



NOTTINGHAM TRENT UNIVERSITY

An investigation into social relationships and social structure in UK and Irish zoo elephant herds

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"What you do makes a difference, and you have to decide what kind of difference you want to make"

– Jane Goodall

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Abstract

Appropriate social groups in zoo-housed animals can enhance welfare, longevity, health status and reproductive success of individuals, and consequently zoo populations. However, inappropriate social groups can be detrimental to individual welfare states. Suboptimal social housing in zoo animals has been linked with increased prevalence of stereotypies, increased aggression and reduced reproductive success. In the wild, elephants predominantly live in herds of related individuals and have a fission-fusion social group structure (i.e. group size and structure fluctuates over time). Concerns have been made over whether elephants in zoos can be kept in appropriate social groups which meet their complex needs. Social interactions have been identified as an indicator of positive welfare in zoo elephants. The aim of this thesis was to ascertain the effect of individual and zoo-level factors including individual personality on herd interactions and social structure, and to gauge the level of change in herd dynamics over a year. Behavioural data were collected over 12 months for each study zoo (January 2016 – February 2017). Subjects were 10 African (1 male: 9 female) and 22 Asian (3 male: 19 female) elephants housed at 7 zoos and safari parks in the UK and Ireland. Methods employed combined extensive behavioural observations (live and video), social network analysis and keeper questionnaires to quantify data on social interactions and personality.

Social interactions were considered to be either positive (e.g. touching with the trunk or walking towards another individual) or negative (e.g. hitting with the trunk or displacement) and were further sub-divided into physical and non-physical interactions. Key demographic factors that could affect social interactions and relationships in zoo elephants, and therefore contributing to cohesive, successful social groups were identified. The results provided evidence for complex herd structures which may not be static over time. Personality was reliably rated by elephant keepers. A sociable personality component was identified from the personality assessment. Level of sociability of elephants as rated by keepers was related positively to frequency of positive interactions given and negatively to frequency of negative interactions given. Interactions in the study herds and within dyads were affected by age, relatedness to others, species, the presence of calves in the group and individual personality. Calves were central to social interactions in many of the herds, interacting with all members of the group and engaging in more physical interactions than older elephants.

The presence of positive social interactions and absence of extreme aggression in the study herds is indicative of current successful social group management of elephants in UK and Irish zoos. This research has identified factors that may contribute to successful social housing of zoo elephants. Based on the results, recommendations for changes to practice and areas for future research are made that will continue to advance knowledge and enhance long-term zoo elephant welfare. Of utmost importance is developing a means of assessing social compatibility between individuals, to facilitate such a measure in long-term welfare assessment.

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CHAPTER 1

Introduction

1.1 Background

Providing animals in zoological collections with environments that optimise their individual health and welfare is considered a primary goal of modern day zoos (Williams et al., 2018a). Whilst the goal appears simple, it is not always easy to achieve for all zoo-housed species. Animal needs encompass both a physical and a psychological aspect. Psychological well-being is thought to be harder to assess than physical welfare and so it can be difficult to understand the psychological needs of zoo animals (Swaisgood & Shepherdson, 2006). Zoo animal housing can have a number of limitations, including a lack of species knowledge, time, funding and space (Williams et al., 2018a). Whilst there is potential for optimum welfare to be obtained in well-managed situations, it has been suggested that zoo animals could still experience poor welfare due to the chronic nature of some zoo stressors, and the inability to react to or to control stressors (Veasey, 2017). Tennessen (1989) highlighted four areas that were considered to be particularly important to zoo animal welfare, and these hold today: amount and complexity of space, social environment, human-animal relationships and the ability to control and predict events. Limited expression of behaviours indicative of stress or poor welfare, and successful reproduction may be considered indicative of social groups which optimise welfare. Using these as guide, some species, such as ring-tailed lemurs (*Lemur catta*) appear to be housed successfully within zoos (Mason, 2010). The welfare of other species, such as cotton-top tamarins (*Saguinus oedipus oedipus*) and gorillas (*Gorilla gorilla gorilla*), are thought to be negatively affected by the presence of humans; individuals show signs of increased aggression, reduced affiliative behaviours and increased stereotypies (Glatston et al., 1984; Wells, 2005). Elephants (*Proboscidae*) experience poor survivorship (Clubb et al., 2008), chimpanzees (*Pan troglodytes*) display abnormal behaviours (Birkett & Newton-Fisher, 2011) and cheetah (*Acinonyx jubatus*) struggle to breed successfully (Marker & O'Brien, 1989) in some zoo settings (reviewed in Mason, 2010). The ability of animals to adapt and thrive in zoos is specific to species and individuals so it is important to investigate factors potentially affecting welfare on an individual, group and species level.

Stable relationships within zoo animal groups can enhance welfare, longevity, health and reproductive success of individuals, and consequently populations (Rose & Croft, 2015). Conversely, inappropriate social grouping of zoo-housed animals can be detrimental to individual welfare states (Price & Stoinski, 2007; Rose & Croft, 2015). Suboptimal social housing has been linked with increased performance of stereotypies, increased aggression and reduced reproductive success (Price & Stoinski, 2007). Disruption to social bonds can also lead to poor welfare and increased stress (Rose & Croft, 2015). It is thus imperative to identify optimal needs for zoo-housed social species.

Elephants are an intelligent and highly social species that display strong affiliative bonds (Moss & Poole, 1983; de Silva et al., 2011). African savanna (*Loxodonta africana*) and Asian

elephants (*Elephas maximus*) are classed as 'Vulnerable' and 'Endangered', respectively, on the International Union of the Conservation of Nature (IUCN) red list (Blanc, 2008; Choudhury et al., 2008). The most recently recognised elephant species, the African forest elephant (*Loxodonta cyclotis*) has not been formally assessed by the IUCN. It is estimated that there are 30,000 to 50,000 Asian and 500,000 African elephants worldwide, with 15,000 to 20,000 Asian and African elephants housed in captivity (Elephant Voices, 2018). Captive situations include zoos, safari parks, circuses, timber camps, tourist parks and other entities where elephants are under some form of human control. Within the UK and Ireland there are currently 41 Asian and 28 African elephants in zoos and safari parks and one Asian elephant in a Buddhist temple (ZIMS, 2017). Considered socially sophisticated and living in fission-fusion societies (Moss & Poole, 1983; de Silva et al., 2011), elephants are believed to exhibit one of the most advanced mammalian social systems known (Sukumar, 2003). Despite recognition of their complex needs, previous research has indicated a lack of ability to meet the physical and social needs of elephants within zoos (Clubb & Mason, 2002; Harris et al., 2008).

Areas of concern over the welfare of elephants in UK and Irish zoos include both mental and physical health. Zoo transfers have been linked with short-term (days) negative changes in behaviour and physiology (e.g. reduced lying rest, increased stereotypies and elevated cortisol levels) (Laws et al., 2007) and longer-term changes such as decreased survivorship in female Asian elephants (Clubb et al., 2008) but there is a need to move elephants in order for zoos to comply with European Endangered Species Programmes (EEP) for breeding. The EEP is managed by studbook coordinators to ensure a viable captive population in order to safeguard species within zoos (EAZA, 2012). Recent moves within the UK and Ireland have involved elephants being moved to new facilities where they will have natural breeding opportunities (Twycross Zoo, 2018) or being moved out of their current environment as zoos phase out elephant herds (McCarthy, 2001), which then may incur a trade-off between the short term stress involved with the move and the longer term benefit. Increasing success of zoo transfers is important in minimising required moves and reducing the potential negative impacts of zoo transfers on individuals. The first British and Irish Association of Zoos and Aquariums (BIAZA) elephant management guidelines were produced in 2002 and then superseded in 2006; however, there was a lack of scientific evidence for some of the recommended minimum standards. The BIAZA Elephant Welfare Group (EWG) set up in 2010 is responsible for the majority of work that has been undertaken in recent years to assess and improve zoo elephant welfare within the UK and Ireland, and suggestions of evidence-based changes to elephant management guidelines (BIAZA Elephant Welfare Group, 2016).

Social needs of zoo elephants have been considered notoriously difficult to cater for, due to their size and complex needs (Zoos Forum, 2010). Individual personality can affect animal experiences, and evidence has shown that personality can affect social group cohesion in cheetah

(Chadwick, 2014) and gorillas (Stoinski et al., 2004), mating success in giant panda (*Ailuropoda melanoleuca*) (Martin-Wintle et al., 2017) and it can be used to predict friendships in chimpanzees (Massen & Koski, 2014). There is evidence that elephants exhibit unique personalities that are stable over time (Grand et al., 2012; Lee & Moss, 2012; Horback et al., 2013; Yasui et al., 2013; Williams et al., 2015; Seltmann et al., 2018), and there is the potential for these to impact on their individual experiences within a zoo (Watters & Powell, 2012). Research suggests that there are a number of indicators of welfare in zoo elephants; physical, physiological and behavioural (Williams et al., 2018b). Social behaviour has been identified as a welfare indicator in elephants, with the occurrence of positive physical interactions and lack of negative interactions indicating positive welfare (Chadwick et al., 2017; Williams et al., 2018b). Social variables such as compatibility and herd structure have predicted behavioural changes indicative of changes in welfare state (Meehan et al., 2016a). Anecdotal evidence suggests that herd compatibility can change over time and that changes in herd members can lead to altered social dynamics (Armstrong, 2015; Cairns pers. comm., 2015). However, the relationship between herd demographics, personality and frequency of occurrence of positive and negative social interactions has not been investigated, despite a recognised need for a greater understanding of factors driving social compatibility in elephants (Asher et al., 2015).

This research measures social behaviour (defined as interactions between conspecifics) and personality (defined by Powell and Gartner (2011) as individual behavioural differences that show stability across time and situations) of zoo-housed elephants in seven social groups in the UK and Ireland. Research was undertaken over a 12-month period (at four discrete time points), in order to ascertain the effect of herd demographics and personality on herd interactions and social structures, and to gauge the stability of herd dynamics over a year. It uses extensive behavioural observations, social network analysis (SNA) and keeper questionnaires to quantify data on social interactions and personality. The aim of the research is to review the potential impacts of the zoo environment on social behaviour in elephants and investigate how herd demographics are affecting social interactions and herd structures in UK and Irish zoo elephant herds. This study will provide information which can contribute to evidence-based suggestions to changes to social grouping aspects of elephant management guidelines, thus contributing to long-term improved welfare for zoo elephants.

1.2 Thesis overview

This thesis is organised into seven chapters. Chapter One outlined the background to the research and briefly introduced the research aim. Chapter Two presents a critical review of the relevant literature, reviewing the impacts of zoos on the social behaviour of elephants. It concludes with an overview of the main aim and the four objectives of the research. Social management of zoo-housed elephants in the UK and Ireland has changed markedly in the last 15 years, yet no publications currently reflect these important changes. In the third chapter this change is evaluated and a comparison of level of compliance of zoo practices in terms of social housing, with relevant regulations is provided. Chapter Four provides an overview of the study population and methodologies used in the data chapters and investigates changes in herd structure over time. Chapter Five focuses on the relationship between elephant personality and social interactions. Chapter Six concludes with an overall assessment of the relationship between herd demographics, individual personality and social interactions, combining data gathered on social interactions in Chapter Four with personality data collected in Chapter Five. Finally, Chapter Seven presents an overall discussion of the research findings, concluding with areas for further investigation and the implications of this research on current zoo elephant management in the UK and Ireland.

CHAPTER 2

Research context

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**A review of the impacts of zoos on
social behaviour in elephants**

2.1 Introduction

Elephants (*Proboscidae*) are an extremely intelligent and highly social species'. Social interactions account for a relatively small proportion of the day of zoo-housed elephants (Schmid, 1995; Gruber et al., 2000; Stoinski et al., 2000; Schmid et al., 2001; Wells & Irwin, 2008; Posta et al., 2013) yet they are an important part of an elephant's behavioural repertoire (Vidya & Sukumar, 2005a) and identification of driving factors behind behavioural choices may have implications for elephant welfare (Mench, 1998). The zoo environment places a number of unique, confinement specific stressors on animals (Morgan & Tromborg, 2007; Williams et al., 2018a) and limiting any negative effects of these on individual animals is paramount in ensuring positive welfare in zoo-housed animals. Elephants exhibit unique personalities (Grand et al., 2012; Horback et al., 2013; Yasui et al., 2013), are highly intelligent and long-lived. This chapter critically reviews the impacts of zoos on social behaviour in elephants. It identifies the importance of appropriate social groups on animal welfare and highlights the need to focus on the finer details of factors affecting interactions in zoo elephants, in order to identify optimum social environments and thus improve welfare. Parts of this chapter have been published in the book *Zoo Animals: Husbandry, Welfare and Public Interactions* (Williams et al., 2018a).

2.2 Defining zoos

The environments where wild animals are held in *ex-situ* captive conditions under human care are zoos, safari parks, circuses, pet shops, small-animal collections in museums, specialist collections, aquariums and bird parks (Hosey et al, 2013). In Europe, a zoo is defined as, 'a permanent establishment where animals of wild species are kept for exhibition to the public for seven or more days per year' (Zoo Licensing Act (Amendment), 1981; European Commission, 2015). As the research undertaken in this study was conducted in zoological collections (UK and Irish zoos and safari parks), the content of this review focuses specifically on research pertaining to animals kept in zoos and safari parks (as defined by the establishments or researchers), hereafter zoos. Worldwide, zoos are governed and legislated for in various ways. However, the basic directives adopted by most zoo governing bodies are conservation, education, science and recreation. The highest operational priority required to achieve these directives is to ensure the optimum care and welfare of animals (Veasey, 2017). Zoos in the UK are governed by the Zoo Licensing Act 1981. The majority of zoos in the UK and Ireland, and all of the zoos involved in this research, are also governed by BIAZA, a professional organisation which aims to be a powerful force in the care and conservation of the natural world (BIAZA, 2018a).

2.3 Zoo animal welfare

Animal welfare has been receiving increasing amounts of press and interest from researchers and animal carers alike and has shown extensive developments over time. Evidence-based assessment of animal welfare has developed rapidly in recent years, with the most recent development involving the use of frameworks designed to assess animal welfare by integrating knowledge and providing practical tools to improve welfare (Sejian et al., 2010). The concept of 'animal welfare' was first introduced in The Brambell Report (Brambell, 1965), which was the report resulting from an examination of the conditions in which livestock were kept in intensive husbandry in June 1964, appointed by the Minister of Agriculture, Fisheries and Food and the Secretary of State for Scotland (Brambell, 1965). There is no single accepted definition of animal welfare in the literature (Carenzi & Verga, 2009), however all definitions follow the same overarching frameworks. Farm and production animal research initially focused on the five freedoms (Farm Animal Welfare Council, 2012), a 'resource based' approach to welfare assessment, but recent work in both farm and zoo industries has shifted to an 'animal based' approach (Whitham & Wielebnowski, 2013). Current zoo animal research predominantly surrounds an animals' *teleos*, and quality of life assessments (Wolfensohn et al., 2018), promoting positive affective states by giving an animal what it wants as well as what it needs. An early definition of welfare that was applied to zoo animals was that provided by Broom (1986): the concept that animal welfare is the state of an individual as regards its attempt to cope with the environment. This has since been updated to include whether or not an animal is healthy and has what it wants (Dawkins, 2008). This is considered to be a concept that encompasses both mental and physical health, engagement with the physical or social environment and the opportunity to exhibit control or choice (Asher et al., 2015).

In order to ensure good welfare for all zoo-housed animals, environmental conditions, and management and husbandry techniques must promote positive physical and psychological health (Blackett et al., 2017), providing the opportunity to have positive experiences, whilst minimising negative experiences (Mellor, 2016). Zoos must move from provision of environments in which animals can cope, to those in which animals can thrive (Maple & Bloomsmith, 2017), an ongoing and continuously developing goal. In order to achieve this, individual experiences and perspectives must be considered, along with how they are integrated with the zoo environment (Brando & Buchanan-Smith, 2017). Environments must be designed to engage animals by providing daily mental and social opportunities and challenges. Environmental and cognitive enrichment, the most appropriate nutrition, provision of appropriate social groups, opportunity for interaction (Blackett et al., 2017; Maple & Bloomsmith, 2017) and personalised approaches to animal care ensure the best opportunity to provide optimal environments.

It has been suggested that zoos should not necessarily use the wild as an optimum welfare standard (Veasey et al., 1996; Hutchins, 2006) and that wild baselines are not always the most accurate indicator of the needs of a zoo animal (Wolfensohn et al., 2018). The disparity between wild and zoo conditions mean that at least to some extent the welfare needs of zoo animals will need to be assessed independently of the wild situation (Wolfensohn et al., 2018). There is great behavioural variation in wild animals, with no one environment depicting the 'wild' for any species. Indeed the situations that animals experience in the wild can be affected by a number of factors including seasonality and resource availability (Hutchins, 2006). Furthermore using the wild as an optimum standard suggests that wild animals are always experiencing good welfare, which may not be the case in food or water shortages, or high parasite load or prevalence of predators (Veasey et al., 1996). The wild is also characterised by a high level of diversity and social flexibility (Swaigood & Schulte, 2010). However, information obtained from wild animals can still be used to inform zoos through recognition of natural behavioural repertoires, as long as the drivers behind the behaviours are clearly understood (Veasey et al., 1996). Unique and novel behavioural patterns specific to geographic areas may occur within sub-populations of wild animals. Studies of groups of wild chimpanzees and orangutans (*Pongo spp.*) have shown evidence of geographic variation in behaviour (Whiten et al., 1999; Van Schaik et al., 2003) and this is a phenomenon which may also be seen in zoo animals (Hill & Broom, 2009). It must however be borne in mind that casual observations of wild animal behaviour may not portray a genuine picture of the more fine scale and complex social systems in which animals are engaging and so therefore may not be truly representative of wild-type behaviour (Swaigood & Schulte, 2010). For example, tigers (*Panthera tigris*) have been described as a relatively asocial species (Sunquist, 1981) who are not socially complex (Borrego & Gaines, 2016) but a range of other work has suggested that wild tigers will associate with others; socially feeding in groups as large as 15 individuals (reviewed in Poddar-Sarkar & Brahmachary, 2014).

The drivers behind animal behaviour in zoos are sometimes unknown and non-performance of wild behaviours may not necessitate poor welfare (Veasey et al., 1996). Prevention of expression of a natural behaviour may be indicative of conditions that do not necessarily support positive welfare; however the absence of a behaviour does not mean that animals are incapable of performing it under different conditions (Hill & Broom, 2009). For example chimpanzees in a zoo environment may not use tools in the same way their wild counterparts would if objects (e.g. food) are not provided in a manner which requires manipulation with tools (Hill & Broom, 2009). Furthermore, just as zoo animals may be protected from wild-specific stressors such as exposure to predators or lack of resources, they may encounter a number of uncontrollable stressors that they would not experience in the wild (Morgan & Tromborg, 2007). These include exposure to novel environments (Carlstead et al., 1992a) and substrates (Beisner &

Isbell, 2008), management regimes (Theil et al., 2017), visitor presence (Choo et al., 2011), restricted or predictable feeding opportunities (Bloomsmith & Lambeth, 1995), abnormal social groups (Waples & Gales, 2002) and reduced opportunity to escape conflict (Young, 2003). Thus the behaviours observed in zoo populations may be beneficial adaptations to their environment (Hill & Broom, 2009). When considering management plans that enhance zoo animal welfare it is thus important to understand and consider their full range of biological requirements and needs (Wolfensohn et al., 2018). A basic understanding of wild behaviour and factors driving the expression of wild-type behaviour is important. This will enable a greater understanding of the implications of animals performing (or not performing) those behaviours within zoos. For example, zoo keepers should be mindful of performance of behaviours that are driven by an unpleasant stimulus. If animals in zoos are performing high rates of 'vigilance' or 'anti-predator' behaviour it could be indicative of a problem with the environment, because that behaviour is driven by a negative stimulus. The key therefore is in understanding what the driving factors are behind animal behaviours and how the presence or absence of those natural behaviours is impacting on individual welfare.

Social behaviour and social interactions linked to zoo animal housing and groupings are complex stressors that have huge implications for animal welfare. Although important it is a relatively understudied area. The nature of social groups and opportunities for avoidance of conflict are crucial when ensuring the positive welfare of social species (Stoinski et al., 2004; Renner & Kelly, 2006). Affiliative behaviour associated with bonding or social bond affirmations are likely to induce states of positive affect in animals (Mellor, 2015). The remainder of this review will focus on the effect of the zoo environment on social species.

2.4 Biological basis of social behaviour

Social structure is a defining characteristic of species (Brando & Buchanan-Smith, 2017). Social animals form potentially complex relationships and social structures (Wey et al., 2008). Social groups range from relatively static (i.e., group membership changes are predominantly through births and deaths only) to fission-fusion (i.e., the group membership and dynamics are flexible and may change over time in relation to fluctuations in environmental conditions) (Aureli et al., 2008). Social behaviour, a term used to describe interactions among conspecifics, is a fundamental attribute of the biology of the majority of species. Social behaviour results in relationships between individuals of variable form, duration and function (Blumstein et al., 2010), termed collectively as social dynamics. Understanding social dynamics in an animal group rather than just group size or demographics is important in successful zoo management (Kleiman, 1994). Close social associations are beneficial and having 'friends' enhances physical and psychological well-being of animals (reviewed in Massen et al., 2010).

Sociality is broadly defined as group living (Blumstein et al., 2010) and is used as a measurement of the degree to which animals interact or form associations, both in the short- and long-term (Brakes, 2019). In wild animals sociality has evolved as an adaptive strategy to cope with environmental pressures, such as increased protection from predation and access to food through information sharing and cooperative defence of resources (Salas et al., 2016), providing the foundation for a range of complex forms of cooperation and conflict in wild species (Nowak, 2006). Dynamics experienced in social groups are an attempt to maintain a balanced relationship between the advantages (e.g. increased protection from predators and increased foraging success) and disadvantages (e.g. increased competition for resources and increased conflict over mates) of group living (Lehmann & Boesch, 2004). Group size has thus been described as an adaptive trait that responds to both ecological and social factors (Lehmann & Boesch, 2004). However, the reasons why associations form and then persist in animal populations is poorly understood (Couzin, 2006).

Neuroendocrine processes regulate animal behaviour, and understanding the relationship between neuroendocrine activity and social behaviour is important in developing understanding of social systems (Blumstein et al., 2010). Social relationships are underpinned by different or interacting hormonal systems, and the development of the neuroendocrine system can be altered by the social environment individuals are exposed to during ontogeny (Ziegler & Crockford, 2017). Sociality in wild animals arises from a combination of genetic, neural and endocrine mechanisms (Figure 2.1). Natural and zoo populations are subject to different evolutionary forces and that can lead to different ultimate processes acting on animal genotypes (Schulte-Hostedde & Mastro Monaco, 2015). Although preservation of genetic diversity in zoo populations is a top priority in zoo populations (Lacy, 2009) maintenance of wild phenotypes in zoo animals can be difficult due to environmental mismatches between the wild and zoos. Zoo animals are exposed to a range of selective pressures that, over generations, can shape behaviours which are adaptive to the zoo environment, e.g. increased tolerance of loud noises (McPhee & Carlstead, 2010). Observed genetic adaptations which may arise from deliberate or accidental artificial selection include behavioural (e.g. temperament, McDougall et al., 2005) and morphological change (e.g. alterations to skull shape and digestive tract, O'Regan & Kitchener, 2005).

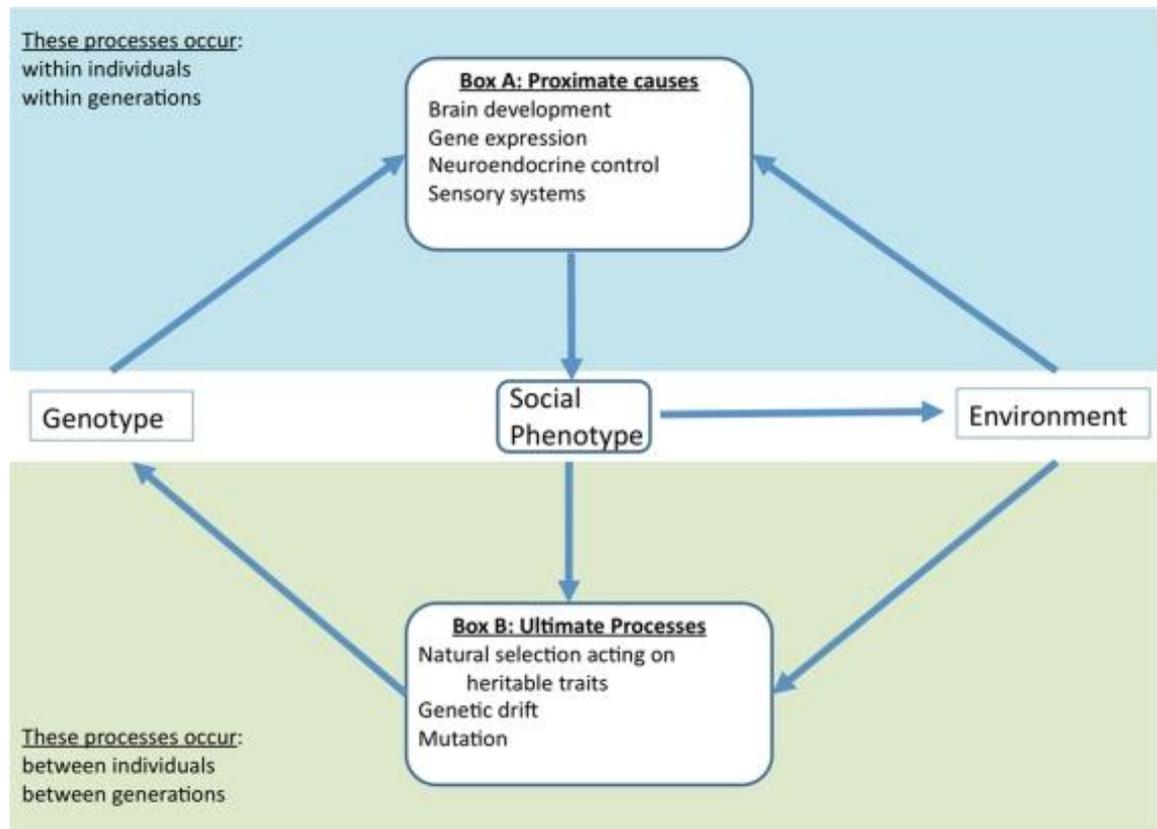


Figure 2.1. An integrative framework for studying social behaviour developed by Blumstein et al. (2010) for wild animal populations

Understanding links between ecological variation, mechanism and sociality can lead to improvements in animal husbandry and welfare. However, our understanding of the genetic and neuroendocrine basis of social behaviour is still limited (Blumstein et al., 2010). In social ungulates, the drivers behind social living are mostly clear; sociality gives protection in the form of reduced predation risk (Molvar & Bowyer, 1994). However, when predation pressures are reduced there must be other drivers behind the maintenance of social groups in order for them to persevere in the wild. Stable social structures can enhance welfare state, longevity, health status and reproductive success of individuals and consequently populations of zoo animals (Rose & Croft, 2015).

2.5 Social groups in zoos

Maintaining functional zoo-housed animal social groups is a primary welfare concern (Mueller et al., 2013), and provision of appropriate social groups is one of the most important factors affecting welfare in some species (Mallapur et al., 2005; Gurusamy et al., 2014). An appropriate social environment leads to improved welfare (de Rouck et al., 2005; Morgan & Tromborg, 2007; Price & Stoiniski, 2007; Chadwick et al., 2017); appropriate and compatible social groups in zoos can provide excellent opportunities for engaging in species-typical behaviours and enriching interactions, offering opportunities for play, companionship and security

(Blackett et al., 2017). However, inappropriate social groups, including housing social species in isolation, housing social groups in situations that do not cater for their social wants or needs, or housing non-social species within social groups can be detrimental to individual welfare states (Morgan & Tromborg, 2007; Price & Stoinski, 2007; Rose & Croft, 2015). Appropriate social groups in zoos have been associated with indicators of poor welfare including increased performance of abnormal repetitive behaviours (ARBs) (e.g., self-injurious behaviour in rhesus macaques (*Macaca mulatta*) (Lutz et al., 2003; Rommeck et al., 2009), reduced reproductive success in small felids (Mellen, 1991), excessive aggression in golden lion tamarins (*Leontopithecus rosalia*) (Inglett et al., 1989) and excessive aggression and physical illness in bottle nosed dolphins (*Tursiops aduncus*) (Waples & Gales, 2002). Chronic social isolation can lead to the development of abnormal behaviours (Blackett et al., 2017; Worlein et al., 2017) including stereotypies in elephants (Kurt & Garai, 2001), abnormal development in young marmosets (*Callithrix jacchus*) (Cinini et al., 2014) and increased aggression in horses when introduced to social groups (Fureix et al., 2012).

It is therefore imperative to identify optimal needs for zoo-housed social species and ensure that the social, reproductive and psychological needs of individuals are being met within zoo environments (Price & Stoinski, 2007). Provision of appropriate social partners and complex social environments enables the opportunity for development of species-specific behaviours (Birkett & Newton-Fisher, 2011), enhancing the opportunity for learning (Galef & Laland, 2005), and potentially reducing the presence of ARBs (Birkett & Newton-Fisher, 2011). It is speculated that for some social species, social partners can be one of the most effective forms of enrichment if the social group is appropriately structured (Rees, 2000). Repeated disruption of established social groups, isolation or exposure to groups of unnatural size or composition have shown to have detrimental effects on behaviour, physiological and psychological states in a number of species, including horses (*Equus caballus*) (Christensen et al., 2011), rhesus macaques (Lewis et al., 2000; Olsson & Westlund, 2007), Geoffroy's tamarins (*Saguinus geoffroyi*) (Kuhar et al., 2003), laboratory housed rats (*Rattus norvegicus domesticus*) and mice (*Mus musculus*) (Olsson & Westlund, 2007).

Provision of socially and physically complex environments that animals can control is critical to promote positive affective states, but can be difficult to achieve (Brando & Buchanan-Smith, 2017). There are many factors in zoos that influence the success of social groups and the zoo environment entails a number of confinement-specific stressors, which are discussed in subsequent sections. Understanding how the zoo environment is affecting animals, enables opportunities for improved management by limiting the effect of the zoo environment on social relationships. Knowledge of why and how individuals choose social partners within zoos allows for evidence-based management decisions to be made regarding group composition (Rose & Croft, 2015). Nevertheless, the factors driving interaction choices in many zoo

species remain largely unknown, despite this being an intrinsic point for ensuring animal welfare in zoos. Further research is needed in this field. A greater understanding of how the demographics of the social group affect herd dynamics may give the opportunity to identify optimum social groups for different zoo-housed species.

2.6 Stressors experienced by social species in zoos and negative effects of inappropriate social groups

Social groups are never completely stable over time. Dynamics of social groups are on a continuum from relatively stable to fission-fusion strategists. Relatively stable groups may have limited change in group social structure, beyond births and deaths in the population. Fission-fusion strategists are more dynamic with fluctuations in group size and structure, however there is usually some level of stability in the most basic or 'core' group (Archie et al., 2006). The term fission-fusion was first coined by Hans Kummer (1971) as a means of describing the social processes undertaken by some species; where the composition of the social group is flexible and can change over periods of time or with environmental conditions, enabling individuals to optimise the benefits of group living (Archie et al., 2006). Species that employ fission-fusion dynamics as a social strategy have the potential to be the hardest to cater for in terms of zoo management. This is predominantly due to complexities and difficulties in dealing with their potential shifting social needs. Provision of environments that incorporate both environmental and social features that enable animals to express species-typical behaviours is important for welfare (Kagan et al., 2015). The ability to provide opportunities for interactions akin to those in the wild, with the space to exist in a number of smaller groups or one larger group, may be determined by the species. Bornean orangutans in Appenheul Primate Park in The Netherlands who were offered the opportunity to choose their own subgroups and sub-enclosures daily as mitigation for potential stressors encountered by being held in a static social group, exhibited reduced effects of group size (Amrein et al., 2014). However, whilst this may be possible in species of this size, it may be problematic or even impossible within a zoo setting for some larger species (e.g. elephants) due to physical space limitations and enclosure designs. Factors that may compromise welfare in social species are discussed in further detail below.

2.6.1 Inappropriate group sizes and compositions

As has been highlighted, social groups may be inappropriate in a number of ways, but generally, if the needs of the animals in the group are not being met then the group could be deemed inappropriate. Common causes of inappropriate social groups within zoos are: (i) inappropriate stocking density (Barnes et al., 2002; Li et al., 2007), (ii) lone housing of social species (Kurt & Garai, 2001), (iii) group housing of naturally solitary species

(Wielebnowski et al., 2002) and (iv) inappropriate group compositions, for example, inappropriate age and sex structures (Anderson, 2005). Inappropriate stocking densities have both short and long-term effects. Overstocking of species of duikers led to an increase in stress-related jaw abscesses (Barnes et al., 2002) and in Pere David's deer (*Elaphurus davidianus*) implications of small enclosure size caused short-term effects on behaviour and elevated levels of cortisol and longer-term effects such as decreased survival and reproduction (Li et al., 2007). Lone housing of elephants has led to the exhibition of stereotypic behaviours (Kurt & Garai, 2001) and, despite the initial recognition that tigers were not social species, paired tigers showed reduced stereotypical behaviour (de Rouck et al., 2005; Vaz et al., 2017). However, group housing naturally solitary species can also be detrimental to individual welfare. Zoo-housed cheetah exhibited more pacing and agonistic behaviour when housed in unnatural social groups (Chadwick, 2014) and showed prolonged anoestrus (which ended once females were separated) (Wielebnowski et al., 2002). The final condition that is encountered, inappropriate group compositions, may lead to groups that do not demonstrate behaviours characteristic of their sex and age (Anderson, 2005). Inappropriate social conditions have potential implications for the future of animals in zoos; if species specific behaviours are not formed during growth and development it can lead to future problems in successful reproduction and development of social relationships (McPhee & Carlstead, 2010).

Knowledge of wild animal behaviour may be key to ensuring appropriate social conditions within zoos. Cotton-topped tamarins housed in colonies of a size and composition that most closely mimic the wild have higher than average infant survival rates and only rare incidences of abortion, stillbirth and parental neglect of infants (Price & McGrew, 1990). Whilst in cheetah, amicable relations and a complete lack of escalated aggression has been observed when wild social conditions were replicated (Caro, 1993). However, replication of the wild is not always physically possible due to the nature of wild animal behaviour, and it is felt that ensuring social animals are not kept solitarily is a priority in these instances (Rees, 2009). Inappropriate group sizes or compositions, in particular solitary housing of social species, can lead to the development of an array of ARBs. In some more extreme cases it may even impede brain function and development if the isolation occurred during a critical development period (Latham & Mason, 2008). It is argued that there is the opportunity for zoos to house animals in a wider range of social groups than they may experience in the wild because some of the limiting factors of wild group size (such as resource and habitat availability) are not present. The lack of space in zoos has led to some solitary species being group housed (Price & Stoinski, 2007). Orangutans and felid species are often housed in this manner, and whilst social partners provide the potential for enrichment and social stimulation (Bond & Watts, 1997), they may also cause chronic stress to some individuals (Mellen et al., 1998). At this point it is not clear whether all social species can be catered for in

zoos. More evidence-based research is needed to identify which species can be adequately cared for within zoological environments, and how best to accommodate them.

2.6.2 Opportunities for social learning and development

Social learning is an over-arching term which is used to refer to a number of behavioural processes that enable social interactions to bias what individuals learn (Galef, 2003). A phenomenon employed by a range of social and often intelligent species, it is a more efficient method of knowledge acquisition than independent trial and error learning (Greco et al., 2013). It takes place in a structured social context for a number of social animals, and it is felt that it varies in biologically meaningful ways. There are a number of different methods of social learning (reviewed in Coussi-Korbel & Frigaszy (1995), but it predominantly incorporates two processes: learning through social interaction (e.g. social play or agonistic interactions) to gain social skills and learning via social information to gain non-social skills (van Schaik & Burkart, 2011) (e.g. predator avoidance or food acquisition; Thornton & Clutton-Brock, 2011). Social learning is an important part of development, and can help to ensure knowledge transfer through generations (Guinet & Bouvier, 1995). For example, elephant learning is considered to be the outcome of an interaction between an individual's behaviour, social experience and the accumulated social experiences of its mother and family members (Lee & Moss, 1999).

Social groups in zoos should be sustainable, without input from wild populations. In order to meet this goal, importation of animals from the wild should not be required and appropriate learning opportunities must be available within zoos to ensure proper development of individuals. For example, successful conception, births and subsequent natural rearing of young elephants require zoo-housed elephants to have had appropriate opportunities for social learning throughout their life. Lack of prior allomothering opportunities/lack of experience with calves are associated with increased likelihood of calf rejection and failure to survive to 5 years of age in female elephants in European zoos (Hartley & Stanley, 2016). In order to sustain the zoo elephant population, the opportunity for young bulls to learn appropriate behaviours from adults is just as important in zoo elephants as the relationship and opportunity for learning is in wild elephants (Evans & Harris, 2008). Conspecifics are as important for bull elephants as for females; the presence of an adult bull during the critical learning period of adolescent bull elephants is believed to be vital for the development of normal behaviours, with young bulls depending on knowledge transfer from adults to enable them to learn appropriate behaviours (Evans & Harris, 2008).

The full benefits of play behaviour are not completely clear but it is thought to strengthen social bonds and assist in development of younger individuals (Heintz et al., 2017). For example, African elephants display a variety of forms of social play throughout their lifetime and it is potentially enriching both in the short and long-term. Play in early development is linked to the

capacity for growth, survival and reproduction in African elephants (Lee et al., 2013). Playful wild African elephant calves have a reduced risk of premature death (<5 years old) but as they age male and female elephants use play differently. Juvenile males use play as a means of gaining relaxed contact with strangers, which enables them to gather information about future friends, associates and competitors. Playfulness in female African elephants, however, is believed to be related to an individual's position within the family herd in later life; playfulness has been identified as an indicator of competence, popularity and sociability, potentially reflecting leadership (Lee & Moss, 2014). Play behaviour is linked to positive affective states (Ahloy-Dallaire et al., 2017). Research in chimpanzees has shown that social play can provide social and motor benefits to individuals; helping with both muscle coordination and locomotor development, and strengthening social bonds (Heintz et al., 2017).

Detailed species knowledge is required to ensure social situations do not impede on natural reproductive function, which may be detrimental to captive breeding programmes. The zoo-housed cheetah population is not considered to be self-sustaining (Wielebnowski et al., 2002) nor is the European (Rees, 2003a) or North American (Olson & Wiese, 2000; Wiese, 2000) Asian elephant population. However, unlike the Asian elephant population, which is considered non self-sustaining due to relatively high infant mortality and reduced fecundity (Rees, 2003a), the unsustainable cheetah population is considered to be due to social factors affected by incompatible female pairs, leading to suppressed ovarian cyclicity (Wielebnowski et al., 2002).

Group composition is critical for the maintenance of stable groups since overcrowding and inappropriate sex and age ratios may result in increased aggression (Gittleman & McMillan, 1996). Animal social preferences and needs may change through different life stages (Evans & Harris, 2008). The composition of groups must be suitably complex as to enable animals to experience the required opportunities for successful development at all points in their life cycle (e.g. litter mates to enable play behaviour, the opportunity to leave groups when animals reach sexual maturity).

2.6.3 Lack of recognition of the effects of social groups at the individual level

Social events that individual animals are exposed to in their lifetime can have important influences on behaviour, development, physiology and overall wellbeing (Prado-Oviedo et al., 2016). Furthermore, a number of factors may affect how animals cope in the zoo environment including position in the social group (or hierarchy) (Sapolsky, 2005) and past individual experiences (Freeman & Ross, 2014; Prado-Oviedo et al., 2016; Williams et al., 2018a).

Many commercially-reared animals experience premature separation from their mothers (Latham & Mason, 2008). Social deprivation in primates has been linked to performance of stereotypies, heightened fearfulness, inappropriate social interactions and disturbed serotonin production (Novak et al., 2006). Young macaques that experience early separation from their

mothers show inability to reconcile with others in their social group, sometimes leading to uncontrolled levels of aggression (Ljungberg & Westlund, 2000). In elephants, demographic and social life events (reviewed in Prado-Oveido et al. (2016) that both zoo born and wild caught individuals may have been exposed to include separation, transfers, births (or exposure to conspecific births) and offspring or conspecific death. The outcomes of exposure to these events include effects on development of social skills, strength of social bonds and success of coping strategies. All of these areas could have an impact on zoo elephant welfare and so must be considered. Taken together, the research in this field suggests that animal life histories have the potential to shape social experiences once they are in a permanent establishment and understanding these on an individual basis will have important implications for welfare.

2.6.3.1 Animal personality

Animals have unique personalities that can affect how they cope with the environment, how they respond to stressors and can even determine reproductive and production success (Wolfensohn et al., 2018). Furthermore, personality can affect the way in which animals react to each other and their environment (Watters et al., 2017). Within the field of ethology it is not uncommon to see the words 'personality', 'temperament' and 'behavioural syndromes' used interchangeably (MacKay & Haskell, 2015). For the purposes of this review and throughout the thesis, personality is defined as 'individual differences in behaviour that are thought to be stable across time and situations' (Powell & Gartner, 2011) as this is most applicable to studies conducted in zoos and it is widely recognised in the zoo community (Watters & Powell, 2012). Understanding how personality varies within species, populations and individuals, has implications for husbandry in domestic animal species (Réale et al., 2000). Indeed, the concept that animals are individuals and have distinct personalities that are likely to affect individual experiences, ability to cope and therefore welfare within zoos is now well established and widely accepted (Watters & Powell, 2012). Personality assessments have been used in a number of areas in both *in-situ* and *ex-situ* conservation, including assessing potential breeding success in captive black rhinoceros (*Diceros bicornis*) (Carlstead et al., 1999b) as a measure of reintroduction success in wild Swift foxes (*Vulpes velox*) (Bremner-Harrison et al., 2004) and as a tool for forming and maintaining social groups in captive gorillas (Kuhar et al., 2006).

Understanding the relationship between personality and well-being in zoo-housed animals enables targeted care that will improve welfare (Gartner et al., 2016). Furthermore, an understanding of animal personality provides the opportunity to predict the response of individual animals to, amongst other things, exhibit design, zoo visitors or introduction to social groups (Powell & Gartner, 2011). Successful breeding in giant panda has been linked with personality profiling to help in identification of potentially compatible mates (Martin-Wintle et al., 2017) and,

in chimpanzees personality types successfully predicted friendships (Massen & Koski, 2014). Familiarisation and kinship can also affect relationships. Researchers have found that in wild kangaroo rats (*Dipodomys heermanni*), a typically solitary species, familiarisation leads to a reduction in physical fights and an increase in communication behaviour designs that are thought to reduce agonistic interactions, such as foot-drumming (Shier, 2000).

Research in both wild and zoo-housed elephants has shown individual personalities and identified specific personality traits, such as fearful, sociable, aggressive and leadership (Grand et al., 2012; Lee & Moss, 2012; Horback et al., 2013; Yasui et al., 2013; Williams et al., 2015; Seltmann et al., 2018). Recognition of the effect of personality on coping abilities within the zoo environment and the influence it is likely to have on the success of formation and perpetuation of relationships between individuals is extremely important for such a long-lived species. Personality can affect how animals behave in social contexts (Réale et al., 2000). Anecdotal evidence has suggested that elephants recognise historic social partners even after many years of separation (Evans, 2014) and so understanding more about the relationship between personality and individual compatibility is important for improving zoo elephant welfare in the long-term. The relationship between bond strength (as rated by keepers) and observed associations and social interactions in elephants herds has been investigated in the US (Bonaparte-Saller & Mench, 2018). To the authors knowledge no studies have investigated links between social interactions and elephant personality or assessed whether certain personality types are more likely to interact positively or negatively. Gaining more knowledge in this area has great practical application in compatibility assessments and could be used in management planning to minimise the risk of inappropriate social grouping in the future.

