certainly, research interest in the subject of animal personality and social networks has increased in recent years due to their potential ecological and evolutionary significance (Wilson et al. 2013). Social interactions do not occur at random. Instead, age, sex, kinship and familiarity all influence interactions and networks structures (Croft et al. 2008). Critically, personality can also influence sociality and, therefore, it can be expected that personality influences who interacts with whom within a social network (Croft et al. 2009).

Individual variation in personality results in behavioural and physiological outcomes that may influence social interactions, and so shape the network structure among group members (Weinstein & Capitano 2008). For instance, a study on yearling rhesus monkeys, *Macaca mulatta* (Weinstein & Capitanio, 2012), found that the quality of an individual's friendship was affected by their own personality. Individuals that scored high Equability (calm, generally inactive animals) had the fewest friendships. In a previous study on great tits, *Parus major* (Aplin et al. 2013), it was found within the results that individual variation in behaviour not only influenced direct interactions with social partners but also interactions between other individuals in an individual's social network. They highlight that songbirds followed alternative social strategies related to personality. Social association in animal groups may also be driven by the behavioural type of the individuals (Wilson and Krause 2015). For instance, Croft and colleagues (2009) demonstrated that in the wild guppies of similar attributes were more likely to be associated as a tendency of predator inspection across strong network ties.

Social interactions in group living species are seldom simply dyadic, but rather occur within a polyadic network. A social network approach is necessary to study individual-level interactions as well as population-level social structures, where not just immediate interactions with individual partners but also indirect relationships are considered (Krause et al. 2010). For instance, Pike and colleagues (2008) tested how personality between individuals, specifically bold and shy, affects the frequency and distribution of their interactions within a network of three-spined sticklebacks, *Gasterosteus aculeatus*. 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; that is, a low mean clustering distribution was observed. In contrast, networks containing bold individuals were characterized by a low interaction frequency and uniform distribution of interactions;

that is, a low mean strength and a high mean clustering coefficient was observed. A more recent study looking at whether individual differences in exploration behaviour 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; to be precise, slower males had the fewest unique contacts.

Whilst an individual's position in a network may depend on their personality, it may also be subject to other non-personality attributes such as age and sex. For instance, age has been observed to have an effect on allogrooming and olfactory inspection networks in lion-tailed macaques, *Macaca silenus*; groups containing several young increased the levels of such behaviour interactions within the group (Mallapur et al. 2005). Similarly, sex was related to grooming interactions in hamadryas baboons, *Papio hamadryas*, in which females play the most important part in such networks by grooming regular female partners (Leinfelder et al. 2001). However, these two factors, personality and other individual traits, are unlikely to be independent of one another. An individuals' personality may be shaped by both morphological traits such as sex and age, as well as other ecological or social factors such as group size. For example, it has been found that older pigtailed macaques, *Macaca nemestrina*, were less cautious and more aggressive as it is commonly observed in humans in age related pattern effects. The increase of aggressiveness can be analogous to the increase in social dominance with age and the decrease in cautiousness can correspond to the decrease in neuroticism in humans as they grow older (Sussman et al. 2014). A study looking at the effects of individual features, such as age, on personality in vervet monkeys, *Cercopithecus aethiops sabaeus*, found that juveniles and subadults scored higher in playful/curious and opportunistic factors than adults (McGuire et al. 1994). Additionally, in the same study, females were found to have higher scores on the opportunistic factor than males. Correspondingly, sex has been correlated to personality in chimpanzees, *Pan troglodytes*, in which males are characterized to be more aggressive than females due to, from an evolutionary point of view, the fact that males need to seek food over a wide and often unknown range of environments, and that the females' principal role is looking after the young (Buirski et al. 1978). A study on Norway rats, *Rattus norvegicus*, has also found a variation between sexes in personality, with males exhibiting lower levels of activity and anxiousness (characteristic traits in rodents) than females (Korpela 2011). Additionally, in an ecologically relevant behaviour such as foraging, the status of an individual can be predicted by personality in mountain chickadees, *Poecile gambeli*. Low exploring birds were significantly more likely to become dominant in the group (Fox et al. 2009). A different study investigating the shy-bold continuum in sheep foraging (Michelena et al. 2009) found within the results that group size was an important component in the group dynamic interactions of foraging, with bold sheep being the ones to split off from the main herd as the group size increased and to graze in two different patches, while shy individuals avoided splitting and exploited the patches alternatively. They highlight that bold sheep may have the propensity to disconnect from conspecifics in order to explore new environments, and consequently the likelihood of animals splitting into subgroups can increase. Therefore, an individual's position within a social network may influence the expression of their personality. Equally, an individual's personality (in conjunction with other factors such as age, sex or dominance position) may determine their position within the social network. Finally, there may be an interplay between an individual's personality and their network position wherein each factor modulates the other.

Social interactions are a pivotal aspect of the behavioural ecology of animals, and a better understanding of the personality social context and the individual variation in behaviour can be employed to improve captive animal conditions, as well as to enhance the success of animal reintroduction (Verdolin & Harper 2013). 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 behaviour (Morgan & Tromberg 2007). Consequently, individuals may be favoured by characteristics dissimilar to those selected for in nature (Einum & Fleming 2001; Salonen & Peuhkuri 2006).

Meerkats, *Suricata suricatta*, are characterized for 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). Previous research on consistent individual differences in wild meerkats has been conducted in cooperative behaviour (see English et al. 2010); however, there is no study exploring personality in the context of social networks in different captive groups of the same species. To achieve this goal, first, meerkat personality was assessed by conducting observations of their behaviour. 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 behavioural traits obtained into broader dimensions or factors that can be used quantitatively to compare individuals, populations and even species (Watters & Powell 2011).

First, it is critical to determine that such measures are robust and therefore repeatable across time (Uher & Asendorpf 2008). I achieved this by surveying a subset of my study groups during two periods, one year apart and testing whether an individual's personality score in one year matched that in the second year. Once this had been confirmed I also explored whether my assumed personality measures differed according to an individual attributes of sex, age and status.

It is expected that personality traits such as playful and sociable are detected mainly in young individuals. Play behaviour occurs at frequencies and there is higher initiation of the behaviour during infancy and juvenile periods (Sharpe 2005b). Curious behaviour, as expressed in exploration, may also be expected from young individuals, as exploration is recognised as being a fundamental form of learning in infants (Degen et al. 2015). Specific to meerkats, females tend to have elevated rates of aggressiveness than males (Clutton-Brock et al. 2006; Kutsukake & Clutton-Brock, 2006, 2008a; Santema & Clutton-Brock 2012); therefore, I tested whether captive females were also more aggressive than males. Finally and critically, I tested whether an individual's personality was influential in determining their social network structure. I took two approaches. First, I explored whether individual's sharing similar network positions also exhibited similar personality types. I predicted that individuals with Friendliness dimension tend to be highly social and to be characterized by being focal in the network. Animals high in sociability can be indexed by the time spent interacting with group partners, involving activities of play and grooming (Freeman & Gosling 2010). A highly social individual, therefore, can be characterized by a central position in the network, by either receiving or giving interactions (high in-outdegree centrality scores in grooming or playing), or for being surrounded by partners that are well connected (the interaction effect from the focal individual can be spread in the local group, high clustering coefficient), or by individuals being important for controlling social connection amongst the group (high betweenness; Madden et al. 2011). Individuals with Aggressiveness dimension can be predicted mostly in individuals with higher outdegree centralisation, that is, individuals that direct larger amounts of aggressive interactions towards other individuals. Second, I investigated how personality scores affected the likelihood of associations between individuals. Personality has been found to influence social network associations in some species including great tits (Snijders et al. 2014) and zebra finches (McCowan et al. 2015). Such networks of preferred association can have fitness consequences for individuals (Ebensperger & Hayes 2016), such as in resource access (Krause et al. 2007) or protection from predators (Croft et al 2009). Association patterns could arise through preferences for similar locations (Ward et al. 2007), Locations in an enclosure can be limited and, therefore, specific individuals, such as non-aggressive or less-aggressive, may find themselves associating with each other and avoid the company of aggressive individuals. Consequently, I may expect that meerkats show stronger associations with other individuals of similar personality type (positive homophily).

5.2 METHODS

5.2.1 Behavioural measures and individual attributes

Fifteen captive groups of meerkats comprising a total of 113 individuals were studied. Social associations and interactions were collected during continuous focal observations. These comprised: grooming, playing, foraging, foraging competitions, resting and dominance behaviour. Three attributes were considered for all individuals: age, sex and status (see Chapter 2-General Methods for the complete description). I wanted to ensure that my 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 behaviour recorded within the same sampling period (see below). I assessed repeatability across time by returning to five groups for a second sampling period approximately one year after my original sampling. This allowed me to compare the same behaviours of 36 individuals over two recording periods.

5.2.2 Personality measures

Four behavioural traits were collected during continuous recording sampling using all occurrence sampling (Martin & Bateson 2007) in order to record various kinds of social interactions (Freeman & Gosling 2010). The method of coding has been used with the objective of assessing personality in meerkats in their captive condition under unmanipulated circumstances. Several trials of behavioural data collection were carried out as a training to recognize and record every behaviour; this was made by a single observer, the author. Each group was observed for 20 hours over the 4 days of observations. Data were collected on all members of the group: infants: 0-3months, juveniles: 3-12months and adults: 12 months over. Personality traits were derived from the species behavioural repertoire from published ethograms which were used to code the behavioural data (Weinstein et al. 2008). The ethogram used was developed from a recompilation of several authors: Drewe et al. 2011; Kutsukake & Clutton-Brock 2008a; Santema & Clutton-Brock 2012; Sharpe 2005a, 2005b.

Four traits were included: playful, curious, sociable and aggressive. Each of the behaviours were counted as equally. Playful personality trait was recorded when the following behaviours were present: play chasing, play biting, clasping, grappling, mounting, pawing, play object (solitary play) and wrestling. Curious personality trait was recorded when approach, exploring and foreleg stabbing behaviours were present. Sociable personality trait was recorded when allogrooming, huddling, side by side and touching the snout behaviour were present. Aggressive personality trait was recorded when the following behaviours were present: attack, bite, charge, chase, chin mark, glare, hit, hip slam and threaten (Table 5.1).

Table 5.1 Ethogram for *Suricata suricatta* and personality category

Category	**State behaviour**	**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
	Touching the snout	an animal is giving another one short touch with the snout
Aggressive	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

Spearman’s correlation was used to test for relationships between the individual scores for each personality trait. Consequently, 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 behavioural variables measured (e.g. Lantová et al. 2010). The scree plot and the Kaiser’s criterion were used, using this rule, 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 tested the repeatability of the PCA measures of personality by re-surveying the behaviours of 36 meerkats in 5 groups one year later. Originally there were 42 meerkats within the five groups, however, after one year there were changes in the composition of the groups. I only included in the observations the same individuals present in both times, and I excluded any new meerkat added to the groups. For the construction of the PCA measures in the two different times of observation I run a separated PCA measure for the replicated group data. Spearman’s correlation was used to test for relationships between the individual scores for each personality traits during the two times of observations.

5.2.3 Network measures and analytical methods

Network positions of individuals and the assortative association of individuals with similar attributes were analysed. 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. Permutation tests in UCInet were used to calculate the probabilities of individuals' categories associating assortatively. Non-random associations probabilities between individuals based on their sex, status and age were calculated based on unweighted interaction data, using 10,000 permutations (see Chapter 2, section 2.4.1. and 2.4.2 for a complete description).

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.

5.3 RESULTS

5.3.1 Principal component analysis.

During the first sampling period, I was able to extract two robust measures of individual personality across the fifteen groups. There was a significant positive correlation between rates of Playful, Curious and Sociable behaviours, but a negative correlation between Playful and Aggressive behaviours. Curious was weakly and positively correlated to Sociable and Aggressive, and Sociable was negatively correlated to Aggressive (Table 5.2). Principal component analysis identified two primary factors with a Eigenvalue greater than 1 and which together explained 60.02% of the total variance (F1: 33.72%; F2:26.34%). Component 1 and component 2 could be described as capturing aspects of ''Friendliness'' and ''Aggressiveness'', respectively (Table 5.3). The first component ('friendliness) had positive loadings with playful, curious, and sociable behaviours. Therefore, an individual with a high PC1 Score exhibited lots of playful, curious and sociable behaviour and thus I use this PC as a measure of Friendliness, describing individuals having a high friendliness score as sociable, curious and playful. The second component had a positive loading with aggressive behaviour and a negative loading with sociable and playful behaviour. Therefore, an individual with a high PC2 score was aggressive, unsociable and non-playful and thus I use this PC as a measure of Aggressiveness and describe high scoring individuals as aggressive.