2.6.4 Space

Enclosure complexity and space can play an important role in the success of social groups. Appropriate space and complexity offer zoo animals the opportunity to choose when to interact with or avoid conspecifics. Research has indicated that excessive aggression can arise when animals are unable to avoid others or when the opportunity to decrease social tension is no longer available. In black rhinoceros, the presence of concrete walls had a negative effect on female breeding success (Carlstead et al., 1999a), which the researchers attributed to the limitation on opportunities to escape from conspecifics. Emperor tamarins (*Saguinus imperator subgriseus*) displayed reduced interactions and increased natural behaviour when they were housed in free-ranging spacious and complex areas instead of cages. The authors suggested that high numbers of interactions observed in caged tamarins were a result of forced proximity in restricted space (Bryan et al., 2017). Extra space and opportunity for more natural behaviours may thus have a positive effect on individual welfare.

Animal management practices place restrictions on zoo animals, including restricting enclosure access for short and long periods of time. The reduction in space leads to a decreased opportunity to make choices, particularly in relation to social dynamics (Herrelko et al., 2015). Reduction in space in zoos may be short-term (hours to days, e.g. for cleaning or maintenance) or long-term (months, e.g. moving from summer enclosures to winter enclosures). This reduction in space, however temporary, may place extra stressors on individuals. Although it has been recognised that it is not always clear whether it is removal from a familiar environment or the reduction in space that is the cause of most stress (Alexander & Roth, 1971).

Three models are proposed that explain the response of a number of mammal species to the spatial restrictions sometimes experienced within zoos. The first model is described as a density-aggression model, whereby a positive relationship is expected to exist between overcrowding and increased aggression. Research supports this hypothesis for a number of species; rodents, galagos, baboons (*Papio spp.*) and macaques. However, more recent work has highlighted the likelihood of more intelligent species adjusting their behaviour in order to avoid conflict (Videan & Fritz, 2007). Two principal strategies have been identified as behavioural adaptation techniques: conflict avoidance (Judge & de Waal, 1993) and tension reduction (de Waal, 1989). Conflict avoidance strategies involve decreasing overall interaction levels. This helps to avoid an increased risk of conflict and aggression during short-term reduction in space, but it cannot be maintained over longer periods. This strategy has been observed in macaques and chimpanzees (Videan & Fritz, 2007). The tension reduction model, described as an active, goal-directed response, is usually utilised under long-term restrictions (up to several years). In this theory, affiliative behaviours or coping strategies should increase, in a bid for animals to actively reduce tension and therefore reduce aggression. This theory has been evidenced in rhesus macaques, bonobos (*Pan paniscus*) and chimpanzees (Videan & Fritz, 2007). There appears to be no specific rule which governs how animals respond to overcrowding, with some animals showing no behavioural change and other studies suggesting it is dependent upon enclosure complexity. In a study on chimpanzees, Videan and Fritz (2007) observed individuals using different strategies for short (1-2 days) and long-term (6 months) increases in spatial density. Males used a tension-reduction strategy for both short- and long-term, whereas females swapped from a conflict avoidance strategy in the short-term to a tension-reduction strategy in the long-term.

2.6.5 Development and destruction of social bonds

Zoo management practices may have a significant negative impact on the development of social bonds and the long-term success of social groups in animals such as fission-fusion species that exhibit changes in social partners periodically (Williams et al., 2018a). Zoo-specific problems that can exacerbate the situation include, but are not limited to: the need to house individuals with

unique atypical life experiences (Jacobson et al., 2017), the need to adhere to EEP studbook recommendations for breeding where appropriate (Wolfensohn et al., 2018), and a lack of living relatives or known social partners within the population (Clubb & Mason, 2002). Animals may need to be transferred between collections for breeding programmes which can cause stress in a number of ways including being removed from the group (or having a conspecific removed from the group), transportation, and introduction to a new group (or having a conspecific introduced to the group) (Wolfensohn et al., 2018). This can contribute to the destruction of social bonds and has the potential to cause disruption to social compatibility and group dynamics.

Disruption to social bonds in terms of permanent physical changes to social groups may lead to poor welfare and increased stress (Rose & Croft, 2015). Observed negative responses to separation in animals have been both physiological (e.g. increased cortisol) as seen in domestic chickens (*Gallus gallus domesticus*) (Jones & Williams, 1992) or behavioural (Tarou et al., 2000). Female giraffe (*Giraffa camelopardalis*) who had a male removed from their group showed decreased habitat utilisation, increased activity and increased stereotypical behaviour, alongside an increase in contact behaviour, which was believed to be used by the remaining giraffe to reinforce social cohesion (Tarou et al., 2000). Within-zoo management regimes can also lead to routine separation of animals, for example, overnight solitary penning, or removal of animals for training or routine veterinary treatment (Bennet pers. comm., 2016; Cairns pers. comm., 2016; Meehan et al., 2016a). In some instances, zoo animals may have had unique and potentially traumatic previous life experiences and so they may be less well equipped to deal with novel or changing situations.

2.6.6 Lack of opportunity for choice

What an animal wants is as important for welfare as what an animal needs (Dawkins, 2017). However, it must be borne in mind that animals may not always make the best long-term decisions for their welfare (Widowski, 2015). The opportunity for choice and a level of control over their environment can help to alleviate some stressors experienced in zoos (Carlstead & Shepherdson, 2000). Animals exhibit individual differences in responses to zoo environments, so it is important that enclosures allow individuals to make changes to meet their needs. The importance of choice in successful social housing of animals is rapidly becoming a more studied field. Choice has been recognised as one of the most important things for zoo animal welfare (Chadwick et al., 2017). Reduced exhibition of stereotypical behaviour was noted when elephants were given the opportunity to choose between inside and outside areas (Greco et al., 2016a) and reduced signs of agitation and lower urinary cortisol were observed when giant panda were given free access between exhibit and off-exhibit areas (Owen et al., 2005). Pair incompatibility is one of the greatest causes of failure in captive breeding programmes (Asa et al., 2011) and the opportunity for choice in social partners and mates has led to improved

reproductive output in giant panda (Martin-Wintle et al., 2015) and cheetah (Wielebnowski, 1999) and successful social group formation in chimpanzees (Schel et al., 2013). Providing optimal levels of choice without negatively affecting welfare in animals who may have unique atypical life histories remains a significant challenge for many zoos (Herrelko et al., 2015).

Understanding how the zoo environment is affecting zoo animals enables opportunities for improved management by limiting some of the stressors that impact social relationships. Furthermore understanding why and how individuals choose social partners within zoos allows for evidence-based management decisions to be made on an individual level (Rose & Croft, 2015). This is particularly true for intelligent, long lived, social species such as elephants. Lack of physical interaction does not necessarily suggest that conspecific companionship is unimportant for zoo elephants (Mueller et al., 2013). It is thought that whilst physical social interactions may account for only a small proportion of behavioural activity budgets in zoo-housed elephants, the opportunity to spend time in the vicinity of conspecifics is important for welfare (Chadwick et al., 2017). Factors driving choice of social partners in zoo-housed elephants are unknown, but research has highlighted the importance of choosing social partners and the opportunity to contact all group members in maintaining individual elephant welfare (Schmid, 1995). Furthermore, social variables have been linked to multiple welfare indicators (Meehan et al., 2016a) and understanding factors affecting compatibility of elephants has been highlighted as a research priority for improved understanding of zoo elephant welfare (Asher et al., 2015). Using their behaviour and ecology as a guide, a more in-depth review of the social needs of zoo elephants is provided below.

2.7 Elephants: behaviour and ecology

Elephants are from the order *Proboscidea*, of which there are now only three extant species; Asian elephant, African savanna elephant and, most recently classified, African forest elephant (Shoshani & Tasse, 1996; Rohland et al., 2010). The IUCN red list currently only provides data for African savanna and Asian elephants as the original two species; African elephants are listed as Vulnerable (Blanc, 2008) whilst Asian elephants are listed as Endangered (Choudhury et al., 2008). Current estimates of population size for wild African elephants are 419,000 to 650,000 individuals, whilst there are thought to be only 39,000 to 43,500 wild Asian elephants, with a further 13,000 domesticated Asian elephants working at logging camps (UNEP et al., 2013).

2.7.1 Determinants of group dynamics in wild elephants

Elephants are socially sophisticated mammals and are known to have one of the most advanced mammalian social systems (Sukumar, 2003). *In situ*, they live in complex fission-fusion

societies (Moss & Poole, 1983; de Silva et al., 2011) and display strong affiliative behaviours. Three broad social unit levels have been documented: family groups, bond groups and clans. The most basic of which, family groups, are composed of one or more related females and their offspring (Moss & Poole, 1983; Sukumar, 1994). Bond groups are considered to be a second tier unit consisting of two or more (usually) related family units (Moss & Poole, 1983). Members of family units or bond groups show high frequencies of association over time, act in a coordinated manner and show affiliative behaviour towards one another (Poole, 1994). Above the bond group is the clan, which is defined as families and bond groups which use the same dry-season home range (Poole, 1994).

The predominant driving force behind wild elephant social structures and herd dynamics are ecological factors (Wittemyer et al., 2005; Pinter-Wollman et al., 2009). It is hypothesised that group size is driven by a number of factors including social evolution, habitat availability, distribution of resources, seasonality and human threat level (Sukumar, 2003; Silk, 2007). Young male elephants stay with their maternal family group until they are early to mid-teenagers (10 – 20 years, mean 14 years) (Lee & Moss, 1999; Lee et al., 2011) whilst females stay with their maternal herd for life, unless the herd reaches carrying capacity. Bull elephants have a different social system to female elephants (Evans & Harris, 2008). Despite early research which described them as relatively solitary species (Croze, 1974 cited in Morris-Drake & Mumby, 2018) more recent research has identified strong social bonds (Chiyo et al., 2011; Goldenberg et al., 2014). Drivers of social affiliation for bull elephants change over time as individuals' needs are affected by changing environments or physical condition (Thitaram et al., 2015). Changes to physical condition are predominantly associated with a phenomenon known as musth; periodic physical and behavioural changes characterised by increased sexual activity and aggression, and associated with elevated testosterone (Poole & Moss, 1981).

The relationship between seasonal group dynamics and spatial distribution is complex (Mcknight, 2015). The size and composition of social groups of wild African elephants varies seasonally (Wittemyer et al., 2005) although the changes in group size and formation seen in Asian elephants is not thought to be affected by seasons (de Silva et al., 2011). Not all individuals will interact with each other and there is much individual variation in long-term fidelity to companions (de Silva et al., 2011). African elephant social networks are much more interconnected than Asian elephants (de Silva et al., 2011). The reason for the difference in social structure between African and Asian elephants has been attributed to the different areas inhabited. This theory is supported by the average group size of elephants in varying habitats; African savanna (>10 individuals), African woodland/Asian dry forests (5 – 10 individuals) and African rain forests (<5 individuals) (Sukumar, 2003). Asian elephants typically reside in forest areas, which have generally higher amounts of rainfall than the African savannas which are typically home to African elephants

(de Silva & Wittemyer, 2012). African elephants reside in open areas, where risk of predation is greater, therefore the large group sizes observed in African herds may be a result of increased safety in larger numbers (de Silva & Wittemyer, 2012). The drivers of Asian elephant social groups dynamics are as of yet unknown, but it is believed they are more likely to be influenced by social factors than ecological factors (de Silva & Wittemyer, 2012).

One of the greatest benefits to group living in wild elephants is when calves are present; the social group provides protection and supports development (Lee & Moss, 1999). Indeed, social groups in reintroduced elephants are not necessarily based on genetic relatedness but they are aided by the presence of a calf (Thitaram et al., 2015). In a reintroduced elephant group in Thailand, social bonding was influenced by the presence of a calf, with calves being at the centre of elephant gatherings (Thitaram et al., 2015), much like the calf centric behaviour observed in natural wild elephant herds (Lee, 1987). Sociality is important for wild elephant survival; they depend on others for knowledge acquisition in the wild. Female matriarchs are known as knowledge repositories for social and ecological knowledge (McComb et al., 2001; Evans & Harris, 2008). Conspecifics are as important for bull elephants as for females; the presence of an adult bull during the critical learning period of adolescent bull elephants is believed to be vitally important for the development of normal behaviours; with young bulls depending on knowledge transfer from adults to enable them to learn appropriate behaviours (Evans & Harris, 2008).

Elephants live in related groups of varying sizes, however, research into social group dynamics in heavily poached populations or reintroduced elephants has indicated that regrouping of individuals is not always based on genetic relatedness (Nyakaana et al., 2001; Thitaram et al., 2015). Gobush and Wasser (2009) observed elephants primarily socialising among kin when they were available, however they also documented behavioural plasticity in the form of diverse responses of adult females to unrelated conspecifics. When close relatives were absent, females frequently socialised with elephants outside of their core grouping; grouping with other females lacking kin or with established groups (Gobush et al., 2009).

2.7.2 Elephant social interactions

Elephants principally communicate in four ways: acoustic, chemical, visual and tactile, with the potential for them to use seismic communication needing further investigation (Langbauer, 2000). The concept of elephant communication is reviewed by Langbauer (2000), but in summary all communication methods in wild elephants are designed to help maintain group cohesion and coordination over distances and advertise hormonal/emotional states. This current study focuses only on visual and tactile communication, as these were the only methods of communication that could be studied reliably through assessment of behaviour. Visual

communication is used by wild elephants in dominance or agonistic displays, group cohesion and advertisement of hormonal/emotional state. Tactile communication is used in both affiliative and agonistic behaviours and principally involves the trunk (Langbauer, 2000).

Tactile interactions are used in a wide range of contexts, including affiliative, aggressive, defensive and exploratory behaviour (Finnegan, 2005) and in the wild it is thought elephants seek reassurance through touch (Sukumar, 1994). Positive social interactions include trunk entwining, play (Figure 2.2), holding the tail of another elephant (Figure 2.3), touching (trunk to-) and rubbing (body to-). Negative social interactions include sparring, pushing, head-butting and kicking (Gruber et al., 2000; Olson, 2004; Wilson et al., 2006; Harris et al., 2008; Posta et al., 2013). Wild elephants may engage in greeting ceremonies which vary in their levels of intensity (Moss, 1981). These ceremonies involve a number of 'excited' behaviours including trunk contact, smelling, spinning, urinating, temporal gland secretions, ear flaps, trunk entwining, sparring and a range of vocalisations including rumbling, screaming and trumpeting (Olson, 2004).



Figure 2.2. Example of play behaviour in two groups of Asian elephants



Figure 2.3. Tail holding behaviour in two Asian elephants

2.7.3 Social learning in elephants

Social learning in wild elephants is most apparent during the development phase, when complex social relationships within the family unit are first formed (Lee, 1986). However, opportunities for social experience and learning among wild elephants are not constrained to this relatively short time period. Elephant learning has been described as an outcome of a series of interactions; between intrinsic behaviour of an individual and its social experience, the accumulated social experiences of its mother and family, and the physical and biotic environment in which it must feed and survive (Lee & Moss, 1999). Elephants in the wild learn through their close social environment, much of which is necessary for survival in an ever changing environment where constant behavioural modification is required (Lee & Moss, 1999). In much the same way as humans, young elephants in particular gather a wealth of life lessons from the wider herd. They learn about the meanings of vocalisations, knowledge of food stuffs (quality, seasonal availability and how to process it; predominantly learning from sampling from the mouths of older elephants while they are feeding), and how to interact socially with others.

Elephants engage in a range of social interactions and communication is central to information transmission within wild elephant groups (Vidya & Sukumar, 2005b). Knowledge transfer has been recorded between experienced and naive female elephants (Bates et al., 2010). There is some disparity in the literature as to whether or not elephants do exhibit social learning. Some field biologists state unequivocally that elephants engage in social learning (Lee, 1986), whilst other researchers suggest the evidence of social learning is predominantly anecdotal, with few studies formally assessing social learning in elephants (Bryne et al., 2009; Greco et al., 2013). Others have reported evidence of social learning influencing behaviour; crop raiding behaviour in young wild male bull elephants (Chiyo et al., 2011) and exhibition of appropriate sexual behaviours in young Asian bull elephants when they are exposed to adult bulls during adolescence in zoos (Rees, 2004). Furthermore, expression of allomothering skills in female African and Asian elephants are acquired through familial herds; where opportunities to assist in the upbringing of young improve reproductive success in zoos (Hartley & Stanley, 2016). Social learning has also been attributed to the ability of wild elephants to identify human voices and distinguish cues that teach them whether they are 'friend' or 'foe' (Plotnik & de Waal, 2014).

2.8 Zoo elephants

Research has begun to identify means of assessing elephant welfare both at a point in time, and over time, specifically by monitoring and documenting changes in behaviour (BIAZA Elephant Welfare Group, 2016). The plastic nature of behaviour makes it an excellent area of focus when investigating welfare of zoo-housed species, because it can be used to gauge a response to an environmental change in a relatively quick and easy fashion.

Historically, the focus of zoo elephant welfare assessments was signs of poor welfare, rather than positive welfare states. More recently the importance of identifying indicators which show positive welfare has been advocated (Maple & Bloomsmith, 2017; Wolfensohn et al., 2018), in order to help identify when animals are beginning to thrive in their environments. Clubb and Mason (2002) identified a number of potential behavioural and physiological indicators of poor welfare (Table 2.1). The indicators they believed applied to elephant welfare in relation to housing, and that were consequently utilised in their study, were: stillbirths, stereotypies, inter-birth intervals, mortality rates, infanticide, maternal rejection rates and some aspects of disease.

Table 2.1. Potential behavioural and physiological indicators of welfare in zoo-housed elephants, identified by Clubb and Mason (2002)

Behavioural	Physiological
Loss of appetite	Changes to basal corticosteroid in blood
Loss of interest in mating	Altered metabolism
Poor parental care (or infanticide)	Low growth rates
Reduced levels of grooming	Poor coats
Reduced interest in exploration of surroundings	Slow healing rates
Increased timidity	Poor milk production
Increased aggression	Immunosuppression
Attempts to escape	Reduced breeding rates
Exhibition of stereotypies	

Hill & Broom (2009) highlighted the importance of using a suite of indicators in assessment of welfare, in order to create an accurate reflection of the welfare state of an animal. These should include some indicators of positive welfare states as well as indicators which capture more negative welfare. A number of indicators have persisted in the literature over time. Harris et al. (2008) used a combination of behavioural, physical health and physiological data to assess the welfare of British and Irish zoo elephants. The suite of measures utilised by the researchers had been created using data gathered through questionnaires sent to 50 elephant and animal welfare experts. Measures included assessment of stereotypies, physical health checks, faecal corticoid metabolites, locomotion, foot health, body condition and ease of lying down.

Asher et al. (2015) and Yon et al. (2019) gathered data in a multidisciplinary approach; using keeper expertise to conduct routine welfare assessments through a combination of qualitative behavioural assessment, answering questions based on *ad hoc* observations of

behaviour and compiling data through production of overnight activity budgets. Indicators of welfare that were included for use in the welfare assessment tool included abnormal behaviour, rest, feeding, environmental interaction, comfort (self-maintenance), activity, inactive, social interactions and 'other' which comprised vocalisations and play. Social behaviour, which is the focus of this thesis, was considered to be an understudied but nevertheless important welfare indicator that has been advocated for use in welfare assessments (Asher et al., 2015; Williams et al., 2018b).

There is little agreement on the precise needs of elephants in zoos (Maple et al., 2008), yet the difficulties of keeping elephants because of their size and cognitive abilities have been widely acknowledged and discussed. More recently, researchers have begun to try to identify the needs of elephants in zoos, through reviews of current literature and consultation with elephant keepers and other elephant experts (Gurusamy et al., 2014; Asher et al., 2015; Chadwick et al., 2017). Resources of importance to elephants are described as physical environment, choice and environmental complexity and the social environment. Physical environmental recommendations included the need for feeding opportunities and appropriate substrate. Social needs include group size, relatedness, the composition of the group and compatibility between individuals.

2.8.1 Elephant welfare concerns

Many social species in zoos are currently housed in, or trials have been undertaken successfully for future housing in, naturalistic social groups. Indeed, there are thought to be benefits to housing social species in naturalistic groups, such as increased breeding in cotton-top tamarins (Price & McGrew, 1990), reduced stereotypies in cheetah (Chadwick, 2014), reduced aggression in chimpanzees (Schel et al., 2013) and an increased ability to cope with group size stressors in orangutans (Amrein et al., 2014). However, elephants are thought to be an exception (Stroud, 2007). High profile reports have suggested that zoo elephant welfare throughout Europe is compromised, and concerns have been voiced over their suitability as a zoo exhibit (Clubb & Mason, 2002; Kiiru, 2007; Mason & Veasey, 2010a; Zoos Forum, 2010). Concerns over the mental and physical health of zoo elephants are detailed in Table 2.2.

Table 2.2. A summary of the main studies which have highlighted concerns over the mental and physical health of zoo elephants

Author	Study details	Main findings
Clubb & Mason (2002)	<ul style="list-style-type: none"> Data gathered from published literature, databases and elephant studbooks (1999 EEP Asian elephant studbook and 2001 EEP African elephant studbook) N = 534 Asian elephants (274 living) N = 242 African elephants (196 living) 	<ul style="list-style-type: none"> Higher mortality rates in zoo elephants than wild counterparts (African elephants) and elephants kept in timber camps (Asian elephants) ($p < 0.05$) Infant mortality rates higher in zoos than timber camps (Asian elephants) Incidence of veterinary conditions caused by excess body weight and/or stress (e.g. coronary and circulatory pathologies, skin infections, lameness, arthritis) Stereotypic behaviour present in approximately 40% of animals High levels of aggression towards other elephants and handlers
Brown et al. (2004b)	<p>Reproductive surveys sent to elephant-holding zoos in N America</p> <ul style="list-style-type: none"> Surveys sent to zoos recorded in the studbooks and those part of the SSP (n=370 Asian elephant collections, n=320 African elephant collections) Surveys returned for >75% elephants in N America Asian elephant: 322/370 (87%) returned surveys African elephants: 257/320 (80%) returned surveys 	<ul style="list-style-type: none"> Reproductive pathologies present in North American zoo elephants Up to 14% of Asian elephants and 29% African elephants in North American zoos are either not cycling at all or have irregular cycles 70% of non-cycling elephants exhibited some type of ovarian or uterine pathology
Harris et al. (2008)	<ul style="list-style-type: none"> Surveyed 77 elephants housed in UK and Irish zoos (n=13 facilities) 41 Asian elephants, 36 African elephants Asked zoos to complete questionnaires, undertook live observations (1634.5 hours of observations ~ 23.7 hrs per elephant) and gathered video footage (9 nights of footage over a 3 week period) for some elephants (n=41) 	<p>Physical health concerns</p> <ul style="list-style-type: none"> Foot health was a major welfare concern: 15/77 (19.9%) had major problems with forefeet, 6/77 (8%) with hind feet Only 11 of the 77 (14%) surveyed elephants had a normal gait; 17 (22%) had imperfect gait, 27 (35%) were mildly lame and 18 (23%) had an obvious limp or were severely lame Only 6 (8%) individuals were normal weight, 58 (75%) were 'overweight' or 'very overweight' <p>Behavioural concerns</p> <ul style="list-style-type: none"> 42/77 (54%) elephants showed stereotypies during the daytime, 25.9% of which stereotyped for >5% of the day 15/41 (37%) elephants who could be reliably identified overnight stereotyped for >5% of the time 19/41 (46%) elephants stereotyped for >5% of a 24hr period
Clubb et al. (2008)	<p>Compared European zoo elephant survivorship with protected populations of wild elephants.</p> <ul style="list-style-type: none"> European zoo elephants: n=786 Wild African elephants: n=1089 Wild Asian elephants (Burmese 	<p>Compromised survivorship (e.g. reduced median lifespans and high infant mortality in European zoo elephants)</p> <p>Median life span (excl. premature and still births):</p> <ul style="list-style-type: none"> African elephants: 16.9 years (zoo), 56

	logging camp): n=2905	<ul style="list-style-type: none"> years (wild) Asian elephants 18.9 years (zoo), 41.7 years (wild) <p>Infant mortality</p> <ul style="list-style-type: none"> No difference between infant mortality for African elephants in zoos or wild (primiparous dams: 23.1% zoo, 17.7% wild; multiparous dams: 0% zoo, 6.8% wild) (p>0.10) Higher infant mortality for Asian elephants in zoos than in the wild population (primiparous dams: 37.5% zoo, 13.2% wild; multiparous dams: 18.5% zoo, 7% wild) (p<0.05)
Lewis et al. (2010)	<ul style="list-style-type: none"> Foot health questionnaire distributed to 80 US elephant-holding facilities in 2006 78/80 (97.5%) response rate 	<ul style="list-style-type: none"> One third of facilities reported at least one foot pathology (n=26) A number of foot pathologies were reported: Onychitis (inflammation/infection of the nail bed), perionychia (lesions/sores between the nails), penetrating erosions and sloughed pads (complete separation of slipper)

There are considerable challenges when attempting to provide zoo elephants with social groups that replicate the wild, and requirements are likely to vary according to individual circumstances (Zoos Forum, 2010). Factors related to the social environment have been identified as the most influential in predicting stereotypy rates, where stereotypies are thought to reduce with increasing time spent with juveniles and increase with time housed separately (Greco et al., 2016a). The main concerns relating to social needs are: (i) unnatural social groupings (small social groups or in some instances social isolation), (ii) lack of relatedness or group stability, (iii) inappropriate herd structure, leading to reduced opportunities for learning or inadequate socialisation during critical periods and (iv) disruption of social hierarchies (Clubb & Mason, 2002; Harris et al., 2008). Disruption of social hierarchies can be caused by movements between facilities or separation of groups. Of particular concern is early removal of young, enforced isolation and breaking of social bonds (Clubb & Mason, 2002). Small herd sizes have also been cited as a serious concern for elephants (Rees, 2009). The negative effects of social isolation are well-publicised (Kurt & Garai, 2001), however, the links between social isolation and stereotypic behaviour may not necessarily be causal. For example, Greco et al. (2016a) found that some elephants are housed alone because their upbringing may have led them to be incompatible with other elephants, rather than the stereotypies arising as a function of their current environment. Some researchers have suggested that elephant groups should be joined together to ensure group sizes are large enough to maintain good welfare (Rees, 2009). However, such a recommendation should be approached with caution as herd size does not necessarily ensure compatibility and moving animals together to meet minimum group sizes may be detrimental to individual welfare (Chadwick et al., 2017).

The research by Clubb and Mason (2002) and Harris et al. (2008) was a catalyst for the formation of a multi-stakeholder working group, the Elephant Welfare Group (EWG), a government advisory body set up in 2010. The remit of the group is to “drive forward a programme of improvements, encourage coordination, develop and share husbandry advice and good practice, and monitor progress” (BIAZA, 2018a). The appropriateness of the methodologies employed by Clubb and Mason (2002) have been questioned (Endres et al., 2003; Rees, 2003b, 2009) and the lack of significant causal links between elephant welfare and housing or husbandry by Harris et al. (2008) have been highlighted (Zoos Forum, 2010). However, in the absence of other research these concerns have remained the focus of the EWG, with researchers working to create long-term welfare monitoring systems (Asher et al., 2015; BIAZA Elephant Welfare Group, 2016). Using evidence-based welfare benchmarks to provide optimum care for zoo-housed elephants throughout the world is essential (Meehan et al., 2016b) and the investment by zoos to try and improve facilities and management of zoo elephants is recognised, as too is the long-term nature of many welfare improvements (BIAZA Elephant Welfare Group, 2016). A number of behavioural indicators of welfare have now been identified (Williams et al., 2018b), stakeholder opinion on resources that are essential for elephants to experience good welfare have been recognised (Chadwick et al., 2017) and an understanding of how zoo environments, elephant social lives and management regimes affect zoo elephants has begun to be developed (Greco et al., 2016b). It is now important to build on these works. Priorities which have been identified in terms of behavioural research include identifying methods to assess demeanour, determining the optimal amount of rest in different life stages, understanding more about overnight activity and identifying factors determining social compatibility between elephants (Asher et al., 2015).

2.8.2 Zoo elephant management guidelines

Elephants are classified as a specialist exhibit and therefore have species specific guidelines (Defra, 2012). Details of the current Association of Zoos and Aquariums (AZA) and BIAZA elephant management guidelines are provided in Table 2.3 (Walter, 2010; AZA, 2011). There is some disparity between AZA and BIAZA elephant management guidelines (highlighted in Table 2.3). In brief, AZA guidelines do not focus on minimum contact time for separated cows and they do not detail overnight access or considerations when caring for geriatric elephants. However both sets of guidelines highlight the importance of calf care and the necessity for bulls to be kept without being socially isolated. AZA guidelines specifically detail the need for a social contact programme to ensure they are given appropriate contact with conspecifics. AZA guidelines focus on social management and keeper knowledge requirements, whereas BIAZA guidelines focus on details of hours of access per day and recognise the need to house different ‘types’ of elephant group. Both organisations highlight the importance of multigenerational groups to enable the transfer of

species-typical behaviours through experience and observational learning, suggest a minimum group size of three to four individuals, and recognise that more information is needed to improve the management of bull elephants. Guidelines do not always truly reflect current practice within zoos, with many zoos recognising the need to cater for a range of different types of individual and types of group. This has resulted in zoos adopting tailor made management plans and consideration of elephant needs on a case-by-case basis (Chadwick et al., 2017). There is no clear evidence base as to where some minimum standards in the BIAZA elephant management guidelines were initially developed (e.g., the recommendation of four cows over the age of two years). It has however been suggested that they were largely based on anecdotal rather than scientific evidence, and that they are examples of minimum rather than optimum standards of care (Clubb & Mason, 2002; Barber, 2009). Evidence-based research is now being conducted to help support and develop guidelines (Asher et al., 2015; Meehan et al., 2016b).

Table 2.3. Current American Association of Zoos and Aquaria (AZA) and British and Irish Association of Zoos and Aquaria (BIAZA) elephant management guidelines (Walter, 2010; AZA, 2011)

Section	American Association of Zoos and Aquaria (AZA, 2011)	British and Irish Association of Zoos and Aquaria (Walter, 2010)	Comparison of guidelines
Housing design	Enclosure designs must allow areas where elephants can exercise/socialise together and avoid socialising if/when desired Enclosures must allow for separation during times of incompatibility.	Facilities must retain the potential to separate elephants as required	Lack of recognition in BIAZA guidelines regarding provision of choice Both organisations highlight the importance of being able to separate elephants when required
Preservation of natural behaviour	Must provide a complex physical and social environment which stimulates natural behaviours, social interactions and activity levels resulting in healthy, well-adapted elephants	Social groups must provide for the preservation of 'cultural' and learnt elements of the natural behaviour	Both guidelines highlight the importance of provision of natural behaviour. Only AZA guidelines detail provision of an environment which stimulates such behaviours.
Mixed species	Nothing specifically detailed	African and Asian elephants must not be mixed	No recommendations in AZA guidelines about housing mixed species exhibits
Cows	Minimum three females, two males or three elephants of mixed gender	Must be maintained in as appropriate a group as possible Compatible females should have unrestricted access to each other for not less than 16 in 24 hours Must strive to keep a minimum of 4 compatible cows over 2 years of age	AZA group sizes are slightly smaller than BIAZA group sizes More detail in BIAZA guidelines relating to hours of access and the need to provide appropriate social groups
Bulls	If males are housed, separate facilities for isolation must be available and a programme of social contact must be in place	Bulls should not be kept in physical and social isolation until required for breeding	AZA guidelines provide more detail than BIAZA guidelines about the type of access that should be given to bull elephants

Section	American Association of Zoos and Aquaria (AZA, 2011)	British and Irish Association of Zoos and Aquaria (Walter, 2010)	Comparison of guidelines
	Adult males (6 years and older) may be housed alone, but not in complete isolation. Opportunities for tactile, olfactory, visual and/or auditory interactions must be provided.		Both AZA and BIAZA guidelines recognize the importance of enabling bull elephants to have social contact with others
Calves	Offspring should remain with mothers until they are at least three years old	Calves should be bought up in a herd nucleus	Both AZA and BIAZA highlight the need for young elephants to be bought up in their natal herd. BIAZA places no age limit on this but AZA states until a minimum of three years. Neither organisation recognises the need for the age of separation to be dependent on the individual.
Relatedness	Multigenerational groups should be maintained where possible	Must establish stable female groups, preferably of related individuals	Both AZA and BIAZA highlight the need to house matrilineal groups where possible, in keeping with wild social structures
Geriatric elephants	Nothing specifically detailed	It may be necessary for some collections to specialise as 'retirement homes' for keeping unrelated, non-reproductive, often older females. Must still strive to ensure they have access for 16 out of 24 hours and make every effort to provide a situation where they are a compatible, stable group. Do not need to house four cows.	AZA do not provide specific details on how to deal with geriatric elephants who may not be part of a captive breeding programme
Overnight access	Nothing specifically detailed	Must strive to keep animals in unrestricted social groupings at night	AZA do not provide guidelines for housing elephants overnight. BIAZA highlight the need for provision of unrestricted social groupings.

2.8.3 Catering for elephant social needs

It has been suggested that the main issues encountered by zoos in the care of elephants have been linked to the failure to maintain 'appropriate' social groups (Veasey, 2006). However there is no science behind 'appropriate' social groups in zoos and social housing can affect males and females in different ways (Swaigood & Schulte, 2010). Some researchers highlight the importance of maintaining social groups that replicate the wild environment (Hancocks, 1980), yet others suggest moving away from nature as an optimum standard (Hutchins, 2006). Veasey (2006) stated 'tension and aggression will almost certainly be reduced in related groups that have grown up together'. Socioecological models support relationships between kinship and social behaviour (Hirsch et al., 2012). However research has indicated that non-kin individuals can still maintain successful social relationships in other zoo-housed species. For example, kinship in ring-tailed coatis (*Nasua nasua*) predicts affiliative behaviour networks but not agonistic interactions (Hirsch et al., 2012) and female rhesus macaques maintain stable relationships that are not restricted to kin relatives (Massen & Sterck, 2013). Moreover, very few studies have objectively investigated social interactions in groups of zoo-housed elephants and those that have indicate the possibility of both related and unrelated elephants developing positive relationships (Garai, 1992; Coleing, 2009; Bonaparte-Saller & Mench, 2018; Harvey et al., 2018).

Elephants in zoos experience different stressors to wild elephants and this must be borne in mind when recommendations for social groups are made. Separating wild elephant behaviour from the needs of zoo elephants is an important first step towards maintaining good physical and mental welfare in zoos, but it is important to consider the range of behaviours we might expect wild elephants to display when considering things zoo elephants may need for good welfare. Developing a greater understanding of zoo elephant herd dynamics will enable informed decisions to be made which will be optimal for elephant welfare.

As has been discussed, wild elephants display fission-fusion dynamics, changing group size and structure, with family groups joining together to form bond groups or even clans when resources allow (Moss & Poole, 1983; Sukumar, 1994). For some species such as chimpanzees it is possible to provide an enclosure which allows them the flexibility to change group size and composition, and choosing their range of affiliative partners at will (Clark, 2011; Schel et al., 2013). Within UK and Irish zoo elephant herds this is much more difficult, in terms of the logistics and space required for such an arrangement. When zoo-elephant group sizes become too large for facilities and they are split into smaller herds to start new groups in other zoos the recommendations are that a number of related individuals are moved together, to create a herd nucleus (Walter, 2010). Herd dynamics in zoo elephants are not always consistent over time (Wilson et al., 2006); births (Whilde & Marples, 2012) and deaths (Armstrong, 2015; Cairns pers. comm., 2016) can cause changes to herd structures and social relationships. It is

unlikely that zoo elephant relationships will change as a function of seasonality, as is observed in the wild, because resources are constant within zoos. But there is the possibility that herd dynamics will show some level of fluctuation; relationships may change as animals age and experience hormonal changes as part of their life cycle or as natural changes to group structures (such as births and deaths) occur. A deeper understanding of how elephant social relationships may change over time could help to identify what is the normal range of relationship flexibility in zoo elephant herds and therefore be more able to distinguish the difference between a normal level of fluctuation and potential incompatibilities forming. To date this information is limited about the UK and Irish zoo elephant population, but the addition of this knowledge to current research would be beneficial for elephant welfare.

2.8.4 Elephant coping mechanisms

Animals need to exhibit some level of adaptability in order to cope with ever changing wild conditions. It is thought that species that are most successful within zoos will be those who show high levels of adaptability (Mason, 2010; Mason et al., 2013). Elephants primarily reside in related social groups in the wild; however, they display behavioural plasticity in the form of diverse responses of adult females to unrelated conspecifics. When close relatives are absent, females socialise with elephants outside of their core grouping; grouping with other females lacking kin or with established groups (Gobush et al., 2009). This level of behavioural plasticity in wild environments suggests that elephants, as with other species, have the potential to adapt successfully to zoo environments, as long as their basic needs are being met. Historic research suggested that we could not meet the social needs of elephants in zoos (Clubb & Mason, 2002; Harris et al., 2008), but more recent research is indicative of positive change (BIAZA Elephant Welfare Group, 2016), and there is evidence of recognition of the importance of appropriate social groups for zoo elephants (Asher et al., 2015; Meehan et al., 2016b; Chadwick et al., 2017). Zoo elephants have been observed to show behavioural change over time (Wilson et al., 2006); the opportunity to enable elephants to alter social interactions and relationships through the provision of free choice is paramount in allowing them to cope with changing social conditions over time.

2.8.5 Changes to practice and future research

There is an ever-increasing body of research and ongoing large-scale projects are being undertaken to help to assess and continually improve the welfare of zoo-housed elephants around the world (Asher et al., 2015; Meehan et al., 2016b). Recent recommendations for changes to Secretary of State's Standards of Modern Zoo Practice (SSSMZP) guidelines in the UK have included more emphasis on social compatibility and additional, more extensive, guidelines for keeping bull

elephants (Asher et al., 2015). Keepers and researchers have highlighted the importance of caring for elephants on an individual basis (Asher et al., 2015; Chadwick et al., 2017). Zoo elephant stakeholders have suggested that a number of social factors influence elephant welfare: group size (Gurusamy et al., 2014), relatedness, group composition and individual compatibility (Chadwick et al., 2017). Following a large-scale epidemiological study, US scientists suggested that in order to improve well-being, zoo-housed elephants should spend time in larger, stable social groupings which include both juveniles and adult elephants, and reducing time in social isolation (Meehan et al., 2016a). No specifics were provided in relation to minimum group size. Changes are constantly being made in elephant housing as knowledge of their needs improves through evidence-based research (Zoos Forum, 2010; BIAZA Elephant Welfare Group, 2016). In order to further improve understanding of social interactions in zoo-housed elephants, further research should focus on trying to identify factors affecting social interactions in elephants. For example, whether relatedness or familiarity are most important to relationships and to identify whether there are any other social needs, such as a critical mass or necessary age structure. Investigation should also be made of how relationships may change over time. These areas for future study will be addressed in Chapters Four, Five and Six of this thesis. It remains unclear whether we can meet the needs of elephants in zoos but ongoing welfare assessment should continue to be incorporated into standard practice, to capture subtle changes in individual welfare, for long-term and evidence-based decisions.

2.8.6 Effects of the zoo environment on elephants

The principal effects of the zoo environment on elephant social groups can be summarised as (i) reduced opportunity to express wild-type behaviour, (ii) inclusion in breeding programmes leading to forced changes in herd structures and (iii) micro management of social groups. As has been highlighted, it is vital to further understand the effects of the zoo environment on elephant social groups and the demographics of social groups on herd dynamics, as this will have a direct impact on their individual welfare.

2.8.6.1 Reduced opportunity to express wild-type behaviour

Despite the lack of need for elephants to retain knowledge transfer within zoos, they retain strong social relationships and so catering for these is important for individual welfare. Bull housing in zoo elephants is difficult, and elephant management guidelines in respect to managing bulls are still vague (outlined in Table 2.2). Inappropriate group composition has been highlighted as an area of welfare concern in UK and Irish elephant herds (Zoos Forum, 2010). Elephants require the opportunity for social interactions, which enables the development of close social bonds between individuals, and provides opportunity for appropriate learning and development, especially when

young (Chadwick et al., 2017). There may be an intrinsic link between performance of stereotypic behaviours and social factors (Greco et al., 2017), so it is imperative that elephants are provided with appropriate and complex social opportunities.

2.8.6.2 Inclusion in breeding programmes: changes in herd structures

African and Asian elephants are part of the EEP captive breeding programme (EAZA, 2018). The EEP produces a plan, based on demographical and genetic analyses, for future management of elephants in zoos, and provides recommendations to participating institutions (EAZA, 2019). Although elephants have relatively low rates of inter-zoo transfers (Prado-Oviedo et al., 2016), in order to enable successful captive breeding some transfers are still required. Transfers between zoos can be detrimental to welfare; female Asian elephants show decreased survivorship for up to four years post-transfer (Clubb et al., 2008) and the process of transportation has been linked with signs of poor welfare such as reduced lying and increased cortisol (Laws et al., 2007). Beyond the stress of the transfer itself, removal from herds and reintroduction to new herds can have a serious impact on individual welfare, even if temporary. Although not believed to be prolonged or severe, transfer and introduction to new elephant herds can cause elevated stress levels in zoo elephants (Schmid et al., 2001), with highest levels of stress occurring in the days immediately following introduction (Dathe et al., 1992; Laws et al., 2007). Breakdown of social bonds may be detrimental to individual welfare. However, elephant reintroductions between familiar individuals might promote positive welfare so it may be important to investigate familiarity between individuals prior to undertaking transfers (Evans, 2014). Introducing unrelated and unfamiliar individuals may lead to potential problems if individuals are incompatible. Although relatively little work has investigated the effect of births or deaths on the behaviour of zoo-housed elephants, evidence suggests these events affect herd dynamics and interactions (Whilde & Marples, 2012; Armstrong, 2015).

2.8.6.3 Micro-management of social groups

Within US zoos, elephant herds are sometimes closely managed with access to social partners restricted by husbandry and management programmes (Meehan et al., 2016a). Meehan et al. (2016a) noted that US zoo elephants sometimes spend their time in multiple social groups, whereby elephants share unrestricted space during the course of normal social management. Instead of all elephants at a facility spending their time as a single herd they were more frequently managed in various group sizes and compositions; some individuals were a member of up to 30 unique social subgroups within a facility, depending on management schedules, elephant characteristics or other factors (Meehan et al., 2016a). This close management of groups may be preventing elephants from associating with their preferred social partners; as was evidenced by Schmid (1995) who found that when shackled elephants were allowed to spend

time in paddocks they associated more frequently with individuals that were not a chain neighbour. This practice is not so prevalent in UK and Irish zoos, where guidelines highlight the importance of access to other elephants and separation of any animals must be justified (Walter, 2010; Defra, 2017). Extensive management further removes the element of choice from an elephant's behavioural repertoire and limits the opportunity for making and sustaining social bonds within zoos. Lack of physical interaction does not suggest that conspecific companionship is not important for zoo elephants (Mueller et al., 2013). Indeed, researchers suggest that the opportunity to spend time in the vicinity of conspecifics is also important for welfare (Stoinski et al., 2000). Factors driving choice of social partners in zoo elephants are unknown, but choice of social partner and the opportunity to contact all individuals in the herd is of paramount importance to elephant welfare (Schmid, 1995). Therefore, zoos should be seeking to give elephants 24-hour access to conspecifics (Wilson et al., 2006; Asher et al., 2015), and to be further understanding factors that are driving social partner choice.

2.9 Conclusion

Social interactions in wild elephants are integral to their strong social structure and, in turn, their survival. Interactions differ between African and Asian elephants, and this is believed to be due to differences in their natural habitats. Factors that enhance social relationships in wild elephants (e.g. migrating over long distances to find food, entering new environments and experiencing extensive habitat variation and predator defence) are not present in zoos and thus these behaviours may have become redundant for zoo elephants. The disparity between wild elephant herds and those in zoos highlights the need for further information on factors driving social interactions in zoo elephant herds, when the environmental factors encountered in the wild are void. There is variability in elephant social housing between zoos. However, the drive to house socially compatible and where possible, related and sustainable populations is a shared long-term goal. At this current time, there is a need to house three types of groups in UK and Irish zoos: related individuals who form principally breeding herds; surplus breeding bulls; and non-breeding, potentially unrelated, individuals. These groups all have different social needs and it is imperative that elephants' needs are catered for on an individual basis. Long-term concerns over the welfare of elephants around the world led to the development of active working groups such as the BIAZA Elephant Welfare Group in the UK. Following long-term research projects, important large-scale changes are being seen in elephant keeping, with enhanced recognition of elephant needs. Research is fuelling recommendations to changes in elephant keeping guidelines, which will continue to improve the welfare of zoo elephants. Despite this there is still relatively little known about what factors are affecting how elephants interact within zoos and precisely what the needs of zoo elephants are.

High-profile research reports in the early to mid-2000s stated that UK and Irish zoo elephants were experiencing poor welfare, and highlighted inappropriate social housing as an area of concern. However, elephant husbandry and welfare is constantly evolving and marked changes have been observed in elephant housing and management since 2002. Recent work has highlighted the importance of social behaviour in elephant welfare assessment and social variables have been linked with changes of welfare state in zoo elephants. There is a limited understanding of social behaviour in zoo elephants. However, in order to make evidence-based suggestions to changes to social grouping aspects of elephant management guidelines, it is imperative to investigate how individual (e.g. personality) and zoo-level (e.g. age structure) factors are affecting social interactions in elephants. In order to improve animal welfare in zoos we must first develop a greater understanding of the motivations behind their choices. It has been suggested that a means of understanding and improving welfare in zoo-housed animals is to compare living and social conditions, to establish if there are any behavioural differences between animals living in different environments. This work builds on this concept, by looking at collections of zoo elephants in the UK and Ireland to try to identify demographic factors which may be affecting social interactions and dyadic relationships.

2.10 Research Aim and Objectives

2.10.1 Aim

This research provides a detailed investigation into social interactions and herd dynamics in zoo-housed African and Asian elephants in UK and Irish zoos. The aim of this research was to identify and investigate social group factors affecting social interactions, and begin to understand whether individual personalities affect social relationships.

2.10.2 Objectives

To fulfil this aim, the following four objectives were set:

- Objective 1: to evaluate the degree to which social management of elephants in UK and Irish zoos complies with relevant elephant management guidelines
- Objective 2: to determine if elephant social relationships are stable over time
- Objective 3: to identify whether a relationship exists between zoo elephant personalities and social interactions
- Objective 4: to identify whether there is a relationship between herd demographics and elephant social interactions

The potential impacts of the zoo environment on social behaviour in elephants have been identified and reviewed. In the remainder of the thesis, changes to elephant social groups from 2002 to 2017 will be investigated and considered in light of updates to elephant management guidelines (Chapter Three). The remaining three data chapters will investigate factors affecting social interactions in UK and Irish zoo-housed elephants and consider the degree to which the needs of elephants are able to be fulfilled within zoos.

CHAPTER 3

Social housing of elephants in UK and Irish zoological collections from 2002 to 2017: investigating change

3.1 Introduction

Elephants are highly intelligent and socially complex (Rees, 2009), which makes it difficult to cater for their needs in zoos (Harris et al., 2008). In the wild elephants live in complex social groups (Rees, 2009) (reviewed in Chapter Two). Two high profile studies have been undertaken to look at elephant welfare in European zoos (summarised in Table 3.1). In 2002, it was suggested by the Royal Society for the Protection of Cruelty to Animals (RSPCA) that it is not possible to adequately meet welfare requirements of elephants in UK and Irish zoos, and so zoo elephants should be phased out of UK and Irish zoological collections (RSPCA, 2002). This statement was based on research by Clubb and Mason (2002). In 2006, researchers at the University of Bristol undertook a survey across UK and Irish zoos and highlighted more problems with elephant welfare (Harris et al., 2008). A number of key welfare concerns related to social conditions were highlighted by these authors and these are detailed in Table 3.1. Both reports, despite being recognised as important, were criticised by researchers (Rees, 2003b, 2009), government advisory bodies (Zoos Forum, 2010) and elephant groups (European Elephant Group (Endres et al., 2003) and the BIAZA elephant welfare group (BIAZA Elephant Welfare Group, 2016). Nevertheless these two early reports led to a number of processes that ultimately led to changes in government policies, and were the catalyst for a plethora of subsequent research undertaken to document and improve the welfare of zoo-housed elephants throughout the UK and Ireland, under the umbrella of the BIAZA EWG (BIAZA Elephant Welfare Group, 2016).

The report published by Harris et al. (2008) was reviewed by the Zoos Forum, a government advisory body. Concerns were such that the Government Animal Welfare Minister, Lord Henley, suggested that measurable improvements must be seen in elephant care or the UK and Ireland should look to phase elephants out of zoos. He requested the development of an independent elephant advisory group, to advise upon, encourage and monitor progress with husbandry and welfare improvements. The Zoos Forum committee stated that the advisory group should be established by, and report to the Department for Environment, Food and Rural Affairs (Defra), working in cooperation with, and through BIAZA, thus ensuring independence of decisions (Zoos Forum, 2010). The independent group was to include zoo specialists but also others with a wider expertise, which would work under direction from the Parliamentary Under Secretary of State for Rural Affairs and Biosecurity. Expertise was to include other elephant, veterinary, reproductive biology, statistics and animal welfare specialists (BIAZA, 2018a). The aim of the multi-stakeholder group was to ensure that decisions made by the UK government on the future of elephants in UK and Irish zoos would be based on evidence and not opinion. The BIAZA EWG works in conjunction with the Elephant Focus Group (EFG) and external researchers to ensure systems are achievable and repeatable for elephant keepers (BIAZA Elephant Welfare Group, 2016). The EFG, previously the elephant Taxon Advisory Group (TAG), concentrates principally on practical

aspects of elephant husbandry and welfare, and includes members of all of the elephant-holding zoos in the UK and Ireland (Zoos Forum, 2010). The BIAZA EWG was set up in 2010 with the remit of 'driving forward a series of improvements in the welfare and care of elephants in UK zoological collections' by conducting strategic research (Zoos Forum, 2010; BIAZA Elephant Welfare Group, 2016). The BIAZA EWG consists of four subgroups, each of whom are undertaking research to document and improve welfare in UK and Irish zoo elephants. Welfare monitoring systems are now in place for foot care, locomotion, body condition scores and behaviour (Asher et al., 2015; BIAZA Elephant Welfare Group, 2016).

This chapter provides an analysis of changes in elephant keeping since 2002. Changes in social housing in terms of group structure are reviewed and discussed in light of concurrent changes in elephant management guidelines. As part of this process an overview is provided of early concerns in elephant keeping with a specific focus on meeting their social needs. The chapter concludes with a summary of development of the elephant management guidelines and recommendations for changes to guidelines going forwards, in order to continue to optimise elephant welfare. This chapter has additionally provided a context and highlighted need for the remainder of the work undertaken as part of this thesis which will be presented in subsequent chapters, in order to further understand elephant social requirements and apply these findings to help secure positive welfare for elephants in zoos.

Table 3.1. An overview of the main publications that have highlighted areas of concern in elephant keeping in UK and Irish zoos since 2002

Report	Commissioned by	Aims	Key findings (relating to social groups)	Validity concerns	Outcome	Critique
Clubb & Mason (2002)	RSPCA	<p>To identify welfare problems associated with keeping elephants in captivity</p> <p>To scientifically identify relationships between such problems and elements of elephant husbandry</p> <p>To make sound, ethically based recommendations for improving welfare of captive elephants</p>	<p>Concerns relating to welfare: unnatural social groupings, small social groups or in some instances social isolation, lack of relatedness or stability in social groups, a lack of adult males, relative rarity of young calves, rarity of older animals, under representation of a range of age classes in facilities and a probable lack of relatedness</p> <p>Suggestion arising: not possible to adequately meet welfare requirements of elephants in UK and Irish zoos. Zoo elephants should thus be phased out from UK and Irish zoological collections (RSPCA, 2002)</p>	<p>Some statements were unfounded and no detailed data were provided to support arguments (Endres et al. 2003)</p> <p>Analysis was undertaken on outdated and/or incorrect data (Endres et al. 2003)</p> <p>Described as “a poorly informed publication of ‘scientific proof’” and presented in a misleading manner (Endres et al. 2003)</p> <p>Report based on anecdotal evidence and extrapolations from other mammalian species (Rees, 2003b)</p> <p>Available data, which was subsequently used in the report, may have masked ‘complex’ situations (Rees,</p>	<p>Formed the basis for many subsequent investigations into the welfare of elephants in UK and Irish zoos, ultimately leading to changes in government policies to protect zoo elephants and improve their future welfare</p>	<p>This report was a catalyst for important future research but there are some methodological concerns in the approach. The report was funded by an animal welfare charity and so there was the potential for bias. The report was based on secondary data, and as was pointed out by Rees (2003b) this was quite limited in its scope. Historical data sets may not be representative of current situations (Zoos Forum, 2010) and there were queries over the appropriateness of the welfare indicators chosen for the review. For example, reproductive/survival problems. One cow could kill one calf but successfully raise another, without any clear reason as to why. Thus this kind of data may have masked situations which were potentially complex (Rees, 2003b). Finally, the application and generalisation of findings from</p>

Report	Commissioned by	Aims	Key findings (relating to social groups)	Validity concerns	Outcome	Critique
				<p>2003b)</p> <p>Report produced based on inaccurate data (Rees, 2009)</p> <p>Data used to calculate survival rates were historical, and potentially not representative of advances in husbandry practices and veterinary medicine (Zoos forum, 2010)</p>		<p>four zoos (three in the UK and one comparative study at a US sanctuary) may not be a genuine representation of facilities throughout Europe and so whilst this work is important it must be interpreted with some caution.</p>
Harris, Sherwin & Harris (2008)	Defra	<p>To provide objective, independent data on the welfare of elephants in UK and Irish zoos</p> <p>Explore some of the research suggestions made by Clubb and Mason (2002)</p> <p>Establish current practices and</p>	<p>Concerns related to atypical social groups; herds skewed towards higher numbers of young individuals and mature bulls lacking from the population</p>	<p>Lack of statistically significant causal links between welfare concerns highlighted and housing or husbandry (Zoos Forum, 2010)</p> <p>Results did not provide any evidence for steps which should be taken to tackle areas of welfare concern (BIAZA Elephant Welfare Group, 2016)</p>	<p>Reviewed by the Zoos Forum (government advisory body) which then led to the attached actions</p>	<p>This study was undertaken in a larger number of facilities than the work undertaken by Clubb and Mason (2002) however the short time spent at each study zoo may have led to conclusions that were still based on fairly limited data. Concerns related to inappropriate social groups were highlighted; however there were a lack of causal links between welfare concerns and housing or husbandry routines at the time</p>

Report	Commissioned by	Aims	Key findings (relating to social groups)	Validity concerns	Outcome	Critique
		facilities which were most associated with better or poorer welfare in the current UK zoo elephant population				(Zoos Forum, 2010). Furthermore, whilst this study again highlighted areas for concern and thus was another step towards the subsequent development of the Elephant Welfare Group (EWG) the authors did not produce any recommendations of how to tackle highlighted problems (BIAZA Elephant Welfare Group, 2016) and so was limited in its practicality.
Zoos Forum (2010)	Defra	To review the report filed by Harris, Sherwin & Harris (2008) and the results of other studies relevant to zoo elephant welfare to help consider and make recommendations about the way forward for elephant keeping in the UK and Ireland	Vigorous and concerted action is needed to address problems seen in zoo elephants, which it should be possible to find solutions for Suggestion arising: If solutions to welfare problems and threats cannot be found, if no or negligible evidence of improved health and welfare can be observed, and if there is no compelling reason to	No validity concerns were published about this report. This report was an analysis of the report filed by Harris et al. (2008) and no new data were presented. Recommendations were to more thoroughly investigate problems that had been previously reported in elephants, and developed evidence-based solutions for areas of concern.	Establishment of an independent Elephant Advisory Group Addition of a section in the SSSMZP guidelines to make species specific husbandry requirements regarding the keeping of elephants A review of	This report did not analyse new data, rather it was a review of the research undertaken by Harris et al. (2008) and a discussion of this in light of other elephant welfare literature. Difficulties and current welfare problems associated with elephant keeping in the UK and Ireland were highlighted. A number of options for the future were presented, and the practicality of the options discussed. Outcomes arising from this report, e.g. the setting up of an independent Elephant Advisory Group; the Elephant Welfare

Report	Commissioned by	Aims	Key findings (relating to social groups)	Validity concerns	Outcome	Critique
			breed elephants in the UK then zoos should take steps to stop keeping elephants		progress in ten years' time (2020), with an interim review in five years' time (2015) (BIAZA Elephant Welfare Group, 2016)	Group (EWG) and subsequent evidence-based research and implementation of long-term welfare assessment tools have been positive for welfare of elephants in the UK and Ireland. Documentation of changes in welfare state in relation to changes in routines or enclosure design will lead to the development of evidence-based mitigation strategies to optimise elephant welfare moving forwards. Development of a logical approach to tackling problems within a fixed time-scale (with the caveat that if problems could not be solved decisions needed to be made as to the appropriateness of elephants in UK and Irish zoos) was an important and rational option in this field.

3.1.1 Elephant management guidelines

In 2002, BIAZA released the first elephant management guidelines, hereafter 'guidelines', to counter the fact that there was not a comprehensive widely-used manual collating standards and best practice in elephant care (Stevenson, 2002). A summary of the guidelines related to social management of elephants from 2002 to 2017 is provided in Table 3.2. This first set of guidelines provided a brief overview of wild elephant behaviour and made basic recommendations for zoo elephant care (Stevenson, 2002). Although an important initial document some researchers have suggested that recommendations were not based on a particularly strong evidence base (Asher et al., 2015). The 2002 guidelines were superseded by a second edition in 2006 (Stevenson & Walter, 2006), and a third edition in 2010 (Walter, 2010). The 2010 guidelines were designed to provide an update in light of recently published research (Walter, 2010). At the time of survey and subsequent analysis of data presented in this chapter, the most recent guidelines, the SSSMZP, were updated in 2012 (Defra, 2012). The terminology has changed since 2002, but the overarching concepts remain consistent: zoos should be aiming to maintain related, family groups with a minimum group size of four individuals. In contrast to later editions, there was no reference to social compatibility in the 2002 guidelines. Instead, initial guidelines (2002 and 2006) advocated replication of wild-type social group structures. In 2010, the first recognition of social compatibility was made (Walter, 2010). The 2010 guidelines stated that there may be a necessity for collections to act as specialist retirement homes for unrelated, non-reproductive, older females. If zoos were catering for the needs of these types of individuals, then it was suggested they did not need to house four adult cows (Walter, 2010).

Changes to guidelines are based on a wealth of strategic research being conducted by elephant keepers and researchers (Zoos Forum, 2010). Since the BIAZA EWG was set up in 2010 evidence-based studies have been undertaken at UK and Irish zoos to provide sound scientific evidence in support of, or recommending amendments to, current practice (Asher et al., 2015; Chadwick et al., 2017; BIAZA, 2018a). Following a review of peer reviewed literature and consultation with expert stakeholders, Asher et al. (2015) suggested a number of evidence-based changes to the SSSMZP guidelines including a focus on social compatibility and additional criteria for bull elephants. The idea of investigating the potential for bachelor herds was highlighted in the 2002 and 2006 guidelines, although in both instances bull elephants were still described as being 'comparatively unsociable' and guidelines did not extend beyond the recognition that bulls should not be housed in social isolation (Stevenson, 2002; Stevenson & Walter, 2006). The third edition of the guidelines (2010) saw the introduction of a section on bachelor herds, but at this point it was still a discussion section and there was recognition that the feasibility of keeping bulls in bachelor herds in UK and Irish zoos had still not been explored. In the wild mature bull elephants are not as antisocial as prevailing theory suggested (Stoeger & Baotic, 2016); research has indicated that they

develop strong relationships with other males and come together to form bachelor herds outside of the mating season (Chiyo et al., 2011; O'Connell-Rodwell et al., 2011).

Table 3.2. An overview of elephant management guidelines from 2002 to 2017: British and Irish Association of Zoos and Aquaria (BIAZA) 2002 (Stevenson, 2002), 2006 (Stevenson & Walter, 2006) and 2010 (Walter, 2010), and Secretary of States Standards of Modern Zoo Practice (SSSMZP) Appendix 8 (Defra, 2012).

Section	BIAZA 2002	BIAZA 2006	BIAZA 2010	SSSMZP 2012
Herd size	Minimum group size should be four cows older than 2 years	Must strive to keep a minimum of four compatible cows over 2 years		Should be at least four female elephants over 2 years
	Breeding herds should be allowed to grow to a 'critical mass'. Suggested size: five to ten animals.			
Herd stability	Must establish stable female groups, preferably of related individuals	If not keeping a bachelor herd zoos must establish female groups, preferably of related animals	Must establish stable female groups, preferably of related individuals	
Access to others	As far as possible, elephants, especially females, should be maintained in social contact with other elephants			Females must have social contact with other elephants at all times
		Compatible females should have unrestricted access to each other for not less than 16 in 24 hours		
	Animals should be kept in social groupings at night		Must strive to keep animals in unrestricted social groupings at night	
	Must be possible to separate bulls from females and other males during musth			Bulls should be run with the herd whenever possible
	Bulls must not be kept in social isolation until required for breeding			Not acceptable to subject bulls to prolonged physical and social isolation

Section	BIAZA 2002	BIAZA 2006	BIAZA 2010	SSSMZP 2012
Appropriate groups and social learning	Must be maintained in as appropriate social group as possible			Matriarchal herds should be the norm
	Social units must provide for the preservation of 'cultural' and learnt elements of the natural behaviour			
	African and Asian elephants should not be mixed			
	Calves should be brought up in a matriarchal group			
	Generally bulls should be removed from the herd during adolescence			Young bulls may benefit from the presence of older adult males
Non-family groups	Feasibility of keeping bulls in bachelor herds should be explored		It may be necessary for some collections to specialise as 'retirement homes' for keeping unrelated, non-reproductive, often older females. Must still strive to ensure they have access for 16 out of 24 hours and make every effort to provide a situation where they are a compatible, stable group. Do not need to house four cows	Zoos which keep unrelated, non-productive, older or problem elephants should comply with standards

Two recent large scale research projects, one in the UK and Ireland (Asher et al., 2015) and one in the US (Meehan et al., 2016b) provided more detailed recommendations on elephant needs. The welfare of elephants in UK and Irish zoos has been described by elephant keepers and other elephant experts as being most influenced by the following social factors: group size, relatedness, and compatibility (Chadwick et al., 2017). An appropriate group size enables variety in terms of group composition and increased opportunities for social interactions. Benefits of relatedness include opportunity for natural social group interaction, close social bonds and opportunity for learning. However, the importance of compatibility has been stressed, especially when catering for individuals who may have no known relatives (Chadwick et al., 2017). An epidemiological study conducted in the US found that good welfare in zoo elephants was supported simply by spending more time in larger, stable social groups that included both juvenile and adult elephants, and reducing time spent alone (Meehan et al., 2016b).

The zoo environment is not static and changes and improvements are constantly being made (Harris et al., 2008). Research into the needs of elephants is ongoing and zoos are making many changes that are leading to substantial improvements in elephant keeping (BIAZA Elephant Welfare Group, 2016). This chapter and thesis focuses on concerns surrounding the social needs of elephants because it is an important area that has been highlighted as requiring further investigation (Asher et al., 2015). Furthermore, elephant keepers have highlighted the importance of providing for elephant social needs (Chadwick et al., 2017). The aim of this chapter is to investigate changes in social housing of elephants in UK and Irish zoos from 2002 to 2017 and to evaluate the extent to which zoos are now meeting the social needs of elephants as set out in the elephant management guidelines.

3.2 Methods

Details of elephants kept in UK and Irish zoos were gathered from five data sources at four time points between 2002 and 2017: (1) 31.12.2002 European Elephant Group (EEP) Survey 2002 (Endres et al., 2003), (2) 01.11.2006 EEP Survey 2006 (Endres et al., 2006), (3) May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012), (4) 30.04.2017 Zoological Information Management System (ZIMS) records. All of these data sources provided accurate details of Asian and African elephants at European zoos and safari parks at the time of their production.

Levels of compliance with guidelines were calculated by investigating the number of facilities that met each specific criterion. If data were not available to investigate the guideline it was recorded as 'no data'. For example, the guideline that 'generally bulls should not be removed from the herd during adolescence' could not be calculated because it was not possible to determine the age of individual animals when they were moved from the herd using studbook data. Moreover, in some instances, conditions were not measurable, so these were recorded as 'not measurable'. For example, the guideline the 'feasibility of keeping bulls in bachelor herds should be explored' was a recommendation that could not be investigated using the numerical data available. Level of compliance was thus calculated for data pertaining to the remaining recommendations: herd size, age of individuals, relatedness, number of calves held in natal groups, number of retirement homes and number of mixed species herds. In order to calculate compliance with these recommendations the following data was gathered at each survey point: number of collections and number of elephants (African elephants/Asian elephants/mixed); median herd size (total/African elephants/Asian elephants/mixed); number and mean age of captive bred and wild elephants; number of elephants at their natal zoo; ratio of males:females overall and ratio of males:females at each zoo; age structure and age structure at each zoo; number of elephants housed with at least one relative; number of elephants and proportion of facilities for different relatives (e.g. housed with sibling, housed with parent, housed with offspring, etc). Where possible and appropriate data were split into study zoo, species and sex for analysis.

For the purposes of analysis of herd structure elephants were grouped into five age categories: calves (0 to 2 years), infants (3 to 4 years), juveniles (5 to 9 years), sub-adults (10 to 15 years) and adults (16 years and older), based on research on Asian elephants by Kurt (2005). Inferential statistical analysis was not considered necessary for the desired outcome of this data set (i.e. to provide a meaningful overview of how elephant social groups had changed in relation to guidelines) so the results presented refer to descriptive statistics only.

3.3 Results

Data were gathered from a median of 15 elephant holding collections (range 13 to 15) over the four time points (2002, 2006, 2011/2012 and 2017). The number of collections holding elephants was lowest in 2006 (n=13), at all other years it was 15. The number of elephants in total was highest in 2002 (n=88) and lowest in 2017 (n=69). Detailed breakdowns of the results are provided in the sections below.

3.3.1 Herd size

Collections housing African elephants remained constant at 7, however collections housing Asian elephants ranged from 6 to 8, generally increasing over the 15-year period. A summary of demographic data detailing the breakdown of number of collections and number of elephants housed is provided in Table 3.3. For the first two time periods one facility held a mixture of African and Asian elephants (one of each). Median herd size across all survey points was 4 individuals (range 1 to 15). When data were separated into zoos and safari parks there was little difference in herd sizes across the survey years, although zoos showed more variation than safari parks when data were separated into survey years (Figure 3.1). Median herd size ranged from 3 to 5 individuals in zoos and was 5 individuals in safari parks. Median herd size (inter-quartile range) across all survey points was 4 (2-8) for zoos and 3 (3-4) for safari parks.

Table 3.3. A breakdown of the number of collections and number of elephants housed in UK and Irish zoos at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

Survey year	Number of collections				Number of elephants		Median* herd size (Range)			
	Total	African	Asian	Mixed	African (Male.Female)	Asian (Male.Female)	Total	African	Asian	Mixed
2002	15	7	7	1	46 (11.35)	42 (10.32)	5 (2 – 15)	5 (2 – 15)	5 (3 – 9)	2 (one herd)
2006	13	7	6	1	38 (10.28)	32 (5.27)	4 (2 – 12)	6 (3 – 12)	4 (3 – 9)	2 (one herd)
2011-2012	15	7	8	0	35 (8.27)	37 (6.31)	4 (1 – 14)	4 (1 – 14)	4 (1 – 8)	0
2017	16	7	8	0	28 (7.21)	41 (8.33)	4 (1 – 13)	4 (1 – 13)	5 (1 – 10)	0

*Rounded to the nearest whole number

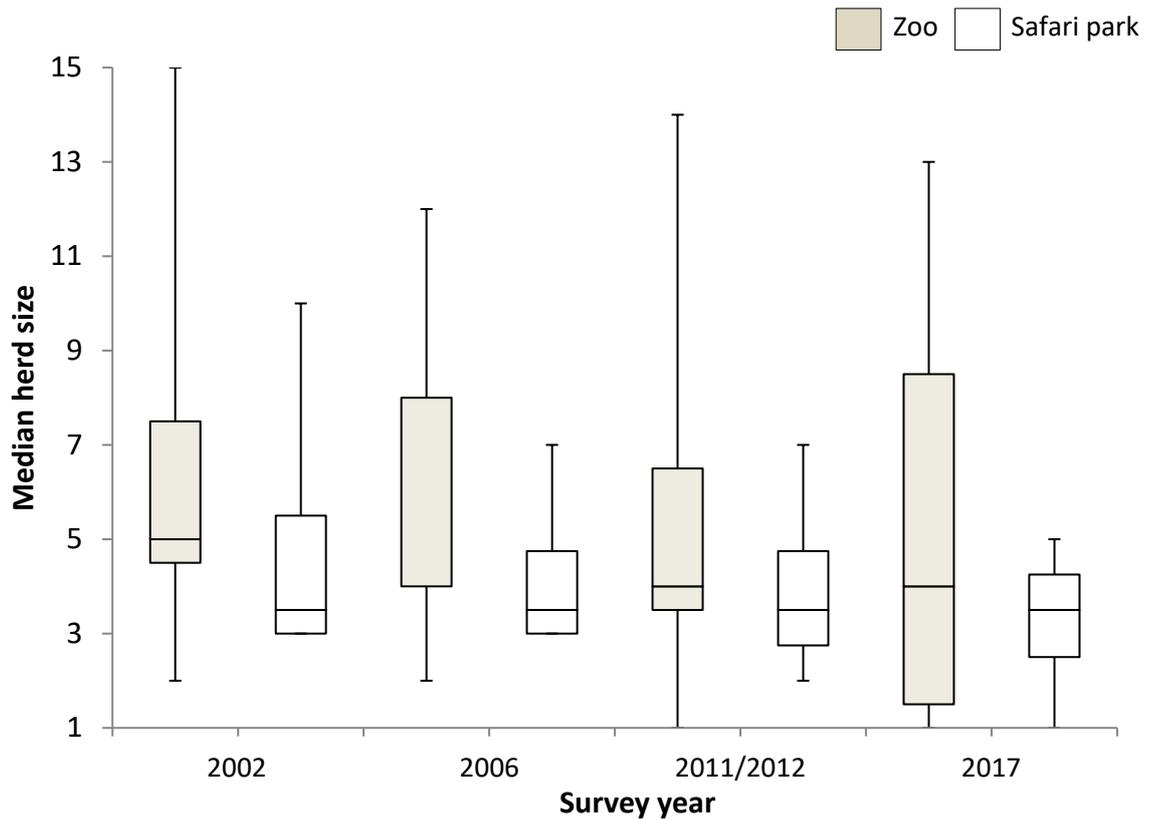


Figure 3.1. Median herd size of elephant groups housed in UK and Irish zoos at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

3.3.2 Origin of individuals

The number of zoo born elephants generally increased over the four survey points; ranging from 34 in 2002 to 45 in 2017, although the smallest population was in 2006 (n=32). The number of wild born individuals decreased over time; numbers reduced by more than half from 54 in 2002 to 24 in 2017. Over the survey period (2002 to 2017) four wild-caught elephants were transferred into the population from other non-UK/Irish collections, 17 elephants died and a further 17 were transferred to other non-UK/Irish collections. Wild born elephants were on average older than zoo born elephants (Table 3.4).

Of those individuals that were zoo born, the number housed at their natal zoo at the survey points increased from 15/34 (44%) in 2002 to 29/45 (64%) in 2017. The number of male elephants housed at their natal zoo fluctuated, but ranged from 5/11 (45%) to 6/10 (60%) in 2006. The number of female elephants housed at their natal zoo increased each year from 8/19 (42%) at the first survey point to 22/32 (69%) at the final survey point (Table 3.5).

Table 3.4. Demographic data detailing number and age of zoo born and wild born elephants housed in UK and Irish zoos at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

Survey Year	Average age (years)						Number					
	Zoo born			Wild born			Zoo born			Wild born		
	Male	Female	Combined Mean±SD (Range)	Male	Female	Combined Mean±SD (Range)	Male	Female	Combined	Male	Female	Combined
2002	10	12	11±8.7 (<1 to 34)	18	25	24±9.4 (9 to 47)	15	19	34	6	48	54
2006	6	12	10±9.1 (<1 to 38)	19	29	27±9.2 (13 to 51)	10	22	32	5	33	38
2011/2012	8	13	12±10.1 (<1 to 43)	29	35	34±9.2 (19 to 59)	11	27	38	3	31	34
2017	9	14	12±11.2 (<1 to 49)	34	38	38±9.1 (24 to 65)	13	32	45	1	23	24

Table 3.5. Number of zoo born elephants housed at their natal zoo in UK and Irish zoos at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

Survey year	Number housed at natal zoo/number zoo born		
	Total	Male	Female
2002	15/34	7/15	8/19
2006	18/32	6/10	12/22
2011/12	20/38	5/11	15/27
2017	29/45	7/13	22/32

3.3.3 Sex ratios and age structures

There were fewer male than female elephants at all survey points, with a mean ratio of 1:4 (male:female) (2002: 1:3.2; 2006: 1:3.7; 2011/12: 1:4.1; 2017: 1:3.6). Four of the 17 collections did not hold elephants at all of the survey points. Across the 17 collections, at the points they did hold elephants, one herd held only male elephants and five held only female elephants. The remaining 11 held a mixed herd at some point (Figure 3.2). Elephants ranged from 2 months to approximately 65 years old (Figure 3.3). A summary of male and female age structures over time is provided in Figure 3.4. Over 50% of the surveyed population each year were adult elephants, aged 16 and over. The number of calves, infants, juveniles and sub-adults fluctuated (Figure 3.3) but the male:female ratio across age categories remained relatively consistent (Figure 3.4). At the adult age category there were considerably fewer males than females at all survey points, with a mean ratio 1:8.4. Three collections only housed adult elephants. All of the other collections had at some point housed elephants from two or more age categories. Eight of the surveyed facilities had held calves within the population during the survey points. Two had calves at all four survey points.

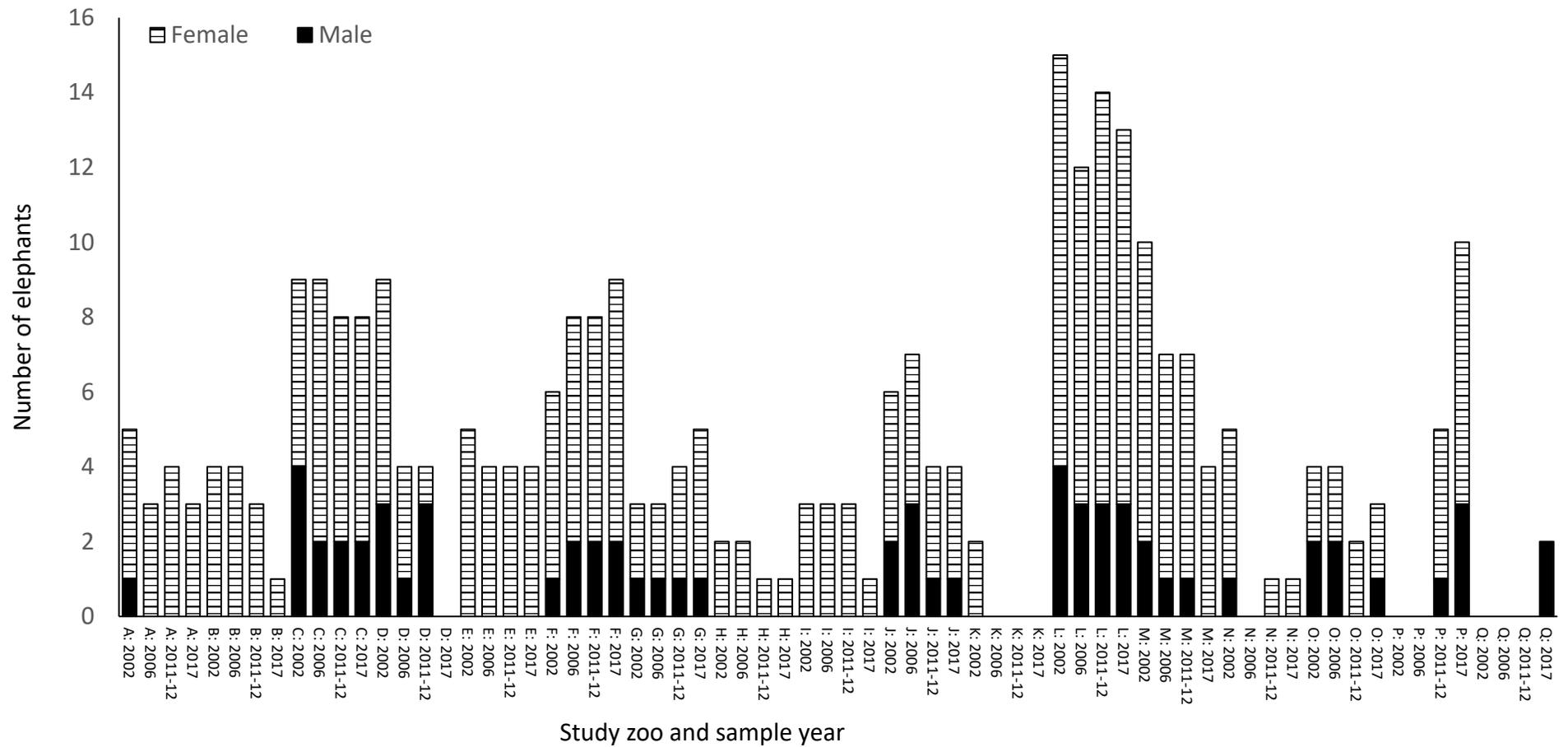


Figure 3.2. Number of male and female elephants in individual UK and Irish zoos (labelled A – Q) at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

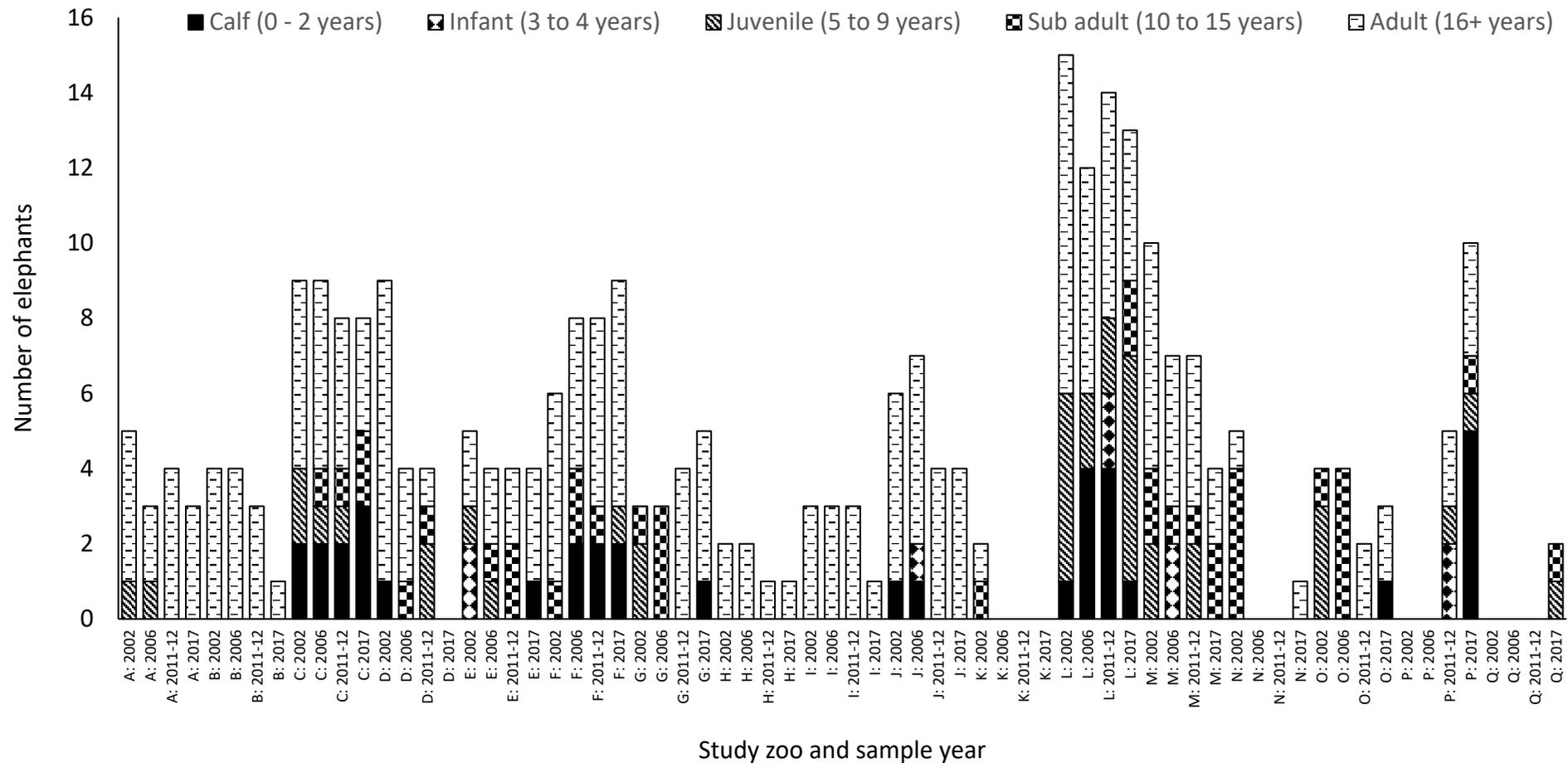


Figure 3.3. A breakdown of age structures of elephants housed in UK and Irish zoos (labelled A – Q) at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

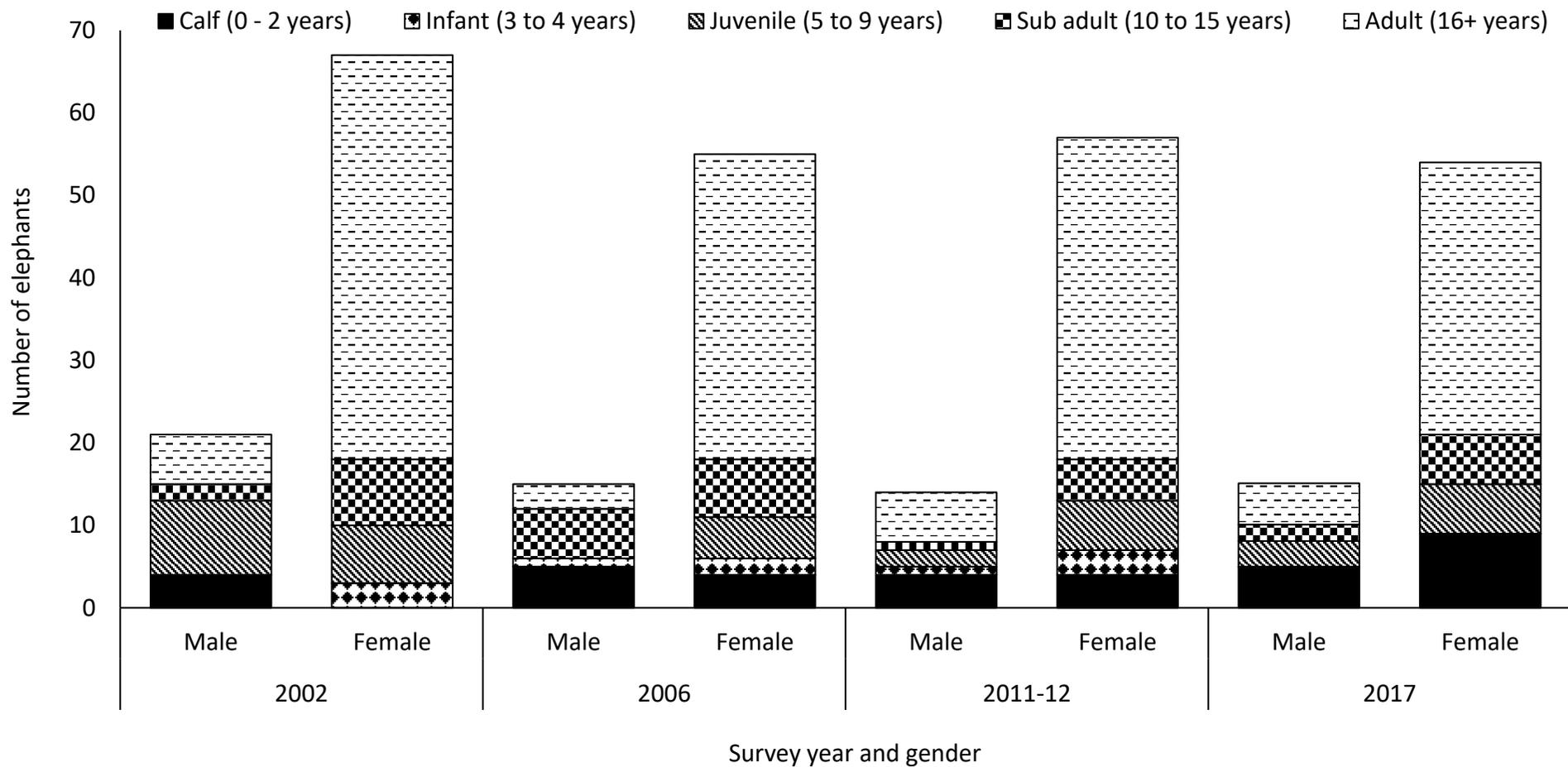


Figure 3.4. A breakdown of the number and age of male and female elephants in UK and Irish zoos at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

3.3.4 Relatedness

Relatedness did not necessarily mean the herds were of a structure similar to wild elephant herds. The number of elephants housed with at least one relative increased from 31/88 (35%) in 2002 to 44/69 (64%) in 2017 and the proportion of male and female elephants housed with at least one relative was greatest in 2017; 11/15 (73%) and 33/54 (61%) for male and female respectively. The number of female elephants housed with at least one relative more than doubled from 20/67 (30%) in 2002 to 33/54 (61%) in 2017 (Table 3.6). This mirrors the increase in females housed at their natal zoo. The number of collections housing elephants with at least one relative increased from 6/15 (40%) in 2002 to 8/13 (62%) in 2006. In 2017 this reduced to 8/15 (53%). A breakdown of the number of elephants housed with relatives is provided in Table 3.7.

Table 3.6. Demographic data detailing number of individuals housed with relatives in UK and Irish zoos at four time points between 2002 and 2017. Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

Survey year	Male with relative/ total number of males	Female with relative/ total number of females
2002	11/21	20/67
2006	10/15	28/55
2011/12	10/14	27/58
2017	11/15	33/54

Not all collections housed multi-generational breeding herds. Herds were considered to be non-breeding if they were same sex herds with no history of young elephants at the four data collection points, or if the zoo had publicly advertised themselves as non-breeding. In 2002, there were four, non-breeding all female herds (4/15). In 2006, this had reduced to three (3/13) before increasing to five (5/15) in 2011-12. 2017 saw the introduction of an all-male herd, at this point there were six same sex herds in the UK and Ireland; one bachelor herd (1/15) holding two young males, and five all-female adult herds (5/15). All of the all-female adult herds described themselves as retirement homes for unrelated non-breeding females.