Table 5.2 Correlation matrix of individual personality traits' scores

Personality measures	Playful	Curious	Sociable	Aggressive
Playful	1.0			
Curious	.168	1.0		
Sociable	.145	.187	1.0	
Aggressive	-.026	.040	-.062	1.0

Table 5.3 Factor loadings from Principal Components Analysis

	Component	
	Friendliness	Aggressiveness
Playful	**.567**	**-.501**
Curious	**.634**	.263
Sociable	**.775**	-.054
Aggressive	.124	**.859**

Factor loadings of 0.50 or above are marked in bold.

5.3.2 Principal component analysis of five groups, first and second observations (Time 1 and 2).

When I restricted my analyses to just the 36 individuals from the five groups that I visited twice, I was only able to extract a single component, likely because of the reduced sample size. In the first period of observations on the five groups, principal component analysis identified only one primary factor with a Eigenvalue greater than 1 and which explained 42.68% of the total variance (Table 5.4). Component 1 was similar to Component 1 in the analysis above (‘’friendliness’’) and had positive loadings with playful and sociable behaviour. In the second period of observations, one year later, principal component analysis identified two primary factors with a Eigenvalue greater than 1 and which together explained 67.05% of the total variance (F1: 40.35%; F2:26.69%) (Table 5.5). The first component had positive loadings with playful, curious and sociable behaviours. The second component had a positive loading with aggressive behaviour and a negative loading with sociable and playful behaviour. Therefore, the first component is equally referred to as ‘’friendliness’’ and the second component as ‘’aggressiveness’’. Because I only extracted a component corresponding to Friendliness in both the first and second set of 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 repeatability in these five group of meerkats (see below).

Table 5.4. Factor loadings from Principal Components Analysis, Time 1 (Five groups)

	Component
	Friendliness
Playful	**.559**
Curious	.378
Sociable	**.525**
Aggressive	-.242

Factor loadings of 0.50 or above are marked in bold.

Table 5.5 Factor loadings from Principal Components Analysis, Time 2 (Five groups)

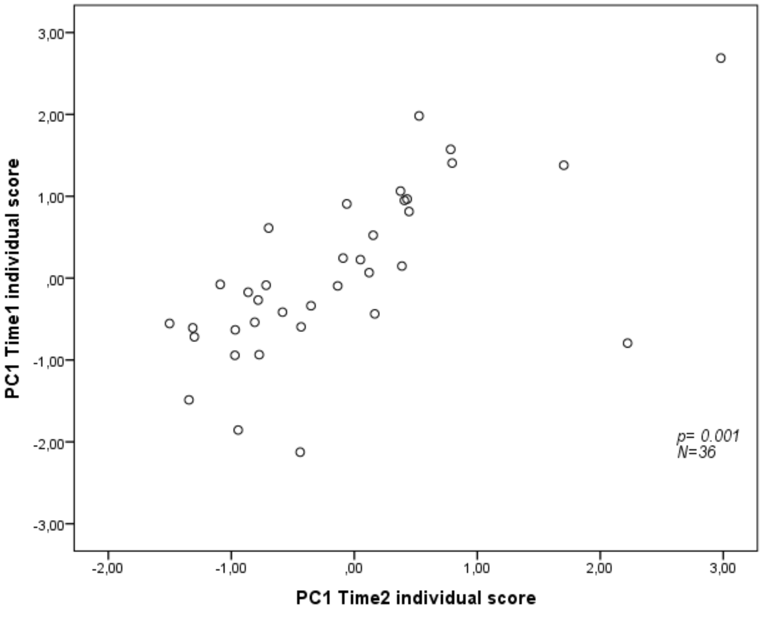
	Component	
	1	2
Playful	**.611**	-.607
Curious	**.709**	.062
Sociable	**.742**	-.044
Aggressive	.111	**.933**

Factor loadings of 0.50 or above are marked in bold.

5.3.3 Measures of Friendliness personality dimension in the two different times of observation in five groups

The personality traits were repeatable within individuals. Scores of personality traits were positively correlated between the two different observation times. The personality dimension of ''friendliness'' had a strong positive correlation between the two times: r= .675, n= 36, *p*=0.001 (Fig. 5.1).

Figure 5.1. Correlation between personality traits measured in two different times in five groups: PC1, ''Friendliness''



5.3.4 Relationships between personality dimensions and individual attributes (sex, age and status) across the fifteen groups.

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 5.6).

Table 5.6. 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	F	*p*	Mean	df	F	*p*	Mean
Sex differences	1	.838	.371	F: .018 M: -.146	1	.820	.383	F: -.164 M: .055
Age differences	2	.280	.756	P: .793 J: -.368 A: -.077	2	.468	.630	P: -.493 J: .370 A: -.092
Status differences	1	.222	.639	D: -.021 S: -.112	1	.002	.961	D: -.087 S: -.071

5.3.5 Network positions of individuals with similar personality attributes in the fifteen groups.

An individual's personality score in friendliness (but no aggressiveness) corresponded to some aspects of their social network position. An individual's position within a social network based on foraging competitions was related to their measure of Friendliness, with friendly individuals having higher clustering coefficients (Table 5.7). Differences were seen also in one group (Longleat) where non-friendly individuals initiated higher rates of foraging competitions (weighted and unweighted data). Non-friendly individuals had shorter paths (outcloseness) to reach the other group members by foraging competitions. There were no consistent differences between individuals in their positions within Dominance networks. Differences were found in on group (Longleat). In the same way as in foraging competitions networks, non-friendly individuals initiated higher rates of dominance (weighted and unweighted data) than friendly individuals. Friendly meerkats acted also like focal individuals within dominance and were well connected to the other group members. Lastly, in the same group, Friendly individuals were focal in playing networks.

There were no consistent differences in any of the four networks related to the measure of Aggressiveness. Differences were found in only one group (Twycross) where individuals with the personality dimension of Aggressiveness had shorter paths to reach the other group members by dominance interactions and were rapidly connected by grooming interactions of other individuals of the group.

5.3.6 Assortative association of individuals

There were no general patterns of assortative association depending of Friendliness and Aggressiveness personality dimensions in the fifteen groups (Table 5.8).

Table 5.7 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, F=Friendly, NF=Non-Friendly, A=Aggressive, NA=Non-Aggressive.

	Friendliness								**Aggressiveness**							
	K	**D. Centrality**		**Kbin**	**Betweeness**	**Closeness**		**Cluster**	**K**	**D. Centrality**		**Kbin**	**Betweeness**	**Closeness**		**Cluster**
	Out	In	Out	In		Out	In		Out	In	Out	In		Out	In	
DOMINANCE																
Africam	0.840	0.249	0.922	0.221	0.419	0.161	0.491	0.245								
Bristol									0.693	0.707	0.693	0.712	0.691	0.701	0.538	
Cotswold	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	
FlamingoG1									0.622	0.587	0.802	0.820	1.0	0.620	0.765	
FlamingoG2	0.401	0.305	0.496	0.500	0.399	0.796	0.711	1.0	0.404	0.399	0.395	0.608	0.800	0.407	0.401	1.0
Longleat	**0.012**	0.057	**0.024**	0.292	0.158	0.647	0.458	**0.004**								
MoreliaG1									0.399	0.494	0.702	0.698	1.0	0.697	0.698	1.0
MoreliaG2			1.0	1.0		0.334	1.0						0.657			
Paignton																
PWPG1	0.757	1.0	0.751	1.0	1.0	0.499	0.756	1.0								
PWPG2									0.500	0.294	0.610	0.704	1.0	0.602	0.500	
Shaldon																
Shepreth									0.197	0.397	0.595	0.407	1.0	0.605	0.587	
Twycross									0.086	0.856	0.079	0.762	0.267	**0.025**	0.094	0.485
WMSP	0.668	0.392	0.542	0.532	0.198	0.525	0.402	0.935	0.169	0.333	0.164	0.330	0.336	0.170	0.166	0.673
Combined P	0.415	0.371	0.699	0.882	0.571	0.629	0.932	0.173	0.189	0.833	0.389	0.977	0.937	0.247	0.490	0.972
Form of diff.	NF>F	NF>F	NF>F	F>NF	NF>F	F>NF	F>NF	F>NF	A>NA	NA>A	A>NA	NA>A	NA>A	A>NA	NA>A	NA>A
FORAGING COMPETITION																
Africam	0.812	0.381	0.785	0.365	0.334	0.594	0.666	0.899								
Bristol									0.832	0.295	0.822	0.915	0.056	0.707	0.439	
Cotswold	0.599	0.691	0.507	0.603	0.698	0.492	0.697		0.095	0.904	0.199	0.106	0.898	0.491	0.598	
FlamingoG1									0.491	0.687	0.689	0.255	0.381	0.560	0.806	0.447
FlamingoG2	0.304	0.899	0.599	0.598	0.301	1.0	1.0	0.904	0.790	0.197	0.303	1.0	0.402	1.0	1.0	1.0
Longleat	**0.011**	0.057	**0.022**	0.298	0.850	**0.016**	0.279	**0.004**								
MoreliaG1									0.401	0.101	0.896	1.0	0.294	0.401	0.198	0.298
MoreliaG2			1.0	0.334		1.0	0.661	1.0					1.0			
Paignton																
PWPG1	0.751	0.503	0.756	0.501	1.0	0.747	0.499	1.0								
PWPG2									0.505	0.804	0.697	0.500	1.0	0.700	0.698	0.497
Shaldon																
Shepreth									0.206	0.801	0.202	1.0	1.0	0.199	0.799	
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	0.696	0.497	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	0.590	0.865	**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	NF>F	NF>F	F>NF	A>NA	NA>A	A>NA	A>NA	NA>A	A>NA	NA>A	NA>A

GROOMING

Africam	0.572	0.161	0.314	0.317	0.260	0.446	0.400	0.490								
Bristol									0.550	0.778	0.555	0.950	0.779	0.488	0.652	0.612
Cotswold	0.502	0.504	0.702	0.499	0.207	0.599	0.486		0.296	0.498	0.396	0.906	0.497	0.396	0.694	
FlamingoG1									0.457	0.715	0.767	0.644	0.429	0.647	0.347	0.498
FlamingoG2	0.392	0.697	1.0	1.0	1.0	1.0	1.0	1.0	0.809	0.805	1.0	1.0	1.0	1.0	1.0	1.0
Longleat	0.175	0.848	0.380	0.699	0.784	0.132	0.347									
MoreliaG1									0.792	0.598	1.0	0.603	0.402	1.0	1.0	0.701
MoreliaG2			0.662	0.33		1.0	1.0	0.670					0.669			
Paignton																
PWPG1	1.0	0.254	1.0	1.0	1.0	1.0	1.0	1.0								
PWPG2									0.196	0.304	0.102	0.305	0.096	0.400	0.402	1.0
Shaldon																
Shepreth									0.199	0.207	0.208	0.402	0.201	0.201	0.595	1.0
Twycross									0.072	**0.034**	0.146	0.099	0.138	0.141	0.064	0.135
WMSP	0.725	0.470	0.338	0.199	0.671			0.663	0.821	0.662	0.839	0.663	0.661			0.301
Combined P	0.612	0.587	0.891	0.789	0.848	0.877	0.335	0.980	0.440	0.512	0.629	0.855	0.528	0.664	0.739	0.891
Form of diff.	NF>F	F>NF	NF>F	F>NF	F>NF	F>NF	F>NF	NF>F	A>NA	A>NA	A>NA	A>NA	A>NA	A>NA	A>NA	A>NA

PLAY

Africam	0.311	0.731	0.350	0.199	0.216	0.202	0.695									
Bristol									0.385	0.514	0.537	0.744	0.534	0.538	0.852	
Cotswold	1.0	0.399	1.0	1.0	1.0	0.500	0.257		0.493	0.399	0.794	0.699	0.902	0.508	0.399	
FlamingoG1									0.590	0.763	0.819	0.896	1.0	0.615	0.360	
FlamingoG2	0.202	0.793	0.390	0.490	0.388	1.0	1.0	0.405	0.397	0.407	0.392	0.395	0.398	1.0	1.0	0.303
Longleat	0.615	0.315	0.888	0.799	0.365	0.448	0.662	**0.044**								
MoreliaG1									0.389	0.105	0.396	0.405	1.0	0.201	0.199	1.0
MoreliaG2						1.0	1.0						1.0			
Paignton			0.669	0.670												
PWPG1	0.253	0.743	0.242	0.252	0.239	0.749	0.751									
PWPG2									0.796	0.802	0.598	1.0	1.0	1.0	1.0	0.296
Shaldon																
Shepreth									1.0	1.0	0.611	0.399	1.0	1.0	1.0	
Twycross									0.284	1.275	0.246	0.244	0.300	0.375	0.380	0.585
WMSP	0.797	0.401	0.800	0.806	1.0	0.369	0.504		0.166	0.339	0.511	0.493	1.0	0.674	0.494	
Combined P	0.641	0.811	0.872	0.825	0.630	0.845	0.960	0.089	0.683	0.648	0.847	0.883	0.999	0.946	0.903	0.658
Form of diff.	NF>F	F>NF	NF>F	NF>F	NF>F	F>NF	F>NF	F>NF	NA>A	NA>A	NA>A	NA>A	NA>A	NA>A	NA>A	A>NA

Table 5.8. Patterns of association for individuals varying in the two personality dimensions in the fifteen groups: F=Friendliness and A=Aggressiveness.