Table 3.7. Demographic data detailing elephant relatedness in UK and Irish zoos at four time points between 2002 and 2017 (number of elephants/facilities out of total elephants/facilities). Data sources: 31.12.2002 EEP Survey (Endres et al., 2003); 01.11.2006 EEP Survey (Endres et al., 2006); May 2011 Asian elephant studbook (Van Wees & Belterman, 2011) and 31.05.2012 African elephant studbook (Schwammer & Fruehwirth, 2012); 30.04.2017 Zoological Information Management System (ZIMS) records

Year	With relative		With father		With mother		With offspring		With maternal sibling		With paternal sibling	
	No. elephants	No. facilities	No. elephants	No. facilities	No. elephants	No. facilities	No. elephants	No. facilities	No. elephants	No. facilities	No. elephants	No. facilities
2002	31/88	6/15	9/88	4/15	15/88	6/15	17/88	6/15	4/88	2/15	15/88	3/15
2006	38/70	8/13	11/70	4/13	19/70	8/13	20/70	8/13	6/70	1/13	18/70	6/13
2011/12	37/72	7/15	13/72	3/15	20/72	6/15	16/72	5/15	13/72	3/15	26/72	6/15
2017	44/69	8/15	12/69	4/15	24/69	8/15	20/69	8/15	17/69	3/15	28/69	5/15

3.3.5 Compliance with guidelines

Calculated compliance with the guidelines is summarised in Table 3.8. Six criteria were either not measurable (e.g. ‘must be maintained in as appropriate social group as possible’) or were not measurable using the data collected during this study (e.g. ‘must strive to keep animals in unrestricted social groupings at night’). Level of compliance of zoos was assessed against the remaining criteria.

Table 3.8. A review of levels of compliance of UK and Irish zoos with social management recommendations detailed in the British and Irish Association of Zoos and Aquaria (BIAZA) and Secretary of States Standards of Modern Zoo Practice (SSSMZP) Appendix 8 elephant management guidelines at four survey points from 2002 to 2017 (Sources: Stevenson, 2002; Stevenson & Walter, 2006; Walter, 2010; Defra, 2012)

Section	Stevenson (2002)		Stevenson & Walter (2006)		Walter (2010)		Defra (2012)	
	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance
Herd size	Minimum group size should be four cows over 2 years old	10/15 facilities compliant	Must strive to keep a minimum of four compatible cows over 2 years old	7/13 facilities compliant	Must strive to keep a minimum of four compatible cows over 2 years old	5/15 facilities compliant	Should be at least four female elephants over 2 years old	5/15 facilities compliant
	Breeding herds should be allowed to grow to a 'critical mass'. Suggested size: five to ten animals.	9/15 housed 5 or more individuals, one housed more than 10	Breeding herds should be allowed to grow to a 'critical mass'. Suggested size: five to ten animals.	5/13 housed 5 or more individuals				
Herd stability	Must establish stable female groups, preferably of related individuals	31/88 elephants with relatives, 6/15 of facilities house related individuals	If not keeping a bachelor herd zoos must establish female groups, preferably of related animals	38/70 elephants with relatives, 8/13 of facilities house related individuals	Must establish stable female groups, preferably of related individuals	37/72 elephants with relatives, 7/15 of facilities house related individuals	Cows in stable groups, preferably related	44/69 elephants with relatives, 8/15 of facilities house related individuals
Access to others	As far as possible, elephants, especially females, should be	None lone housed*	As far as possible, elephants, especially females, should be	None lone housed*			Females must have social contact with other elephants at all times	No data

Section	Stevenson (2002)		Stevenson & Walter (2006)		Walter (2010)		Defra (2012)	
	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance
	maintained in social contact with other elephants		maintained in social contact with others					
			Compatible females should have unrestricted access to each other for not less than 16 in 24 hours	No data	Compatible females should have unrestricted access to each other for not less than 16 in 24 hours	No data	Cows should have unrestricted access to other elephants for not less than 16 in 24 hours	No data
	Animals should be kept in social groupings at night	No data			Must strive to keep animals in unrestricted social groupings at night	No data		
	Must be possible to separate bulls from females and other males during musth	No data					Bulls should be run with the herd whenever possible	No data
	Bulls must not be kept in social isolation until required for breeding	None lone housed*	Bulls must not be kept in social isolation until required for breeding	None lone housed*	Bulls should not be kept in physical and social isolation until required for breeding	None lone housed*	Not acceptable to subject bulls to prolonged physical and social isolation	None lone housed*

Section	Stevenson (2002)		Stevenson & Walter (2006)		Walter (2010)		Defra (2012)	
	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance
Appropriate groups and social learning	Must be maintained in as appropriate social group as possible	Not measurable	Must be maintained in as appropriate social group as possible	Not measurable	Must be maintained in as appropriate social group as possible	Not measurable	Matriarchal herds should be the norm	8/15 facilities
	Social units must provide for the preservation of 'cultural' and learnt elements of the natural behaviour	Not measurable	Social units must provide for the preservation of 'cultural' and learnt elements of the natural behaviour	Not measurable	Social units must provide for the preservation of 'cultural' and learnt elements of the natural behaviour	Not measurable		
	African and Asian elephants should not be mixed	14/15 facilities	Asian and African elephants must not be mixed	12/13 facilities	Asian and African elephants must not be mixed	15/15 facilities	African and Asian species must not be mixed	15/15 facilities
	Calves should be brought up in a matriarchal group	5/5 calves housed with natal group	Calves should be brought up in a matriarchal group	9/9 calves housed with natal group	Calves should be brought up in a herd nucleus	8/8 calves housed with natal group	Calves must be brought up in matriarchal group	14/14 calves housed with natal group
	Generally bulls should be removed from the herd during adolescence	No data					Young bulls may benefit from the presence of older adult males	19/23 bulls aged 9 or below housed

Section	Stevenson (2002)		Stevenson & Walter (2006)		Walter (2010)		Defra (2012)	
	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance	Guideline	Compliance
								with an adult bull
Non-family groups	Feasibility of keeping bulls in bachelor herds should be explored	Not measurable	Feasibility of keeping bulls in bachelor herds should be explored	Not measurable	It may be necessary for some collections to specialise as 'retirement homes' for keeping unrelated, non-reproductive, often older females. Must still strive to ensure they have access for 16 out of 24 hours and make every effort to provide a situation where they are a compatible, stable group. Do not need to house four cows	5/15 zoos retirement homes. None in groups of four or more. 1/15 zoos housed a lone elephant.	Zoos which keep unrelated, non-productive, older or problem elephants should comply with standards	5/15 zoos retirement homes. None in groups of four or more. 4/15 zoos housed a lone elephant.

*No facilities held just a single elephant but it was not possible to ascertain from the available data whether or not any elephants were lone housed

As can be seen in Table 3.8, common areas of non-compliance were: related matriarchal female herds and minimum group sizes. The number of elephants housed with at least one relative increased over time, however a number of individuals had no known relatives within the population. Some of these individuals were housed in a social group with other unrelated elephants, some were housed with family herds and two were lone-housed. One of the lone-housed females had recently lost another group member (March 2016). The other was lone-housed for safety as she is blind; the elephant with which she was previously housed died in March 2010. The number of zoos keeping a minimum of four cows over the age of two years halved from 10/15 (67%) in 2002 to 5/15 (33%) in 2017. Both of these areas of non-compliance reflect the need to house a range of individuals, and the steps zoos are taking to cater for individual elephant needs. Common areas of compliance were: no African and Asian elephant mixed species exhibits, no lone-housing of individuals and calves being brought up in their natal groups. For the first two survey points one facility housed both an African and Asian elephant, from 2010 onwards all zoos were compliant with this guideline. Calves (aged 2 years and below) were always housed in their natal herd and in 2012, when the guideline was first documented, the majority of bulls aged nine and under were housed with an adult bull. No collections housed a single adult bull over the survey points, but the data did not show the number of hours per day in which the bull had the opportunity for physical contact with the rest of the herd; it is however likely that this varied between collections.

3.4 Discussion

The data presented in this chapter represent changes to the UK and Irish zoo elephant population over time. Guidelines have been developed, with more recent editions providing evidence-based recommendations for best practice. Median herd size over time was five elephants, with an average ratio of 1 male: 4 females. There was a dramatic and important increase in elephants housed with at least one relative, from 31/88 (35%) in 2002 to almost double 44/69 (64%) in 2017. The most common herd type in 2017 was breeding herds. The guidelines are only recommendations for elephant keeping, and levels of compliance across the assessed criteria varied over time. Areas of compliance were no mixed African and Asian species exhibits, no lone housing of individuals (no facilities held just a single elephant but it was not possible to ascertain from the available data whether or not any elephants were lone housed) and calves bought up in their natal group. Areas of non-compliance were related herds and minimum group size of four or more cows over the age of two years. This finding represents the need to house a range of individuals with unique backgrounds and social needs, not just related females and their young, and that these requirements are recognised by zoos.

To the authors' knowledge this chapter provides the first review of elephant social housing in UK and Irish zoos since the high-profile report by Clubb and Mason (2002). A number of key changes that have not been previously documented arose from this analysis, and these have been highlighted and discussed. These changes indicate that the way we are keeping elephants is showing positive change, but that a greater understanding of social structures within herds is still required, in order to proactively manage social groups to optimise individual and group welfare.

Recommendations for changes to the guidelines are detailed in Table 3.9. These principally include the recognition of the need to house different types of social groups and acknowledgment of the importance of social compatibility, including understanding how to document social compatibility. After the completion of the data analysis for this chapter an update to the SSSMZP guidelines was released (Defra, 2017). Important updates related to social factors were the implementation of long-term management plans both for the collection and for individual elephants, including ongoing behavioural and health assessments and the creation of behavioural profiles. These are discussed in further detail, and comparisons are made between recommendations for change arising from this chapter and actual updates to the SSSMZP guidelines (Section 3.4.5, Table 3.9). The updated data provided in this chapter is evidence that zoos are focusing on catering for elephants on an individual basis. Recent updates to management guidelines are also indicative of the focus and importance zoos are placing on caring for elephants on an individual basis.

3.4.1 Herd size

Inappropriate herd sizes were highlighted as an area of concern in 2002 (Clubb & Mason, 2002). However, results from this study showed that, on average, herd sizes were in line with the lower end of figures reported for wild elephant groups (Moss & Poole, 1983; Sukumar, 2006). Keeping a minimum group size of four or more cows over the age of two years was an area of low-compliance at all survey points, ranging from 10/15 zoos compliant in 2002 to 5/15 compliant in 2017. For the first two survey points, there were no lone-housed elephants. In 2012, one adult female was lone-housed following the death of a conspecific. By 2017 this figure had risen to four adult females; one imported ex-circus elephant and three following conspecific deaths. No bulls were housed in a zoo alone. However, no data were available on how long they had access to other elephants.

The presence of other elephants is considered to be the most effective enrichment for zoo-housed elephants (Rees, 2000); social environments can be used to promote positive welfare in managed groups (Meehan et al., 2016a). Herd size has been identified as one of the most important issues for welfare of elephants in zoos (Gurusamy et al., 2014). However, herd sizes may be constrained by the logistic challenges of keeping large groups of elephants (Veasey, 2006); this

critical mass is recognised in the guidelines (Stevenson, 2002; Stevenson & Walter, 2006). The importance of not keeping elephants in social isolation, especially from a young age, is well documented (Kurt & Garai, 2001; Clubb & Mason, 2002; Stevenson, 2002; Stevenson & Walter, 2006; Walter, 2010; Meehan et al., 2016b; Chadwick et al., 2017). However, whilst this point is undisputed, elephant keepers have suggested that concentrating solely on a recommended fixed number of elephants may be detrimental to individual welfare and thus compatibility is of greater importance than a minimum group size when identifying suitable social housing arrangements for female elephants (especially those who have had a difficult upbringing or been housed in zoos for many years) (Chadwick et al., 2017).

It is important to note that the data presented here do not allow investigation of number of hours elephants are separated. Elephants were only considered lone-housed if only one elephant was in the collection. However, there is the possibility that elephants were separated during routine husbandry and management. Current guidelines state that cows should have unrestricted access to each other for no less than 16 in 24 hours, and zoos should be striving to ensure that animals are kept in unrestricted social groupings overnight (Defra, 2012). In order to gather such data a questionnaire would need to be sent to all of the elephant-holding zoos in the UK and Ireland. Data for this chapter was gathered using readily accessible sources and so this information could not be ascertained at this time. Further research should be conducted to identify how many elephants in the UK and Irish population are periodically lone-housed within collections, in order to identify the true number of lone-housed elephants. There is no evidence of whether lone-housed elephants (in single institutions) would be socially compatible for future group housing, although this is likely to be affected by individual experiences and personalities.

The findings presented here on changes in herd size suggest that zoos are not mixing social groups to meet an arbitrary minimum group size, rather they are looking at individual elephant and individual herd requirements; growing breeding herds naturally and mixing only compatible elderly elephants in retirement herds where appropriate. Whilst it is important to maintain elephants in a herd size that enables and encourages appropriate, species-typical, social interactions, it is paramount that individual elephant needs are assessed and prioritised to ensure good welfare. Transporting elephants and introducing them to new groups can induce behavioural and physiological indicators of reduced welfare both temporarily and more long-term e.g. reduced resting behaviour and increased levels of faecal corticoid metabolites (Schmid et al., 2001; Laws et al., 2007). It is not yet clear whether integrating lone-housed individuals into other larger groups, or merging multiple small groups together would be detrimental. Elevated levels of agonistic interactions within an elephant herd, arising from incompatibilities, may be a cause of chronic stress and therefore poor welfare in affected individuals (Harvey et al. 2018). Further

research should investigate the potential for changes in short- and long-term welfare state when small elephant groups or individuals are combined to create larger groups.

3.4.2 Origin of individuals

The number of captive-bred males remained consistent whilst the number of females increased over time. The number of wild-caught elephants declined. The decrease in number of wild caught elephants is reflective of BIAZA and European Association of Zoos and Aquaria (EAZA) policy. Neither organisation permits the import of wild-caught animals into their member institutions (EAZA & BIAZA, 2017), and thus, as would be expected, wild-caught elephants are becoming older and less frequent within the population as they are phased out of collections naturally via mortality. The last wild-caught elephants to come direct to a UK or Irish zoo were imported in 1998. The increased number of captive-bred individuals suggests that breeding programmes are successful in UK and Irish collections. 2017 also saw the greatest number of female calves in the population, which suggests successful breeding within zoos. Researchers consider reduced reproductive success to be a sign of poor welfare (Broom, 1991). This increased breeding of young in the population is indicative of appropriate and stable social groups (Carlstead & Shepherdson, 1994). This finding has great importance because it suggests that the UK and Irish zoo elephant population are self-sustaining. Whilst elephants in UK and Irish zoos are not bred for reintroduction to the wild, researchers have indicated previously that European elephant populations are not sustainable (Rees, 2003a). A self-sustaining zoo population affects the sustainability of the zoo elephant population and suggests that if good welfare can be guaranteed there is a potential for the zoo elephant population to thrive.

3.4.3 Sex ratios and age structures

The age range of elephants increased but the mean age of the population remained relatively consistent. Captive bred individuals were on average younger than wild elephants. The ratio of male:female elephants across all age categories remained consistent over time, despite the fluctuation in overall population size. The ratio was largest at the adult age category (16 years and over), with relative equality seen in numbers of male and female elephants up until 16 years old. Eight of the surveyed collections had held at least one calf at the survey points; two had held calves at all of the four survey points.

The increasing age range over time with maintenance of a consistent average age is indicative of the presence of older elephants within the population. This may suggest that elephants are living longer than first thought, but it may also indicate the persistent presence of calves and younger individuals, who are a product of breeding programmes. Analysis of data from 2006 shows that six collections had elephants from three or more of the five age categories and of

those that did not, none housed calves or infants. This suggests that the concerns voiced by Harris et al. (2008) that there was a lack of multi-aged herds in 2006 was unlikely to be such a concern. The skewed sex ratios observed in the study at the adult age category is to be expected due to the nature of housing adult bulls. Whilst reports suggest that young bulls benefit from being housed with adult bulls, it is rare for more than one adult bull elephant to be housed in a collection at the same time unless in a bachelor herd, due to the specialised needs of bulls (Defra, 2017). Social bonding and group formation in reintroduced wild elephants is related to the presence of calves (Thitaram et al., 2015), however large numbers of young elephants in social groups are thought to potentially be causing a lack of social stability (Harris et al., 2008). Further research should seek to identify the position of calves within social networks, to investigate their effects on group structure. This will be investigated in Chapter Six.

3.4.4 Relatedness

In 2017, 7 out of the 15 collections had at least one calf/infant in the herd. However, only one herd was a multi-generational family herd comprising only related cows, their young and a breeding bull. A setup that was more commonly observed were collections comprising one or more breeding cows and their young, plus one or more unrelated individuals. In some instances, the breeding cows were related and the herd was multi-generational, but in others it was a number of unrelated mothers with their offspring. The number of elephants housed with at least one relative increased over time. There was a greater proportion of male than female elephants housed with at least one relative at all survey points; this finding is representative of both the number of retirement homes for unrelated female elephants, and the presence of breeding bulls with multiple offspring in some collections.

Males housed with a relative increased from 11/21 (52%) in 2002 to 11/15 (73%) in 2017. Although this is not broken down into sex or age classes, it is likely that the majority of those elephants were calves or infants, as bull elephants are moved away from family herds at sexual maturity or when their behaviour becomes disruptive to the herd (McKenzie pers. comm., 2015). This finding therefore indicates the increased housing of young with older bulls, which is important for social learning, especially in bull calves (Evans & Harris, 2008). No collections housed a single adult bull over the survey points, but the data did not show the number of hours per day in which the bull had the opportunity for physical contact with the rest of the herd; it is however likely that this varied between collections. This would be a very important area for further investigation as bulls having access to the rest of the herd is considered by elephant keepers 'essential' for elephant welfare (Chadwick et al. 2017).

The proportion of captive bred elephants that continued to be housed at their birth zoo fluctuated over time for males but steadily increased for females. This increase of related

individuals in zoo herds has great importance. The 2012 SSSMZP guidelines state that female elephants should stay with their natal herd for life, unless the herd reaches a maximum carrying capacity (Defra, 2012), in which case a number of related females should be moved together to start a new herd. The increase in females remaining at their birth zoo indicates that, for elephants born in more recent years, this guideline is being adhered to. This has importance for welfare because zoo transfers may decrease survivorship in female Asian elephants (Clubb et al., 2008).

Housing female elephants in related, multi-generational breeding herds, akin to their wild social structure is a recommendation that has persisted in the guidelines (Stevenson, 2002; Stevenson & Walter, 2006; Walter, 2010; Defra, 2012). As the data from this study reveals, this recommendation should be split into two parts: i) housing females in related units, and ii) facilitating breeding herds. This is because in some instances, females in breeding herds are completely related, but this is not always the case. Whilst it is considered difficult to keep elephants in social groups that mimic the wild, due to space requirements and a need to house unrelated elephants in the zoo population, this is an area which has seen considerable and important change. The increased frequency of related elephants being housed together in the last 15 years is representative of the phasing out of wild-caught individuals (whose relatives may be unknown) and the success of breeding programmes. Perceived benefits to housing elephants in related groups include: improved welfare, increased opportunities for learning and decreased social tension (Walter, 2010).

Early reports highlighted a probable lack of relatedness as an area of welfare concern, because it may result in a lack of formation of strong social bonds in zoo elephants (Clubb & Mason, 2002). However, evidence from literature on both zoo (Garai, 1992; Evans, 2014) and wild (Nyakaana et al., 2001; Charif et al., 2005; Poole & Moss, 2008) populations suggests that this concern may be unfounded as kinship is not the only determinant of social bonds; unrelated individuals can successfully join other herds or create their own herds. Investigation of compatibility was not possible from this data set but the presence of successful breeding in herds that contain unrelated individuals is indicative of successful social groups. Kinship amongst elephant groups has been identified as a 'gold standard' in elephant keeping (Stevenson 2002; Stevenson & Walter, 2006; Harvey et al. 2018). However, as these results show, there are some potentially unrelated elephants in the current zoo population. To provide zoo-housed elephants with appropriate social groups the weight of value of kinship relationships must be identified, as a means of assessing compatibility and predicting factors which will enhance compatibility. This will be investigated in further detail in Chapter Six.

3.4.5 Recent updates to elephant management guidelines

The purpose of this chapter was to investigate changes in elephant management in terms of social groups since 2002. In doing so this chapter provides a context for the research being undertaken and highlights potential areas for more research and/or change in the management guidelines in order to continue to improve zoo elephant welfare. Data for the chapter was updated and the chapter subsequently completed on 30.04.2017. Since this chapter was completed Defra have released updated SSSMZP elephant management guidelines (Defra, 2017). Therefore, it is prudent to include a brief summary of the revised guidelines and consider them in light of the recommendations for change arising from this data chapter. An overview of recommendations arising from this research and comparison with actual changes to the elephant management guidelines are provided in Table 3.9.

Table 3.9. A comparison of recommendations for future research/change to 2012 Secretary of States Standards of Modern Zoo Practice (SSSMZP) Appendix 8 elephant management guidelines arising from data analysed in this chapter and updated 2017 SSSMZP elephant management guidelines (Defra, 2017)

Recommendations for future research/ change to guidelines from current research	New 2017 elephant management guidelines (Defra, 2017)
Recognise the need to house three social group types: <ul style="list-style-type: none"> • Breeding herds • Bachelor herds • Non-breeding (unrelated) herds 	Implementation of long-term management plans for each collection including the purpose of the collection and compatibility details
Provide a means of assessing compatibility and predicting factors which will enhance compatibility. Identifying compatible animals will help to maximise the likelihood of long-term social compatibility	Creation of individual elephant plans including ongoing behavioural and health assessments and behavioural profiles
Understand the value of kinship relationships	

It is important to note that data on elephant keeping reflects the point of time that the research was undertaken and may not directly reflect the social group in which elephants are currently housed. Recommendations arising from this chapter were that the need to house specific social groups should be recognised and guidelines developed accordingly. Guidelines should begin to highlight the importance of group social compatibility, and researchers and UK and Ireland zoo governing bodies should be looking to identify reliable ways to assess compatibility and understand more the value of kinship relationships to individual elephants. Two important developments have been included in the 2017 guidelines that relate to social management of elephants and also support the recommendations arising from this chapter. First, there is now the requirement for inclusion of a long-term management plan for each collection. Within this plan it should include what the purpose of the collection is (and thus what type of group they intend to house) and herd

compatibility details. There is also the inclusion of an individual elephant plan including ongoing behavioural and health assessments and behavioural profiles, with the behavioural profiles contributing directly to informing herd compatibility (Defra, 2017). Behavioural profiles include qualitative assessments of behaviour, along with daytime and night-time activity using a suite of behavioural indicators of welfare as reference points (Asher et al. 2015). Behavioural indicators incorporated measures of engagement with the social and physical environment, occurrence of affiliative and agonistic behaviour, performance of stereotypies and resting behaviour (Asher et al., 2015; Yon et al., 2019). Health assessments include locomotion, body condition and foot health scoring (BIAZA Elephant Welfare Group, 2016). The inclusion of ongoing welfare assessments into the SSSMZP management guidelines is a recent addition and so at this point it is not possible to accurately assess whether they are working. However, as these are detailed in SSSMZP guidelines they are now included in inspections carried out as part of zoo licencing protocols. Zoo licencing inspectors refer to current SSSMZP management guidelines when undertaking site inspections. Elephant holding zoos are expected as part of their compliance with the Zoo Licensing Act 1981 to provide evidence in support of or achieving the SSSMZP standards. When standards are not met, zoo inspectors will assess justifications or circumstances of mitigations (Defra, 2017). Formal inclusion of such measures in the guidelines is very important in the process of continuously optimising zoo elephant welfare moving forwards.

3.4.6 Catering for elephant needs

There are considerable challenges when attempting to provide zoo elephants with social groups that replicate the wild and there is no clear recommendation as to the appropriateness of this approach for individuals. Requirements are likely to vary according to individual experiences (Zoos Forum, 2010), which is important to recognise in order to promote positive welfare for all individuals. This chapter illustrates the need to house three groups: related individuals who form principally breeding herds; surplus breeding bulls; and non-breeding, potentially unrelated, individuals. Most recent guidelines recognise the need to house these types of social group and have highlighted the importance of ongoing welfare assessment and identification of socially compatible animals. Evidence-based welfare assessments have been produced to facilitate this goal (BIAZA Elephant Welfare Group, 2016; Yon et al., 2019). These new steps will play an important part in improving zoo-elephant welfare. However, more work still needs to be undertaken to maximize the likelihood of the formation of a long-term socially-compatible group. In recent years, large scale projects have been undertaken to identify, amongst other things indicators of welfare and elephant social needs, including group size, relatedness, composition, individual compatibility, age range and time spent in social groupings (Gurusamy et al., 2014; Asher et al., 2015; Meehan et al., 2016a; Chadwick et al., 2017).

Guidelines have developed over time, and so too has the way in which elephants are kept in UK and Irish zoos. The data presented in this chapter indicate that some of the concerns raised in early reports may not have been an accurate reflection of the situation. Furthermore, they highlight the ongoing important changes that have been made since 2002 and are continuing to be made. It is clear from consultation with keepers (Chadwick et al., 2017) and the implementation of ongoing forms of welfare assessment (Yon et al., 2019) that elephant welfare is at the forefront of decision making in UK and Irish zoos and that elephant care will hopefully continue to evolve in light of evidence-based recommendations arising from research. Zoo elephant social interactions have been identified as a potential indicator of welfare (Williams et al., 2018b) and they are one of a number of measures that have been incorporated into the long-term behavioural assessment of elephant welfare protocols now included in the SSSMZP guidelines (Yon et al., 2019). In order to gather further information and contribute towards the recommendations provided in the new guidelines, there must be a continuous, ongoing cycle of documented research and evidence-based recommendations to help zoos to create and maintain socially compatible elephant herds. Understanding how herd demographics may be influencing compatibility will help to understand more about zoo elephant social relationships and allow zoos to cater for their needs. As is now recognised in the most recent guidelines, due to the low number of elephants housed in UK and Irish zoos it is not unreasonable to suggest that future management plans should be considered on an individual basis to cater for the social needs of individual elephants (Defra, 2017).

3.5 Conclusion

Since 2002 there have been three editions of the BIAZA elephant management guidelines and two updates to the SSSMZP appendix for elephant care. Revisions to management guidelines have been based on evidence-based scientific research and the most recent guidelines include the requirement of regular welfare monitoring by zoos, not just as part of periodic welfare audits by zoo inspectors. Important changes include the recognition of the need to house a range of individuals and more extensive guidelines for bull elephants. Elephant keeping in terms of herd demographics has also shown changes over time, although levels of compliance with elephant management guidelines have been variable since 2002. The male:female demographic remained largely consistent over the survey periods, whilst the number of elephants housed with at least one relative increased over time. Areas of non-compliance were related herds and minimum group size of four or more cows over the age of two years. These areas of non-compliance are not necessarily an area of concern. Rather they are indicative of the drive by zoos to cater for elephant needs on an individual elephant or individual herd basis, looking at individual circumstances and maximising individual welfare, rather than bringing elephants together to meet arbitrary minimum group sizes. They represent the need to house a range of individuals with unique backgrounds and social needs,

and crucially, indicate that these requirements are recognised by zoos, which is something that other research involving keeper interviews has also found. This chapter has highlighted the variability encountered when looking at social housing in UK and Irish zoo elephants and has identified important changes in guidelines over time. Recommendations arising from the chapter included the need to recognise three distinct types of social group: breeding herds, bachelor herds and non-breeding herds, and ensure good welfare for the different groups according to individual needs. Other recommendations included the need to understand the effect of kinship on relationships and to assess compatibility in elephant herds to help to improve welfare. After the data had been analysed for this chapter SSSMZP elephant management guidelines were updated. The most recent edition included the need to identify the purpose of the collection and implementation of long-term behavioural and health assessments to assist in individual elephant plans for improved welfare. Frameworks are in place to assess elephant welfare through the study of behaviour and physical health, but further information still needs to be gathered on the social needs of zoo elephants for this to reach full potential. Understanding how herd demographics are affecting social behaviour will add to the growing scientific evidence-base which is allowing research-fuelled changes to be made to policies. Understanding how different herd structures and herd demographics affect elephant social relationships will help to identify social groups which will promote optimum social welfare. A greater understanding of the effect of herd demographics and individual personalities on social interactions (a measure of welfare in zoo elephants) are provided in Chapters Four, Five and Six.

3.6 Chapter summary

The results from this chapter have highlighted the variability encountered when looking at social housing in zoo-housed elephants in the UK and Ireland, and have identified important changes in management guidelines over time. Furthermore, this chapter has identified a need for further information on the social needs of zoo-housed elephants; to inform future guidance and improve elephant welfare by enabling research-fuelled changes to policy. Further investigations into the social needs of zoo-housed elephants will be undertaken in Chapters Four, Five and Six through the collection of primary data.

CHAPTER 4

**Zoo elephant relationships:
monitoring changes in herd interactions over time**

4.1 Introduction

4.1.1 Background

Social groups and the opportunity to engage in social interactions and develop friendships can benefit animals in a number of ways, including cooperation to achieve common goals, enhancement of physical and psychological well-being and enhanced reproductive output (Massen et al. 2010). Sociability is defined as the reaction of an individual to the presence or absence of conspecifics; sociable animals will seek the presence of others whereas unsociable animals will avoid conspecifics (Reale et al., 2007). An animal's level of sociability, their 'friendships' or relationships can be assessed via proximity to others (Silk et al. 2013; Bonaparte-Saller & Mench, 2018) or through physical interactions (Silk et al. 2013). Tactile behaviour is an important part of the maintenance of social relationships in several mammalian species (Yasui & Idani, 2017). Social grooming in primates can be used to establish and maintain affiliative bonds (Cooper & Bernstein, 2000) and pectoral fin contact in bottlenose dolphins is used to establish, maintain and manage inter-individual relationships (Dudzinski & Ribic, 2017). In elephants, tactile behaviour has been recognised as important (Vidya & Sukumar, 2005a) and is used to reinforce social bonds, communicate information and provide comfort in times of stress (Poole & Granli, 2011; Plotnik & de Waal, 2014).

Wild elephants engage in fission-fusion relationships, with group size and structure changing over time. This changing social structure is thought to be driven predominantly by ecological factors and resource availability in wild African elephants, whilst drivers of social group change are believed to be social factors in Asian elephants (Moss & Poole, 1983; Archie et al., 2006; de Silva & Wittemyer, 2012; Fishlock & Lee, 2013). Individuals in fission-fusion societies frequently change groups, but there remains some level of persistence in social affiliations in even the most fluid societies (Rubenstein et al., 2015). Social ties in Asian elephants are generally weaker than those seen in African elephants. However, despite this the majority of individuals will maintain a few strong and consistent ties (de Silva et al. 2011). Female Asian elephants do not engage in completely random interactions, rather they 'shuffle' amongst a set of preferred companions with individual variation at the dyadic level. Long-term fidelity to companions is variable but stability at the population level is indicative of some long-term stable associations (de Silva & Wittemyer, 2012). Wild African elephants show variability in social structures over time, but interactions are non-random. That is, the most basic social groups (families) are composed of stable, tightly associated groups (Wittemyer et al., 2005). During the dry season social cohesion decreases, which is believed to be related to the reduced capacity of the environment in terms of support of larger groups (Moss & Poole, 1983; Vance et al. 2009). However, the different tiers of organisation seen in African elephant herds (family groups, bond groups and clans) are affected to different degrees (Wittemyer et al., 2005). Social networks of African elephants are far more

interconnected than the Asian elephant networks; each individual is more closely connected to more individuals by fewer steps than in the Asian elephant network (that is, associates of a female African elephant are more likely to be associated with one another than associates of a female Asian elephant) (de Silva & Wittemyer, 2012).

Elephants are held in relatively static social groups within zoos, and may be subject to routine changes in social group composition as part of management regimes (Meehan et al. 2016a). Researchers have highlighted concerns relating to elephant social requirements and an inability of UK and Irish zoos to provide for their social needs (Clubb & Mason, 2002; Harris et al. 2008). Social interactions have been highlighted as an indicator of welfare (Williams et al., 2018b) and elephant keepers have advocated the importance of social groups engaging in positive social interactions (Chadwick et al., 2017). The opportunity for appropriate social contact is considered more important in zoo elephant welfare than environmental space (Meehan et al., 2016a). To date limited research has been undertaken to develop a greater understanding of zoo elephant social relationships, however this area of study is gaining traction. The current knowledge of social relationships in zoo elephants indicates that social networks are unbalanced to some degree, that is some members are engaged in more physical contact whilst others sit on the periphery of social groups (Coleing, 2009), and unbalanced affiliative ties occur within dyads (Harvey et al. 2018). Interactions do not appear to be dominated by a single individual (Coleing, 2009) but most interactions occur between related individuals or are instigated by younger group members (Coleing, 2009; Harvey et al., 2018). Some level of fluidity has been described in zoo elephants (Bonaparte-Saller & Mench, 2018), despite the range of social partners being more limited than that found in wild elephants, and zoo elephants can be successfully housed in a range of social groups within zoos (Garai, 1992).

Individual social preferences and social needs can change throughout an individual's lifetime (Evans & Harris, 2008), and social compatibility at one point in time does not guarantee compatibility throughout the lifetime of that social group (Cairns pers. comm., 2016). Understanding zoo elephant relationships at the level of herds and dyadic interactions is paramount in improving welfare. Social network analysis can be used to capture such data. For example, by understanding at what point aggressive interactions move from a natural and stabilising level within a social group to escalated and problematic aggression, or determining rates of avoidance within social groups (Rose & Croft, 2015). Advancing knowledge in this area provides the opportunity to improve welfare on an individual level, by informing decisions relating to housing and husbandry regimes. Recent advances in elephant management guidelines highlight the need to understand more about individual elephant needs and herd compatibility, and for such information to be included in elephant welfare plans (Defra, 2017). Changes to social groups can lead to disruption in social hierarchies, changes in social networks (Armstrong, 2015) and in

extreme cases a temporary breakdown of social relationships (Cairns pers. comm., 2016). The opportunity to understand social networks and identify key individuals ensures management decisions can be made and executed with minimal effects on the overall stability of the social group (Snijders et al., 2017). Furthermore, regular sampling of social dynamics can allow managers the opportunity to detect changes to social relationships and put in place intervention strategies to prevent conflict escalating (Koontz & Roush, 1997). Use of knowledge in this manner is particularly important in zoo-housed Asian elephants, where social group stability has been linked with calf survival (Hartley & Stanley, 2016).

If the drivers of changes in social structure of wild elephants are predominantly driven by environmental factors then fluctuations in behaviour of zoo elephants may not be expected. Social networks and relationships in zoo elephants have been, until recently, little studied, but planning management programmes around known social group preferences has been shown to improve the welfare of individuals (Hacker et al., 2015). Individual animals play different roles in social networks in zoos (Coleing, 2009; Harvey et al., 2018). An imbalance in social networks or within dyads has important potential effects on welfare, especially in negative interaction networks. The work that has been conducted on social networks in zoo elephants has thus far been conducted in the US (Bonaparte-Saller & Mench, 2018) and in the UK (Coleing, 2009; Harvey et al., 2018). However elephants in the US are subject to more manipulation in terms of social groups (Meehan et al., 2016a) and work conducted within the UK has looked only at one or two study herds which may limit its application (Coleing, 2009; Harvey et al., 2018).

4.1.2 Aim and objectives

The aim of this chapter was to use SNA to investigate herd structures and dyadic relationships in UK and Irish zoo elephants, and to determine if social relationships are stable over a 12 month period. It was hypothesised that there would not be any significant behavioural change over time and that social relationships would remain generally static, because the factors driving group structure change in the wild (i.e. level of resources, predation threats) are absent from zoos, and social groups are more static. It was also hypothesised that interactions would be equally spread amongst group members and that there would be no special dyadic relationships. This chapter will address Objective Two of the thesis; to determine if social relationships are stable over time. The information provided in this chapter will provide zoo keepers and other elephant professionals with increased knowledge of herd dynamics and enable them to identify 'normal' relationship fluctuations. Understanding these fluctuations could help to identify potential relationship breakdowns and enable management that alleviates social pressures before they become a compatibility issue. On an individual zoo level, the results from this chapter aim to provide in-depth knowledge of dyadic relationships and help to identify key individuals in the herds. This information has the potential for application as a measure of well-being and methodologies used in this chapter could be applied to future studies. The findings could also be incorporated into long-term elephant management plans and help to improve welfare on both an individual elephant and herd basis, thus contributing to requirements laid out in SSSMZP elephant management guidelines.

4.2 Methodology

A number of methodological and analytical approaches were required to address research Objectives Two to Four. Objective One was answered in Chapter Three. To answer Objective Two, to determine if social relationships are stable over the year, a combination of both behavioural observations and analysis of social networks and dyadic relationships were utilised (this chapter). The third objective, identifying whether individual personality influences social interactions and social relationships combined Objective Two methods with a survey of elephant keepers to capture information on elephant personality (Chapter Five). Finally, Objective Three, to identify whether individual or herd demographics affect social interactions, utilised behavioural observations and general linear modelling (Chapter Six).

This chapter provides background information on the study sites and subjects, recording equipment, the pilot study and consequent ethogram and sampling method development. Further details on the collection of behavioural data (live and video observations), the use of SNA and personality assessment in zoo animal behaviour and welfare research are included in the relevant data chapters. Within each data chapter the rationale behind the chosen method is presented prior to a description of the method.

4.2.1 Methodology development – pilot study

In September 2015 a pilot study was undertaken at Zoo G, the most local study zoo. The aim of the pilot study was to test the practicality and feasibility of the proposed data collection methods. The objectives of the pilot study were to: i) optimise an ethogram designed for the study and ii) identify appropriate and representative sampling intervals.

4.2.1.1 Subjects and study sites

Subjects were five female Asian elephants aged 2 to 32 years. The group included two mother-daughter pairs and an unrelated female. Elephants were housed together and had 24-hour access to both inside and outside enclosures.

4.2.1.2 Data recording

Elephants were identified using visually discernible differences: height, size and shape of ears, length of tail and presence/absence of hair, scars and tattoos (Figure 4.1).



Figure 4.1. An example of features used to identify study elephants (a) both elephants have no hair on their tails, the elephant on the left has a star tattoo on her rump, (b) elephant has a ridge in her back and a forward fold on her ear, (c) elephant has long tail with lots of hair, rounded back and small ears.

Video footage of outdoor enclosures was captured using high definition video cameras with infrared capability (Hikvision IR network camera, Model DS-2CD2632D-IS, Hikvision Europe, The Netherlands) (Figure 4.2). Cameras had a 20m IR light range and recorded at 20FPS onto bespoke recording kits designed by Carnyx Wild (Carnyx Wild, UK). To comply with data protection laws no sound recordings were made to avoid inadvertently capturing voice recordings of zoo visitors or keepers. Footage gathered from existing indoor cameras was provided by the zoo for analysis. Video footage was gathered 24-hours a day for 5 days in September 2015. Behavioural studies must be systematic and designed in such a way as to reduce sampling bias as far as possible by strategically sampling across an entire time period. The sampling period was thus divided into 12 x 2-hour periods throughout the week to systematically sample across a 24-hour period throughout the 5 days of data collection (Table 4.1).



Figure 4.2. Video recording kit used to gather video footage throughout a 24-hour period

Table 4.1. Details of the 12 x 2-hour time periods the data collection was split into for data analysis

Day	Observation period (24 hours)																									
	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	22:00	23:00	00:00	01:00	02:00	03:00	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00		
Mon	Sample	Target	Target	Sample																						
Tues			Sample	Target	Target	Sample												Sample	Target	Target	Sample					
Weds							Sample	Target	Target	Sample											Sample	Target	Target	Sample		
Thurs														Sample	Target	Target	Sample							Sample	Target	
Fri																									Sample	Target

 Sample period
  Target observation period

4.2.1.3 Ethogram development

A comprehensive ethogram which was previously created from multiple sources and designed for use in welfare assessment of zoo elephants (Asher et al., 2015) was modified and developed to suit the purposes of this study. Social behaviour categories were expanded and other categories which were being used to create only overall activity budgets (e.g. feeding) were condensed into the broader behavioural categories. Similar behaviours were grouped for the purposes of analysis. The finalised ethogram with details of modified categories is presented in Table 4.2.

Table 4.2. Elephant behaviour ethogram (based on Asher et al. 2015)

Behaviour			Description	
Environmental interaction*			Investigating or interacting with things in the environment (other than food)	
Resting*	Standing		Standing motionless (either upright or leaning on an object or conspecific), not performing any other behaviour	
	Lying		Lying down in a recumbent position	
Abnormal repetitive behaviour (ARB)*			Repetitive behaviour with no apparent goal or function	
Comfort*			Any self-maintenance or grooming behaviour, e.g. wallowing, rolling, scratching, dust bath	
Feeding*			The process of locating, manipulating and consuming food stuffs	
Locomotion (non-social)*			Taking two or more steps in any direction in a non-repetitive pattern. Only one foot is removed from the ground at any one time. Movement is unrelated to other elephants in the herd and no social interaction occurs immediately after the movement.	
Standing (alert)			Standing still performing no other behaviour but eyes open and elephant is responsive to changes in the environment	
Human-animal interaction**			Any interaction between keeper and the study animal	
Social**	Affiliative	Positive physical	Conspecific play	Engaging in active play with another elephant, including head-to-head sparring, trunk wrestling, mounting, chasing and rolling on one another. Does not include behaviours observed following an agonistic encounter or courtship.
			Touching (trunk to)	Touching another elephant with the trunk in a non-aggressive manner
			Touching (body to)	Touching/rubbing another elephant with the body
	Positive non-physical	Protecting	Standing over another elephant	
		Huddling	Formation of a tight circle with calves at the nucleus. Calves hidden in the middle, adults surrounding them.	
		Approach	Walking towards another elephant in a non-threatening manner. Recipient stays in position during and after the approach.	
		Approach with trunk	Trunk outstretched towards another elephant. Not close enough to make physical contact.	
		Walking with	Walking side by side with another elephant	
		Following	Walking closely behind another elephant (within one elephant body length)	
Agonistic	Negative physical	Pushing	One elephant forces or pushes against the body (usually the rump) of another elephant,	

Behaviour		Description	
		resulting in the elephant that is being pushed moving at least two steps	
	Pulling	Using the trunk to pull at another elephant in a non-playful manner. May pull at the trunk or an accessible body part such as tusks/tushes or the tail.	
	Sparring	An escalation of a push/pull incident into more physical aggression	
	Hitting/kicking	Aggressive physical contact with the trunk or leg, e.g. trunk strike or kicking out	
	Negative non-physical	Displace	Movement of one elephant results in another elephant leaving its location (within 10 seconds). Usually occurs when a more dominant elephant approaches a more subordinate individual
		Approach	Walking towards another elephant in an aggressive or hostile manner (head held high, ears wide or flapping). Receiving elephant may either respond to this by standing as tall as possible, head raised, ears flapping or turning away from/walking away from the approaching elephant
		Walking/turning away from	Avoiding or shying away from another elephant; the individual either walks forwards away from or backwards away from the other elephant
		Frozen	Standing still and alert as another elephant approaches
		Charge/mock charge	Move towards another elephant with the head held high, pace usually quickens as individual gets closer to the target elephant. In the case of a mock charge the individual charging stops further away from the target elephant.
		Blocking	Blocking from food source or other resource (e.g. door)
Maternal*		All interactions between mother and calf. Includes nursing, suckling and soliciting suckle.	
Mounting		A male elephant places his trunk length-wise on another elephants back, rests his head/tusks on the back of the elephant and rears up on his hind legs, with his front legs either side of the spine of the other elephant. This may be a female elephant (sexual, i.e. mating) or a male elephant (dominant or play).	
Other		Any other behaviour being performed that is not listed on the ethogram	
Out of view		Out of sight of observer	

*Categories in the original ethogram (Asher et al., 2015) were condensed for use in this study, **categories were expanded with extra detail added for behaviours specific to this study

4.2.1.4 Data analysis – identification of appropriate and representative sampling intervals

In order to identify an appropriate and representative sampling interval it was important to use the most accurate methodologies to capture the data. Initial attempts were made to analyse the video footage using continuous sampling for the most detailed data collection. However, this method was not pursued due to the difficulties in accurately simultaneously identifying individuals involved and the context of interactions without missing subsequent interactions. Video footage was consequently analysed using instantaneous 30-second scan sampling as this method was considered to be the most practical whilst remaining reliable. It provided the smallest scan sample whereby individuals and contexts could be accurately identified and analysed. Any social interaction that occurred at the time of the sample was recorded, along with the recipient of the interaction and the reaction of the recipient. The reaction of the recipient was used to identify the nature of the interaction. To optimise the sampling interval, i.e. collecting maximum data whilst minimising the sampling effort, data were analysed to identify the largest scan sampling interval that would provide data that was representative of observed behaviour. Data collected using 30-second scan sampling formed a 'baseline' of behaviour. Data points were then systematically removed at 30-second intervals. This created the effect of 30-second scan sampling up to 5-minute scan sampling (e.g. 0.5 minutes, 1 minute, 1.5 minutes etc).

SPSS version 21 (SPSS Inc., Chicago, IL) was used for statistical analyses. Significance levels were set at 0.05 unless otherwise stated. A Kolmogorov-Smirnov test was used to assess distribution normality across the data set. Data were abnormally distributed. A Wilcoxon signed-rank test was thus used to investigate statistical data loss at the different sampling frequencies. All sampling frequencies were compared to the initial sampling period of 30-second intervals. Statistically significant loss was recorded at the 1-minute scan interval for the behaviour 'touching' ($Z=-2.401$, $p<0.05$). Touching was considered one of the most important behaviours to accurately capture due to the importance of tactile behaviours in elephant social interactions (Makecha et al., 2012). Scan sampling with a 30-second interval was consequently used throughout the study for greatest accuracy and minimal data loss, whilst maintaining practicality.

4.2.2 Main study

4.2.2.1 Study sites and subjects

All of the zoos in the UK and Ireland that housed elephants when this study commenced were contacted (via email) and invited to be included. Seven of the 15 zoos contacted gave approval for the study to be undertaken. Data collection was carried out at all seven study sites. Study elephant herds consisted of a range of structures including related and unrelated individuals, African and Asian species, mixed sex groups and single sex groups and a range of ages and group sizes. Table 4.3 provides demographic data of each of the study elephant herds. The 32 study

elephants in the participating seven study zoos represented 49% of the zoo elephant population (n=68) in the UK and Ireland at the start of this study. Of the 32 elephants 10 were African (1 male: 9 females) and 22 were Asian (3 male: 19 female).

Table 4.3. Elephant and herd demographics for the study elephants at the onset of the study period (October 2015)

Zoo	Elephant	Species	Sex	Age	No. relatives in herd	Wild or captive born	If zoo born, at natal zoo?	Calf in herd	Herd size	Observation period (mins)	Proportion observations in sight
A	E1	African	F	45	0	Wild	NA	N	2	5817	0.66
	E2	African	F	47	0	Wild	NA	N	2	5817	0.98
B	E3	Asian	F	54	0	Wild	NA	N	3	5842	0.89
	E4	Asian	F	44	0	Wild	NA	N	3	5842	0.89
	E5	Asian	F	40	0	Wild	NA	N	3	5842	0.85
C	E6	Asian	F	49	0	Captive	N	Y	6	5838	0.75
	E7	Asian	M	15	1	Captive	N	Y	6	5838	0.16
	E9	Asian	F	1	4	Captive	Y	Y	6	5838	0.90
	E8	Asian	F	36	3	Wild	NA	Y	6	5838	0.78
	E10	Asian	F	19	3	Captive	Y	Y	6	5838	0.87
	E11	Asian	F	13	3	Captive	Y	Y	6	5838	0.87
D	E12	African	M	34	0	Wild	NA	N	2	7666	0.20
	E13	African	F	35	0	Wild	NA	N	2	7666	0.27
	E14	African	F	35	0	Wild	NA	N	2	7666	0.67
	E15	African	F	31	0	Wild	NA	N	2	7666	0.69
E	E16	Asian	F	32	8	Captive	N	Y	9	3267	0.65
	E17	Asian	F	26	8	Captive	N	Y	9	3267	0.66
	E18	Asian	F	13	8	Captive	N	Y	9	3267	0.71
	E19	Asian	F	10	8	Captive	Y	Y	9	3267	0.75
	E21	Asian	M	2	9	Captive	Y	Y	9	3267	0.61
	E22	Asian	F	2	9	Captive	Y	Y	9	3267	0.65
	E20	Asian	M	2	9	Captive	Y	Y	9	3267	0.60
	E23	Asian	F	<1	9	Captive	Y	Y	9	1569	0.51
	-	Asian	M	22	9	Captive	N	Y	9	-	-
F	E24	African	F	14	1	Captive	Y	N	4	5031	0.79
	E25	African	F	30	0	Wild	NA	N	4	5031	0.76
	E26	African	F	14	2	Captive	Y	N	4	5031	0.81

Zoo	Elephant	Species	Sex	Age	No. relatives in herd	Wild or captive born	If zoo born, at natal zoo?	Calf in herd	Herd size	Observation period (mins)	Proportion observations in sight
	E27	African	F	30	1	Wild	NA	N	4	5031	0.80
G	E28	Asian	F	33	0	Wild	NA	Y	5	5016	0.69
	E29	Asian	F	22	1	Captive	N	Y	5	5016	0.70
	E30	Asian	F	3	1	Captive	Y	Y	5	5016	0.63
	E31	Asian	F	19	1	Captive	Y	Y	5	5016	0.68
	E32	Asian	F	34	1	Wild	NA	Y	5	5016	0.67

4.2.2.2 Behavioural observations

Behavioural observations are common in studies of zoo animal welfare due to their relative ease of execution, ability to provide a wealth of information, and most importantly, non-invasive nature. Assessment of changes in behaviour has been identified as a reliable and non-invasive means of assessing elephant welfare (Williams et al., 2018b). There are a number of methods employed by behavioural researchers to document behaviour (see Martin & Bateson (1993) for a full review); briefly, they cover: ad libitum, focal, scan and behaviour sampling, using a continuous or time sampling recording technique (Altmann, 1974; Martin & Bateson, 1993). Each method has limitations, and these must be assessed carefully within the context of zoo research to ensure the appropriateness of the study design. Accurate documentation of behaviour allows changes over time to be captured.

This research utilised scan sampling and instantaneous recording to capture social behaviour and overall activity budgets of the study elephants. Scan sampling is generally not recommended for less common behaviours such as social interactions (Altmann, 1974; Martin & Bateson, 1993), however as has been detailed in Section 4.2.1.4, scan sampling was considered to be the most practical and reliable option following the pilot study. This method enabled inclusion of a comparatively large number of study elephants and collection of data over a relatively long period of time (one year). Scan sampling and instantaneous recording with a short inter-scan interval (30-seconds) was employed during this project to reduce sampling bias. Social interactions were a rare group of behaviours in terms of overall activity budget, but when they occurred they were sometimes performed at a high intensity. This meant that continuous sampling had the potential to lead to sampling bias, for instance, only recording the first elephant to take part in an interaction, or to introduce an error in interpretation of the context of the interaction. Whilst utilisation of scan sampling as a sampling method may have led to some instances of physical social interaction being missed, it was considered to be the most appropriate method for this study as it (i) enabled identification of individuals, (ii) allowed the context of the interaction to be identified during the scan break and (iii) gave time for the entire group to be recorded accurately before the next scan began. Point three was particularly important for accuracy during live observations.

Types of interactions

At every sampling point the behaviour of each visible elephant was recorded. Elephants that were not visible were recorded as being out of sight. If elephants were engaging in social interactions then extra information was also captured: the type of behaviour, the individuals involved, details of the context of the interaction (which enabled identification of whether it was positive or negative) and the directionality of the interaction. Elephants engage in a range of social interactions (Stoinski et al., 2000; Olson, 2004; Wilson et al., 2006; Posta et al., 2013;

Asher et al., 2015). For the purposes of data analysis interactions were identified as either positive or negative (see Ethogram, Table 4.2). Behaviours were considered to be positive if they were non-aggressive contact or non-aggressive approaches (e.g. touching with the trunk), and negative if they were instances of aggression or a reaction to aggressive behaviour (e.g. walking away from another elephant) (Garai, 1992). Positive and negative social interactions were then further subdivided into physical and non-physical interactions. Previously, non-physical interactions have been grouped with physical interactions for analysis (Wilson et al., 2006). In this study it was felt that it was important to distinguish between these interactions as they may represent different levels of relationship, and being able to identify whether elephants were engaging in physical interactions or only non-physical interactions may reveal extra information in relation to social networks and individual relationships. Positive and negative interactions were thus separated into physical and non-physical interactions for analysis.

4.2.3 Live observations & video recordings

Data were gathered via live and video observations. All live observations were conducted from public viewing areas during zoo opening times to minimise the observer effect. Wherever possible, live observations were used as an addition to video recordings. However, where it was not possible to gather video footage, only live observations were used (Table 4.4). Live observations followed the same sampling protocol as video observations for continuity and accuracy. Video footage was either provided by the study zoo or cameras were temporarily installed on site (see details in Section 4.2.1.2).

4.2.4 Data collection and schedules

The data collection period ran from January 2016 to February 2017. Four days were spent at each zoo prior to commencing data collection to allow familiarisation with the study site and the subjects prior to the start of observations. Identity cards were created for each elephant. Photographs were taken of each elephant and keeper descriptions were used to identify individuals. As with the pilot study elephants were identified using a number of visually discernible differences (Figure 4.1). A data collection schedule, including months of data collection and number of sampling days is provided in Table 4.4. As per the pilot study, data were collected over a five day period with each day split into 12 x 2-hour periods (Table 4.1) to reduce bias and ensure data collected was representative of behaviour throughout the 24-hour period and did not just provide a snapshot of one time period. Previous research has suggested that elephant behaviour is variable between days (Asher et al., 2015). Wherever possible data were collected during the 'target' observation period, which fell in the middle of the 2-hour period. A minimum of one month was taken between the data collection periods to ensure independence of the sampling periods.

Research has indicated that the presence of a handler can affect elephant social behaviour (Yasui & Idani, 2017). Therefore, to reduce the effect of keeper presence on elephant behaviour, recordings were stopped when elephants were interacting directly with keepers (e.g. public feeding displays or training). There is still however the potential for the zoo routine to have an impact on elephant behaviour, but this is a factor that could not be controlled and would be present at all study zoos to some extent.

Unbalanced periods of data collection are common in zoo research, where due to the nature of zoo schedules observations may need to be taken on an opportunistic basis. There was a discrepancy in the hours of observations that were able to be undertaken at the study zoos due to circumstances beyond the control of the researcher (e.g. failure of recording equipment), and it was not always possible to view all of the study elephants for the full duration of each observation period due to enclosure set-ups. For example, the bull at Zoo E was run with the herd daily in the main paddock, however, video footage from the zoo was only from the cow house (to which the bull had no access). He was therefore removed from the study. Where possible, recordings and observations were undertaken in both inside and outside enclosures. However, in some instances it was only possible to observe one or the other. Table 4.3 provides total hours of observation per study zoo and the proportion of observations that each elephant was in-sight for during the recording periods. Measures were applied during the data analysis stage to account for this; data were analysed as a proportion of total possible observations, to enable comparisons to be made across the study zoos. Data were analysed as a proportion of possible observations rather than as a proportion of recorded activity to prevent false representation of behaviour in elephants who spent long periods of time out of sight of the observer, where their behaviour was unknown. This may have led to an under-representation of perceived levels of sociability in elephants who spent longer periods of time out of sight. The results have been interpreted with this limitation in mind.

Table 4.4. Data collection periods and hours of observation for each study zoo

Zoo	Observations	Enclosures observed	Familiarisation period (4 days)	Data collection period (study months, days)				Total period of observation (minutes)
				1	2	3	4	
A	Video only (provided by zoo)	Inside only	October 2015	January & February 2016 (10 days)	April & May 2016 (10 days)	July & August 2016 (10 days)	October & November 2016 (10 days)	5817
B	Live only*	Outside only	November 2015	May 2016 (5 days)	August 2016 (5 days)	December 2016 (5 days)	February 2017 (5 days)	5842
C	Video only (provided by zoo)	Inside and outside	November 2015	January & February 2016 (10 days)	April & May 2016 (10 days)	July & August 2016 (10 days)	October & November 2016 (10 days)	5838
D	Live and video (cameras installed)	E14 & E15: Inside and outside E12 & E13: outside only	December 2015	January & February 2016 (10 days)	April & May 2016 (10 days)	July & August 2016 (10 days)	October & November 2016 (10 days)	7666
E	Video only (provided by zoo)	Inside only	October 2015	February 2016	April & May 2016	September 2016	October & November 2016	3267
F	Live and video (cameras installed)	Inside and outside	November – December 2015	January & February 2016 (10 days)	April & May 2016 (10 days)	July & August 2016 (10 days)	October & November 2016 (10 days)	5031
G	Live and video	Inside and outside	Pilot study	January &	April & May	July & August	September &	5016

Zoo	Observations	Enclosures observed	Familiarisation period (4 days)	Data collection period (study months, days)				Total period of observation (minutes)
				1	2	3	4	
	(Outside: cameras installed, Inside: provided by zoo)			February 2016 (10 days)	2016 (10 days)	2016 (10 days)	November 2016 (10 days)	

*Live observations only were undertaken at this study zoo due to practical difficulties associated with installing video cameras

4.2.5 Social network analysis

4.2.5.1 Using social network analysis to identify relationships

Social network analysis enables an understanding of the nature of interactions within a group (Wasserman & Faust, 1994), through the calculation of quantitative metrics describing social structures at individual and population levels (Croft et al., 2008). Although not new it has been increasingly used to investigate social systems in a range of species including dolphins (Lusseau et al., 2003), feral horses (Krueger et al., 2014), wild Asian elephants (de Silva et al., 2011), zoo Asian elephants (Coleing, 2009) and wild African elephants (Schuttler et al., 2014). There are predominantly four categories of network studies: (i) a description of social structures, (ii) studies of the causes and consequences of individual variation in the individuals position in the network, (iii) studies of social processes and implications of network structure for information transfer and disease or parasite spread between individuals and (iv) the relationship between environment and network structure (Farine & Whitehead, 2015).

4.2.5.2 The use of social network analysis in zoo animal welfare research

Quantification of social relationships is extremely important for zoo animal welfare (Koene & Ipema, 2013), as advanced knowledge of social structures can play an important role in improving welfare by allowing zoos to make informed decisions about management and husbandry routines (Rose & Croft, 2015). Fine scale structures of zoo animal populations have consequences at both the individual animal and population level (Rose & Croft, 2015). In social animals as a whole there is a lack of robust methodologies capable of identifying what gives social systems their form and temporal stabilities (Dunbar & Shultz, 2010). Rubenstein et al. (2015) highlighted the need to capture temporal changes in social relationships, and SNA can be used to garner such data.

The use of SNA in understanding interactions in animal social groups has been reviewed in depth (Wey et al., 2008) but it is briefly summarised here. Within a social group each node (individual) is connected via social ties, which can arise from both direct and indirect interactions. Understanding where an individual sits within a network helps to understand social groups, and it can facilitate the execution of management practices which will cause minimum disruption to overall group structure (Lusseau & Newman, 2004). In order to identify an individual's position in the network some degree of 'centrality' must be calculated. Centrality, which can be measured by looking at measures of betweenness or degree, is described as 'the extent to which a given node occupies a position that is important to the structure of the network' (Croft et al., 2008) and it can be used to quantify the structural importance of an individual within a social group (Wey et al., 2008). Understanding the centrality of individuals within a social network allows an enhanced understanding of the nature of the social group, and the role individuals play within the network. Centrality is commonly described in four ways: degree centrality, closeness centrality,

betweenness centrality and eigenvector centrality. The degree of an individual is a simple measure of centrality and provides information on the number of different social connections an individual has in the population. Nodes with many neighbours are considered to be 'well connected', sitting at the centre of the social networks. Nodes with fewer connections will sit on the network periphery (Croft et al., 2008). Closeness centrality describes how well connected an animal is to others in the network, and reflects an individual's potential influence on the social group (Wey et al., 2008). Betweenness centrality operates in much the same way but it additionally indicates how important an animal is as a point of social connection and knowledge transfer (Wey et al., 2008). Betweenness can be described as a measure of how information (or disease) spreads within a network (Newman, 2005) and it has been used to identify how important individuals are in terms of network cohesion (Lusseau & Newman, 2004). Finally, eigenvector centrality is the measure of the influence of nodes in a network. It factors in the importance of neighbours and considers their individual connectivity scores. Eigenvector centrality can be a useful measure of sociability in association networks (Newman, 2004).

4.2.5.3 The use of social network analysis in this study

Application of social network theory to identify social structures in zoo-housed animals is particularly important in highly social species such as elephants, who have known flexibility in their social relationships (Wittemyer et al., 2005; Chiyo et al., 2011; Archie & Chiyo, 2012; de Silva & Wittemyer, 2012). Social network analysis was utilised in this study to investigate social relationships, document frequencies of social interactions and understand in more detail dyadic relationships in the study herds. This study dealt with directed networks using interaction data in order to measure how important an individual was in terms of cohesion of overall herd structure. Betweenness centrality was thus used as the centrality measure as this was considered to provide the most useful and relevant information. Data were treated as being from individual time points to investigate temporal change, and then grouped together in order to look at overall group structure. Directionality was also important, in order to identify whether there was a balanced relationship within dyads, or whether one individual was giving or receiving proportionally more interactions than the rest of the group, or their dyadic partner. Mantel tests were used to investigate whether positive/negative matrices were correlated over periods of time and to identify levels of reciprocity in dyads within the herds. This enabled the investigation of whether or not overall herd structures or dyadic relationships had changed over time, and whether or not dyadic relationships were balanced.

One of the main challenges in SNA is the lack of ability to compare networks across contexts (Farine & Whitehead, 2015). In this study, methods used to gather data were kept the

same to maximise the opportunity for comparison between study herds. To optimise the use of SNA in this study, networks were compared across the zoos to identify common themes.

4.2.6 Social interactions versus association data

In some instances associations may be a better representation of relationships than dyadic interactions (Farine & Whitehead, 2015). However, determining association partners can be ambiguous. When elephants are housed within inside enclosures it is possible for there to be a false representation of sociability, if associations were recorded when elephants were within a certain number of body lengths of another elephant (Harvey et al., 2018). Likewise, in larger enclosures it is possible that under usual association or disassociation criteria, elephants who were in a group with others were considered to be not associating because of their physical distance apart despite them being in the same area of the enclosure. Previous work in other species, such as rhesus macaques, yellow bellied marmots (*Marmota flaviventris*), bottlenose dolphins and flamingos (*Phoenicopterus roseus*) have used both interaction data (McCowan et al., 2008; Wey & Blumstein, 2010) and association data (Lusseau et al., 2003; Rose & Croft, 2017) to identify group social structures, with association data more frequently used in large groups where it is not always possible to identify individual interactions (Lusseau et al., 2003). The work on wild elephant social structure has focused on the use of associations to identify group members and monitor changing association patterns (Wittemyer et al., 2005; Archie et al., 2006; Vance et al., 2009; de Silva et al., 2011). Zoo elephant relationship studies have assessed both interactions and associations (Coleing, 2009; Armstrong, 2015; Bonaparte-Saller & Mench, 2018; Harvey et al., 2018). In some instances, a combination of both were used, and in others one or both of these measures of sociability was coupled with keeper assessments of social bonds or hierarchy.

It is possible that whilst rates of affiliation provide a measure of relationship strength between individuals they are not necessarily capturing all of the social dynamics between individuals (Silk et al., 2013). Very limited work has focused on analysis of dyadic relationships (Silk et al., 2013), which may be more accurately represented using interactions to be able to identify directionality of relationships. Secure relationships have been defined as those that are predictable and consistent over time (Silk et al., 2013). However, limited research has tried to capture the dynamics of social relationships in zoo elephants (but see Coleing, 2009; Armstrong, 2015; Bonaparte-Saller & Mench, 2018; Harvey et al., 2018), so any information that advances our knowledge in this area of study has an important place in the literature and has implications for elephant welfare.

4.2.7 Data analysis

R (Version 1.1.383) was used for all statistical modelling. SPSS Version 21 (SPSS Inc., Chicago, IL) was used for all other statistical analyses. Elephants were grouped into five age categories for analysis: calves (0 to 2 years), infants (3 to 4 years), juveniles (5 to 9 years), sub-adults (10 to 15 years) and adults (16 years and older), based on research on Asian elephants by Kurt (2005). Unless otherwise stated significance values were set at 0.05. A Kolmogorov-Smirnov test was used to assess distribution normality across all data sets. Appropriate statistical tests are detailed in the relevant data chapters.

Data analysis for this chapter was undertaken using two methods: (i) analysis of frequency of social interactions given by individual elephants and (ii) analysis of social interactions given and received by the whole herd in terms of social matrices. Analysis of social matrices was further subdivided into analysis of herd social matrices over time and reciprocity in dyads. A breakdown of analysis methods is provided below.

4.2.7.1 Analysis of frequency of social interactions given by individual elephants

Data were split into four time points (P1, P2, P3, P4) (Table 4.4) to investigate whether herd dynamics changed over the 12-month period of data collection and thus to establish stability of social relationships. Changes to elephant social structure were investigated in terms of frequency of interactions given by individuals at the four data collection periods, and fluctuations in overall herd structures between the first and last periods of data collection. Frequency of interactions at the four time points were compared for differences. Data were analysed at the individual level and in dyads across all of the study zoos. A Friedman's test with a Wilcoxon post-hoc was undertaken to analyse how frequency of interactions had changed in terms of frequency of interactions given as a total by individual elephants and within dyads over time. Bonferroni adjustments were applied (reducing the significance value to $p=0.008$) to cater for replicates in data analysis. Additional data analysis was carried out to investigate the birth of a calf on the frequency of social interactions with the herd at Zoo E. Data were pooled for P1 and P2 to create a 'pre-birth' period, and for P3 and P4 to create a 'post-birth' period. Frequency of interactions during the 'pre-birth' and 'post-birth' periods were then compared using a Wilcoxon test.

4.2.7.2 Analysis of herd social matrices

Social network analysis was used to represent relationships between individuals in the herds. Weighted diagraphs were constructed from each asymmetric matrix for each type of interaction (physical positive, physical negative, non-physical positive and non-physical negative) using UCINET 6.0 Version 1.00 (Borgatti et al., 2002) and NetDraw Version 2.160 (Borgatti, 2002). Two elephants were removed from this section of the analysis due to missing data. E2 (Zoo A)

passed away after the first period of data collection. E23 (Zoo E) was not born until after the second data collection period and so too was removed from analysis of herd matrices over time.

4.2.7.3 Assessment of herd structure change over time and reciprocity in dyads

To assess changes in herd structure over time and reciprocity in dyads mantel tests were undertaken in R (Version 1.1.383) using packages 'ade4' and 'vegan'. 999 permutations were used per test, with the Pearson product moment correlation coefficient as the test statistic. Significance levels were set at 0.05. All data entered into the matrices were averaged to give an accurate representation of individual sociability.

Change in herd structure over time

Social interaction matrices were created for individual herds using frequency of interaction data for physical positive, physical negative, non-physical positive and non-physical negative interactions. Matrices were created for each data collection period. Each period was then compared with the subsequent data collection period. The three analyses that were undertaken were therefore (1) P1 – P2, (2) P2 – P3, (3) P3 – P4. Stability of interactions over the four time points were assessed using mantel tests. Mantel tests were used to test for correlations between matched interaction matrices at each data comparison point. This enabled the investigation of whether interactions within the whole herd had changed over time or remained stable. Significant correlation between interaction matrices over time indicated no change to herd structures, non-significant values indicated a difference between interaction matrices and hence a change in herd structure in terms of frequency of social interactions.

Reciprocity in dyads and equality of relationships

Tests of reciprocity were undertaken to determine whether dyadic social interactions were reciprocal (i.e. to determine whether the rate of interaction elephant E1 directed towards E2 was correlated with the rate of interaction that E2 directed to E1). Mantel tests were undertaken to examine absolute reciprocity. No correlation between the matrix and its transpose indicated unidirectional interactions. Equality of relationships within the whole herd matrix were also assessed using simple ratio methods. Dyadic interactions were considered to be relatively balanced if the ratio of interactions given to interactions received was between 0.5:0.5 and 0.41:0.59.

4.2.8 Ethical approval

All research protocols were approved by the Nottingham Trent University School of Animal, Rural and Environmental Sciences school ethics committee. Support for the study was obtained from the

BIAZA Research Group and permission to conduct the study was granted by all of the participating zoos prior to the commencement of data collection.

4.3 Results

4.3.1 Frequency of social interactions

For all zoos and all elephants combined, there was a significant difference between the types of interactions observed. Elephants ($n=32$) engaged in more positive interactions than negative interactions (expressed as percentage of total activity) (positive physical (median, IQR): 4.33% (0.48 – 24.49), negative physical: 0.09% (0.04 – 0.19), positive non-physical: 8.46% (3.31 – 17.51), negative non-physical: 0.46% (0.21 – 1.17) ($\chi^2(3)=62.687$, $p<0.001$). Positive physical interactions were more frequent than negative physical interactions ($Z=-4.623$, $p<0.001$) and negative non-physical interactions ($Z=-3.606$, $p<0.001$). Positive non-physical interactions were more frequent than negative physical ($Z=-4.860$, $p<0.001$) and negative non-physical interactions ($Z=-4.742$, $p<0.001$). Negative non-physical interactions were more frequent than negative physical interactions ($Z=4.644$, $p<0.001$).

4.3.2 Change over time

When the data were analysed in terms of frequency of interactions given by each elephant there was no significant difference for positive physical, negative physical and non-physical negative interactions between the four time periods ($p>0.05$). Frequency of non-physical positive interactions was significantly different across the time periods ($\chi^2(3)=21.125$, $p<0.001$) (Table 4.5). Post-hoc tests revealed differences between periods 1 and 3 ($Z=-3.795$, $p<0.001$), 1 and 4 ($Z=-2.822$, $p<0.01$) and periods 2 and 3 ($Z=-2.865$, $p<0.01$) (Table 4.5).

Table 4.5. Median percentage of social interactions given by each study elephant

Interaction type	Time period	Median	IQR	Range (%)
Positive physical	1	0.96	0.09 – 4.28	0 – 8.55
	2	0.19	0.19 – 5.3	0 – 18.27
	3	0.86	0.86 – 4.77	0 – 14.03
	4	1.16	1.16 – 6.56	0 – 13.73
Negative physical	1	0	0 – 0.05	0 – 0.3
	2	0.02	0 – 0.07	0 – 0.19
	3	0.02	0 – 0.04	0 – 0.16
	4	0	0 – 0.06	0 – 0.48
Positive non-physical	1* ²³⁴	3.35	3.35 – 8.19	0.13 – 50.65
	2* ¹³⁴	1.57	1.57 – 6	0.03 – 16.84
	3* ¹²	1.04	1.04 – 1.96	0 – 11.34
	4* ¹²	1.29	1.29 – 2.24	0.15 – 6.52
Negative non-physical	1	0.19	0.06 – 0.34	0 – 1.1
	2	0.09	0.04 – 0.23	0 – 0.85
	3	0.09	0.03 – 0.24	0 – 3.28
	4	0.06	0.03 – 0.18	0 – 0.52

*Indicates a significant difference. The number in superscript indicates with which time period the significant differences occurred

When frequency of social interactions given were analysed within dyads there were significant differences between the time periods for physical ($\chi^2(3)=11.912$, $p<0.01$) and non-physical ($\chi^2(3)=76.188$, $p<0.001$) positive interactions, and negative non-physical interactions ($\chi^2(3)=15.544$, $p<0.01$). There were no significant differences in frequency of physical negative interactions across the study periods ($p>0.05$). Median values at the time points for each interaction type are provided in Table 4.6. Differences were found between period 1 and period 4 for positive physical interactions ($Z=-3.198$, $p<0.01$). Non-physical positive interactions differed between time period 1 and the other three time periods (period 2: $z=-5.531$, $p<0.001$; period 3: $z=-7.951$, $p<0.001$; period 4: $z=-5.086$, $p<0.001$), between time period 2 and 3 ($z=-4.755$, $p<0.001$) and between time period 3 and 4 ($z=-2.944$, $p<0.01$). For non-physical negative interactions differences were recorded between time period 1 and the other three time periods (period 2: $z=-3.157$, $p<0.01$; period 3: $z=-3.029$, $p<0.01$; period 4: $z=-4.037$, $p<0.001$).

Table 4.5. Median percentage of social interactions given within elephant dyads

Interaction type	Time period	Median	IQR	Range (%)
Positive physical	1 ^{*4}	0	0 – 0.15	0 – 7.52
	2	0	0 – 0.07	0 – 12.01
	3	0	0 – 0.16	0 – 8.89
	4 ^{*1}	0.03	0 – 0.71	0 – 11.65
Negative physical	1	0	0 – 0	0 – 0.23
	2	0	0 – 0	0 – 0.15
	3	0	0 – 0	0 – 0.09
	4	0	0 – 0	0 – 0.48
Positive non-physical	1 ^{*234}	0.27	0 – 0.97	0 – 17.16
	2 ^{*13}	0.13	0 – 0.53	0 – 10.81
	3 ^{*124}	0.07	0 – 0.27	0 – 10.81
	4 ^{*13}	0.13	0.12 – 0.31	0 – 6.14
Negative non-physical	1 ^{*234}	0	0 – 0.06	0 – 0.76
	2 ^{*1}	0	0 – 0.04	0 – 0.85
	3 ^{*1}	0	0 – 0.03	0 – 3.28
	4 ^{*1}	0	0 – 0.03	0 – 0.44

*Indicates a significant difference. The number in superscript indicates with which time period the significant differences occurred

At Zoo E a calf was born part way through the period of data collection. To investigate the effect this had on the behaviour of the herd an additional comparison was made between the periods pre- and post-calf. There was no change in the frequency of physical positive (median, IQR: 0.53%, 0 – 5.13 pre; 0.84%, 0 – 6.36 post) ($Z=-0.114$, $p>0.05$) and physical negative (median, IQR: 0%, 0 – 0.06 pre; 0%, 0 – 0.05 post) ($Z=-0.533$, $p>0.05$) interactions by herd members before and after the birth of the calf, nor was there a change in the frequency of non-physical negative interactions (median, IQR: 0.04%, 0.04 – 0.09 pre; 0.04%, 0 – 0.10 post) ($Z=-0.800$, $p>0.05$). However there was a significant reduction in the frequency of non-physical positive interactions observed following the birth of the calf (median, IQR: 7.05%, 0.54 – 11.8 pre; 0.96%, 0.12 – 1.9 post) ($Z=-3.067$, $p<0.05$) (Figure 4.3 & Figure 4.4). In terms of dyadic interactions there was no significant change in positive physical interactions pre- and post-birth (median, IQR: 0.1%, 0 – 0.53 pre; 0.09%, 0 – 0.8 post) ($Z=-1.017$, $p>0.05$), nor negative physical interactions (median, IQR: 0%, 0 – 0 pre; 0%, 0 – 0 post) ($Z=-1.014$, $p>0.05$) or negative non-physical interactions (median, IQR: 0%, 0 – 0.005 pre; 0%, 0 – 0.02 post) ($Z=-0.121$, $p>0.05$). Positive non-physical interactions were less frequent amongst the dyads following the birth of the calf (median, IQR: 0.36%, 0.13 – 2.78 pre; 0.1%, 0.06 – 0.15 post) ($Z=-4.895$, $p<0.001$).

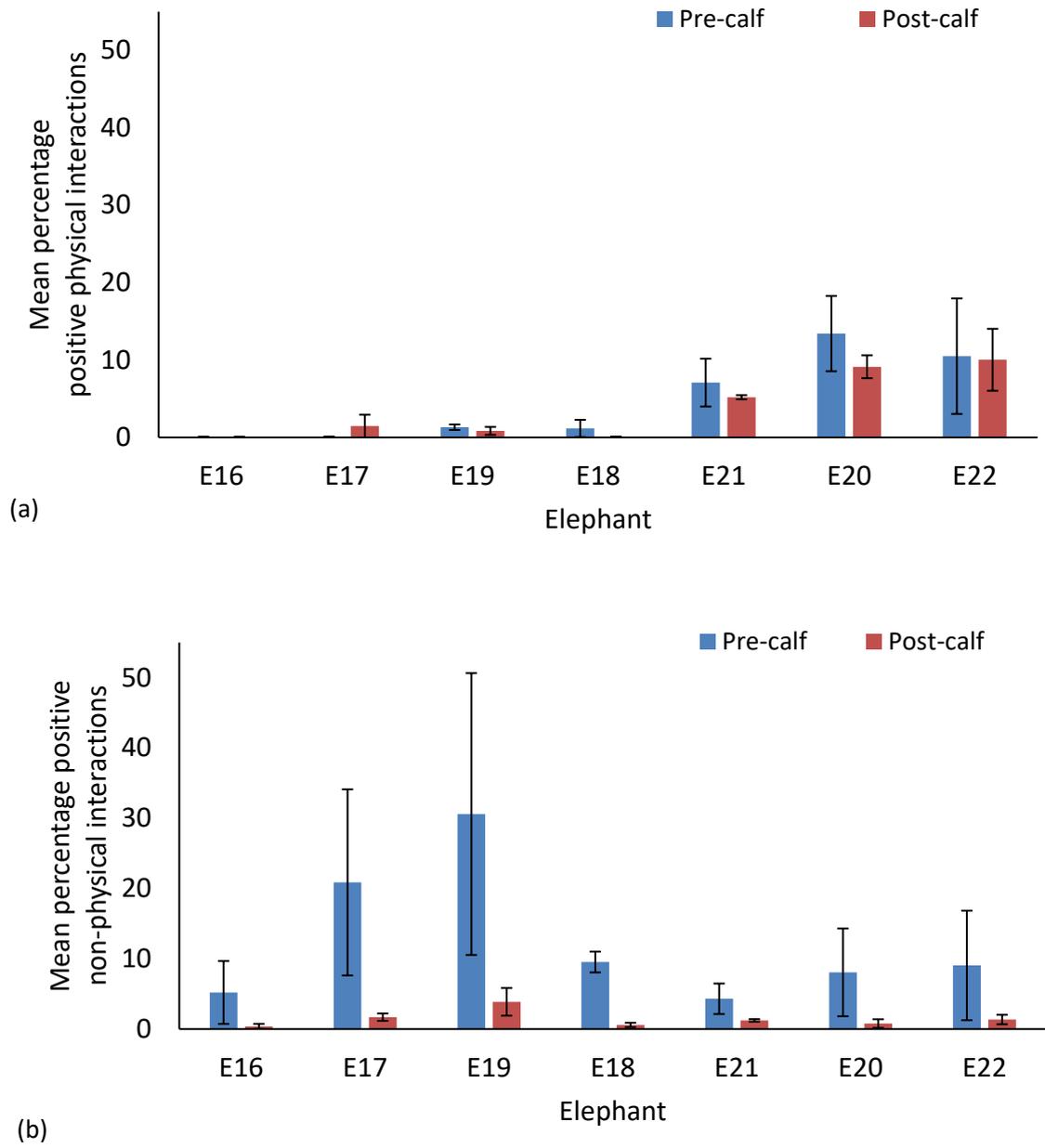


Figure 4.3. Change in positive social interactions given by each elephant in the herd at Zoo E, pre- and post- the birth of the calf. E19 was mother of the calf

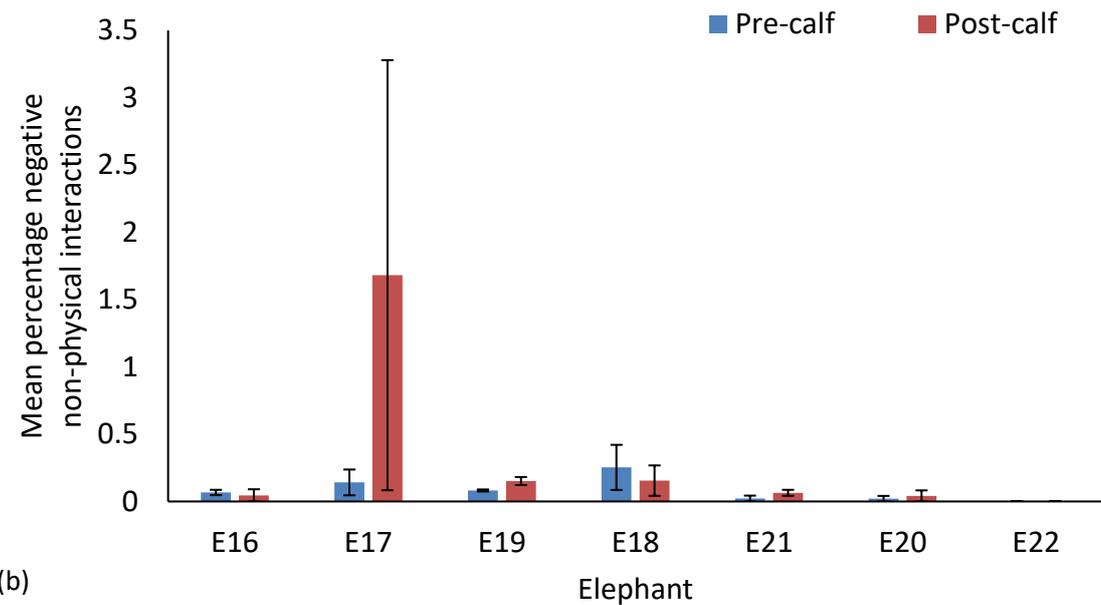
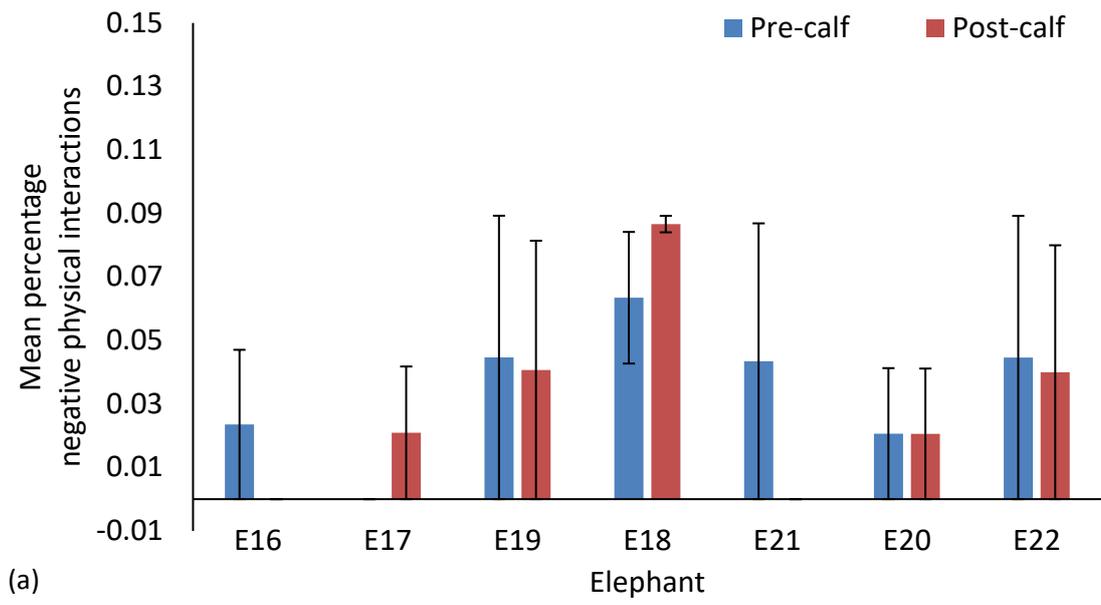


Figure 4.4. Change in negative social interactions given by each elephant in the herd at Zoo E, pre- and post- the birth of the calf. E19 was mother of the calf.

4.3.2.1 Herd social matrices

Zoo A was not included in this section of the analysis as one of the two elephants in the group was euthanised after the first month of data collection. A calf (E23) was born at Zoo E half way through data collection. Because data was missing from some of the study months, the calf was also excluded from this section of the analysis. All other elephants were included in the association matrices. The findings are detailed on zoo by zoo basis in Table 4.7 and Table 4.8. The positive non-physical social interaction network at Zoo G was the only network to remain consistent across all three comparison points. Elephants at Zoos B, D and E showed no stability in their positive interaction networks over time. The negative physical and non-physical networks were stable at Zoo C across all comparison points. The stability of the negative physical network could not be fully analysed at Zoos D, E and F due to an absence of negative physical interactions.

Table 4.6. Mantel test correlation scores showing stability over time for positive social interactions in the study herds

Zoo	Comparison points					
	Positive physical			Positive non physical		
	1	2	3	1	2	3
A	N/A	N/A	N/A	N/A	N/A	N/A
B	NS	NS	NS	NS	NS	NS
C	r=0.9834**	NS	NS	NS	NS	r=0.7289*
D	NS	NS	NS	NS	NS	NS
E	NS	NS	NS	NS	NS	NS
F	NS	r=0.8279*	NS	NS	NS	r=0.9113*
G	r=0.9204***	NS	NS	r = 0.9206*	r = 0.8353*	r=0.9444*

N/A: Mantel tests were not calculated for Zoo A due to the death of E2 following the first month of data collection.

Significance values are indicated by *p<0.05, **p<0.01, ***p<0.001

Table 4.7. Mantel test correlation scores showing stability over time for negative social interactions in the study herds

Zoo	Comparison Points					
	Negative physical			Negative non physical		
	1	2	3	1	2	3
A	N/A	N/A	N/A	N/A	N/A	N/A
B	N/A	NS	NS	NS	NS	NS
C	r=0.6784*	r=0.8668**	r=0.93**	r=0.6346*	r=0.6478*	r=0.5476*
D	N/A	N/A	N/A	NS	NS	NS
E	NS	N/A	N/A	NS	NS	NS
F	N/A	N/A	NS	NS	NS	NS
G	NS	NS	NS	NS	NS	NS

N/A: Physical negative interactions could not be analysed due to no occurrence of these interactions in one of the matrices. Mantel tests were not calculated for Zoo A due to the death of E2 following the first month of data collection.

Significance values are indicated by *p<0.05, **p<0.01, ***p<0.001

Significant values presented in Table 4.7 and Table 4.8 represent correlations in the social interaction matrices at the comparison points, suggesting that behaviour in terms of frequency of interaction within dyads remained consistent for the entire herd at the compared data collection points. Non-significant values (NS) suggest that social interactions (in terms of dyadic interactions of the whole herd) differed over time. At Zoo B physical interactions were only recorded between two members of the herd. The third member of the herd did not engage in any physical interactions during the study. At Zoo E, part way through the study a calf was born. To assess the effect of this birth data were investigated in terms of pre-calf birth and post-calf birth. There was no correlation for positive or negative physical interaction matrices pre- and post-calf, or non-physical positive interactions. Non-physical negative behaviours were correlated between the pre- and post-birth periods ($r=0.57$, $p<0.05$).

4.3.3 Social networks

Networks were visualised for the four separate behavioural categories: positive physical, negative physical, positive non-physical and negative non-physical social interactions. For the majority of the study zoos the highest frequency of positive physical interactions was given or received by the matriarch, or elephant considered by keepers to be the most dominant in the group. The only exception to this was at Zoo E where the greatest frequency of interactions was observed between a male and female calf (half-siblings). The highest frequency of positive non-physical interactions was observed at Zoos C and E. At Zoo E the greatest frequency of interactions was from an adult female to her maternal half-sister and at Zoo C between mother and daughter. No physical interactions (negative or positive) were observed between the elephants at Zoo A.