	Personality associations											
	Associate more			Associate less			Associate more			Associate less		
	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
	Resting						Foraging					
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

5.4 DISCUSSION

Principal component analysis of the four personality traits revealed two personality dimensions, Friendliness and Aggressiveness, across the fifteen groups of meerkats. However, within a subset of my data (five groups), Friendliness was the only measure that robustly captured consistent individual differences across at least one year. A relationship was not found between attributes and personality dimensions due to age, status, and sex. Individuals with high Friendliness scores were more central in networks of foraging competitions. There were no other consistent predictors of SN position across all 15 groups, although, in individual groups personality score did correspond to SN position. Aggressiveness did not explain an individual's position in any form of interaction. There was no evidence that meerkats preferentially associated with or avoid others based on each of their personality scores.

5.4.1 Repeatability of personality dimensions

A long-term repeatability (over a year) assessed in 36 meerkats was detected in the personality dimension of Friendliness. Repeatability is widely acknowledged as a main criterion for animal personality. It can be perceived in single traits and in behavioural syndromes, that is, between individual correlations of two or more behavioural traits (Wuerz & Krüger 2015). Even though repeatabilities in traits are revealed, particular changes over time can be expected. It is suggested that animal personalities can be chosen if fitness payoffs rely on both the frequency of the individual's behavioural strategy and the individual's behavioural history (Dall et al. 2004). It has also been suggested that changes in personality can be due to 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 & Krüger 2015). In addition, the syndrome structure may be unstable due to the shift in hormonal levels during sexual maturation (Bell 2004). For instance, a study on the development of behavioural differences in juvenile, sub adult and adult sticklebacks (Bell & Stamps 2004) found that particular personality syndromes that were present during the juvenile stage were not present anymore in sub adults but reappeared in the adult stage. They suggest therefore that ecological and development circumstances may favour different suites of traits. In the present 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 that I observed in their personality. Han and Brooks (2013), emphasize that genetic architecture may be a cause of personality syndrome stability over time and that more genetic studies on personality can provide important insights into how behavioural syndromes are maintained or disrupted across life stage transitions. Records of personality characteristics of individuals' parents (or overall ancestry records) can be valuable for future investigations of this sort. A second explanatory factor could be that conditions which rarely change and are fairly predictable, such as a zoo environment, may favour higher levels of repeatability than unpredictable and fluctuating conditions.

5.4.2 Structure of personality dimensions and individual attributes

The first principal components corresponded to the Friendliness dimension with positive loadings from playful, curious and sociable behaviours. This dimension has similarities with the dimension of Sociability in rhesus macaques, *Macaca mulatta* (Weiss et al. 2011; Freeman & Gosling 2010), in chimpanzees, *Pan troglodytes* (Koski 2011; Freeman & Gosling 2010), 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). These dimensions tend to be associated with the traits of playful, curious, and sociable.

In contrast to my predictions Friendliness did not differ with age, nor sex or status in the captive meerkats. A quite straightforward relationship between age and play behaviour may be expected considering that young animals are typically characterised by practicing play behaviour (Bekoff & Allen 1998; Bekoff & Byers

1998; Kuczaj & Eskelinen 2014). Play between adults has been found in species like birds, canids, rodents, primates and ungulates (Mancini & Palagi 2009), nonetheless, in wild meerkats, social play has been observed more frequently between young than adults (Sharpe et al. 2005b). Nevertheless, a confined 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 behaviours that are considered as luxury in the wild. Play behaviour can be performed by individuals only when their immediate needs are met so that their welfare is not compromised (Held & Spinka 2011). Thus, parallel levels of play behaviour in adult and juvenile meerkats could have been observed in the captive groups. Second, several functions of play behaviour 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. 2015). Despite captive environments meeting basic physiological and survival needs, they can still produce stressful situations (Held & Spinka 2011), such as an escalated intrasexual conflict caused by individuals' deprivation for natural dispersal. Play can contribute to general stress resilience (Tacconi & Palagi 2009) and to reduce aggression between group members (Soderquist & Serena 2000). Therefore, play, regardless 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.

Explorative behaviour, sub-trait related behaviour to Curious, can be understood as a function of foraging behaviour; a foraging efficiency is related to an exploration foraging strategy (Evans & Raine 2014). It is known that pup meerkats are usually reared by helpers until they are able to forage independently (approximately aged 3 months; Clutton-Brock 2001b) and find food by themselves. Young meerkats in the wild, with good body condition, still invest more time in foraging to develop foraging skills and hence develop high foraging efficiency, notwithstanding they already have a full stomach (Thornton 2008a). In contrast, young meerkats in captivity may not act in accordance with their wild conspecifics as they may possibly not perceive the development of foraging skills as a proximate need because food is already provided by humans, and therefore, may decline to invest in extensive exploratory.

The first principal components corresponded to the Aggressiveness dimension with positive loadings from aggressive behaviour. This dimension has similarities with the dimension of Proactive in rats (de Boer et al. 2003), Dominance in rhesus macaques, *Macaca mulatta* (Weiss et al. 2011), and Confidence in rhesus macaques and chimpanzees, *Pan troglodytes* (Freeman & Gosling 2010), which tend to be associated with the trait of aggressive. Contrary to my predictions, an individual's aggressiveness was not related to their sex, status or age. In wild meerkats it can be expected that females will be more aggressive than males due to their intense intragroup reproductive conflict (Jordan 2007); however, captivity conditions may result in atypical group compositions and in the unfeasibility of female eviction and/or male emigration. 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 general aggressiveness personality in wild female meerkats may not be reflected in captive females but can be equally reflected in both, males and females. A similar condition can happen with age where juvenile or adult meerkats may be equally aggressive in a captive environment but still modulate aggression. An additional explanation of missing relationship between Aggressiveness and age can be linked to food quantity and availability. Hodge et al. (2009) suggest that food availability can be an important factor in aggression. They point out that juvenile wild meerkats tend to be more aggressive between littermates when the amount of food available is low (during low rainfall). They further explain in their work that when food was supplied to individuals before a foraging session, juveniles significantly reduced their frequency of aggression in comparison to unfed controls. Correspondingly, research looking at the effects of fat on social behaviour in the Cynomolgus monkey, *Macaca fascicularis* (Kaplan et al. 1991) found that the quantity of food (luxury or prudent food) had an effect on aggressiveness between individuals, with animals on a prudent diet behaving more aggressive that animals on a luxury diet. Meerkats in captivity are usually well fed and sometimes overfed which could be an alternative explanation of the present results.

5.4.3 Network positions, assortative association of individuals and relationship between personality and group attributes

Individuals with high Friendliness dimension scores were more central in networks of foraging competitions. Generally, small individuals (young) or individuals lower in hierarchy and which can be more playful, curious or sociable (see prediction in section 5.1) can be poorer competitors in foraging and may be individuals with a high centrality 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 factor in shaping the structure of ecological communities (Jeglinski et al. 2013) and the extent of competition varies with the abilities of the foragers, the ecological context and the distribution in time and space of the resources (Ward et al. 2006). Competition often results in the dominance of one individual over another with the winner gaining priority access to resources such as food (McFarland 1999). Moreover, it is known that dominant individuals may use information produced by subordinates on new food patches (Kurvers et al. 2010), such scrounging phenomenon for dominant individuals has been well described in literature (McCormack et al. 2007); which may be an additional explanation of subordinate meerkats been sought out by the other members of the group.

In contrast to my predictions, personality seemed not to affect patterns of assortative association. Behavioural assortment between individuals of similar personality can provide anti-predator benefits (Croft et al. 2009) or other important adaptive benefits such as increased foraging efficiency in which such a structure may be mediated by behavioural factors rather than just morphological differences between individuals

(Pike et al. 2008). Here yet again, potential short and long-term benefits can be perceived differently in a captive habitat and, consequently, association based on personality type may diverge from animals in the wild.

In conclusion, a generalisation of the results should not be done about the observed patterns in the captive groups of meerkats. Friendliness and Aggressiveness personality dimensions differed depending on the attributes of age and status, and an individual’s position in the network of foraging competitions could be predicted by the Friendliness personality dimension. Additionally, a long-term repeatability was perceived in the same dimension within particular groups. A consistent influence of personality on an individual’s association with others was not detected. In the wild, individuals of certain personality types may adjust their network assortment among them to modify selective pressures, and balance their cost and benefits (Aplin et al. 2013). In a captive environment such characteristics may vary and therefore social associations may be adjusted accordingly. Broader use of personality in social contexts will help us to clarify complex social dynamics and elucidate the mechanisms sustaining the patterns of personality assortment.

Chapter Six

Housing conditions and management effects on the group structure of captive meerkats.

6.1 INTRODUCTION

Zoos have evolved tremendously from their foundation, where little consideration was given to the needs of the animals in exhibition. Nowadays a modern zoo has the important role of supporting and promoting the conservation of global wildlife, dedicating itself to scientific research to improve animal husbandry and management, and increasing the level of understanding, knowledge and awareness that visitors have about wildlife and the environment (Hosey et al. 2013). Many zoos today have very high standards of animal husbandry and welfare, yet, zoos with low standards still exist around the world. It stands to reason that the captive environment of many species differs greatly to those of their wild conspecifics. The physical environment can be much simpler, less challenging, with restricted space where migration is not possible, and there are no predators (Huntingford 2004). Therefore, much research in zoological parks has been focused on understanding how the captive environment may influence the animals' behaviour and welfare. Examples include the effect of husbandry (Clark 2011; Baker & Pullen 2013; Tan et al. 2013), enclosure (Jensvold et al. 2001; Liu et al. 2003), environmental enrichment (Wood 1998; Wells 2009) and visitors (Wells 2005; Fernandez et al. 2009). However, less attention has been paid to their social environment (see Cassinello & Pieters 2000; Valuska et al. 2014; Leeds et al. 2015). This is critical since an adequate social environment facilitates expression of natural behaviour, especially in group living species, and an abnormal social environment leads to poor individual welfare (Hosey 2005; Hosey et al. 2013).