4.3.3.1 Reciprocity in dyads

Interactions in the whole herd network were considered balanced if mantel tests revealed significant correlation between the matrix of social interactions and the inverse matrix. A summary of mantel test correlation scores for each study zoo are provided in Table 4.9. The most balanced network across all study zoos was the positive physical network. Negative physical networks were not balanced at any of the study zoos. The positive non-physical interaction network was only balanced at Zoo C and the negative non-physical interaction was only balanced at Zoos C and E.

Table 4.8. Mantel test correlation scores showing dyadic reciprocity in the study herds

Zoo	Physical		Non-physical	
	Positive	Negative	Positive	Negative
A	N/A	N/A	N/A	N/A
B	NS	NS	NS	NS
C	r=0.8455*	NS	r=0.8965**	r=0.8551*
D	NS	NS	NS	NS
E	r=0.5341**	NS	NS	r=0.6821**
F	r=0.9761*	NS	NS	NS
G	r=0.9348*	NS	NS	NS

N/A: No physical interactions were observed at Zoo A. Mantel test statistics could not be performed on the data entered for non-physical interactions.

Significance values are indicated by *p<0.05, **p<0.01, ***p<0.001

Within each study a number of dyadic interactions were considered to be approximately balanced (Table 4.10). At Zoos A and B there were no balanced dyads in any of the social networks. At Zoo D only the non-physical networks had balanced interactions between one of the dyads. Zoos C, E and F had balanced dyads in all of the four social networks. In all of these instances the greatest number of approximately balanced dyads was in the non-physical positive network. Zoo G had balanced dyads for all but the physical negative interaction network.

Table 4.9. Dyadic interactions considered to be balanced (assessed using simple ratios) in the study herds

Zoo	Physical positive		Physical negative		Non-physical positive		Non-physical negative	
A	-	-	-	-	-	-	-	-
B	-	-	-	-	-	-	-	-
C	E6 – E10 E7 – E8 E8 – E9	Unrelated Unrelated Related	E6 – E10 E6 – E11 E7 – E8 E7 – E9	Unrelated Unrelated Unrelated Related	E6 – E8 E6 – E9 E6 – E10 E6 – E11 E7 – E8 E7 – E10 E9 – E10 E10 – E11	Unrelated Unrelated Unrelated Unrelated Related Unrelated Related Related	E6 – E9 E6 – E10 E10 – E11	Unrelated Unrelated Related
D	-	-	-	-	E14 – E15	Unrelated	E14 – E15	Unrelated
E	E19 – E21 E18 – E22 E20 – E21	Related Related Related	E16 – E17	Related	E16 – E17 E16 – E18 E17 – E19 E18 – E19 E21 – E23 E22 – E23	Related Related Related Related Related Related	E16 – E21 E17 – E19 E17 – E20	Related Related Related
F	E24 – E25 E26 – E27	Unrelated Related	E24 – E25	Unrelated	E24 – E25 E24 – E26 E24 – E27 E25 – E27	Unrelated Related Unrelated Unrelated	E24 – E25 E26 – E27	Unrelated Related
G	E28 – E30 E28 – E31 E28 – E32 E29 – E30 E29 – E31 E30 – E31	Unrelated Unrelated Unrelated Related Unrelated Unrelated			E28 – E29 E28 – E31 E29 – E31 E30 – E32	Unrelated Unrelated Unrelated Unrelated	E29 – E31	Unrelated

4.3.3.2 Visualisation of social relationships through sociograms

Sociograms were used to create a visual representation of social relationships in the study herds. Interaction frequency is depicted using the thickness of the arrow. Directionality of the interactions is shown by numbers next to the nodes; numbers represent the mean frequency of interactions received by that elephant from the corresponding elephant. If no number is listed near the node then this elephant was not receiving an interaction within that dyad. If no line is present joining the two nodes this means that no interactions were observed in either direction throughout the period of the study. Betweenness was used as a measure of social connectedness. A higher value indicates a greater influence within the social group.

Zoo A

The two elephants were unrelated adult females (Table 4.11). Due to the death of E2 data could only be analysed from the first period of data collection (P1). Interactions during the first two months of data collection were unbalanced and relatively infrequent. No physical social interactions were observed between the two elephants. Non-physical positive interactions from E1 to E2 were on average over three times higher than the reverse (Figure 4.5). Negative non-physical interactions, which included walking away from another elephant were twice as high from E2 to E1 (Figure 4.5), indicating that E1 is the more dominant and sociable elephant.

Table 4.10. Zoo A: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E1 ^M	Adult	Female	None	ALL
E2	Adult	Female	None	ALL

^M denotes the matriarch or elephant considered to be the most dominant herd member

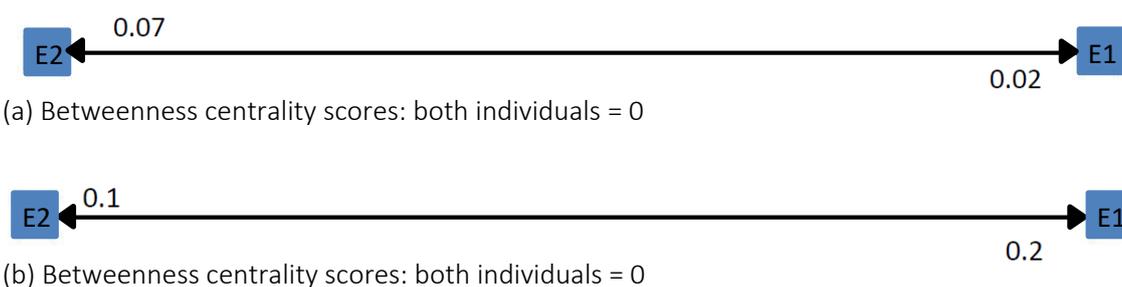


Figure 4.5. Sociograms depicting (a) non-physical positive interactions (b) non-physical negative interactions recorded at Zoo A.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. A higher number of non-physical positive interactions were given by the matriarch. Non-physical negative interactions were approximately equal.

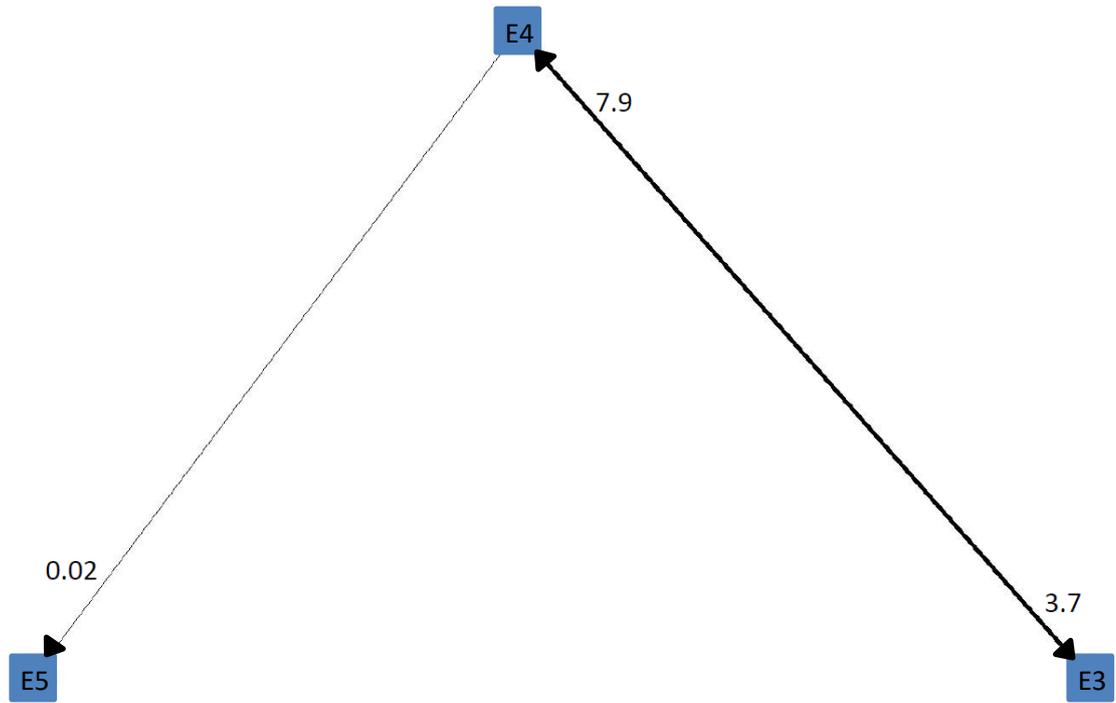
Zoo B

Elephants were unrelated adult females (Table 4.12). None of the dyads were balanced. This herd was separated during the daytime due to historic aggression between E3 and E4. Aggression started in 2013 following the death of another elephant in the herd. E4 and E5 were housed together in one section of the enclosure. E3 was housed alone in an adjacent enclosure although she could have tactile contact with E4 and E5 through the enclosure bars. The sociograms in Figure 4.6 indicate that E4 is the only elephant to engage in physical social interactions with both of the other elephants and so thus is considered central to the network. Limited interactions were observed between E5 and the rest of the herd, none of which were physical (Figure 4.6 & Figure 4.7).

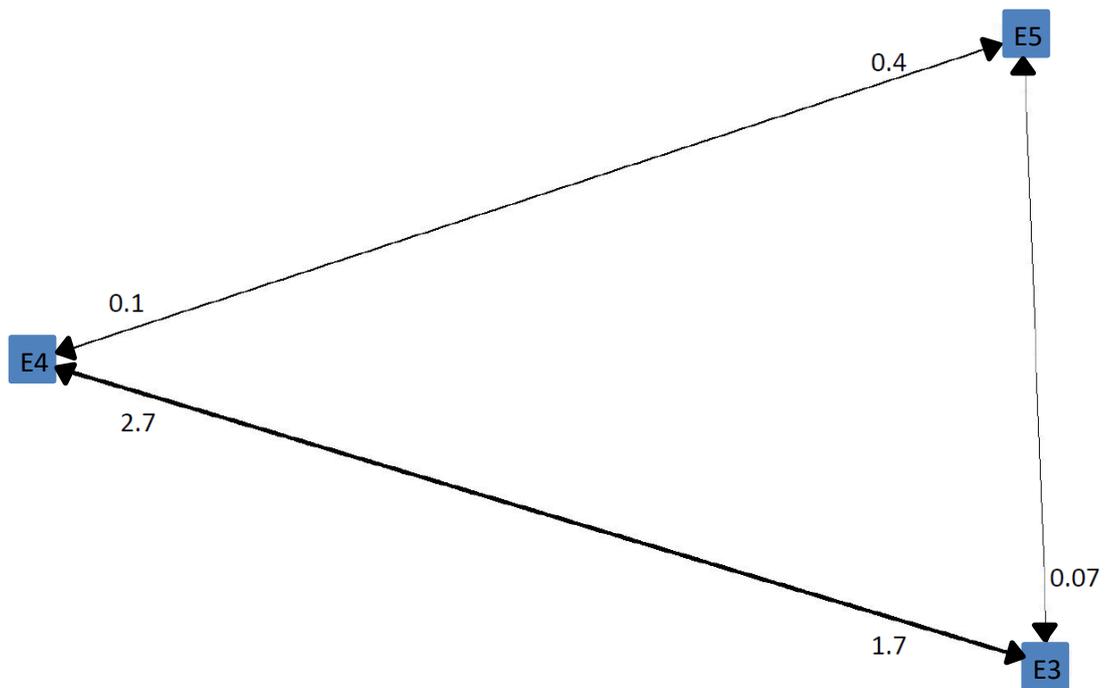
Table 4.11. Zoo B: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E3 ^M	Adult	Female	None	Alone at all times*
E4	Adult	Female	None	E5 (day), alone (night)*
E5	Adult	Female	None	E4 (day), alone (night)*

*Tactile contact possible through enclosure bars, ^M denotes the matriarch or elephant considered to be the most dominant herd member



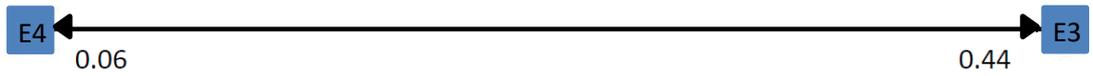
(a) Betweenness centrality scores: E3 = 1, E4 = 0, E5 = 0



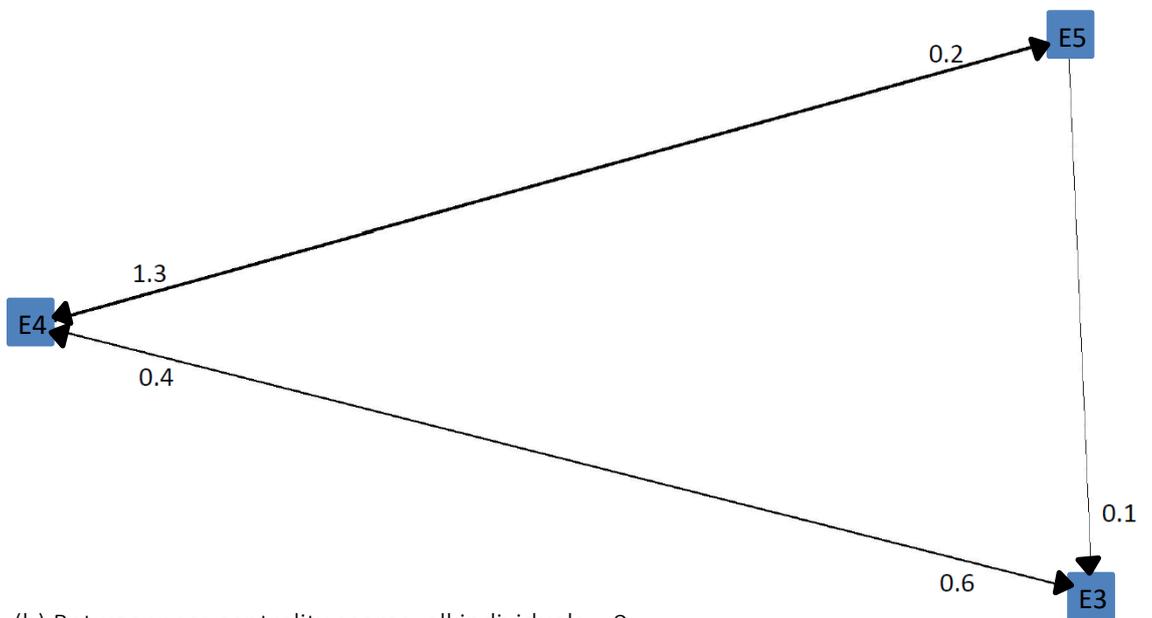
(b) Betweenness centrality scores: all individuals = 0

Figure 4.6. Sociograms depicting (a) physical positive interactions and (b) non-physical positive interactions at Zoo B.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. E4, considered by keepers to be matriarch, was most central to the positive physical network (identified via highest betweenness score). Betweenness scores were equal across the group for the positive non-physical network. E5 gave no physical interactions during the study.



(a) Betweenness centrality scores: all individuals = 0



(b) Betweenness centrality scores: all individuals = 0

Figure 4.7. Sociograms depicting (a) physical negative interactions and (b) non-physical negative interactions recorded at Zoo B.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Betweenness scores were equal across the group for both networks. E5 gave no physical negative interactions during the study.

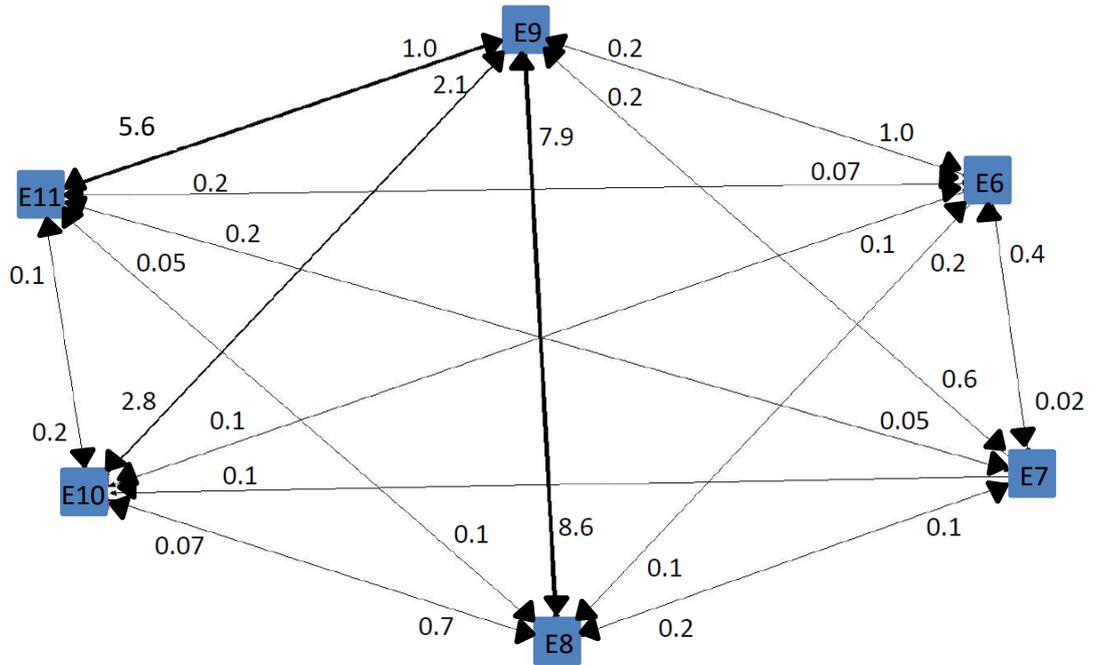
Zoo C

This herd contained a three generational family group, a breeding bull and an unrelated adult female (Table 4.13). In the negative non-physical network E6, E8, E10 and E11 are central to the network. Physical positive and non-physical positive and negative networks were all balanced (i.e. there is an equal spread of interactions between all individuals). The dyad with the greatest frequency of positive interaction was E8 and E9, a mother and her calf. The youngest herd member received most positive interactions (both physical and non-physical). An adult female (E11) received the most negative interactions (both physical and non-physical) from the other herd members. All members of the herd engaged with one another in the positive network whilst not all elephants received negative interactions (Figure 4.8 & 4.9).

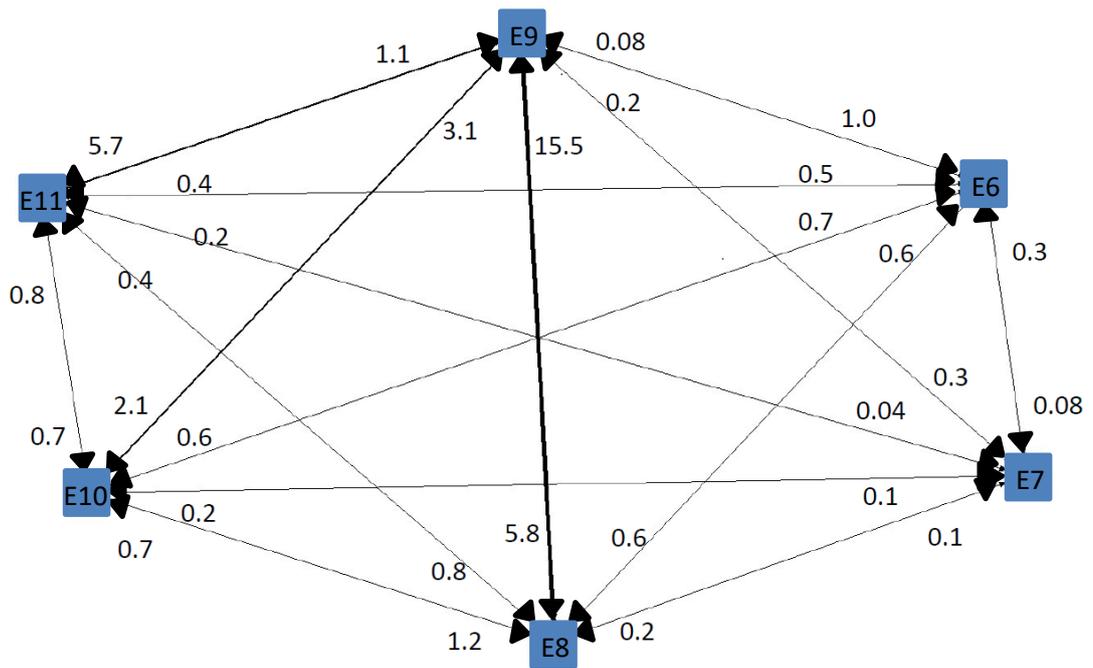
Table 4.12. Zoo C: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E6	Adult	Female	None	ALL (day), E8,9,10,11 (night)
E7	Adult	Male	Father to E9	ALL (day), alone (night)
E8 ^M	Adult	Female	Mother to E9 Mother to E10 Grandmother to E11	ALL (day), E6, E9,10,11 (night)
E9	Calf	Female	Daughter to E7 and E8 Sister to E10 Niece to E11	ALL (day), E7,8,10,11 (night)
E10	Adult	Female	Mother to E11 Sister to E9 Daughter to E8	ALL (day), E6,8,9,11 (night)
E11	Adult	Female	Granddaughter to E8 Daughter to E10 Aunt to E9	ALL (day), E6,8,9,10 (night)

^M denotes the matriarch or elephant considered to be the most dominant herd member



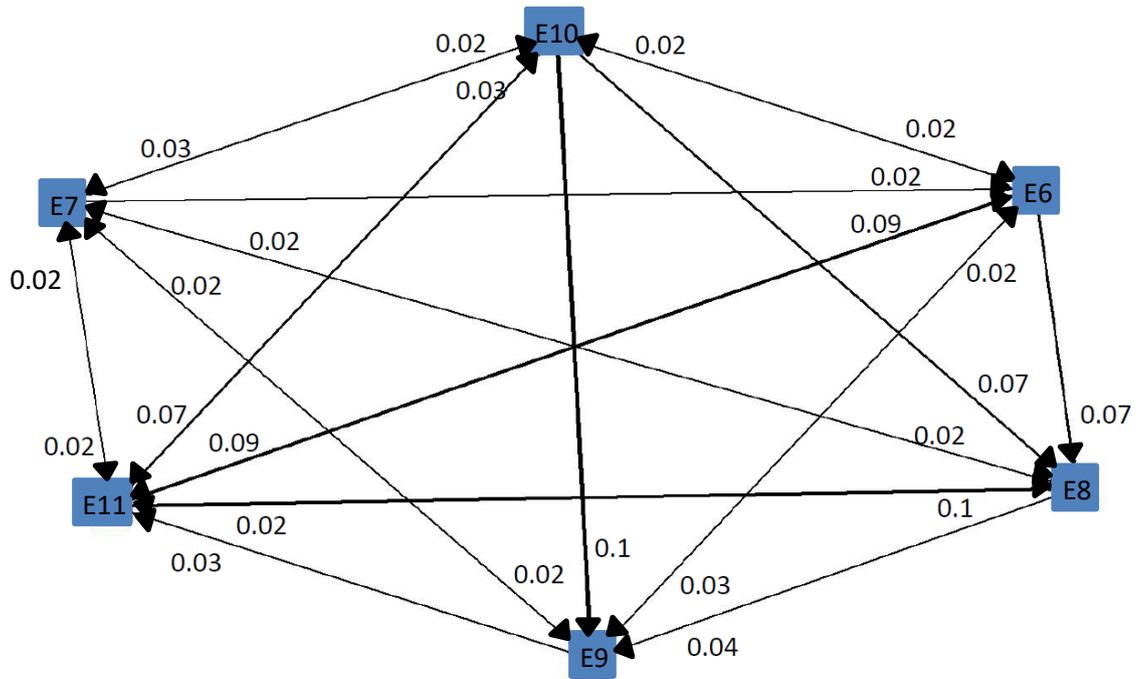
(a) Betweenness centrality scores: all individuals = 0



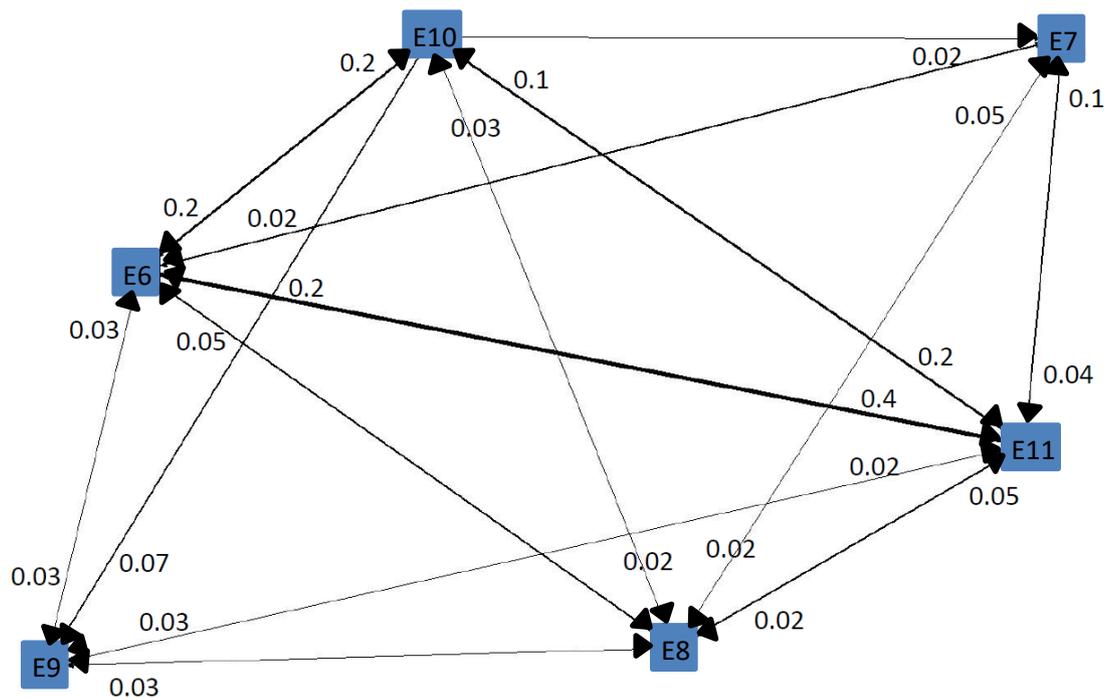
(b) Betweenness centrality scores: all individuals = 0

Figure 4.8. Sociograms depicting (a) physical positive interactions and (b) non-physical positive interactions at Zoo C.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. The greatest number of physical and non-physical interactions were between the matriarch and her calf (E8 & E9) although betweenness scores were equal across the group.



(a) Betweenness centrality scores: all individuals = 0



(b) Betweenness centrality scores: E6 = 0.25, E7 = 0, E8 = 0.25, E9 = 0, E10 = 0.25, E11 = 0.25

Figure 4.9. Sociograms depicting (a) physical negative interactions and (b) non-physical negative interactions at Zoo C.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Negative physical interactions were fairly low and evenly spread throughout the group (equal betweenness scores across all individuals). Negative non-physical interactions were greatest between E6 and E11, unrelated adult females. E6, E8, E10 and E11 were considered most central to the network (indicated via highest betweenness scores).

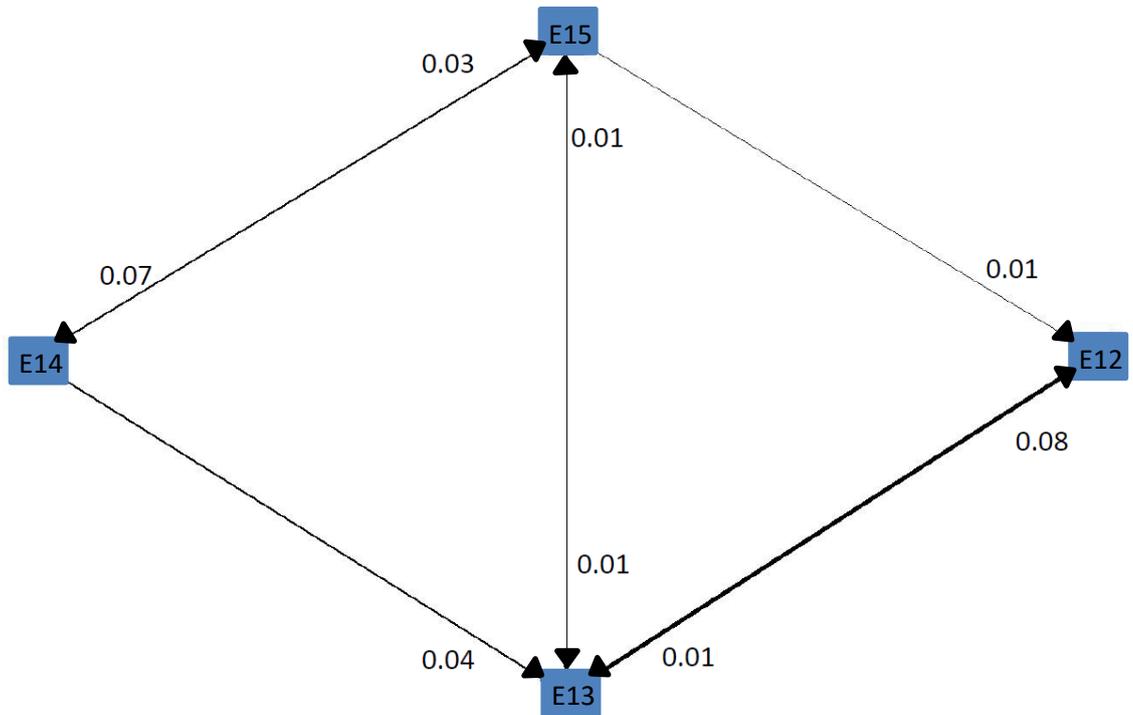
Zoo D

Four unrelated elephants were housed at Zoo D (1 male: 3 females) (Table 4.14). Elephants were split into two herds (E12 and E13, E14 and E15). E14 and E15 had 24-hour access to one another. E12 and E13 had unrestricted access to each other during the daytime, when they were housed in the outside paddock. Overnight they were housed alone, although they had the opportunity for tactile contact with one another and also with E14 and E15 through enclosure bars. The two groups did not have chance to engage in social interactions with elephants housed in the other social group during the day. None of the social interaction networks were balanced (Figure 4.10 & Figure 4.11). E12 and E14 directed more positive physical interactions than they received from their corresponding enclosure partners. E12 gave more non-physical positive interactions (e.g. approach) than he received, whereas E13 gave more non-physical negative interactions (e.g. walking away from) than she received as well as giving no negative physical interactions to E12, which is indicative of the social hierarchy. E15 directed positive non-physical interactions to E12 but received none in return. This was likely due to the enclosure setup, which enabled her to approach his pen in the inside enclosures.

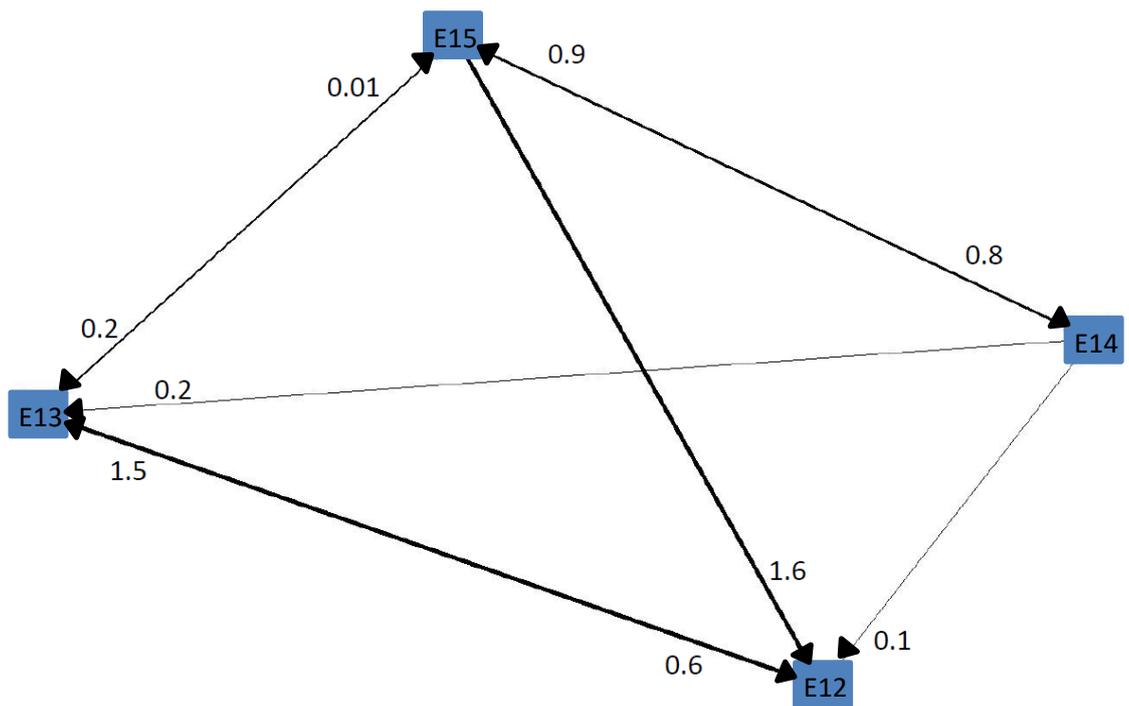
Table 4.13. Zoo D: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E12 ^M	Adult	Male	None	E12 (day), alone (night)*
E13	Adult	Female	None	E13 (day), alone (night)*
E14 ^M	Adult	Female	None	E15
E15	Adult	Female	None	E14

*Tactile contact possible with the rest of the herd overnight, ^M denotes the matriarch or elephant considered to be the most dominant herd member



(a) Betweenness centrality scores: all individuals = 0



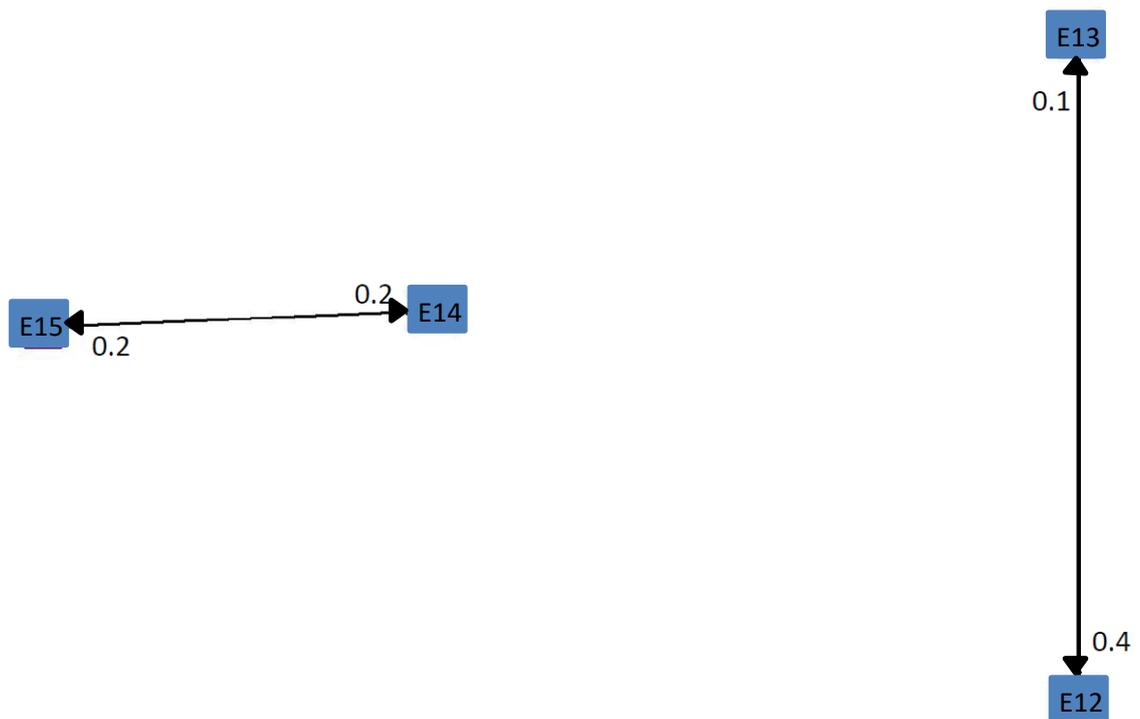
(b) Betweenness centrality scores: all individuals = 0

Figure 4.10. Sociograms depicting (a) physical positive interactions and (b) non-physical positive interactions at Zoo D. Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant.

E12, the adult bull, gave the most non-physical interactions to the female with which he was housed and received most non-physical interactions from another female. E14, the matriarch only received non-physical positive interactions from the female with which she was housed. Betweenness scores were equal in both networks.



(a) Betweenness centrality scores: E12 = 0.5, E13 = 0, E14 = 0.5, E15 = 0



(b) Betweenness centrality scores: all individuals = 0

Figure 4.11. Sociograms depicting (a) physical negative interactions and (b) non-physical negative interactions at Zoo D.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Negative interactions were only observed between elephants housed together. E12 and E14 were considered central to the physical negative network (indicated by highest betweenness scores). Interactions were equal in the non-physical negative network. Betweenness scores were equal in both networks.

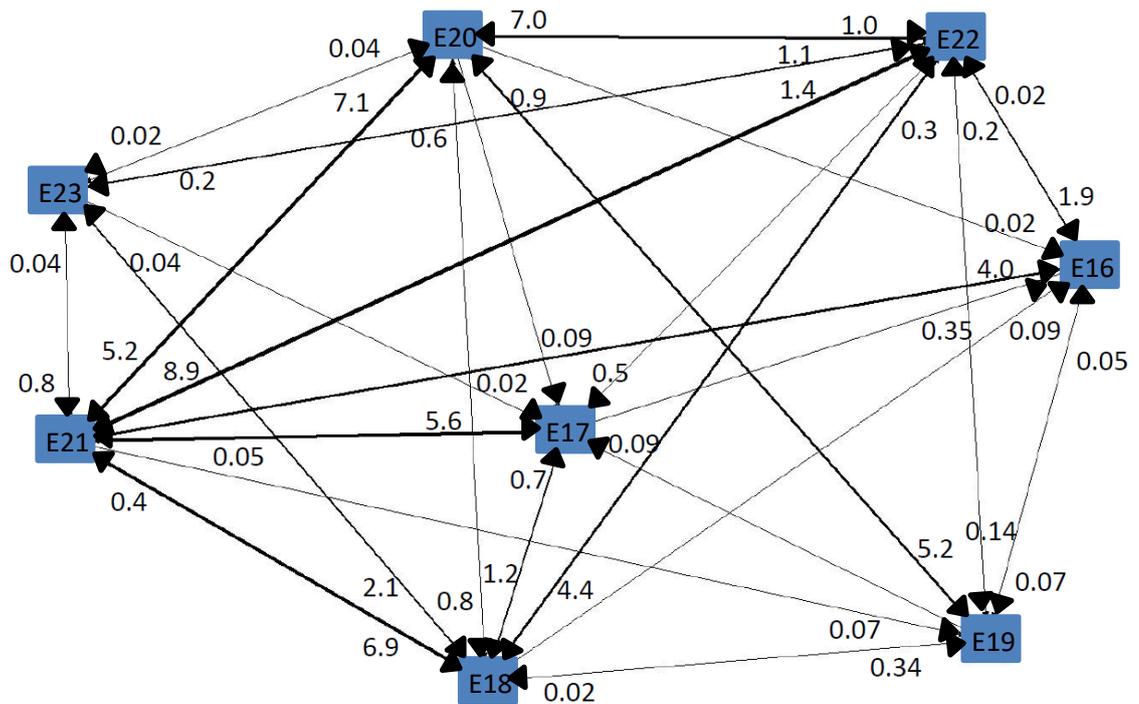
Zoo E

A herd replicating wild social groups comprising two full sisters and their offspring, and a breeding bull who had access to the females and young in the outside paddock were housed at Zoo E (Table 4.15). The positive network was more complicated than the negative network, and far more interlinked (Figure 4.12 & Figure 4.13). All individuals engaged with one another in the positive network however not all engaged in negative interactions. The positive physical network was balanced, as was the negative non-physical network. In the negative physical interaction network E21 (a young bull calf) received the most interactions. In the non-physical interaction network E22 and E23 received no interactions at all, whilst E18 was central to the network.