A social environment can be manipulated by the social factor itself (group composition, group size, stability and so forth) and physical factors (husbandry management, enclosure size, complexity, barrier type, etc.). Different physical factors in a confined setting are likely to alter different aspects of interactions and, hence, social structure. Social network analysis can focus on the structural properties of an individual's standpoint or a network as a whole. This approach can provide a visual map trough quantitative measures such as degree centrality, betweenness centrality, clustering coefficient, reciprocity and fragmentation which indicate how a social system divides or integrates within its overall structure (McCowan et al. 2008). These maps can help us to visualise the social stability or instability that can, for instance, lead to elevate rates of deleterious aggression and injuring (McCowan et al. 2008). Such direct impacts of social relations upon individual or group well-being indicate the utility of SNA in the study of animal welfare. SNA can be a very useful tool to study animals in captivity where some features of the captive environment help to avoid sampling issues and enable collection of continuous fine-scale interaction data that is difficult to collect in the wild. Additionally, group sizes in captivity are usually smaller and close-range, and observations can be achieved more easily over a sustained period (Clark 2011). Analysing the social structure of a group within multiple housing areas, such as indoor and outdoor housing, breeding sites and enclosure furnishings, will contribute to the design of enclosures with the objective of reducing, for instance, antagonistic encounters and thus, maintain the welfare of the individuals housed in the exhibit (Rose & Croft 2015). Moreover, comparative analysis of social networks and inter-individual distances can be an important tool to understand the different responses of animals in order to change and help predict how social organizations may possibly be disrupted after relocation or modification in group structures (Dufour et al. 2011).

In addition to characteristics such as an optimal group size, good management of the group, and the availability of space, enclosure design has been shown to be an important factor influencing the behavioural repertoire of animals. The complexity of the environment can provide the necessary sensory input that can stimulate the individuals to exhibit species-specific behavioural patterns (Mallapur et al. 2005; Ross et al. 2011a). The promotion of naturalistic environments has been considered in numerous zoological parks where enclosures aim to reproduce the aesthetic characteristics of the wild setting (Ross et al. 2011b). Buchanan-Smith et al. (2013)

claim that factors such as a good enclosure design and adequate husbandry may be substantial for promoting positive interactions between individuals. For instance, in a study on captive orang-utans (Perkins 1992) looking at the variables that influence the behaviour of the captive animals, it was found that enclosures enriched with moveable objects promoted higher activity levels in individuals than the size of the enclosure per se. A further study, also in primates (Jensvold et al. 2001), found that provision of enriching structures facilitated by good enclosure design was the most essential element that determined the quality of the captive primate's life. As the housing environment comes to be more austere and socially or spatially restrictive, detrimental changes in behaviour may be more prevalent. Such inadequate housing conditions can be linked to reduced fecundity, self-injurious behaviours and chronic stress (Brummer et al. 2010). In enclosures with restricted space, animals are in closer proximity than they would be in the wild and therefore, such captive conditions may change animal social behaviour (Buchanan-Smith et al. 2013). In the wild, group members can choose whether to remain in the group or to leave, individuals may opt to stay closer to their groupmates in order to reduce the risk of predation, or they may opt to keep greater distances in order to minimize competition for resources (Leone & Estevez 2008).

The size of the enclosure has been correlated to aggressive interactions between individuals. Animals may have a preferred inter-individual distance, wherein a minimum distance is allowed by an animal before responding aggressively towards a conspecific approach (Valuska & Mench 2013). In addition, captive animals may naturally have higher inter-individual distances, as well as a decrease in aggressive interactions, in larger spaces (Dufour et al. 2011).

It is not simply the content of an enclosure or its area, but the barriers that surround the enclosure may also influence the behaviour of its inhabitants. Diverse barrier types have been used to keep animals inside the enclosure and to keep visitors and animals separated. Besides keeping visitors safe, barriers or fences are needed so that animals are not bothered. Hosey et al. (2013) give an overview of some of the most commonly used barriers along with their advantages and disadvantages. Some of these are: solid barriers (made of brick walls, wooden fence panels and glass), bars, netting and mesh. Hosey (2000), in his work on the visitor effect on zoo animals, explains that more naturalistic cages including a not so obvious barrier between visitors and animals may produce a more naturalistic profile behaviour without the disruption of the visitor presence. Unfortunately, the number of studies in this area focusing on the barrier effect on animal welfare is still limited (e.g. Blaney & Wells 2014; Wells 2005; Lindblom 2014). Furthermore, there is no study to date exploring the probable effects of the type of enclosure barriers on the social structure of animal groups.

Finally, the social behaviour of captive animals may be influenced by their human observers; that is, the zoo visitors who provide the reason why animals are in the enclosure. These behavioural changes can include a decrease in social behaviour, an increase of aggression and an increase of abnormal behaviours (Fernandez et al. 2009; Farrand et al. 2014; Quadros et al. 2014). Aspects such as visitor density (Wells 2005), audience activity and noise (Birke 2002; Quadros et al. 2014) have been found to influence the behaviour of animals. However, most of the studies have focussed predominantly on investigating behavioural changes such as aggression, abnormal behaviours and avoidance, and physiological measures such as urinary cortisol and faecal glucocorticoid metabolite concentrations (Sherwen et al. 2015).

Meerkats provide a very good opportunity to study social network structures as they are identified as a highly social and cooperative species that repeatedly interact with each other (Madden et al. 2009). They are composed primarily of a dominant pair and subordinates of both sexes (Clutton-Brock et al. 1999), living in groups of 2 to 50 individuals that will remain stable for years (Bousquet & Manser 2011). Critically, meerkats are a very popular species within zoos and are included in a large number of zoological parks. Therefore, a better understanding of how captivity influences their social structure would benefit many individuals. Furthermore, the variety of zoos provides the opportunity to study them in a great variety of housing conditions. Even though there is little work on the effects of captivity on the structure of animal social networks (e.g. Rose 2010; Clark 2011: Rose & Croft 2015), there is a large body of evidence on the effects of captivity on animal behaviour (e.g. Veasey et al. 1996; Shulte 2000; Mallapur et al. 2005; Santiago-Moreno et al. 2007; Tan et al. 2013; Crast et al. 2014; Mattiello et al. 2014; Talbot et al. 2014). Behaviour is expressed as a response to intrinsic and extrinsic factors that will manifest in a network of inter-individual interactions and associations that will vary in strength, type and dynamics (Croft et al. 2008). Therefore, if the individual behaviour is affected by captivity conditions, certainly, the social network structure will be transformed.

In the present work, I will explore how physical and husbandry factors vary across enclosures and how this corresponds to a variation in the social structure of meerkats. Precisely, I will measure six different forms of social interaction and their resulting networks, and correlate measures of network structure with husbandry and enclosure measures. It was predicted that meerkat interactions and association networks could be affected by the management and housing conditions of the zoo. Specifically, I predicted that non-random associations of dissimilar sex or status will be observed in enclosures with more satisfactory conditions (such as more complex enclosure and adequate type of shelter). When adequate and complex spaces are provided to animals in confinement, individuals will have more likelihood to choose whom they wish to associate with (Schel et al. 2012). I also predicted that denser networks in smaller enclosures can be observed, indicating more equal patterns of interactions. In addition, I predicted that enclosures with less human contact, will show less central patterns of interactions. Interactions between group partners may decrease with a high number of visitors because of the animal´s increasing interest towards visitors (Farrand et al. 2014).

6.2 METHODS

6.2.1 Behavioural measures, network measures and individual attributes

Fifteen captive groups of meerkats comprising a total of 113 individuals were studied. Social associations and interactions were collected during continuous focal observations. These comprised: grooming, playing, foraging, foraging competitions, resting and dominance behaviour. Three attributes were considered for all individuals: age, sex and status (see Chapter 2 for the complete description).

In order to construct social networks, a total of 14012 observed social associations and 9408 interactions (grooming interactions: 3564, playing interactions: 3719, foraging associations: 10052, foraging competitions: 1353, resting associations: 3960, dominance interactions: 772) were used (see Chapter 2 for the complete description).

6.2.2 Zoological Parks' enclosure and management

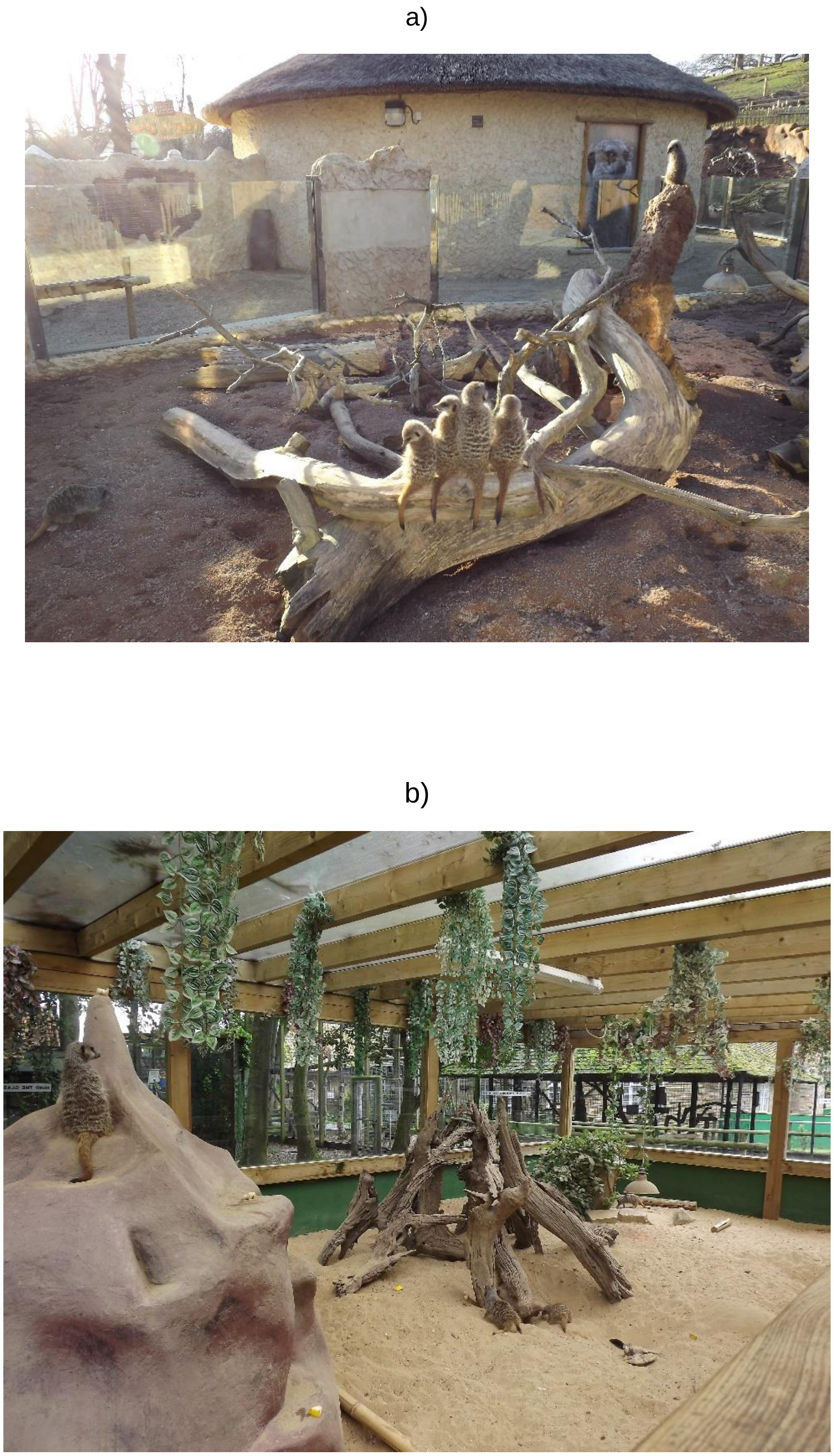
Information from zoos, such as zoo records and enclosure design sketches helped to classify the fifteen enclosures conditions into the six following categories:

Table 6.1 Classification and description of the enclosure types and management.

	Description
a) Enclosure size	1=small (15m^2-40m^2) 2=medium (41m^2-75m^2) 3=large (76m^2-160m^2) 4= very large (161m^2-240m^2)
b) Enclosure complexity (see Fig. 6.1)	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)
c) Enclosure barrier type (see Fig. 6.2)	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
d) 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.
e) 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.
f) 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)

Figure 6.1 Representative pictures for enclosure complexity comparison. Low a) medium b) and high c).



c)

Figure 6.2 Representative pictures for enclosure barrier type. Inadequate a) and good b).

a)

b)

6.2.3 Analytical methods

Ten network measures for the six forms of interactions and associations were analysed. 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 across the three ways of interactions for every group. Additionally, I analysed the differences of individuals varying in three attributes, sex, status and age by using degree centrality, cluster coefficient, betweenness and closeness. Network positions of individuals and the assortative association of individuals with similar attributes were also analysed (see Chapter 2, for the complete description).

Spearman's rank correlation was used to test relationships between the network level measures and measures of enclosure design and husbandry regimes because there was a small data set with a non-normal distribution of data. I tested whether there was a correlation between the different network measures and the different type of enclosure/management (enclosure size, complexity and barrier, type of shelter, enrichment and human contact).

6.3 RESULTS

6.3.1 Assortative association of individuals and enclosure/husbandry factors

In general, there were no consistent correlations at the $p<0.05$ level (Table 6.2 and 6.3). Enclosure size and complexity were negatively related to strengths of associations between sexes and between individuals of differing status when considering networks of resting interactions (Fig. 6.3). That is, in smaller or less complex enclosures, there were stronger patterns of affiliation between individuals. In addition, the measure of day shelter quality was negatively related to both heterophily associations based on sex and status in resting associations. That is, in groups with inadequate day shelter provision, different sexes and individuals of different status associated less than expected by chance.

Table 6.2 Spearman's correlations between enclosure measures, husbandry measures and the association patterns of foraging and resting varying in sex (n=15).

	Sex association											
	Foraging						Resting					
	F-F		F-M		M-M		F-F		F-M		M-M	
	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*
Enclosure size	.299	.298	-.447	.109	-.395	.162	-.482	.081	-.766	**.001**	-.718	**.004**
Enclosure complexity	-.054	.848	-.413	.126	-.597	.126	-.644	**.010**	-.710	**.003**	-.710	**.003**
Human contact	.066	.815	.051	.857	.162	.564	.135	.631	.041	.885	.187	.505
Barrier type	.248	.374	-.410	.129	.069	.806	.209	.455	-.392	.149	-.025	.929
Environmental enrichment	.426	.113	-.039	.889	.245	.379	.035	.900	-.171	.543	-.031	.913
Day shelter	.439	.102	-.332	.227	-.056	.843	-.135	.631	-.574	**.025**	-.310	.261

Table 6.3 Correlation between enclosure measures, husbandry measures and the association patterns of foraging and resting varying in status (n=14).

	Status association											
	Foraging						Resting					
	D-D		D-S		S-S		D-D		D-S		S-S	
	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*
Enclosure size	-.141	.632	-.395	.162	-.248	.393	-.639	**.014**	-.841	**.000**	-.424	.130
Enclosure complexity	-.304	.291	-.502	.067	-.387	.172	-.654	**.011**	-.788	**.001**	-.535	**.049**
Human contact	-.105	.720	.075	.798	-.105	.720	.189	.518	.146	.618	.032	.913
Barrier type	-.156	.574	-.102	.730	-.255	.378	-.141	.631	-.257	.376	-.164	.576
Environmental enrichment	.000	1.0	.038	.898	-.095	.748	-.075	.799	-.318	.268	-.038	.898
Day shelter	-.058	845	-.331	.248	-.148	.613	-.527	.053	-.694	**.006**	-.367	.197

Figure 6.3 Relationship between the enclosure complexity (1. Low, 2. Medium, 3. Highly) and male association patterns (M-M) of resting.

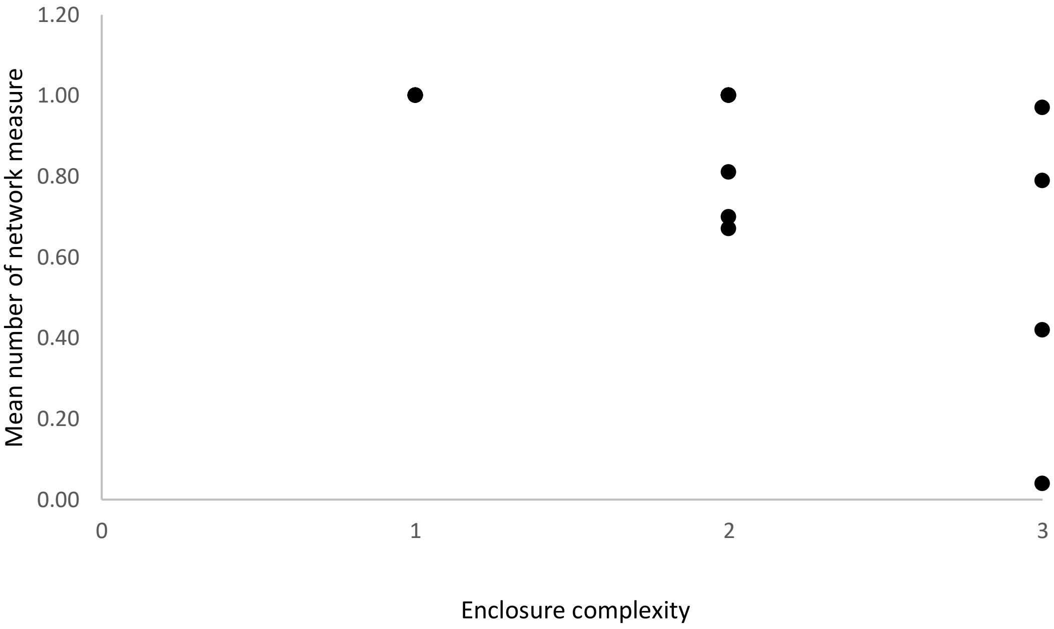
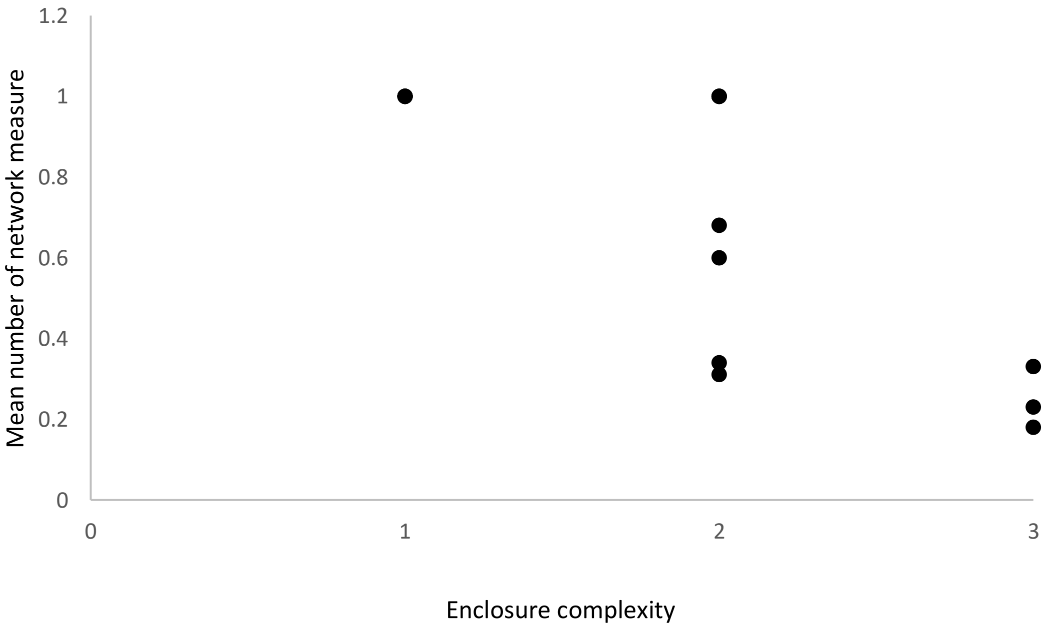


Figure 6.4 Relationship between the enclosure complexity (1. Low, 2. Medium, 3. Highly) and dominant-subordinate association patterns (D-S) of resting.



Within status associations, strong negative correlations were detected between the size/complexity of the enclosure/day shelter and dominant-subordinate associations (r=-841, n=14, *p*=0.000; r=-0.788, n=14, *p*=0.001; r=-0.694, n=14, *p*=0.006; Fig. 6.4), dominant associations (r=-0.639, n=14, *p*=0.014; r=-0.654, n=14, *p*=0.011) and subordinate associations (r=-0.535, n=14, *p*=0.049). That means that as the size, complexity of the enclosure and the availability of a good shelter increased resting networks became more dispersed between status associations.

6.3.2 Individual interaction patterns and enclosure/husbandry factors.

Overall, there were no consistent correlations at the $p<0.05$ level (Table 6.4). Correlations were found within grooming, playing and dominance interactions (Fig. 5, 6, 7 and 8). Within grooming network, strong negative correlations were found between enclosure size and outdegree centrality (weighted data; r=-0.570, n=15, *p*=0.027), compactness (r=-0.601, n=15, *p*=0.018),), density (r=-0.594, n=15, *p*=0.020), and cluster coefficient (r=-0.572, n=15, *p*=0.026). These results suggest that as the enclosure was larger grooming interactions directed to other individuals were more widespread. A positive correlation was found between enclosure complexity and cluster coefficient (r=0.584, n=15, *p*=0.022), which indicates that as the complexity of the enclosure increased, networks of grooming interactions were more dense with meerkats linking themselves with all neighbours. A negative correlation was found between the frequency of human contact and indegree centrality (unweighted data; r=-0.543, n=15, *p*=0.036) which it can implies that as the human disturbance was more frequent grooming events were more strongly directed to specific individuals..

Negative correlations were found between environmental enrichment and indegree centrality (weighted data; r=-0.558, n=15, *p*=0.031), and between day shelter and the same network measure (r=-0.606, n=15, *p*=0.017). This implies that in zoos providing enrichment at a high frequency, and in zoos with good shelters, grooming received by individuals were less centralized.

Within playing networks, a strong positive correlation was found between enclosure size and the distance measure L (r=0.610, n=15, *p*=0.016) and a negative correlation between the same extrinsic factor measure and cluster coefficient (r=-0.566, n=15, *p*=0.028). That is, as the enclosure size increased playing interactions were more indirect. A negative correlation was found between day shelter and cluster coefficient (r=-0.572, n=15, *p*=0.026), imply that when better quality shelter was available, most individuals were not linked to themselves during playing. Within dominance network, a strong negative correlation was found between the barrier type and outdegree centrality (unweighted data; r=-0.599, n=15, *p*=0.018), suggesting that when the barrier was adequate, I observed lower rates of dominance exhibited to other individuals.

Table 6.4 Relationship between enclosure measures, husbandry measures and network measures of grooming, playing, dominance and foraging competitions.