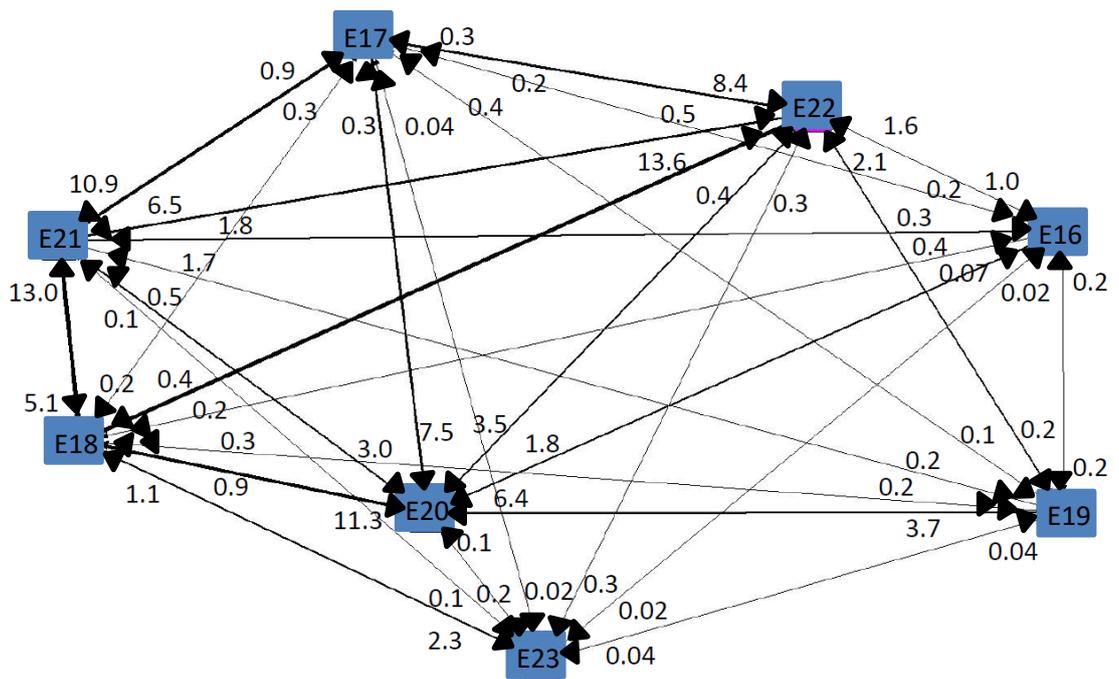
Table 4.14. Zoo E: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E16 ^M	Adult	Female	Sister to E17 Mother to E19,22	ALL
E17	Adult	Female	Sister to E16 Mother to E18,20	ALL
E18	Adult	Female	Mother to E21	ALL
E19	Adult	Female	Mother to E23	ALL
E20	Calf	Male	Son to E17 Half-sib to E21,22,23	ALL
E21	Calf	Male	Son to E18 Half-sib to E20,22,23	ALL
E22	Calf	Female	Daughter to E16 Half-sib to E20,21,23	ALL
E23	Calf	Female	Daughter to E19 Half-sib to E20,21,22	ALL

^M denotes the matriarch or elephant considered to be the most dominant herd member



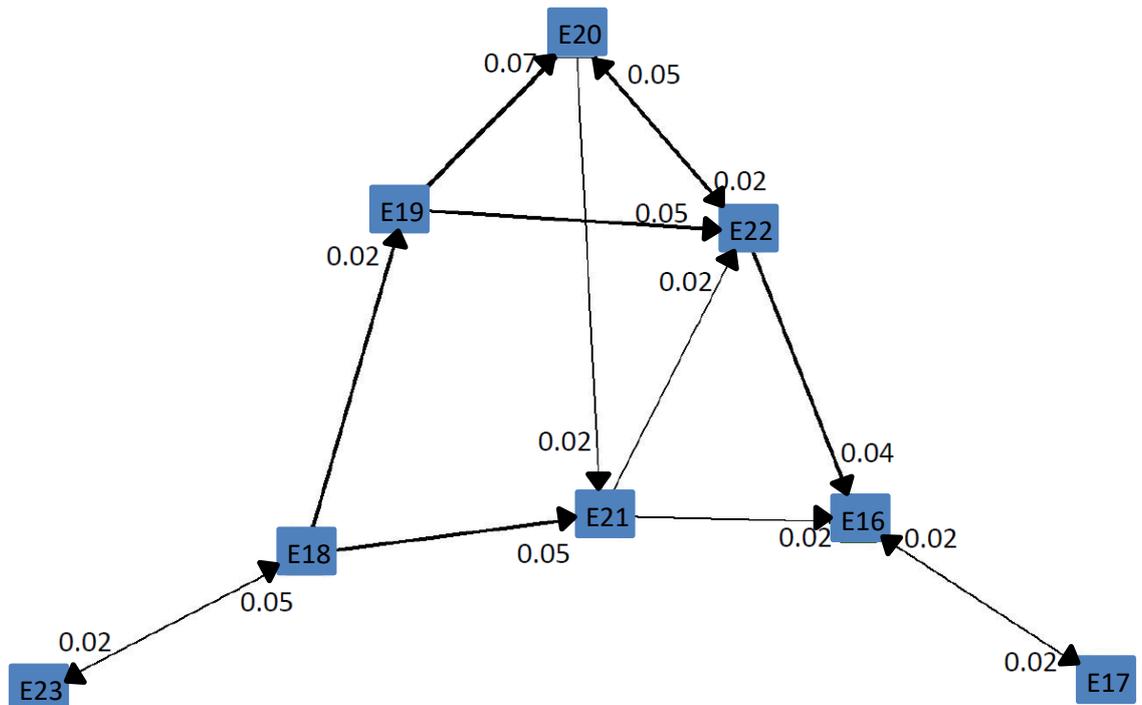
(a) Betweenness centrality scores: E16 = 0, E17 = 0.4, E18 = 0.4, E19 = 0, E20 = 0.4, E21 = 0.4, E22 = 0.4, E23 = 0



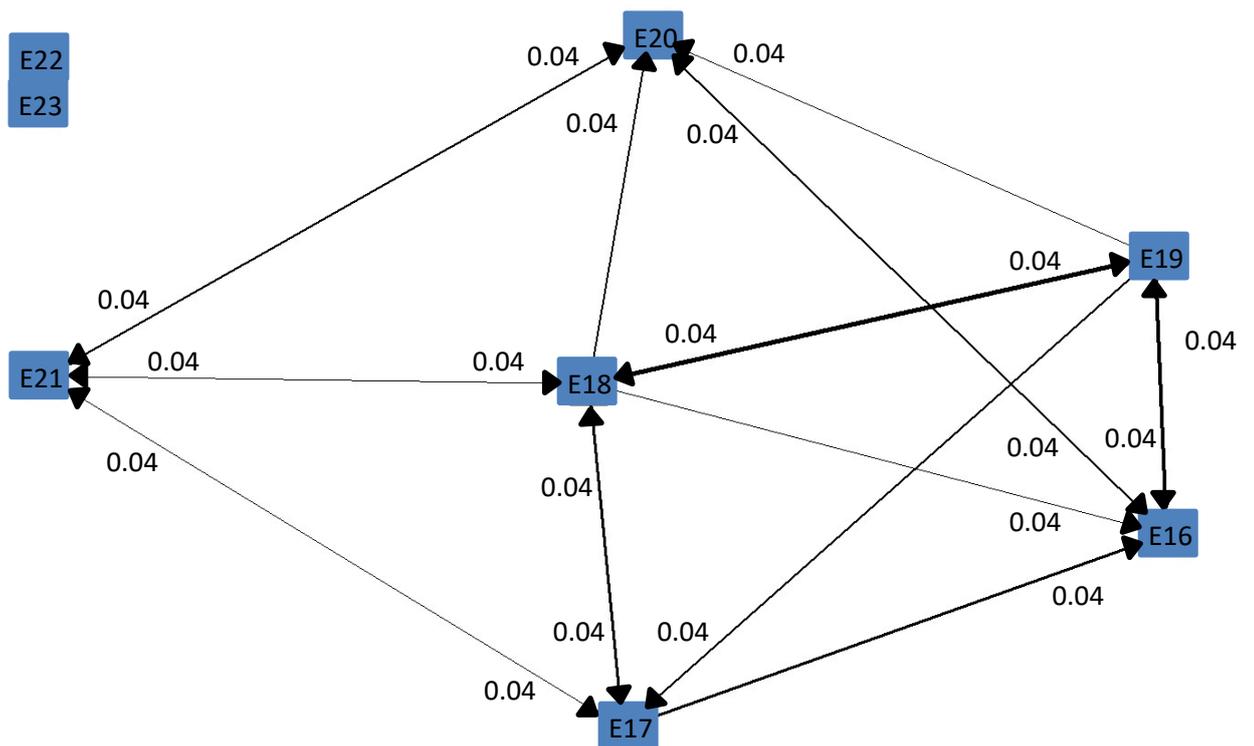
(b) Betweenness centrality scores: all individuals = 0

Figure 4.12. Sociograms depicting (a) physical positive interactions and (b) non-physical positive interactions at Zoo E

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. The networks are highly interlinked with calves giving and receiving most interactions. E17, E18, E20, E21 and E22 were central to the positive physical interaction network (indicated by highest betweenness scores). Non-physical positive interactions were equally distributed.



(a) Betweenness centrality scores: E16 = 6, E17 = 0, E18 = 6.33, E19 = 2, E20 = 0.33, E21 = 7, E22 = 3.33, E23 = 0



(b) Betweenness centrality scores: E16 = 0.25, E17 = 0.67, E18 = 0.92, E19 = 0.25, E20 = 0.67, E21 = 0.25, E22 = 0, E23 = 0

Figure 4.13. Sociograms depicting (a) physical negative interactions and (b) non-physical negative interactions at Zoo E.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Negative interactions were performed in low frequencies and did not include all members of the group. E21 was most central in the physical negative interaction network and E18 was most central in the non-physical

network (indicated by highest betweenness score). E22 and E23 did not give or receive any negative non-physical interactions.

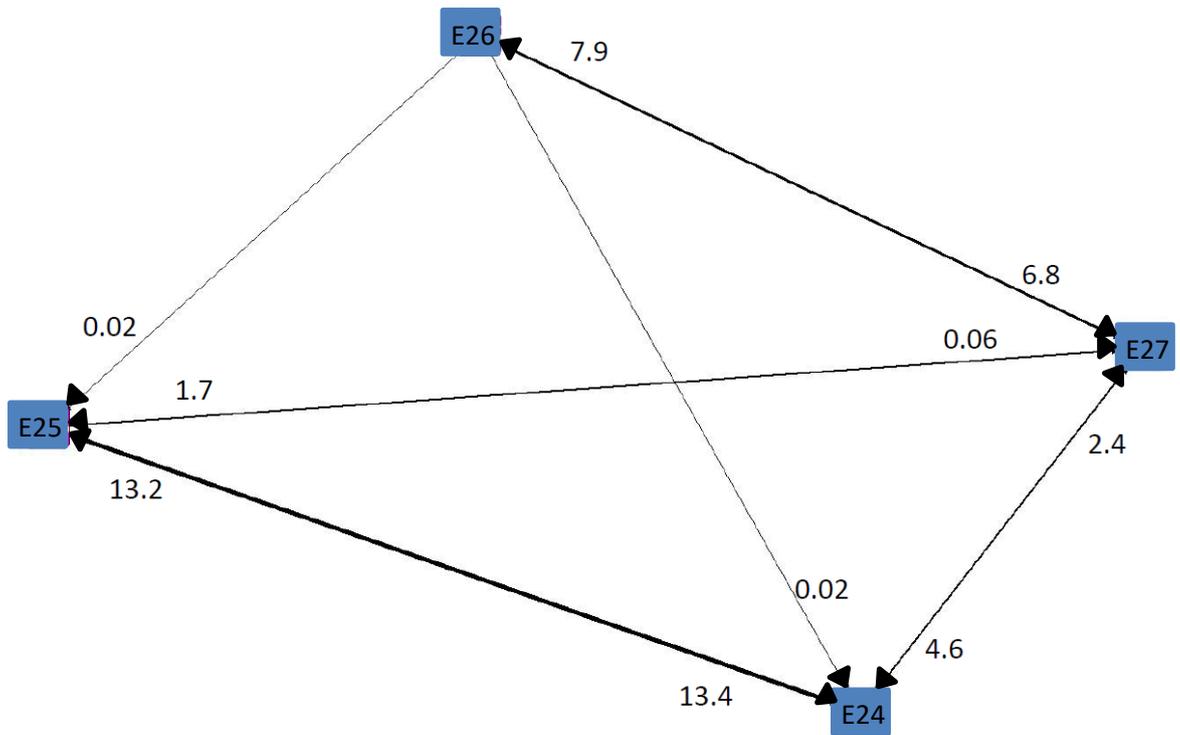
Zoo F

The herd at Zoo F was four cows; two adults and two sub-adults (Table 4.16). The two sub-adults had the same sire. E26 and E27 were mother and daughter. E24 and E25 were a sub-adult and the matriarch, who had taken the role of surrogate mother to E24 following her mother's euthanasia in 2015 (Cunningham pers. comm., 2015). The positive physical interaction network was the only network to show balance within dyads. The positive and negative physical interaction networks predominantly showed the group split as two pairs (E24 and E25, and E26 and E27) (Figure 4.14 & Figure 4.15). In the positive non-physical social interaction network E27 received the greatest number of interactions, from her daughter, E26. In the negative non-physical social interaction network E27 received the most interactions from E24, an unrelated elephant.

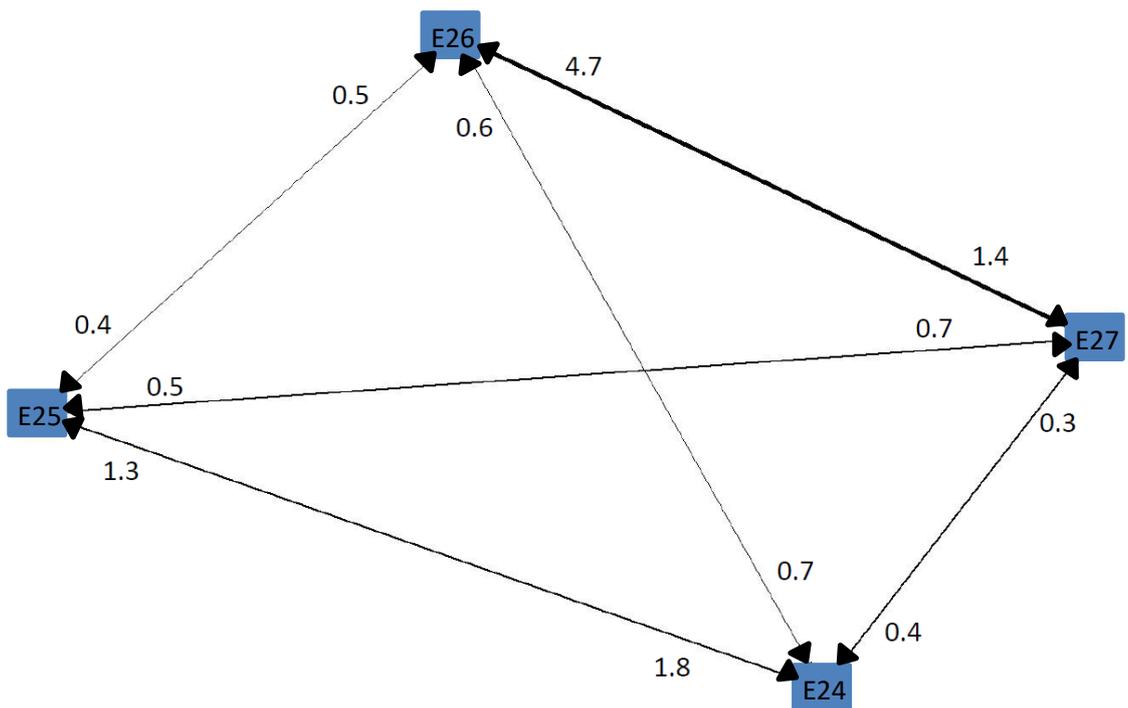
Table 4.15. Zoo F: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E24	Sub-Adult	Female	Half-sib to E26	ALL
E25 ^M	Adult	Female	None	ALL
E26	Sub-Adult	Female	Daughter to E27 Half-sib to E24	ALL
E27	Adult	Female	Mother to E26	ALL

^M denotes the matriarch or elephant considered to be the most dominant herd member



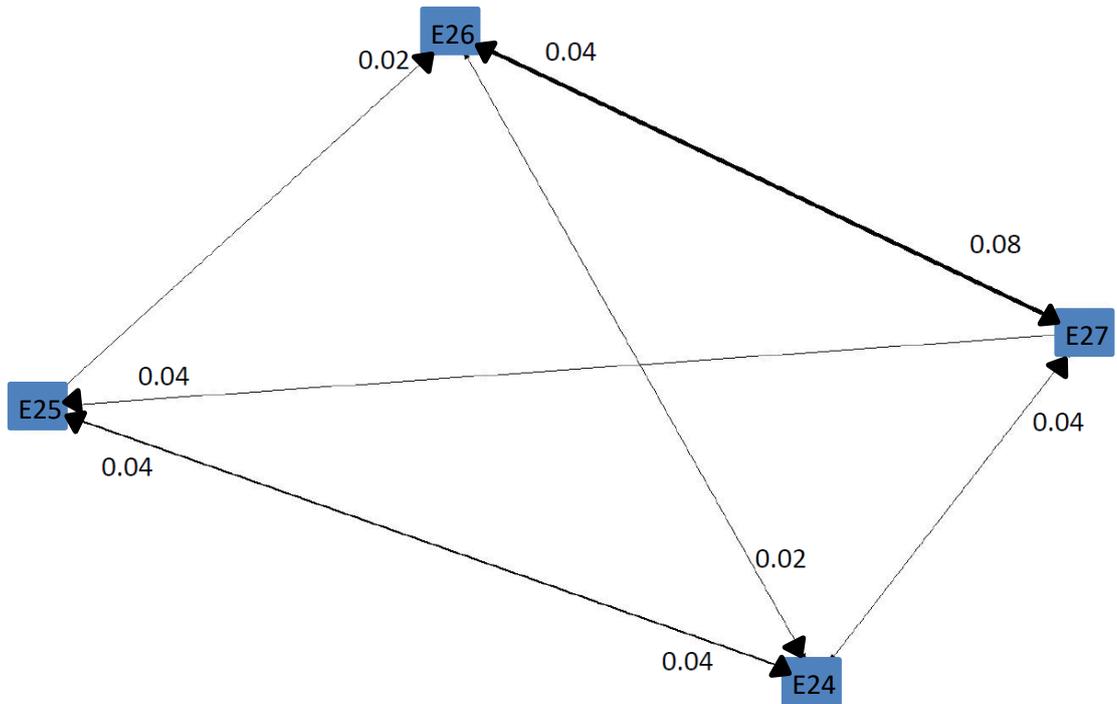
(a) Betweenness centrality scores: all individuals = 0



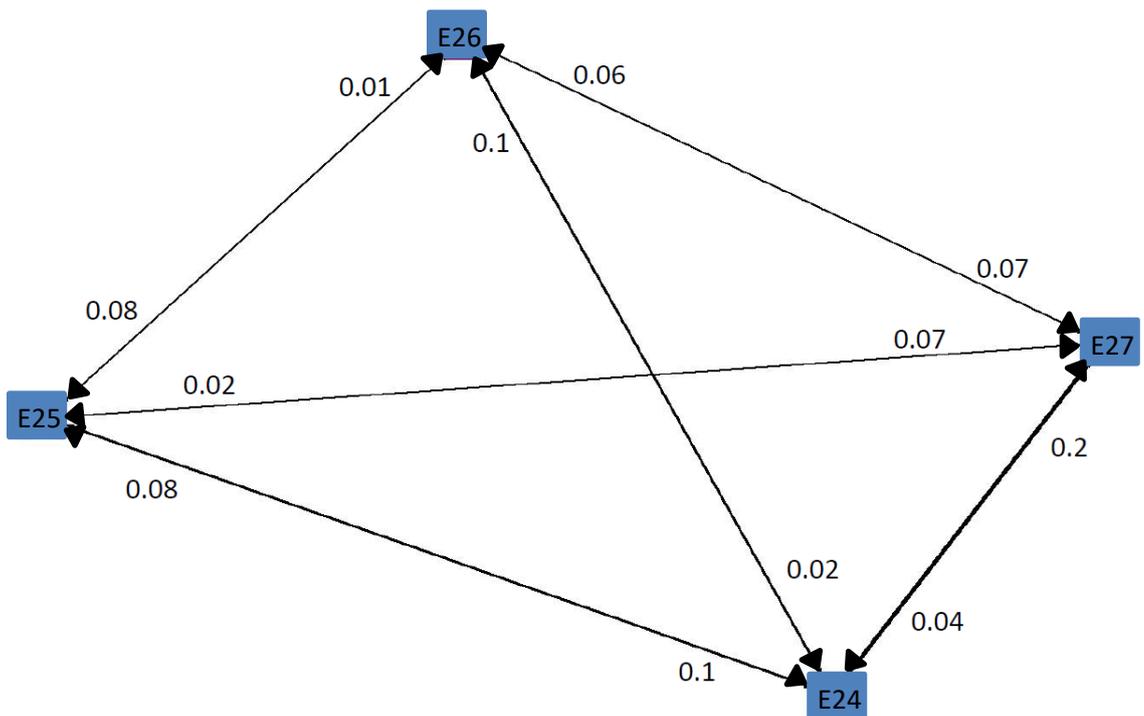
(b) Betweenness centrality scores: all individuals = 0

Figure 4.14. Sociograms depicting (a) physical positive interactions and (b) non-physical positive interactions at Zoo F.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Interactions were greatest between the two dyads (mother/surrogate mother – daughter), interactions were seen across the whole group but they were less frequent. Betweenness scores were equal in both networks.



(a) Betweenness centrality scores: all individuals = 0



(b) Betweenness centrality scores: all individuals = 0

Figure 4.15. Sociograms depicting (a) physical negative interactions and (b) non-physical negative interactions at Zoo F.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Physical negative interactions were greatest between the two dyads (mother/surrogate mother – daughter). Non-physical negative interactions were more evenly distributed across the group. Betweenness scores were equal in both networks.

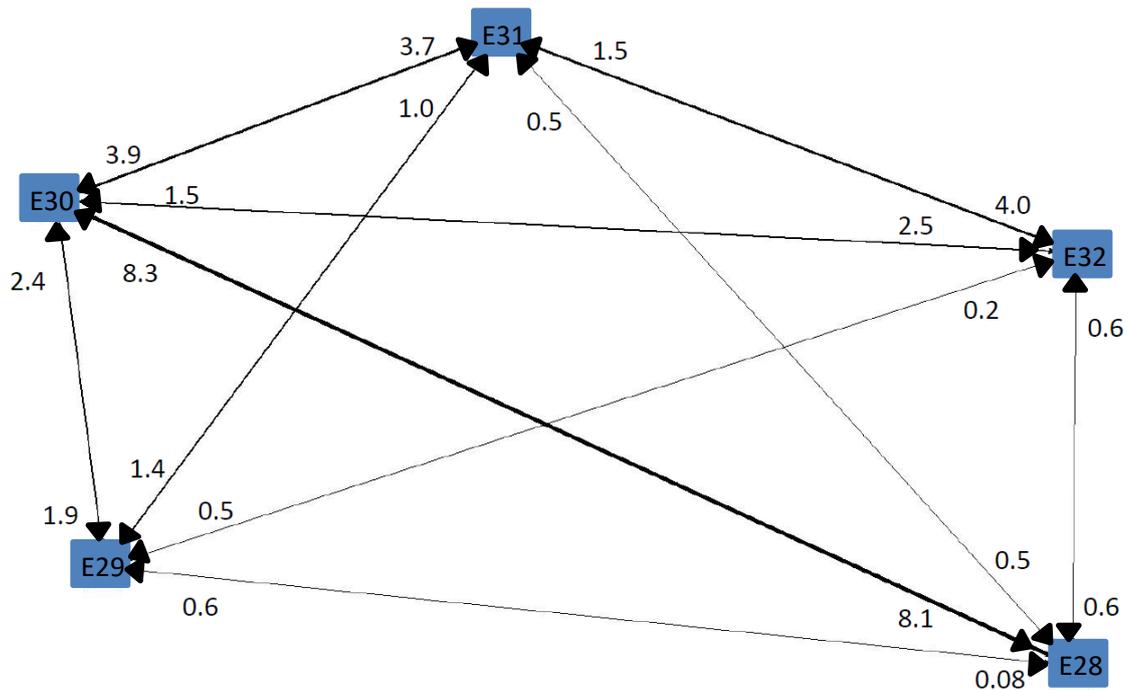
Zoo G

Zoo G held two mother-daughter pairs and an unrelated matriarch (Table 4.17). The positive physical interaction network was the only network to show balance in the dyads. The most positive interactions (physical and non-physical) were received by the infant. The most positive physical social interactions were between the infant and the matriarch (Figure 4.16). The greatest frequency of negative physical interactions was between E28 and E29. In the negative non-physical interaction most interactions were given from E28 (the matriarch) to E29 (mother of the infant) and from E29 to E32 (the eldest in the herd) (Figure 4.17).

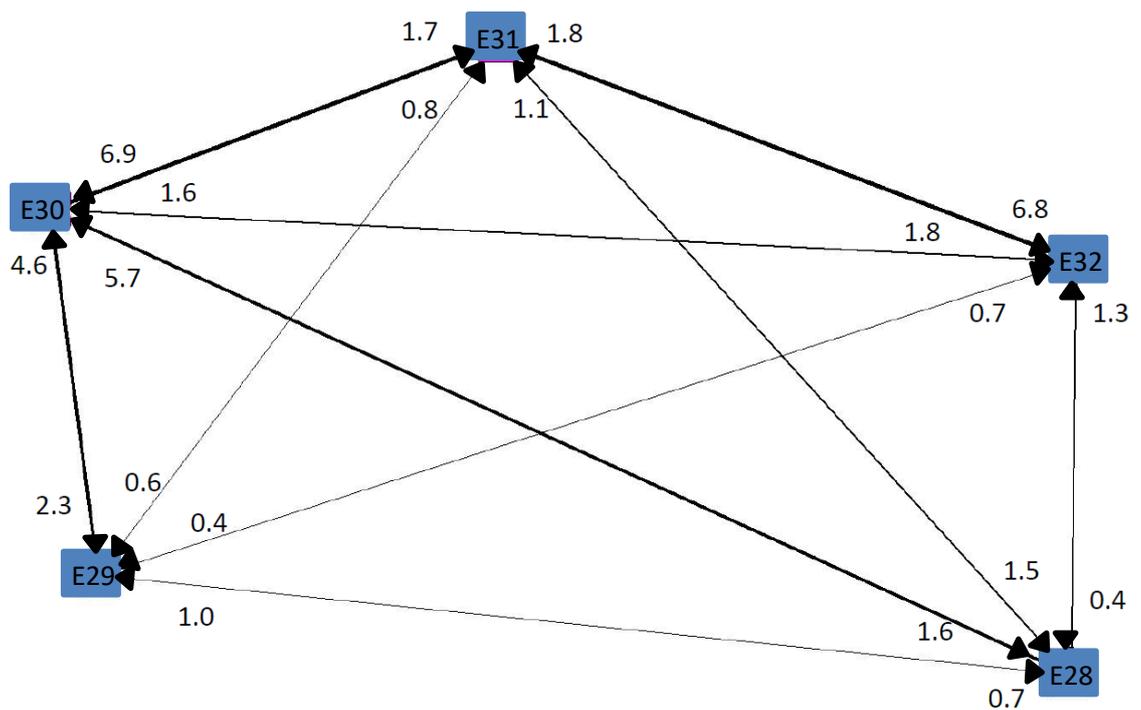
Table 4.16. Zoo G: Table of relatedness

Elephant	Age	Sex	Related to	Housed with
E28 ^M	Adult	Female	None	ALL
E29	Adult	Female	Mother to E30	ALL
E30	Infant	Female	Daughter to E29	ALL
E31	Adult	Female	Daughter to E32	ALL
E32	Adult	Female	Mother to E31	ALL

^M denotes the matriarch or elephant considered to be the most dominant herd member



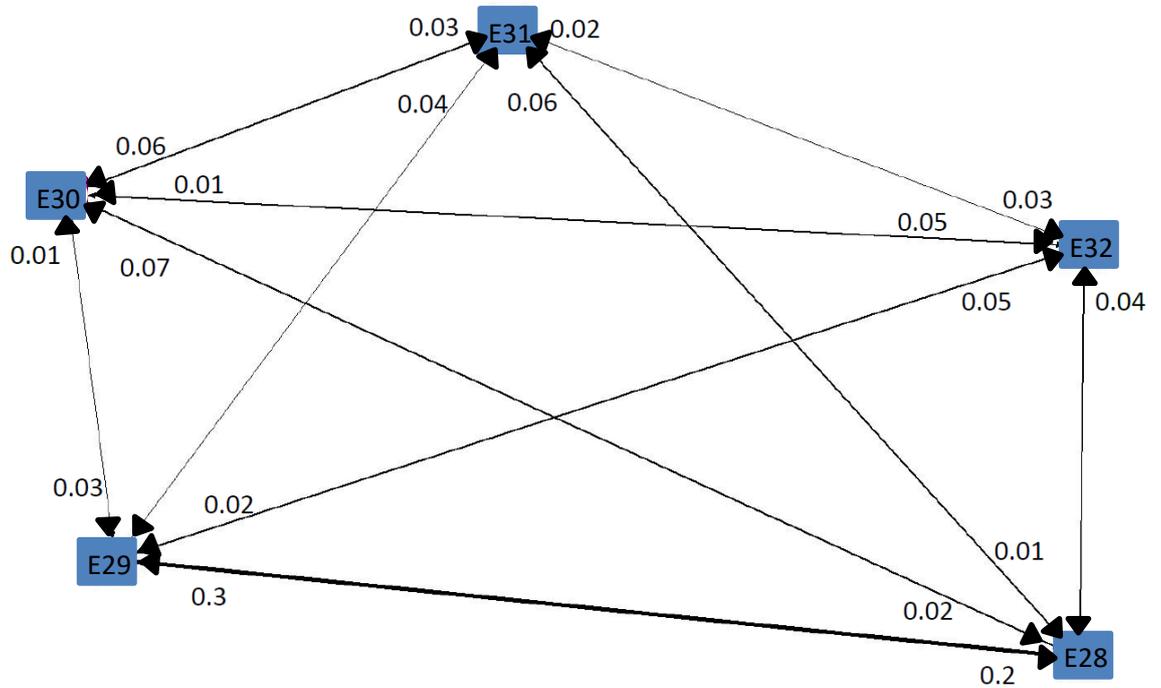
(a) Betweenness centrality scores: all individuals = 0



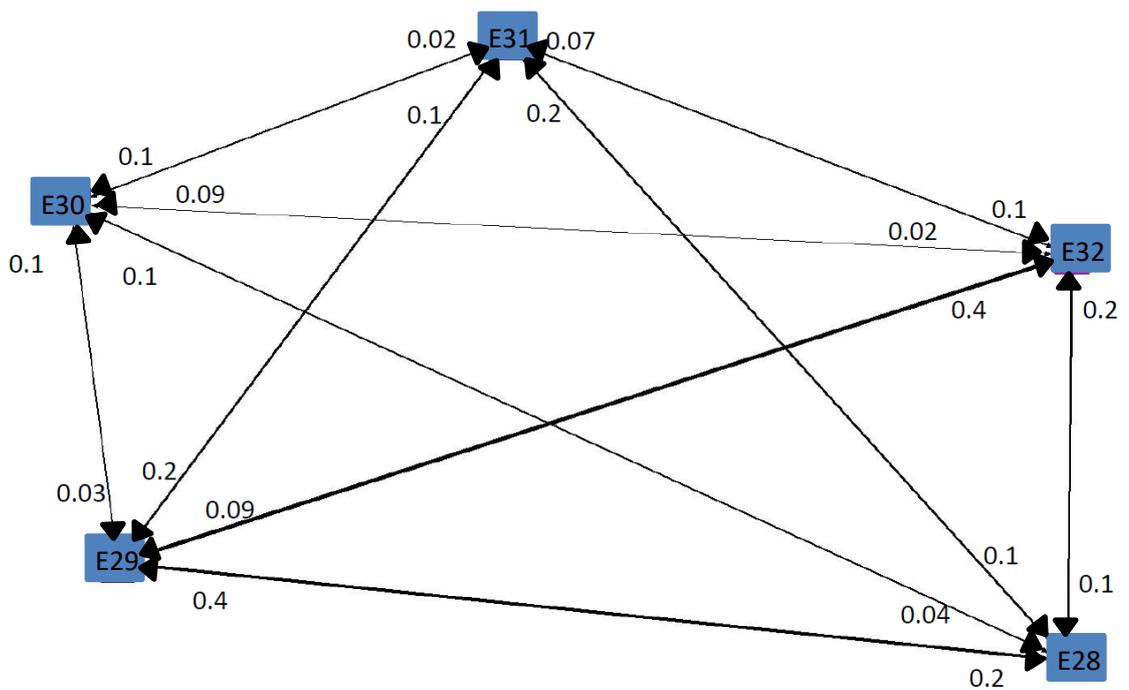
(b) Betweenness centrality scores: all individuals = 0

Figure 4.16. Sociograms depicting (a) physical positive interactions and (b) non-physical positive interactions at Zoo G.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. Physical positive interactions were greatest between the matriarch and an unrelated infant. Non-physical interactions were highest between the matriarch and an unrelated infant and the infant and her mother. Betweenness scores were equal in both networks.



(a) Betweenness centrality scores: all individuals = 0



(b) Betweenness centrality scores: all individuals = 0

Figure 4.17. Sociograms depicting (a) physical negative interactions and (b) non-physical negative interactions at Zoo G.

Interaction frequency is depicted by line thickness. Numbers next to nodes are indicative of the mean percentage of interactions received from the corresponding elephant. The matriarch gave most physical negative interactions; highest frequencies were between her and the mother of the infant. Non-physical negative interactions were highest from the mother of the infant to E32; the lowest ranking elephant in the herd. Betweenness scores were equal in both networks.

4.4 Discussion

Four social interaction networks were created and assessed: positive physical, positive non-physical, negative physical and negative non-physical. Elephants engaged in more positive interactions than negative interactions (positive interactions were over ten times more frequent than negative interactions) for both physical and non-physical interactions. Positive networks were more complex and interlinked than negative networks. Non-physical interactions were more frequent than physical interactions. Not all elephants engaged in physical interactions and not all elephants were part of negative social networks. No extreme aggression was observed. Whilst the absence of excessive negative interactions and the presence of positive interactions have been identified as indicators of positive welfare (Chadwick et al., 2017; Williams et al., 2018) it is not clear whether an absence of social interactions may be indicative of poor welfare for those individuals or whether it may have an impact on the rest of the herd. Certainly a change in an individual from positive engagement with others in the herd to not engaging in any interactions may be indicative of an underlying welfare problem and an area which would require further investigation. Further research should focus on developing our understanding of the welfare state of individuals who do not engage in any physical interactions, to ascertain whether this is indicative of good or poor welfare, and to determine the effect of this lack of interaction on group cohesion and consequently welfare for the rest of the herd.

The most complicated and interconnected networks were those containing calves. The high frequency of positive social interactions and the balance in these relationships would be expected. Positive interactions strengthen social bonds (Matoba et al., 2013; Yasui & Idani, 2017) and thus it would be expected that all individuals would benefit from engaging in these types of interactions to some degree. Prior research has highlighted the importance of the choice of conspecifics for zoo animal welfare. Close social associations in animals are beneficial, and having ‘friends’ enhances physical and physiological well-being (Massen et al., 2010).

4.4.1. Network structures

4.4.1.1. Change over time (a comparison between time points)

Consistency in sociability over time was variable but elephants showed fluidity in their social relationships. At one of the study zoos consistency could not be assessed due to the death of an elephant after the first data collection period. None of the study zoos showed completely consistent correlation matrices for all of the observed interactions over time. When data were analysed in terms of percentage of interactions given by each individual elephant the frequency of non-physical positive interactions given differed across the data periods. It was higher in the first period than any of the others. Frequency of interactions was considerably lower in the second two periods of data collection. When the data were analysed in terms of frequency of dyadic

interactions given there were changes to behaviour over time for physical and non-physical social interactions and also negative non-physical interactions.

There is some disparity in recent work on social behaviour, with some authors suggesting that Asian elephants show a strong consistency in sociability over time (Harvey et al., 2018), whereas others suggest that dyadic interactions, particularly tactile contact, can be variable over time (Bonaparte-Saller & Mench, 2018). The results of this study support the notion that elephants show variability in sociability over time. Previous research has indicated that there is a lot more variability in social interactions than associations (Bonaparte-Saller & Mench, 2018). Wild elephants, particularly African, exhibit changes in group structure, driven by ecological factors (Wittemyer et al., 2005; Pinter-Wollman et al., 2009; de Silva & Wittemyer, 2012). This was not expected to be the case due to the lack of variation in terms of resource provision throughout the year. As differences observed in this study were not consistent across study zoos it can be concluded that the changes were unlikely to be linked to seasonality, despite changes to management routines during winter months at some of the zoos. Three of the seven study zoos gave their elephants 24-hour access to outside enclosures during the study months so this may have negated the effect of winter housing. It is therefore more likely that the variability represents natural behavioural fluctuations. There were a number of factors that were not formally assessed during this study but which could have affected physical relationships. For example, hormonal cycles or events occurring at the periods of data collection such as unique stimuli, maintenance work, fluctuations in visitor numbers or a change of keeping team. These would have been present at all of the study zoos. They were controlled for by the 12-month period of data collection, which should have minimised any effects.

It is important to note that a lack of consistency in the interaction matrices over time is not indicative of an incompatible social group or a cause for concern. In two studies of the same group of elephants initial researchers found no significant differences in frequency of positive behaviours across two sample periods (Brockett et al., 1999), whereas a later comparative study found a decrease in social behaviour, which the authors attributed to increased age in the elephants (Wilson et al., 2006). This theory will be investigated in more detail in Chapter Six.

4.4.1.2. Change over time (temporal changes in social interactions)

Stability of herd matrices between the beginning of the study and the end of the study assessed using three comparison points showed variability across the study zoos. Only one zoo had a consistent non-physical positive social network over all three comparison points. Three of the study zoos showed no stability of interactions over time for either the positive physical or positive non-physical social networks. The negative physical and non-physical interaction networks were only stable at one study zoo across all three time periods. These results indicate that zoo elephants

do show fluctuations in social interactions in terms of frequency of interactions. It was not possible to record elephants consistently and proportion of time in sight of the observer varied for individuals, but the range of fluctuations in the results suggest that elephant social structure is changeable and that this is independent of the period of time spent in front of the camera.

Elephant social relationships can also change as a result of changes to herd structure. This was also anecdotally documented by elephant keepers at one of the study zoos. At the time of the onset of the study, elephants at Zoo B were separated into two social groups, because of aggression between two of the females, which began in 2013 following the death of a fourth herd member (Cairns pers. comm., 2016). The three elderly cows were individually housed overnight and during the day they were separated into one group of two and a single elephant. All elephants had the opportunity for tactile contact. Since completion of the study one of the elephants in the herd passed away (E5) and the other two elephants, who were previously separated, were reintroduced to one another in 2018. The reintroduction of these elephants indicates that the relationships had changed, which supports the theory of developing relationships. Furthermore, this highlights the impact that group structure can have on individual relationships. Changes to herd social structure following elephant deaths are not unheard of. In a study of zoo African elephants Armstrong (2015) found an increase in positive behaviours from the matriarch and between the youngest herd members, following the death of the bull. Being able to monitor subtle behavioural change has important ramifications for welfare; it provides an opportunity to identify problems and implement mitigation strategies to prevent escalation into more serious long-term issues.

There may be natural developments in elephant social behaviour over time and elephant social relationships can change as a result of changes to herd structure. The importance of not losing temporal changes in social networks by aggregation of data over time has been highlighted for Onager (*Equus hemionus*) and Grevy's zebra (*Equus grevyi*), which also engage in complex fission-fusion dynamics (Rubenstein et al., 2015). The data in this study was analysed as four separate time points in order to capture temporal changes as far as possible. The recognition that elephant social interactions are fluid however is important to consider in zoo elephant management. Identification of preferred social partners at one point in time may not be a long-term preference and thus management decisions must not be made from a snapshot in time. Fluidity of interactions leads to a necessity to monitor for change. In order to understand social group structures in zoo elephants it is important to monitor relationships over time. Further work should look to validate a minimum period of observation which is required to produce accurate reflections of social relationships. Being able to identify factors that have the potential to affect social relationships is important in being able to undertake targeted and appropriate monitoring. A number of factors will be investigated in further detail in Chapters Five and Six.

4.4.1.3. Changes to herd social structure

Provision of social enrichment for social species is important to maintain good welfare (Rees, 2000; Coleman et al., 2012), however changes to social groups can be a stressful experience (Dathe et al., 1992; Schmid et al., 2001). Two natural structural changes to social groups occurred during this study: one birth and one death. The elephant that died was one of only two housed at that zoo and so it was not possible to analyse social structure in her absence. As the birth occurred during the study however, the effect of this could be analysed. There was no change in physical positive or negative interactions, or non-physical negative interactions in the group. However, the frequency of non-physical positive interactions reduced by, on average, ten times following the birth of the calf. Non-physical interactions performed by the mother of the calf showed the greatest reduction, which likely highlights a behavioural shift from engaging with the rest of the herd to focusing on protecting her new-born calf. When the effect of the birth of the calf was looked at in terms of the whole herd structure only the non-physical negative network correlated between the pre- and post-birth periods. Reproductive states of breeding females and variability in ages and points of development of calves have been suggested as factors affecting social unit stability in wild African elephants (Wittemyer et al., 2005), and care of calves is a centralising component in elephant society (Schulte, 2000). The effect of a birth on the behaviour of zoo-housed Asian elephants in previously published research identified few behavioural changes overall; the researchers surmised that a natural birth had a positive effect overall with minimal disruption to herd structure (Whilde & Marples, 2012). The results from this research support that theory. Variability was observed in the interaction matrices pre- and post- the birth of the calf but there was no particular social disruption in terms of their social interactions, aside from a reduction in non-physical interactions. This finding could be a factor of analysis methods, which did not enable investigation of whether social interactions had been redirected from other group members to the calf. The lack of change in positive physical interactions however suggests this social change did not negatively impact on the group structure.

4.4.2. Dyadic relationships

Understanding dyadic relationships between zoo elephants is an important consideration in zoo management and can have implications for individual welfare (Bonaparte-Saller & Mench, 2018), yet it is a vastly understudied area (Silk et al., 2013). This chapter investigated how interactions at the level of dyad had occurred within the study zoos, and how they changed over time. Assessment of reciprocity within dyads highlighted that the most equally reciprocated network was the positive physical network, with the negative physical network showing no reciprocity in terms of whole herd structure. The negative non-physical network was reciprocated at Zoos C and E and positive non-physical network was reciprocated at

Zoo C. At Zoo C the highest frequency of balanced dyads involved an unrelated adult female, which suggests that in this instance relatedness is not affecting her relationships with herd members.

It was possible to measure the effect of factors such as relatedness, but it was not always possible to directly and accurately measure other important factors, such as reasons for strong relationships between unrelated group members. For example, at Zoo F, keepers highlighted a group change following the euthanasia of the mother of one of the sub-adults in the herd in 2015. The matriarch had become a 'surrogate' for the younger female, and in doing so changed the position of the younger female within the social hierarchy (Cunningham pers. comm., 2016). This was supported by the network analysis in this study; two main dyads were observed at Zoo F, strongest relationships (in terms of frequency of social interactions) were between the mother and her daughter and the elephant that keepers had described as a 'surrogate' and the orphaned female. At Zoo G a particularly strong relationship was observed between the matriarch and the unrelated infant. These findings are contradictory to what Harvey et al. (2018) recently reported; unbalanced social ties in the positive network in two groups of Asian elephants. These differences may have arisen because of the different periods of time over which the present study and the work by Harvey et al. (2018) were undertaken, and the inclusion of a greater number of elephants in the current study. Harvey et al. (2018) compared just two time points (four days of observation, five months apart) and two elephant herds (one representative of the wild social structure and one with two separate related dyads and an unrelated matriarch). Elephant keepers have highlighted the need to provide elephants with appropriate social environments (Chadwick et al., 2017), yet the discrepancy in findings from the studies which have since been undertaken highlight the need for more research using identical methodologies to enable comparisons to be made and to aid understanding of zoo-elephant social structures. Development of reliable metrics to document association patterns and to ascertain whether associate partners are the same as interaction partners in zoo-housed elephants is recommended in order for this data to be incorporated into future studies. A greater understanding of factors driving dyadic interactions will help to interpret this data further. This area will be further developed in Chapters Five and Six.

4.4.2.1. Identification of key individuals in social networks

The relationships between elephants varied across study zoos and between the interactions investigated. In some of the study zoos there were clearly identifiable key individuals, who either gave or received a larger amount of interactions than others in the herd. Whilst in other study zoos, interactions were more evenly distributed throughout the herd. For the majority of the study zoos the highest frequency of positive physical interactions was given or received by the matriarch, or the individual considered by elephant keepers to be the most dominant in the group. The only exception to this was at Zoo E where the greatest frequency of interactions was between

a male and female calf (half-siblings). The highest frequency of positive non-physical interactions was observed at Zoos C and E, which both housed a matrilineal group. At Zoo C the highest frequency was between mother and calf and at Zoo E the greatest frequency was from an adult female to her maternal half-sister.

The number of individuals considered central to networks was sometimes reflective of herd management, whilst in other instances it could be more considered reflective of the age and structure of the herd. For example, at Zoo B elephants were separated due to incompatibility and at Zoo D elephants were managed as two separate social groups. At zoo B one elephant was considered central to the network, with two of the elephants not interacting during the study. At Zoo D, negative interactions were only observed between the elephants that were housed together whilst for the positive network some interactions were observed between individuals that were housed separately. All other study groups however had free access to one another, apart from the bull at Zoo C, who was housed with the females during the day and separated at night. At Zoo C all herd members engaged in the positive social network but not all engaged in the negative network. The youngest herd member received the most positive interactions. This reflects findings from other research that suggests elephant calves are central to elephant social relationships (Thitaram et al., 2015).

The most complicated and highly interlinked network was the positive social network at Zoo E, which housed a multi-generational completely related family herd. At zoos D, F and G no 'core' social group was identified for any of the four networks. Literature regarding wild elephants suggests that African elephants have a much more interconnected social network than Asian elephants (de Silva & Wittemyer, 2012). This finding was not replicated within this research. The most interconnected network was an Asian elephant group, however it is possible that the interconnectedness was due to the size and composition of the group rather than a genuine species difference. It has been hypothesised that the social behaviour in wild African and Asian elephants is resource and predator driven (de Silva & Wittemyer, 2012) so it is not surprising that the strict species differences observed in the wild are not replicated within zoos, when resources and protection are constant. Furthermore the static nature of social groups in terms of members likely alters relationships.

Having a greater understanding of social relationships between zoo elephants is important for their welfare and management moving forwards, to ensure they are being cared for to the optimum standards, through provision of the most appropriate social groups. Being able to identify key individuals will enable managers to make informed decisions if members of social groups need to be moved for breeding, and will help to understand the effect the loss of a herd member may have on the rest of the group. A greater understanding of dyadic relationships will help managers to identify particularly strong social bonds and account for these if groups need to be temporarily

split for routine management. Further understanding of the way demographic factors and individual elephant personalities influence dyadic and herd level relationships will contribute to improved understanding of zoo elephant social relationships and potential social needs. These areas will be added to the data presented in this chapter in the subsequent two chapters.