	Network centrality								**Distance**				**Density**		**Cluster Coefficient**	
	Unweighted data				Weighted data				L		Compactness					
	Outdegree		Indegree		Outdegree		Indegree									
	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*	r	*p*
									Grooming							
Enclosure size	.316	.251	.334	.224	-.570	**.027**	-.275	.320	.643	**.010**	-.601	**.018**	-.594	**.020**	-.572	**.026**
Enclosure complexity	-.341	.213	-.254	.360	.000	1.0	-.042	.881	-.203	.469	.424	.115	.511	.051	.584	**.022**
Human contact	-.221	.428	-.543	**.036**	.090	.750	-.499	.059	-.176	.530	.191	.495	.304	.270	.331	.228
Barrier type	-.016	.956	-.294	.287	-.139	.622	-.208	.456	.074	.793	.050	.859	.082	.772	.035	.902
Environmental enrichment	.071	.800	-.253	.364	-.067	.813	-.558	**.031**	-.028	.922	-.113	.690	.069	.806	-.028	.922
Day shelter	.143	.612	-.097	.730	-.247	.375	-.606	**.017**	.145	.607	-.246	.377	-.147	.600	-.206	.461
									Playing							
Enclosure size	.285	.303	.152	.589	-.342	.212	-.275	.320	.610	**.016**	-.066	.814	-.238	.393	-.566	**.028**
Enclosure complexity	.381	.162	.507	.054	.127	.653	.148	.599	.054	.849	.444	.098	.402	.137	.064	.821
Human contact	.244	.381	.169	.547	.036	.898	-.274	.323	.348	.204	.199	.477	.008	.979	-.337	.219
Barrier type	.247	.375	.262	.345	.185	.509	-.332	.227	.208	.456	-.093	.743	-.224	.422	-.214	.443
Environmental enrichment	.149	.597	.047	.867	.149	.595	-.356	.193	.315	.253	.330	.229	.099	.724	-.214	.443
Day shelter	.320	.244	.110	.696	.036	.898	-.393	.147	.472	.075	.146	.603	-.040	.888	-.572	**.026**

Dominance																
Enclosure size	-.381	.162	-.095	.736	-.266	.338	-.323	.240	.097	.731	-.295	.286	-.239	.392	.363	.184
Enclosure complexity	.159	.572	-.191	.496	.285	.302	.109	.497	.043	.879	.275	.321	.244	.380	-.032	.909
Human contact	-.197	.481	.083	.770	-.305	.269	-.229	.411	.131	.642	.026	.927	.006	.982	.118	.676
Barrier type	-.599	**.018**	.124	.661	-.197	.482	-.112	.691	-.106	.706	-.243	.382	-.275	.321	.035	.900
Environmental enrichment	-.272	.327	.221	.430	-.140	.619	-.213	.447	.158	.573	.034	.903	.001	.997	.429	.111
Day shelter	-.475	.075	.066	.816	-.291	.293	-.106	.708	.102	.719	-.195	.486	-.206	.461	.289	.295
Foraging competition																
Enclosure size	-.038	.893	-.334	.224	-.057	.840	-.484	.067	.435	.105	-.057	.840	-.219	.434	-.228	.414
Enclosure complexity	-.042	.881	.021	.940	.201	.473	.338	.218	-.215	.441	.285	.302	.243	.382	.074	.793
Human contact	.208	.458	.460	.085	.285	.303	.208	.458	-.194	.489	-.087	.759	-.016	.955	-.090	.750
Barrier type	-.320	.224	.000	1.0	-.089	.753	-.031	.913	-.149	.595	-.081	.774	-.100	.722	.054	.848
Environmental enrichment	.049	.862	-.120	.669	.169	.547	-.033	.906	-.100	.723	-.101	.719	-.099	.725	-.163	.561
Day shelter	-.109	.698	-.212	.449	-.041	.885	-.167	.552	.083	.768	-.117	.678	-.169	.547	-.091	.746

Figure 6.5 Relationship between the enclosure size (1. Small, 2. Medium, 3. Large, 4. Very large), average path length (L, black dots) and compactness network (grey dots) measure of grooming.

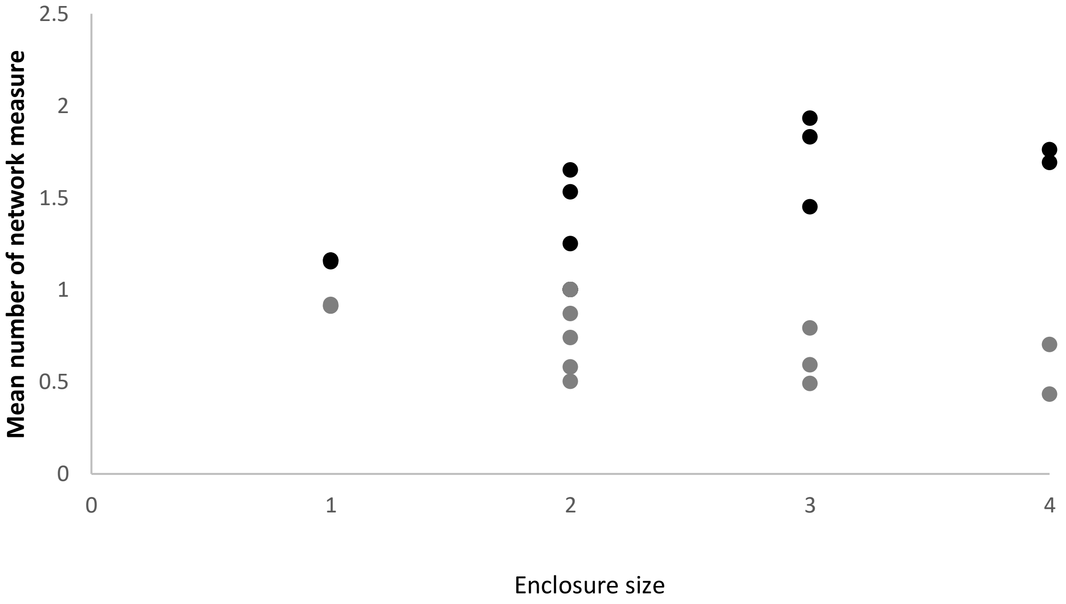


Figure 6.6 Relationship between day shelter type (1. None, 2. Available, 3. Available for all group members) and weighted indegree centrality network measure of grooming.

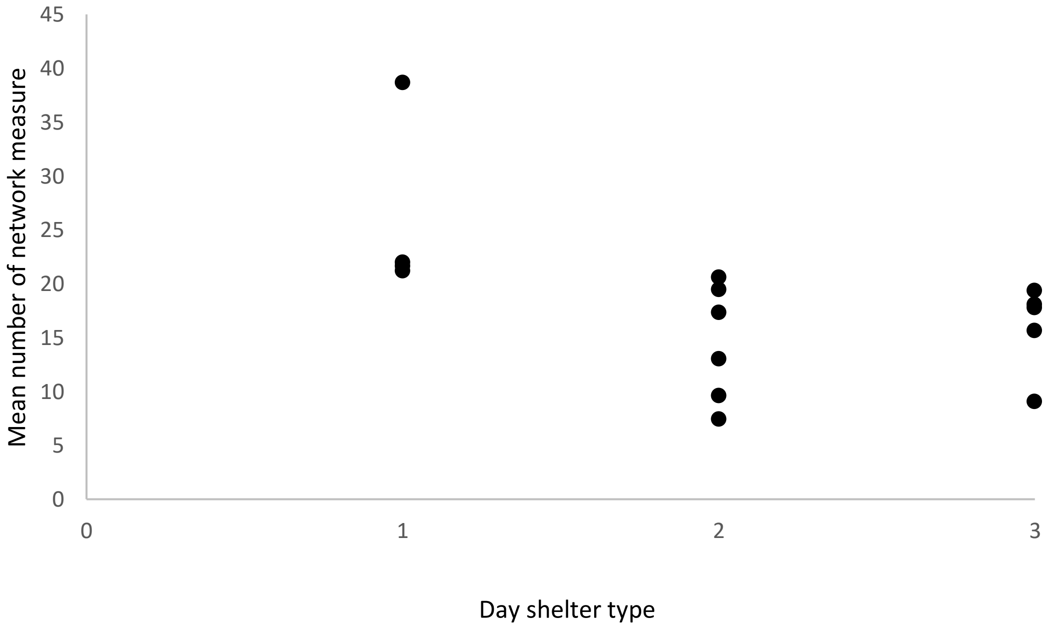


Figure 6.7 Relationship between day shelter (1. None, 2. Available, 3. Available for all group members) and cluster coefficient network measure of playing.

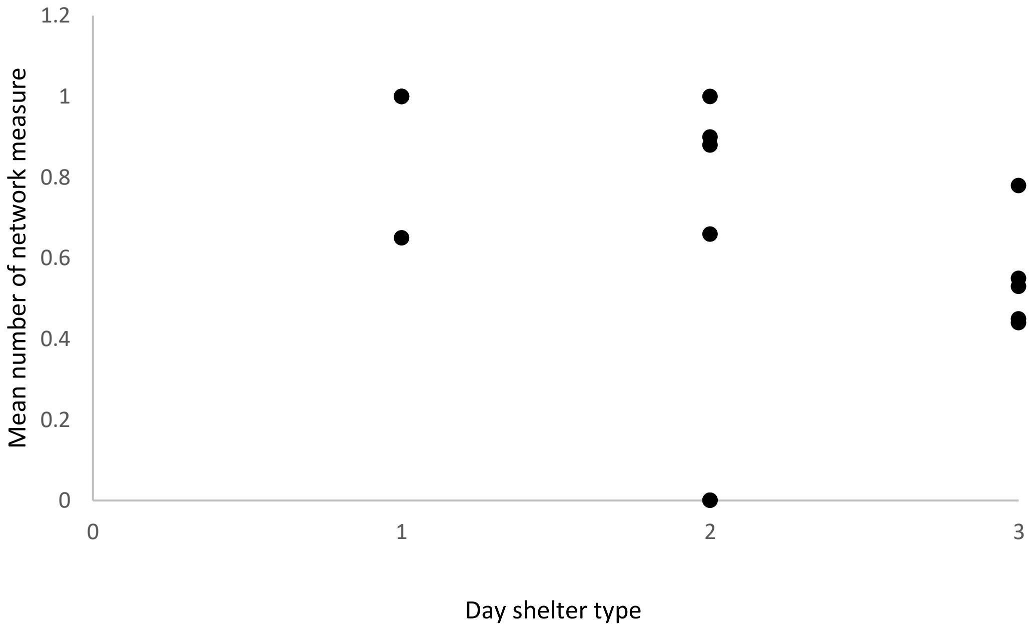
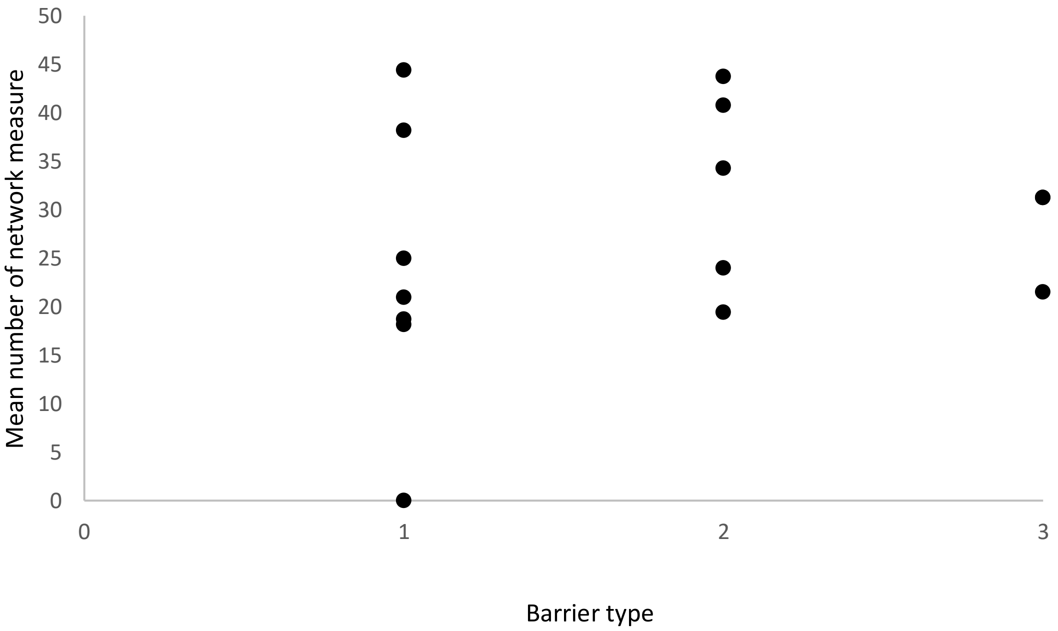


Figure 6.8 Relationship between barrier type (1. Inadequate, 2. Acceptable, 3. Good) and unweighted outdegree centrality network measure of dominance.



6.4 DISCUSSION

6.4.1 Association networks

A relationship was found in the way meerkats associate with one another in the resting network based on the size and complexity of the enclosure and the type of shelter. Individuals were less likely to associate with others of the same sex or dominance status in enclosures that were larger or more complex.

In mammals more generally, the degree of sociality variance in individuals can be reflected in group patterns of resting. In captive and free ranging wild dogs, it has been documented that they consistently rest close to or in contact with specific companions of the group (McCreery 2000). Likewise, meerkats are animals with tightly knit social groups that are repeatedly in connection (Drewe et al. 2011). In the wild, meerkats spend much of their time, usually in the morning or evening, in close contact in their communal burrow (Drewe 2010). In the present study, results showed that resting association networks were influenced by the area they inhabit. As predicted, mixed-sex and mixed-status associations were found in resting networks within larger, more complex enclosures and with the availability of an appropriate shelter. It appears to be that an enclosure with such characteristics can give more opportunities to each individual in the group to select a convenient resting site and a convenient resting partner(s). Schel et al. (2012) found in communities of chimpanzees that larger captive spaces with complex designs allows animals to adopt their natural social system and choose who they wish to associate and interact with. In addition, animals may choose to change their resting sites often if suitable sites are abundant (Genin 2010). Thus, if resting patterns are indicative of choice in the present captive meerkats, females may choose to rest close to males rather than other females due to the constant agonistic relationship between females and less aggressiveness toward males (Kutsukake & Clutton-Brock 2008). Dominant individuals usually obtain a greater share of benefits and they may also get better access to favourable positions to rest (Estevez et al. 2007). Further investigation of the use of sleeping sites and time spent resting may be useful to the further understanding of status associations in a captive setting. It would have also been interesting to add to the data the factor of group longevity as strong bonds can be manifested in a close sleeping distance. That is, individuals that had slept close to each other over a period of years can be expected to have stronger bonds (Zimen 1976). It is increasingly clear that the sleep patterns of zoo-housed animals can be influenced by the environment, husbandry routines and visitors' proximity (Whitham & Wielebnowski 2013). In view of that it is important to monitor sleep and/or resting patterns since they have been considered as a method of determining whether animals are experiencing positive affective states.

It can be presumed then that in smaller spaces and less complex environments inter-individual distances can become shorter and may result in individuals changing their resting sites less often. Consequently, individuals may occupy the same location and associate repetitively with the same individuals in the group rather than specifically choosing their partners. Apropos of the mixed-sex association, Génin (2010) affirms that sleeping associations between females and males during the nonbreeding season can be a tactical method that males use to increase their reproductive success. While seasonality was not considered in this study (groups were observed in different seasons), such an explanation cannot be ruled out completely and should be tested in future resting networks in meerkat studies along with zoo husbandry and enclosure characteristics. The pair-living sleeping association can be seen as a reproductive strategy. This kind of association during sleeping has been observed in several primate taxa where females may profit from these relations through paternal care, territorial defence or long-term reproductive success due to the stability of pair bonds between the pair-living (Dröscher & Kappeler 2013). As Estevez et al. (2007) point out, a particular environment and specific group compositions may stimulate more than others factors the formation of affiliative relationships and positive bonds between individuals. This type of social association may be driven by additional factors such as thermoregulation, territoriality (Génin 2010), group size (Drösher & Kappeler 2013), age (Knick & Mech 1980), social bonds (McCreery 2000), type and quantity of resting sites (Weidt et al. 2004) and the distribution of the home range (Radespiel 2000). Certainly, variation between environment conditions may show different association patterns. This has been documented in wolves where a marked difference in the resting patterns of captive and wild wolves has been detected (Altmann 1987), with the former presenting a larger space between group members. However, studies on the same species indicate that the variation of the distances between captive members can also be related to rank, age, season and other types of affiliative behaviour (Knick & Mech 1980). Differences in resting associations of this sort have been indicated in other species such as owl monkeys (Fernandez-Duque et al. 2013) and tarsiers (Driller et al. 2009).

6.4.2 Interaction networks

All the six external measures (the size and complexity of the enclosure, the type of barrier and day shelter, environmental enrichment frequency and human contact) influenced how individuals interacted with other group members within grooming, playing and dominance networks. In brief, as the enclosure conditions improved in size, barrier type and day shelter type, and the frequency of environmental enrichment and human contact was more frequent, grooming interactions were more disperse and indirect. Also, in more complex enclosures, most of the individuals (if not all) were themselves linked in grooming interactions. Playing networks seemed to be more dispersed when the size of the enclosure increased and when the condition of a shelter was superior. Lastly, rates of dominance to other individuals were lower when the barrier was appropriate.

Levels of human contact did not influence the social organization of the groups. Human contact only affected one measure of grooming. Undoubtedly, in a confined environment, animals face unfamiliar humans, visitors and new keepers who may be a source of stress. Negative responses have been observed across a range of species, such as in chimpanzees, *Pan troglodytes*, where a decrease in foraging and playing has been found (Wood 1998), and in ring-tailed lemurs, *Lemur catta*, Diana monkeys, *Cercopithecus diana*, and cotton-toped tamarins, *Saguinus oedipus*, where grooming behaviour decreased and agonistic behaviour increased (Claxton 2011). Group cohesion in ungulates was affected by visitor behaviour because of the animals' increasing interest towards visitors and keepers (Farrand et al. 2014). Positive responses toward visitors have also been observed, such as an increase in play and feeding in short-clawed otters, *Aonyx cinerea*. However, the effect of visitor presence has not been seen in cheetahs, *Acinonyx jubatus* (Claxton, 2011). Unfortunately, a visitor count was not undertaken in the present study to know whether large or small quantities of visitors provoked a specific behavioural response in the animals. However, I noticed that keeper rotation in most of the meerkat groups was minimal, which could also be an important factor in the animals' interactions. In Claxton (2011) work on the human-animal relationships of zoo-housed animals, he discussed how keeper rotation can be significant in animal reactions when a high number of animal keepers rotate at the facilities. For example, a study on North American clouded leopards, *Neofilis nebulosa*, assessing adrenal activity with husbandry and behavioural factors (Wielebnowski et al. 2012), came across higher concentrations of faecal glucocorticoid metabolite and social interaction differences between females and males if a greater number of keepers worked in the same facility. Sherwen and colleagues (2014) discuss how meerkats, explicitly, may not perceive humans as threatening. They argue that meerkats, in addition to being considered a highly social species with extensive social learning attributes, also habituate easily to a human presence. This is especially true for pups born in the groups where adults were already unafraid of people. This leads them to conclude that if habituation to humans can occur in wild individuals, it is also likely to happen in captive individuals. This habituation to humans seemed to be reflected in the fifteen groups investigated in this study. It is also important to highlight that social behaviour may be more plastic and dynamic than previously thought, allowing animals to change strategies and adapt to varying environmental conditions within a confined group (Estevez et al. 2007).

Limited space may create a competitive environment for resources and this may consequently increase aggression and social stress within group members, as seen in farm animals (Estevez et al. 2007). 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. However, in other studies (e.g. on marmosets, *Callithrix jacchus jacchus*; Kitchen

& Martin 1996), it was observed that an increase of allogrooming occurred after a decrease of stress due to the enrichment within the enclosure. Thus, perhaps because meerkats are inclined to repeatedly groom particular members of the group (which indicates a more centralised grooming network) in order to gain tolerance in critical circumstances, a quite diffuse network of grooming (links between all members) 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 a quota of grooming across all members of the group. In wild meerkats, patterns of grooming between the dominant pair has been observed to reflect their value of social relationships (Kutsukake & Clutton-Brock 2010). Similarly, patterns of grooming between dominant males and subordinate males has been observed to maintain valuable relationships so that male subordinates help to protect the group from extra group males (Kutsukake & Clutton-Brock 2010). Subordinate females tend to exchange grooming patterns with dominant females as a form of placating the dominant female and gaining social benefits, such as tolerance, due to the strict dominance hierarchy (Kutsukake & Clutton-Brock 2010). 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 (mainly between females) and may interact in frequent grooming relationships since it is a technique (detected in mice) to reduce beta-endorphin concentrations, which reduce stress (Keverne et al. 1989). Grooming interactions in communities of capuchin, *Sapajus apella*, and squirrel monkeys, *Saimiri sciureus*, 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). I could not collect physiological measures of stress via cortisol samples of blood, saliva or faeces because I did not have relevant permissions. Having such samples would have allowed me to provide an insight into the animal’s tress response to captive conditions and grooming interactions (but see Scott 2014 work on behaviour and endocrinology of meerkats in captivity).

It is suggested that enclosure design is one of the most important factors in promoting positive interactions between individuals (Buchannan-Smith et al. 2013). Enriched or impoverished conditions can increase or decrease the frequency of play depending of the environment type in which the animals live (Wood-Gush et al. 1990; Donaldson et al. 2002). The importance of play as a welfare issue within populations and as a useful biological measure of well-being has been discussed. Cronin et al. (2016) and Whitham and Wielebnosky (2013) assert that play is one of the most promising positive welfare indicators because it is reduced when animals live under deficient conditions. Zoos researchers have been looking for different ways of promoting such positive states, and they have found that by making, sometimes minor, modifications to their enclosures and routine can have positive results. For example, Ross (2006) discovered an increase within play interactions when giving polar bears, *Ursus maritimus*, the option of accessing indoor and outdoor enclosures. Hence, it appears that the captive group of meerkats who had an enhanced environment responded positively by playing with partners of their choice, as likely commonly occurs in their wild counterparts. Wild meerkats are known to favour play with individuals of the opposite sex (subject to age) or to play with younger individuals that they could dominate, or older individuals that they could not. (Sharpe 2005b). It is also reported that adult meerkats can devote only 0.3% of their time to play (Sharpe 2005b); however, in this study a considerable amount of play was observed in adults. In line with this, Hill and Broom (2009) state that adult play in captivity may take place at higher percentages compared with the wild since play is considered as a luxurious behaviour (see Chapter 5, section 5.4.2 for the discussion of play results in adults). Besides the human contact assessment tested here, it would have been useful to monitor visitor number and visitor behaviour (agitated or calm) during the study to complement the results presented here on animal play and its dynamics in captive conditions. Research on this topic has found that larger crowds of people were associated with a decrease in playing and other social behaviours (Fernandez et al. 2009).

Animals in captivity can be exposed to several simultaneous stimuli from visitors, such as auditory, olfactory, vibratory and visual signals. Visual stimuli can be a key component in responses to zoo visitors. Adequate types of barriers have been recognised to be an important factor in reducing abnormal behaviour and stress. For instance, in a study on gorillas that looked at the effects of enclosure design (Blaney & Wells 2004), it was found that visitors tended to be quieter after the installation of a camouflage netting barrier and animals were seen to be more comfortable. Additionally, gorillas considerably decreased their intra-group aggression. Some level of intra-group aggression can be beneficial in maintaining stable social hierarchies (dominance interactions) although high levels of aggression can be injurious and may compromise welfare. Meerkats are known to have a stable hierarchy and dominant interactions are not exclusive of the dominant pair (Madden & 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 may exhibit more dominance assertions when contesting for the immediate benefit. This may be an explanation of the decrease of dominance interactions when the type of barrier was more appropriate, making the feeding of meerkats by visitors unlikely or much more difficult.

In conclusion, the present research is subject to several limitations (mentioned throughout the discussion and methodology) which limits the ability to generalize about captive meerkat social networks with respect to enclosure conditions and management. However, the present study can demonstrate that inter-individual distance and social network interaction analyses can play an important role in understanding species response to dissimilar conditions that may disrupt their social organization. Further information on how management factors (i.e. husbandry procedures and enclosure style) impact social group stability through patterns of social relationships will allow us to gain greater insight into management practices for group-housed animals in order to maximize their welfare. In concordance, Rose and Croft (2015) affirm that social network analysis can be highly applicable for enclosure designers who can construct exhibits based on the particular needs of the individual and the group that will be housed.

Furthermore, social network analysis can helps us to understand how management practices can alter social bonds between group members (Rose &

Croft 2015) and how they can reduce severe aggressive outbreaks in groups. It would be also beneficial to undertake a post-occupancy evaluation (before and after environmental enrichment, refurbishment or any change in the enclosure and management) in these types of investigations in order to extend our knowledge of animal social networks in captivity and to be able to provide adequate social opportunities for the entire group. In addition, understanding these potential effects of captivity on animal behaviour and group dynamics could be vital for animal conservation and maintaining animals in good conditions.

Chapter Seven

General Discussion

The overall aim of this thesis was to investigate how a captive environment can modify social structure in group-living animals, in this case meerkats (*Suricata suricatta*), and to explore personality in the context of social networks in captive groups. Four research chapters addressed these aims.

7.1 Evaluation of social network structure in captive meerkats and comparison to their wild counterparts.

Previous work has indicated that animal social behaviour may differ between the two conditions, wild and captive, and consequently the range of animal social structure in confined conditions may overlap to different degrees with the one observed in the wild (Hosey et al. 2013). Two field studies (chapter 3 and 4) were carried out in fifteen captive groups of meerkats to investigate how captivity may alter social structures within meerkats. A first study explores the probable effect of housing and husbandry aspects on association patterns, specifically foraging and resting. The second study specifically repeats previous work by Madden et al. (2009, 2011) in which they explore interaction networks across eight wild groups of meerkats. The same ten network measures were analysed for the three forms of interaction (grooming, dominance and foraging competitions): measures of (indegree and outdegree) degree centrality (unweighted and weighted data), distance, betweenness, closeness, density (average path length and compactness) and cluster coefficient (unweighted data).

Research into the social behaviour of wild animals living in groups has demonstrated the importance of social structure dynamics and their consequences for an individual's fitness. Animal social interactions may facilitate or impede the spread of disease within a population (Pinter-Wollman et al. 2013) or may predict future social status in early life (McDonald 2007). Individual positions may also have important implications, such as in mating: males with high betweenness centrality can have a greater paring success (Oh & Badyaev 2010). Physical proximity between individuals of a group is a requirement for social interactions and the developing and maintenance of relationships (Vonhof et al. 2004). The particular way of interacting and associating can be a result of group specific attributes, such as sex, status or age, as well as the physical environment.

Results in Chapter 3 shows that group size may have generated different forms of foraging network structures, with small groups having more centralized networks and larger groups having diffuse networks. Literature affirms that groups with less individuals tend to be more cohesive than groups with a large number of individuals (Lehmann et al. 2007; Michelena et al. 2008; Herbert-Read et al. 2013). Captive conditions seemed to be an additional factor of the association network structure as shown in the results of Chapter 6. Resting associations were more centralised in small groups and groups with fewer pups presented a low indegree centrality. Here again, the conditions of captivity influenced resting association networks as illustrated in Chapter 6. Literature affirms that variation between environment conditions may show different association patterns, as it has been documented in wolves (Altmann 1978) where a marked difference in resting patterns has been observed between captive and wild wolves, with the former presenting a larger space between group members. Individual positions in foraging networks differed according to the individuals' status. Subordinate individuals are said to be the first to arrive at new food patches and dominant individuals (usually having higher proportion of successful joining than subordinates) may profit from that information when joining them (Stahl et al. 2001). Foraging associations also revealed patterns of association based on age. The preference of juveniles joining adults seemed to be because, typically, young meerkats obtain much of their food from adult helpers by following them closely (Clutton-Brock et al. 2001).

In resting behaviour, dominant and juveniles meerkats joined more other members of the group than subordinates and adults. The selection of resting sites can be influenced by territoriality where animals scent mark in the vicinity of sleeping sites (Génin 2010). In the same way, resting networks may reveal social territoriality where dominant meerkats, which typically have a high rate of scent marking (Carlson et al. 2004; Jordan 2007), are given priority in choosing a high quality sleeping site and, also, have the privilege of choosing who they want to interact with.

Results in Chapter 4 illustrate that groups of captive and wild meerkats differed in various aspects of their social network structure. Captive meerkats had a more highly skewed grooming distributions 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. Factors such as the number of individuals in the group, kinship, and an individual's sex and age seemed to be a consequence of the network centrality difference.

In dominance and foraging competition networks, captive meerkats had a higher score in the overall rates of dominance and in foraging competitions than wild meerkats. Competition for food plays a fundamental role in the social organization of group-living animals, in which, individual foraging success is, to an extent, regulated by dominance relationships (Barton & Whiten 1993). Consequently, even supposing that food is continually available in captivity, strong competition for food may still be present. For example, captive bonobos have been observed to exhibit higher levels of aggressive reactions to food and strong dominance hierarchies (Jaeggi et al. 2010). A similar situation has been observed in wolves, where captive groups of wolves presented higher levels of aggression than in wild packs (Sands & Creel 2004).

Network positions in grooming of captive meerkats did not differ according to the attributes of sex, status and age. In individual captive groups, male meerkats could easily connect with others in the group by grooming interactions, and at the same time, males were the ones who gave more grooming. These results contrast with the ones observed in wild populations, where grooming interaction are most common between females as a function of placation of dominants by subordinates and intra-sexual reproductive conflicts (Kutsukake & Clutton-Brock 2006b). The explanation of such an outcome in this study is that the specific groups with more allogrooming between males had a great number of them, which may elevate the tension between males because they cannot disperse like their wild counterparts. Individual positions in dominance networks showed differences between captive and wild groups, with captive individuals being more quickly connected by the rest of the group members because of their restricted living area and their smaller group size. Similar patterns of outdegree and closeness scores in wild meerkat interaction patterns based on status were found in captive groups, showing the typical dominant-subordinate dominance interactions. Juvenile and subordinate captive meerkats were more easily reached by other members of the group within foraging competition networks than in the wild groups. In a captive environment, this situation may be magnified because young and subordinate individuals have less room to escape competition, and therefore, a high inclosenness in this interaction was seen in the present groups. Females in captive groups initiated more foraging competitions than in wild groups. In a captive environment, females may have the need to fight more for resources in order to divide the available food patches and maximize their own foraging efficiency as territories are practically restricted by space and competition for food can be higher (Gibeault & MacDonald 2000).

In general, differences and some similitudes were found between captive and wild groups in their social network structure. Such differences may be explained by the dissimilar living environment both live in. Social network analysis permits the examination of social interactions and associations to help us understand individual roles within the social dynamics of a group. Castles et al. (2014) suggest that a combination of proximity and interaction measures should be applied to a population at multiple time periods. Social networks vary temporally and between social groups. Therefore it would be interesting to do further work with groups that have a similar group composition in terms of number, age and sex during the same period in the year, and if possible, during similar husbandry conditions in order to produce more comparable metrics.

7.2 Personality as a factor influencing social network structure in captive meerkats

The social environment is a major site of selection in many animal populations where important social behaviours have been found to vary depending on the individual personality type, and personality-dependent behaviour can, inversely, vary depending on the social context (Snijders et al. 2014). Despite the fact that numerous studies have investigated personality traits, the maintenance of personality variation within a population and their responsible processes are still not well understood (Cote et al. 2008). Literature suggests that behavioural differences can affect an individual’s interaction with other members of a social group. For instance, particularly aggressive animals may be avoided by others or more active animals may have more encounters with other individuals. A field study (Chapter 5) was carried out on fifteen groups of meerkats to explore personality in the context of social networks in different captive groups of the same species. Meerkat personality was assessed by conducting observations on their behaviour and used PCA to consolidate the four behavioural traits obtained into larger dimensions to be able to compare individuals and groups. I first assessed whether personality score of individuals was repeatable within one year. I also tested whether it differed according to individual attributes. And lastly, I sampled affiliative and antagonistic interactions by using the same network measures used in Chapter 3 and 4.

Data on chapter 5 illustrates that personality dimensions were present within meerkats from fifteen captive groups. Two personality dimensions were revealed across such fifteen groups: Friendliness and Aggressiveness. Yet, within the five groups, used for a second sampling period approximately one year after to assess repeatability across time, Friendliness was the only measure that robustly captured consistent individual differences after my original sampling.

The Aggressiveness dimension has similarities with the Proactive dimension in rats as well as the Dominance and Confidence dimensions in apes and monkeys, which tend to associate with aggressive trait, as in the present study. A relationship between the three traits (sex, age and status) and the dimension was not detected. The Friendliness dimension has similarities with the Sociability and Openness dimensions in several apes and monkeys where the personality traits of playful, curious and sociable were associated as in the present study. A long-term repeatability was detected in the personality dimension of Friendliness. An explanatory explanation regarding this founding was that fairly predictable environments, such as Zoos, may possibly favour higher levels of repeatability in animals. It is important to highlight that the pressures imposed by captivity, along with genetic processes, are likely to affect the frequency and characteristics of personality traits (McCowan et al. 2014).

Relationships between attributes and personality dimensions were not found.

Sub-traits including play and explorative, related to Sociable and Curious dimension, were expected to be related to age. Play (behaviour that contributes to general stress resilience), regardless individual’s age, may help animals living in a confined environment to cope with the constant hostility of others. Despite captive environments meeting basic physiological and survival needs, they can still produce stressful situations (Held & Spinka 2011). The investment of explorative behaviour in captivity may be differently expressed by individuals, regardless their age, as basic survival needs like food are already controlled in zoos. Aggressiveness dimension was expected to be mainly related to individual's sex. However, in a captive environment were female eviction or male emigration is not possible, aggressiveness personality can be equally reflected in both, females and males.

Data on network positions in foraging competitions revealed individuals with Friendliness dimension scores being more central in the network. Animals high in sociability can be indexed by the time spent interacting with group partners, involving activities of play and grooming (Freeman & Gosling 2010). A highly social individual, therefore, can be characterized by a central position in the network. Competition often results in the dominance of one individual over another where young or individuals with low hierarchy can be easier targets and less able to defend their resources.

Assortative association based on personality type was not revealed in the results. It was suggested that short and long-term benefits including protection from predators or increased foraging efficiency may be perceived differently in a captive habitat.

7.3 Housing conditions and management effects on social network structure of meerkats

A substantial amount of research on zoological parks has been focused on understanding how the captive environment may influence animal behaviour and welfare. The level of sophistication in the husbandry of zoo animals has progressed considerably in recent years, as has the recognition that animal caretakers have a responsibility not only to provide humane treatment for zoo animals, but also to create captive conditions which actually enhance their quality of life. Improvements in animal management have resulted from an increasing awareness of both the physical and the psychological needs of captive animals (Kleiman et al. 2010). However, less attention has been paid to their social environment.

Chapter 6 looks at how physical and husbandry factors vary across enclosures and how this corresponds to a variation in the social structure of a group-living species, meerkats. Six different forms of social interaction and their resulting networks were measured. In addition, correlate measures of network structure with husbandry and enclosure measures were also assessed.

In the present study, when considering resting association networks, differences were found in enclosures of different sizes, complexity and the type shelter. It was presumed that in smaller space and less complex environment inter-individual distances become shorter and may result in individuals changing their resting sites less often. Consequently, individuals may occupy the same location and associate repetitively with the same individuals of the group rather than specifically choosing their partners. Schel et al. (2012) found in communities of chimpanzees that, indeed, larger captive spaces with complex designs allows animals to adopt their natural social system and choose who they wish to associate and interact with. In addition, animals may choose to change their resting sites often if suitable sites are abundant (Genin 2010)

The external measures considered in this study influenced interaction networks of grooming, playing and dominance in the fifteen captive groups. Grooming interactions were more disperse and indirect when enclosure conditions improved in size, in the type of barrier and day shelter, and when the environmental enrichment and human contact were more frequent.

Limited space may create a competitive environment for resources and this may consequently increase aggression and social stress within group members (Estevez et al. 2007). This may explain the increase and the direction of grooming events to preferred individuals, as meerkats in captivity may still face an intense intrasexual conflict and may interact in frequent grooming relationships to reduce stress. A further probable cause of these results is that animals housed in austere and limited spaces, without any kind of enrichment, tend to multiply their inter-individual interactions (Hediger 1950), which may also explain why meerkats in this study were inclined to interact repeatedly and specifically with some individuals.

Playing interactions were observed to be more dispersed when the size of the enclosure increased and when the condition of a shelter was superior. Such results may suggest that the captive group of meerkats who had an enhanced environment responded positively by playing with partners of their choice, as likely commonly occurs in their wild counterparts.

Dominance interactions were lower in frequency when the barrier was appropriate. Animals, in enclosures with inadequate barriers, may intensify their dominance assertions towards others when contesting for food handed from visitors,

In general, it seems to be that the key features to address in meerkat management in zoos are those of enclosure size and complexity (and perhaps provision of adequate shelters). Providing captive meerkats with more naturalistic and complex enclosures can help to preserve their natural social system.

7.4 Conclusion

This work does not generalize the results beyond the particular groups of meerkats studied here. Nonetheless, this thesis shows how the social interaction of captive meerkats may vary from their wild counterparts and that such variation in the degree to which members of a group interact with one another could be due social and non-social factors. It also shows that the association preferences of individuals are likely to differ and the factors that drive such preferences may be singular to each member of the group with the main purpose of maximizing potential short and long-term benefits. This thesis also highlights the importance of applying social network analysis and personality assessments on captive populations in order to extend our knowledge on such areas, and in that way help to provide better animal management and improve individual and group welfare.

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