4.5. Conclusion

The findings from this chapter indicate that SNA can be used successfully to monitor zoo elephant social relationships and investigate changes in dyadic interactions and herd structures over time. The fluid nature of elephant social interactions within zoos has been highlighted; these results thus reinforce the point that social relationships and social networks may change over time, and this should be borne in mind when future assessments of social relationships are being undertaken. Furthermore they highlight the need to understand the roles of each herd member in social networks, as individuals may hold unique positions in networks. Being able to monitor relationships and identify problems before they escalate is important in zoo animal welfare, when there may be reduced opportunity to escape conflict. Within elephant dyads it is possible that there are some immeasurable factors influencing interactions. Being able to account for factors which may cause social change in the future is a vital area for inclusion in welfare assessment. Being able to identify key individuals within a social network is important when animals are being considered for moving to other collections as part of breeding programmes or for observing herd interactions when potentially disruptive events occur, such as births or deaths. This will enable an understanding of how the addition of new individuals or removal of old individuals will affect group social structures. Furthermore, this information can be incorporated into herd management plans, which are now included in SSSMZP elephant management guidelines.

The aim of this chapter was to investigate herd structure and dyadic relationships, and to determine if relationships in zoo-housed elephants are stable over time. Positive networks were far more complex and interlinked than negative networks. Moreover, networks were different across the study zoos and there were many unbalanced ties within dyads. The results of this chapter suggest that within positive networks, interactions may include the entire social group, whereas negative networks may be restricted to specific individuals or a subset of individuals from the entire social group. Furthermore, they suggest that some level of fluidity in elephant social relationships should be expected. Having a greater understanding of social relationships between zoo elephants will enable evidence-based social management decisions to be made moving forwards, to ensure their social needs are being cared for to optimum standards and they are thus experiencing optimum welfare within their social groups. Further understanding of the way social group factors and individual elephant personalities influence dyadic and herd level relationships will contribute to improved understanding of zoo elephant social relationships and networks within

zoos. Future research should also look to include proximity to others as a measure of social cohesion, and to investigate the relationship between proximity to others and physical interactions on a multi-institution scale within UK and Irish zoos.

4.6. Chapter summary

- Elephants engaged in more positive interactions than negative interactions overall
- Elephants engaged in more non-physical interactions than physical interactions
- The most inter-connected networks (those with the most links between elephants) were those containing calves
- Highest frequencies of positive physical interactions were given by the matriarch (or animal considered to be most dominant)
- Study zoos showed variability in social interaction matrices over time
- Dyadic relationships were not always balanced in the study elephants; some individuals were giving more interactions than they received and vice versa

This chapter provided an overview of social relationships in the study herds and quantified frequencies of interactions given by individual elephants. It then investigated whether interactions were stable over the period of a year or whether some level of fluidity is to be expected in elephant social groups. Whilst zoos in the UK and Ireland do not provide elephants the opportunity to physically move social groups, elephants are given the opportunity to interact relatively freely with social companions, within their static social groups. The data in this chapter indicated some level of fluidity in elephant social relationships in terms of positive and negative interactions, and identified 'key' individuals in networks. Networks containing calves were the most interconnected and the highest frequency of positive physical interactions were given by matriarchs (or individuals considered by keepers to be most dominant). Understanding more how individual factors may be affecting elephant relationships is key to interpreting this data further. The following data chapter, Chapter Five, will build on this work by investigating if there is a relationship between individual elephant personalities and social interactions.

CHAPTER 5

Personality and social relationships in zoo-housed elephants

5.1. Introduction

5.1.1. Background

Assessment of social networks has been utilised to identify relationships within zoo animals (see Chapter Four) but incorporation of unique individual differences are needed to interpret this data further. Personality is defined as ‘individual differences in behaviour that are thought to be stable across time and situations’ (Powell & Gartner, 2011). Individual personalities are important to recognise in order to promote good animal welfare; understanding individual differences as well as differences in group dynamics can help to ensure more efficient zoo management (Racevska & Hill, 2017). The importance of personality in animal welfare and survival is well documented; researchers suggest that as personality is likely to affect an individual’s experience within a zoo, then it should be a primary concern for zoo managers (Watters & Powell, 2012). Personality of animals within zoos is being increasingly investigated in a number of species including chimpanzees, black rhinoceros, cheetah, clouded leopard (*Neofelis nebulosa*), African and Asian elephants, lion tailed macaque (*Macaca silenus*), Vancouver island marmot (*Marmota vancouverensis*), gorilla, orangutan, tiger (*Panthera tigris*), giant panda, bonobo (*Pan paniscus*) and snow leopard (*Panthera uncia*) (Tetley & O’Hara, 2012). Personality can be used to ‘personalise’ environmental enrichment, is indicative of coping ability and may allow keepers to identify appropriate roles within a group for individuals e.g. identifying social compatibility or who to transport to a new facility (Horback et al., 2014). Furthermore, developing an understanding of current and future social group members can provide information about individual experiences but also reduce the potential for stress through minimisation of the risk of housing incompatible individuals and reduction of the risk of aggressive encounters (Tetley & O’Hara, 2012).

Application of knowledge of animal personality has contributed to formation of successful social groups and improved mating success (Carlstead et al., 1999b; Fox & Millam, 2014; Martin-Wintle et al., 2017). In black rhinoceros personality predicted breeding success; compatible pairs were assertive females and submissive males (Carlstead et al., 1999b). Moreover, in cockatiels (*Nymphicus hollandicus*), birds that were more ‘agreeable’ and showed lower intra-pair aggression had higher breeding success (Fox & Millam, 2014). Combinations of personality traits can enhance or impair reproduction in giant panda; excitable males and low excitable females had higher rates of breeding success, and low fearful males performed better overall (Martin-Wintle et al., 2017). Social animals in a number of species also show preferences in social companions; these ‘relationships’ have been termed ‘friendships’ (Massen et al., 2010). Friendships and choice of social partner can be affected by individual differences (Massen & Koski, 2014); in chimpanzees friendships were more likely in individuals with similar sociability and boldness scores (Massen & Koski, 2014). Furthermore, researchers have suggested that assessment of personality

can be used to increase success and decrease risks when forming new groups of great apes (Gartner & Weiss, 2018).

Zoo transfers are an essential element of captive breeding programmes, and they can come with a number of different stressors, which may be impacting negatively on animal health and welfare (reviewed in Chapter Two). Maximising the likelihood of compatibility in social groups is thus extremely important. Stressors associated with transportation and introduction to new social groups include: the transportation, changes in keepers, introduction to new environments and change in social hierarchies (Wolfensohn et al., 2018). A number of animals have been shown to have elevated cortisol during- and post-travel (tigers, Dembiec et al., 2004; cattle, Palme et al., 2000; and elephants, Laws et al., 2007; Millspaugh et al., 2007), and in some instances behavioural changes have also been observed (increased stereotypies and breathing rates in tigers, Dembiec et al., 2004; and reduced lying rest in elephants, Laws et al., 2007). Inter-zoo transfers have also been linked with reduced life expectancy in female Asian elephants (Clubb et al., 2008). Despite the potentially negative experiences surrounding inter-zoo transfers, there is still a need to move individuals between collections, as part of breeding programmes (BIAZA, 2018b) or as part of long-term collection planning (Twycross Zoo, 2018). Being able to predict future social compatibility prior to moving individuals has the potential to improve the long-term welfare of zoo species, by increasing the likelihood of success post-transfer and thus reducing numbers of transfers required. Elephants have unique and stable personalities which can be discriminated reliably and accurately by expert keepers/primary carers (Grand et al., 2012; Horback et al., 2014). Furthermore elephant personalities have an underlying biological basis (Yasui et al., 2013) and are related to levels of serum cortisol (Grand et al., 2012). If personality assessments can be used to predict social compatibility in elephants, as has been seen in other species, it will have value in the introduction of individuals into new groups.

The three predominant forms of personality assessment are rating behaviour, coding behaviour and behavioural or preference tests (Watters & Powell, 2012). In terms of identification of individual differences in animals, rating and coding of behaviour are the principle chosen methods (Highfill et al., 2010). The rating method of assessment involves human observers; an animal's behavioural tendencies are rated along a number of behavioural dimensions. These ratings are based on the raters experience with the observed animal (Highfill et al., 2010). Behavioural coding involves scoring an animals behaviour in specific contexts, which can either be naturally occurring or experimental (Highfill et al., 2010). The rating method proves most useful when objective knowledgeable raters are available to complete questionnaires (Highfill et al., 2010) and is the most common method of personality assessment in zoo animal research (Tetley & O'Hara, 2012; Watters & Powell, 2012). The use of keeper questionnaires to study personality in zoo animals makes it possible to measure traits and capture expert knowledge in a

standardised and repeatable manner (Gartner & Weiss, 2018) and the importance of this is recognised (Chadwick et al., 2017).

Previous work within both wild and captive elephants (semi-captive logging camps in range countries and western zoos) have identified between three and five personality components, with most research combining to produce three principal components on which elephant personality can be accurately described: sociability, dominance/aggression and leadership, with an additional component related to responsiveness to/relationship with handler for elephants in some captive settings (Table 5.1).

Table 5.1. A summary of published personality studies in captive and wild elephants

Author	Setting	Species	Number animals	Components	Adjectives	Key findings	Critique of study
Grand <i>et al.</i> (2012)	Zoo	African	5	Effective	Confident Effective Motherly Slow Strong Playful Understanding	Correlations between cortisol and personality: <ul style="list-style-type: none"> • Positive correlations between morning cortisol and 'fearful' component • Negative correlations between cortisol and 'effective', 'sociable' and 'aggressive' components 	Combined behavioural and physiological approach to personality assessment, with the aim of establishing a link between basal cortisol and personality. An elephant behaviour index was used which was modified from a rhesus macaque personality assessment. The personality assessment was based on 23 adjectives. Keepers (n=16) rated the five elephants in their care using a 5-point likert scale. All adjectives were related reliably (ICC>0.6). Spearman's rank was used to create four components with good internal consistency. Five adjectives didn't fit in to the components. Findings seen mirrored other species however this was only undertaken at one study zoo. It is important to build on this work to validate the relationship between elephant personality (as rated by keepers) and basal cortisol.
			Fearful	Apprehensive Fearful Insecure Subordinate Tense			
			Sociable	Popular Sociable			
			Aggressive	Aggressive Opportunistic			
Lee & Moss (2012)	Wild	African	11	Leadership	Effective Permissible Intelligent Insecure (negative) Confident Opportunistic Equable Strong Maternal	Elephants had individually variable traits on four components. Component 3 (Gentle) and Component 4 (Constancy) reflected social integration. The matriarch scored highly on elements associated with 'leadership'. Suggests personality may underlie interfamilial variation in long-term survival and	Observers (n=4) rated elephant personality (n=11 wild elephants) based on 28 adjectives. Adjectives chosen for inclusion in the assessment were those that described wild elephant behaviour. Raters were asked to complete ratings on a 7-point likert scale. Only two adjectives were dropped from the PCA due to negative ICC scores. The remaining 26 adjectives were retained in the PCA despite some very low consistency between raters (e.g. 'confident', ICC = 0.02). This could lead to potential problems in their PCA. The four identified factors (leadership, playfulness, gentleness and social
			Playful	Active			

					Curious Playful Excitable Eccentric Social Slow (negative)	reproduction.		integration) relate to the social structures of wild elephants. The ICC scores are comparable to (and frequently higher than) those reported by Seltmann (2018) and so may mark the difference between relationships between humans and wild elephants and humans and zoo-elephants. Wild elephants are subject to a range of different environmental pressures that may not be applicable to zoo-elephants and so it is possible that they may not be comparable populations. Nevertheless, identified factors related to the research undertaken by Yasui et al. (2013). This study was only undertaken on one family so extension of this work into other wild elephant families is beneficial.
				Gentle	Irritable (negative) Gentle Aggressive (negative) Deferential			
				Constancy	Predicable Fearful (negative) Popular Protective Sensitive			
Horback <i>et al.</i> (2013)	Zoo	African	12	Playful	Environment play Conspecific play Conspecific tolerant Human playful	<ul style="list-style-type: none"> Assessment demonstrated temporal stability, construct validity and cross-method consistency. Researchers suggested that the rating of zoo elephant personalities by expert caretakers may be a valid proxy for long-term behavioural monitoring. Three personality traits were determined based on 	Keepers (n=12) completed personality assessments of 12 elephants based on 25 adjectives. 7-point likert scale was used, 4 was a 'neutral' mid-point and keepers had the option to say 'do not know' although the authors do not detail whether this was used by any keepers. 18 (of 25) adjectives were reliably rated (ICC>0.8). 15 of these traits were clustered (using spearman's rank correlation) into 4 composite groups. 15 behaviours (ethologically coded) were clustered into three traits (playful, curious and sociable). The clusters are not always completely clear. E.g. Although assigned using spearman's rank correlations behaviours such as 'body touch' was assigned to 'sociable' and not 'playful' whilst 'approach' was coded to	
				Observant	Environment curious Environment energetic Environment observant Human observant			
				Confident	Environment			

					<p>confident Conspecific confident Conspecific dominant</p> <hr/> <p>Shy Environment timid Conspecific shy Human gentle Human shy</p>	<p>behaviour events. Playful, curious and sociable were most significant.</p> <ul style="list-style-type: none"> • Personality traits correlated over time demonstrating temporal stability • Coded playful trait correlated with the rated playful trait, demonstrating construct validity and cross-method consistency. 	<p>‘playful’. However, personality scores were consistent over time and cross-method consistency (keeper ratings and ethological coding) was demonstrated for some traits. This is indicative of the reliability of the use of keeper assessments of elephant personality but suggests more work may be required before keepers can be used as a sole proxy for behavioural observations.</p>
Yasui <i>et al.</i> (2013)	Zoo	45 Asian 30 African	75	<p>Dominance</p> <hr/> <p>Neuroticism</p> <hr/> <p>Agreeableness</p>	<p>Defiant Dominant Irritable Aggressive Moody Mischievous</p> <hr/> <p>Nervous Anxious Fearful Timid Vigilant Cautious</p> <hr/> <p>Friendly Sociable Gentle Adaptable Affectionate</p>	<p>Association identified between a genetic polymorphism in a gene expressed in the brain and personality (ASH1 affected neurotic personality dimension)</p>	<p>Keepers (n=95) completed personality assessments based on 30 questions. Some adjectives included in the assessment are of questionable relevance in elephants (e.g. distractible, quitting) and a four-point scale reduced the opportunity for choice for raters. However, reliability between raters was high (mean 0.7 across terms, range 0.5 – 0.9). The authors used predefined factors (n=5) rather than creating factors based on the data. The identified factors related to work by Lee & Moss (2012) and the work demonstrated face validity; findings made biological sense. E.g. females were considered by keepers to be more agreeable than males; which makes sense in terms of natural history of elephants, and younger elephants were more curious and impulsive, which are traits which are associated with young animals in a range of species.</p>

					Calm		
				Impulsiveness	Focused Distractible Attentive Restless Impulsive Excitable Quitting		
				Curiosity	Inquisitive Curious Playful Inventive Active		
Williams <i>et al.</i> (2015)	Zoo	Asian	11	Assertive	Aggressive Dominant Sub-ordinate (negative)	<ul style="list-style-type: none"> Elephants who scored higher on the 'vigilant' component engaged in shorter lying rest bouts and longer standing rest bouts 	<p>The study focused only on a relationship between elephant personality (as rated by keepers) and rest behaviour, no other ethological coding was taken into consideration in analysis. The assessment, which comprised 22 behavioural adjectives, was created based on assessments published by Grand <i>et al.</i> (2012) and Yasui <i>et al.</i> (2013). 11 keepers at 3 zoos rated their elephants (n=14) using a visual analogue scale (VAS). The inclusion of a VAS instead of a likert scale may have given raters more freedom when completing the assessment. Only adjectives with an ICC > 0.6 were included in further analysis. The 9 reliably rated adjectives were then entered into a PCA, which revealed 3 components with good internal consistency. The study indicated that elephant keepers could reliably rate the personality of their elephants and that the components did fit with the published literature. However there was no biological significance of the findings, so the relationship between</p>
				Confident	Confident Sociable Solitary (negative)	<ul style="list-style-type: none"> Elephants who scored higher on the 'assertive' and 'confident' components engaged in shorter standing rest bouts 	
				Vigilant	Active (negative) Eccentric Vigilant		

							elephant personality and resting behaviour still requires further investigation.
Seltmann <i>et al.</i> (2018)	Timber camp	Asian	257	Attentiveness <hr/> Sociability <hr/> Aggressiveness	Attentive Obedient Slow Vigilant Confident Active <hr/> Mischievous Social Playful Friendly Affectionate <hr/> Aggressive Dominant Moody	Data gathered did not fit the traditional 5 factor model. Instead, personality was manifested as three factors and did not differ between the sexes	Mahouts (n=316) caring for 257 semi-captive Asian elephants rated elephant personality using a 28-adjective questionnaire. Mahouts rated the frequency with which each elephant usually displayed a particular behaviour or behavioural propensity, which is slightly different to the other reported studies. Ratings were made on a 4-point likert scale. ICC values ranged from 0.09 to 0.33 (mean 0.19), which is very low in comparison to other personality assessments in elephants and would not normally be considered statistically acceptable (Shrout & Fleiss, 1979). Nevertheless all adjectives were included in analysis. The data did not fit the 5-factor model which had been proposed by Yasui <i>et al.</i> (2013) but the adjectives used in the two studies were different so this may have explained this. The authors instead used an exploratory factor analysis (EFA). Of the 28 adjectives rated only 15 were kept in for this, although it is not clear why (or how the 15 adjectives were selected for inclusion). Ratings were separated for male and female elephants and three factors were found in both instances. The highlighted factors were similar to those reported by Grand <i>et al.</i> (2012), Lee & Moss (2012) and Williams <i>et al.</i> (2015). This study had an extremely large sample and it is possible it is this that led to some lack of reliability across raters. Nevertheless the authors advocate the need for a greater understanding of wild elephant personality and inclusion of personality assessments in semi-wild elephant care.

The components identified in the elephant personality literature are what would be expected from a social and gregarious species with a relatively strict social hierarchy (Wittemyer & Getz, 2007). They are also in line with what has been identified in other species. The most frequently assessed personality dimensions in the general personality assessment literature (as identified using factor analysis) are sociability, confidence/aggression and fearfulness (Freeman & Gosling, 2010). Apart from the research conducted by Seltmann et al. (2018) all of the personality traits described in Table 5.1 have been reliably rated by elephant keepers (Grand et al., 2012; Horback et al., 2013; Yasui et al., 2013; Williams et al., 2015) or wild-elephant researchers (Lee & Moss, 2012). The study by Seltmann et al. (2018) used rankings from mahouts. The term mahout is derived from Hindi and means 'elephant keeper' (Blaine & Winkler, 2019). Inter-rater reliability is a measure of agreement between raters (Shrout & Fleiss, 1979). The mahouts in the study by Seltmann et al. (2018) had relatively low inter-rater reliability of ratings and the study did not support the traditional five-factor model of personality as described by Yasui et al. (2013). However the researchers suggested that the reliability scores were within accepted thresholds and recognise that mahout personalities could affect ratings of elephant personality (Seltmann et al., 2018). Despite the different conditions in zoo, timber-camps and the wild there is still consistency in use of personality terms. All of the adjectives used in the personality assessments related to traits that are appropriate to the natural behaviour of elephants, in terms of social hierarchies, behaviour towards conspecifics and behaviour towards keepers. Appropriateness of behavioural adjectives has been highlighted as important by researchers who suggest that the human-focused five factor model may not be completely appropriate for animal personality assessments (Gosling & John, 1999). The generally high inter-rater reliability scores and the persistence of evolution of similar factors from the data suggests reliable rating in the studies and appropriate use of the assessments. Furthermore, the relationship between genetic traits (Yasui et al., 2013) and the link with behavioural coding (Horback et al., 2013) lends support for the validity of keeper assessment of elephant personality, when only reliably rated personality traits are used.

Identifying a relationship between personality and sociability in individuals has the potential to improve the welfare of zoo elephants, by providing them with conspecifics with whom they are more likely to be socially compatible. A link has been established between keeper assessments of social bonds and social association patterns in US elephants (Bonaparte-Saller & Mench, 2018). To date no work has investigated the relationship between personality as rated by keepers and social interactions in UK and Irish zoo elephants.

5.1.2. Aim and objectives

The aim of this chapter was to apply the knowledge of keepers in the UK and Ireland to assess individual personalities, and to investigate the relationship between individual elephant personalities and frequency of social interactions in the study herds. This ensures Objective Three of the thesis, to identify whether there is a relationship between individual personality and social interactions in zoo elephants, was achieved. It is hypothesised that the frequency of social interactions observed will be related to personality, and that some elephants will have a more 'sociable' personality type than others. This will build on the data presented in Chapter Four, looking at social relationships within the herds in light of personality types and identifying whether there is a relationship between personality types and dyadic relationships.

5.2. Methodology

5.2.1. Subjects and study sites

Details of the study elephants (n=32) and participating zoos (n=7) are provided in Chapter Four. Elephant personality assessment questionnaires were distributed to keepers at all of the study zoos for the study elephants at the onset of the study.

5.2.2. Personality assessment

5.2.2.1. Keeper ratings of elephant personality

This study utilised a 'trait rating by knowledgeable informants' method to assess elephant personality using a keeper questionnaire. An adapted version of the questionnaire devised by Williams et al. (2015) was used. Modifications were made following consultation with keepers at the onset of this study. Modifications included removal of terms that may not be considered to be personality traits (e.g. dominant, subordinate) and inclusion of extra options for 'towards keepers' and 'towards elephants' for relevant terms (e.g. affectionate, calm, fearful and play).

The questionnaire (Figure 5.1) comprised 21 behavioural adjectives with the option of adding additional relevant comments. Ratings were made on a 10cm visual analogue scale with the anchors 'disagree' (0cm) and 'strongly agree' (10cm). An exact score was determined by measuring the distance (in centimetres, to 1dp) along the line that the rating was placed. Keepers were asked to complete the questionnaires independently of one another, though there was no means of assessing whether this had been adhered to or not. However, rating bias was controlled by including a mix of positive and negative traits within the assessment. Keepers were asked to provide information about themselves, including how long they had worked with elephants in general and how long they had worked with the specific herd. Elephant keepers who had worked with the herd for less than three months were excluded from analysis as the assessment required knowledge of the individual over time and in a range of contexts.

Keeper assessment of elephant personality participant consent form

Researcher: Miss Ellen Williams, Nottingham Trent University

Contact details: ellen.williams@ntu.ac.uk, 07912 755482

Supervisory team: Dr Samantha Bremner-Harrison, Dr Anne Carter, Dr Carol Hall

Project title: An investigation into social relationships and social structure in European zoo elephant herds

African and Asian elephants display strong affiliative behaviours and are known to live in a fission-fusion society in the wild (Moss & Poole, 1983; de Silva *et al*, 2011). Inappropriate social groups in European zoo elephants have been cited as a serious welfare concern (Clubb & Mason, 2002; Harris *et al*, 2008). EAZA and BIAZA state that elephants must be kept in minimum groups of four compatible females, however there are no clear definitions as to what makes a compatible female and how to assess compatibility between individuals (Leeuwen, 2004; Walter, 2010).

Personality has been used to assess compatibility of individuals in captive animals (Tetley & O'Hara, 2012). It could be expected that personality would play a role in social interactions within a captive elephant herd. In order to assess personality of elephants in captivity a keeper assessment of elephant personality has been developed. Each full time keeper at participating collections will be asked to complete a short assessment of personality for each elephant in their care once per quarter (one assessment per season).

Interactions with conspecifics have been largely overlooked as an area of research in captive elephants. Given the high-functioning levels of sociality observed in wild African and Asian elephants it is an area that warrants considerably more investigation. This project will create reliable methodologies for documenting social behaviour and investigating the effect of environmental and social factors on social interactions and social structures of captive elephant herds in Europe. The results from this study will enable evidence-based recommendations to be made with regards appropriate social groups which could be used to inform future decisions in European zoos.

I am aware that:

1. The information I provide during the keeper assessment of personality will be used to investigate the relationship between individual elephant personality and social interactions
2. I am requested to complete this assessment for each elephant in the herd at the beginning (and again at the end if required), of the study period
3. My name will be used only by the researcher as a means of investigating intra-rater reliability over the course of the study, in order to assess the reliability of the questionnaire for assessing personality in captive elephants
4. The information I provide during this questionnaire will be stored securely and will be accessible only by the researcher for the purposes of this study and any future reports or presentations arising from this study
5. All information I provide during this questionnaire will be anonymised before production of reports or presentations
6. I can withdraw my input into this study at any time during the study by emailing the researcher directly. If I withdraw from the study any contributions I made to the project will be destroyed and removed from the study.

I have read and understood the above information and agree for the information I provide to be used in the manner as outlined.

Signed: _____ Date: _____

Name (print): _____

Name of facility: _____

Elephant Personality Assessment

This assessment should be filled in for each elephant in the collection by as many full time elephant keepers as possible. Please describe each elephant's personality using the scale below, by placing a mark on the line where appropriate for each behaviour. Please add any further important comments or information to the bottom of this form.

Elephant Name: _____

Keeper Name*: _____

Years spent working with elephants: _____ Years spent working with this herd: _____

*All data gathered will be anonymised before production of reports. Keeper name will be used to document intra-rater reliability for each behavioural adjective over the period of the study. This, along with inter-rater reliability will be used to investigate the **reliability of the elephant personality assessment** when used at a wide range of establishments.

0=Disagree, 10=Strongly Agree

Active: Has high motivation to be physically active



Adaptable: Quickly adapts to novel situations



Affectionate (keepers): Seeks close relationships to keepers



Affectionate (elephants): Seeks close relationships to elephants (please place two lines if there is a difference for related or un-related elephants)



Aggressive: Causes harm or potential harm to conspecifics, e.g. displays, chases, bites



Apprehensive: Seems anxious; fears or avoids risk



Calm (unfamiliar people): Reacts to unfamiliar people in a calm and peaceful manner



Calm (novel situations): Reacts to novel situations in a calm and peaceful manner



Confident: Behaves in a positive, assured manner



Curious: Shows interest in novel objects
 0 10

Fearful (conspecifics): Retreats readily from conspecifics
 0 10

Fearful (disturbances): Retreats readily from outside disturbances
 0 10

Inquisitive: Explores new situations and tries to learn new things
 0 10

Mischievous: Shows a fondness for causing trouble in a playful way, e.g. sand kicking or trunk grabbing
 0 10

Playful (conspecifics): Initiates or readily engages in play with conspecifics
 0 10

Playful (objects): Readily engages in play with objects
 0 10

Placid: Reacts to conspecifics in an even, calm way; is not easily disturbed
 0 10

Restless: Rarely relaxes, always walking or moving around the enclosure
 0 10

Sociable: seeks companionship of conspecifics
 0 10

Solitary: Spends time alone
 0 10

Vigilant: Carefully watches or listens for possible dangers in the surroundings and easily becomes alerted
 0 10

Figure 5.1. Elephant personality assessment questionnaire sent to keepers at the study zoos

5.2.2.2. Inter-rater reliability and principal components analysis

To determine inter-rater reliability, a measure of reliability between raters, intra-class correlation coefficients (ICC (3,k)) were calculated for each personality adjective (Shrout & Fleiss, 1979). In general, an ICC (3, k) of >0.5 indicates a good level of agreement between raters; therefore any adjectives with an average ICC of <0.5 were removed from further analysis. A single score for each personality adjective was calculated for each elephant by averaging scores across raters. A principal components analysis (PCA) was conducted to reduce the remaining personality adjectives into components. The component solution was rotated using varimax rotation and components with eigenvalues >1 were extracted. The Kaiser-Meyer-Olkin Measure of Sampling Adequacy was >0.5 and the Bartlett's Test of Sphericity was <0.001. Adjectives with salient loadings (>0.4) on more than one component were assigned to the component on which it had the higher loading. None of the adjectives loaded negatively onto the components. Cronbach's alpha was used to detect internal consistency. Composite scores were calculated as the mean of the adjectives within each component.

5.2.3. Data analysis

None of the data were normally distributed (Kolmogorov-Smirnov test, $p < 0.05$) therefore all tests conducted were non-parametric. A Mann-Whitney U test was carried out to investigate the difference in personality component scores and: origin, sex, species and whether individuals were related to others in the herd. Elephants were grouped into six age categories for analysis: calf (0-2 years), infant (3-4 years), juvenile (5-9 years), sub-adult (10-15 years), adult (16+ years) (Kurt, 2005). A Kruskal Wallis test was used to identify the effect of age category and individual elephant on component scores. Spearman's rank correlations were undertaken to look at the relationship between age (in years), number in herd, number of individuals in the herd interacted with (positive and negative) and frequency of social interactions given (split into positive physical interactions, positive non-physical interactions, negative physical interactions and negative non-physical interactions). Data were also investigated in terms of dyadic interactions, to assess whether elephants were more likely to spend longer interacting with an elephant to whom they had a similar level of sociability. Sociability was split into low (0 – 3.3), medium (3.4 – 6.6) and high (6.7 – 10) categories, where low scoring elephants were considered 'unsociable', medium scoring elephants were considered 'mid-sociable' and high scoring elephants were considered 'highly sociable'. A Kruskal Wallis test with a Dunn post-hoc test for multiple comparisons was used to investigate whether there was a difference between sociability scores of givers/receivers in dyads and frequency of interactions, i.e. whether there was a higher propensity for 'givers' of social interactions to have higher, lower or equal sociability scores to the 'receivers' of the interaction.

5.3. Results

5.3.1. Keeper ratings

Personality assessments, were completed by 27 elephant keepers across the seven study zoos for 30 (4 males, 26 females, Table 5.2) of the 32 study elephants (4 males, 28 females; Chapter Four, Table 4.3). Elephants were rated by between 3 and 6 keepers (Table 5.2). At Zoo C one keeper had worked with elephants (and the herd) for less than one month and so those ratings were not included in the analysis. E6 who was housed at Zoo C was rated by only two keepers and so this elephant was also withdrawn from further analysis to ensure consistency within that zoo, as the rest of the study herd had been rated by three keepers.

Table 5.2. Subjects for which completed personality questionnaires were received from the study zoos

Zoo	Species	Number of elephants (Males. Females)	Number of keepers
A	African	2 (0.2)	4
B	Asian	3 (0.3)	4
C	Asian	5 (1.4)	3
D	African	4 (1.3)	3
E	Asian	7 (2.5)	3
F	African	4 (0.4)	4
G	Asian	5 (0.5)	6

5.3.2. Inter-rater reliability and principle components analysis

Intra-class correlation coefficients were used to examine inter-rater reliability at all zoos. Inter-rater reliability was established for 21 personality adjectives. Those that achieved average ICC values of 0.5 and above (Table 5.3) were entered into a PCA. A PCA yielded three components with eigenvalues >1 (Table 5.4), which accounted for 78.7% of the total variance. The three components were named according to the adjectives within them as 'adaptable', 'sociable' and 'engaged with the environment'. The loadings of each trait onto the three components are presented in Table 5.4. Cronbach's alpha revealed good internal consistency for each component.

Table 5.3. Intra-class correlation coefficient (ICC*) scores for each adjective rated in the keeper assessment of elephant personality

Adjective	ICC* (3, K)							Average Score (1dp)
	Zoo A	Zoo B	Zoo C	Zoo D	Zoo E	Zoo F	Zoo G	
Active	0.95	0.86	0.67	0.96	0.51	0.79	0.73	0.8
Adaptable	0.92	-0.02	0.01	0.72	0.40	0.59	0.57	0.5
Affectionate (keepers)	-0.14	0.55	0.12	0.95	0.74	0.80	0.37	0.5
Affectionate (elephants)	0.95	0.76	0.30	0.69	0.62	0.52	0.40	0.6
Aggressive	0.47	-0.22	0.44	0.02	0.75	0.74	0.94	0.4
Apprehensive	0.96	0.08	-0.11	-0.01	0.42	0.15	-0.08	0.2
Calm (unfamiliar people)	0.18	0.7	-0.22	0.88	-0.30	0.75	-0.06	0.3
Calm (novel situations)	0.77	0.61	0.40	0.93	-0.02	0.47	0.36	0.5
Confident	0.95	0.56	-0.28	0.73	0.45	0.24	0.04	0.4
Curious	0.79	-0.08	0.28	-0.25	0.40	0.79	0.35	0.3
Fearful (conspecifics)	0.99	0.24	0.01	0.23	0.66	0.37	0.76	0.4
Fearful (disturbances)	-0.32	-0.26	-0.29	0.01	0.15	0.26	0.16	0.0
Inquisitive	0.92	0.01	0.58	-0.03	0.50	0.82	0.36	0.5
Mischievous	0.98	0.62	0.03	-0.13	0.21	0.41	0.63	0.4
Playful (conspecifics)	0.59	-0.18	0.69	-0.08	0.86	0.76	0.60	0.5
Playful (objects)	0.75	0.50	0.60	-0.07	0.74	0.55	0.42	0.5
Placid	0.85	0.36	0.08	0.47	0.52	-0.23	0.08	0.3
Restless	-0.18	0.17	0.27	0.28	0.42	-0.08	0.70	0.2
Sociable	0.96	0.71	0.74	0.76	0.08	0.18	0.73	0.6
Solitary	0.77	0.26	0.92	0.08	0.11	0.34	0.52	0.4
Vigilant	0.66	0.22	0.01	0.40	0.60	0.77	0.40	0.4

Adjectives with an average ICC value of >0.4 (in bold) were entered into a PCA

*ICC refers to an intra-class correlation coefficient, which is used as a measure of reliability between raters

Table 5.4. Factor loadings of the 21 personality adjectives in the keeper questionnaire with intra-class correlation coefficient (ICC) scores >0.4

Personality adjective	Component 1 (adaptable) $\alpha = 0.856$	Component 2 (social) $\alpha = 0.857$	Component 3 (engaged with the environment) $\alpha = 0.459$
Adaptable	0.910		
Calm – novel situations	0.873		
Active	0.735	0.431	
Inquisitive	0.578*		0.568*
Sociable		0.925	
Affectionate – elephants		0.878	
Playful – conspecifics	0.435	0.697	
Affectionate – keepers			0.838
Playful - objects		0.447	0.658
Eigenvalue	4.623	1.387	1.076
% of variance	51.4	15.4	12%

Factor loadings of <0.5 have been omitted. Only adjectives whose loadings are highlighted in bold contributed to the formation of the component scores. Cronbach's alpha scores for each component were as follows: component 1 = 0.841, component 2 = 0.857, component 3 = 0.459.

*Due to cross-loading on components 1 and 3, 'inquisitive' was removed from both components

Component 1 was labelled 'adaptable' and had high positive loadings on the traits 'adaptable', 'calm in novel situations' and 'active'. This component loaded highly for 'inquisitive' however due to cross loadings on this and component 3 it was removed from both components. Elephants scoring highly on this component were considered to be quite calm and adaptable. Component 2 had high positive loadings on 'sociable', 'affectionate with elephants' and 'playful with conspecifics', and was labelled 'sociable'. Elephants who scored highly on this component were considered to be more sociable than individuals with lower scores, actively seeking interaction with other individuals or engaging in conspecific play. The final component, component 3, was labelled 'engaged with the environment'. This component had high loadings for 'affectionate with keepers' and 'playful with objects'. It also loaded highly for 'inquisitive', however this personality adjective cross loaded on component 1 so was removed from both components.

5.3.3. Component scores and social interactions

Frequency of social interactions were calculated as part of data collection and analysis in Chapter Four (see Section 4.3.1). Social interactions accounted for a relatively small percentage of total activity, median frequencies as an average per study zoo are provided in Table 5.5. There was a difference between the frequency of interactions for physical positive ($\chi^2=16.012$, $df=6$, $p<0.05$), physical negative ($\chi^2=15.438$, $df=6$, $p<0.05$) and non-physical positive ($\chi^2=14.175$, $df=6$, $p<0.05$) across the study zoos.

Table 5.5. Median percentage of social interactions (as a percentage of total activity) given by elephants at each study zoo

Zoo	Physical positive		Physical negative		Non-physical positive		Non-physical negative	
	Median	IQR	Median	IQR	Median	IQR	Median	IQR
A	3	0.95 – 4.5	0.08	0.06 – 0.11	3.56	3.39 – 4.39	0.27	0.13 – 0.37
B	5.78	4.4 – 6.71	0.05	0.04 – 0.05	1.17	1.02 – 1.58	0.08	0.07 – 0.1
C	1.06	0.78 – 7.65	0.03	0.02 – 0.06	1.32	0.92 – 4.11	0.04	0.04 – 0.1
D	0.05	0.05 – 0.07	0.01	0.01 – 0.01	0.65	0.53 – 0.87	0.09	0.07 – 0.12
E	0.41	0.23 – 1.71	0.03	0.01 – 0.04	2.12	0.96 – 3.48	0.2	0.05 – 0.34
F	2.16	1.08 – 3.15	0.03	0.02 – 0.11	1.08	0.59 – 1.16	0.34	0.26 – 0.56
G	0	0 – 0	0	0 – 0	0.14	0.09 – 0.20	0.26	0.16 – 0.36

5.3.3.1. Component 1 – Adaptable

Male elephants were considered by keepers to be more ‘adaptable’ than female elephants (mean \pm SD: male 7.95 \pm 0.40; female 6.04 \pm 1.77) ($t_{(22,9)}=4.75$, $p<0.001$) however there was no correlation between attentiveness component scores and any of the other variables (origin: $Z=-1.539$, $p>0.05$; species: $Z=-0.220$, $p>0.05$; relatedness to others: $t_{(26)}=1.982$, $p>0.05$; number in herd: $R_s=0.170$, $p>0.05$; presence of a calf in the herd: $t_{(28)}=0.462$, $p>0.05$; age: $F_{(3,26)}=0.905$, $p>0.05$). There was no correlation between adaptable component scores and frequency of social interactions (positive physical: $R_s=0.098$, $p>0.05$; negative physical: $R_s=0.061$, $p>0.05$; positive non-physical: $R_s=-0.158$, $p>0.05$; negative non-physical: $R_s=-0.174$, $p>0.05$) or with number of individuals interacted with in the herd in either a positive ($R_s=0.105$, $p>0.05$) or a negative manner ($R_s=-0.02$, $p>0.05$).

5.3.3.2. Component 2 – Sociable

Elephants considered more sociable by elephant keepers interacted positively with more elephants in the herd than did less sociable elephants ($R_s=0.395$, $p<0.05$). There was no correlation between personality and the number of individuals interacted with in the herd in terms of negative interactions ($R_s=0.184$, $p>0.05$). Sociable personality scores decreased linearly as age of the individuals increased, both when this was looked at as age as a continuous variable ($R_s=-0.714$, $p<0.001$) and when it was condensed down into categories ($\chi^2=13.218$, $df=3$, $p<0.01$) (Figure 5.2). There was no correlation between herd size and how sociable keepers perceived elephants to be ($R_s=0.332$, $p>0.05$). There was also no relationship between the sociable personality component and the origin of elephants ($Z=-1.450$, $p>0.05$) so being born into a zoo was not reflective of personality type as perceived by elephant keepers. Nor was there a relationship between personality and sex ($Z=-1.497$, $p>0.05$), species ($Z=-0.022$, $p>0.05$), relatedness to others in the herd ($Z=-1.547$, $p>0.05$) or between individual elephants ($\chi^2=29$, $df=29$, $p>0.05$). There was a positive correlation between the sociable component score and physical positive interactions ($R_s=0.627$, $p<0.001$) and a negative correlation with non-physical negative interactions ($R_s=-0.505$, $p<0.01$). There was no correlation between negative physical interactions ($R_s=0.168$, $p>0.05$) or non-physical positive interactions and the sociable personality component score ($R_s=0.468$, $p>0.05$).

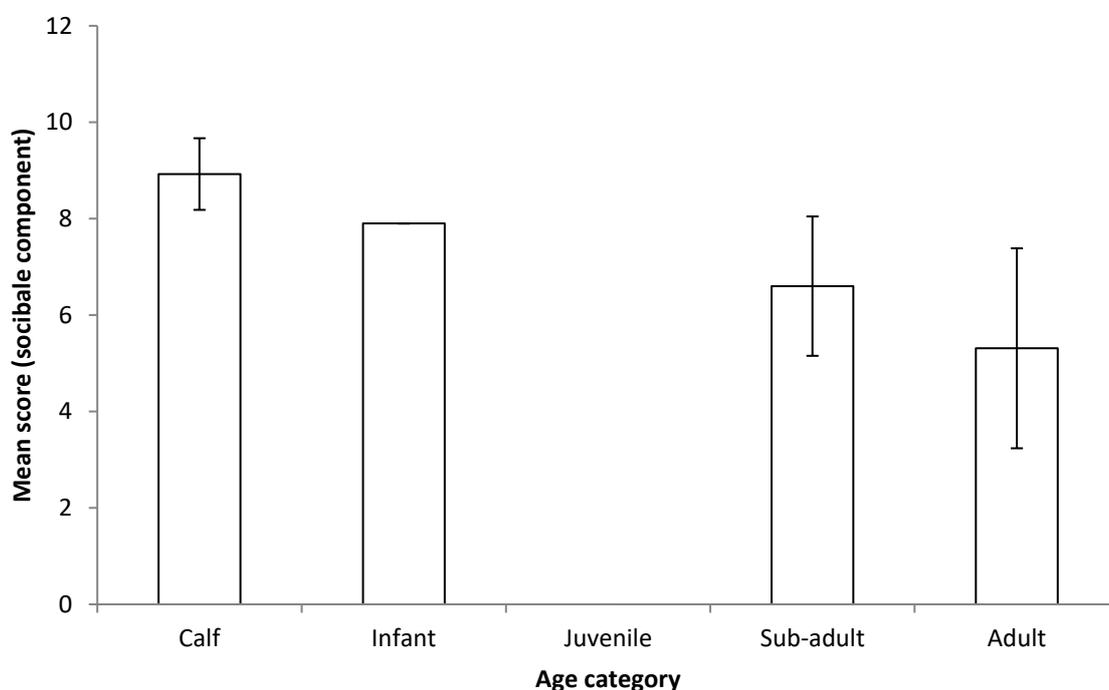


Figure 5.2. Mean scores on the social personality component for each age category. There were no juvenile elephants and only one infant elephant in the study population. Absolute figure is therefore represented for the infant age category.

Where data for dyads were combined (i.e. sociability component scores for both individuals were added together) to investigate the combined sociability level of the dyad, there was a positive correlation between the combined score and non-physical positive interactions ($R_s=0.515$, $p<0.001$) indicating that elephants with a higher combined sociability scores engaged in a greater percentage of non-physical positive interactions than elephants with lower combined scores. There was a negative correlation between the combined sociable score and non-physical negative interactions ($R_s=-0.479$, $p<0.001$) indicating that the higher the combined sociability score for the dyad (i.e. highly sociable giver highly sociable receiver), the fewer non-physical negative interactions were given/received. Analysis of the sociable personality scores indicated that for positive non-physical interactions there was a significant difference between partner types ($\chi^2=17.461$, $df=4$, $p<0.01$). A post-hoc test revealed that highly sociable elephants engaged in positive non-physical interactions with other highly sociable elephants more frequently than unsociable elephants engaged with mid-sociable elephants ($\chi^2=37.250$, $p<0.05$), and mid-sociable elephants engaged with each other ($\chi^2=-26.635$, $p<0.01$). No interactions were recorded for unsociable – unsociable, unsociable – highly sociable, mid-sociable – unsociable or highly sociable – unsociable combinations so these could not be analysed (Figure 5.3).

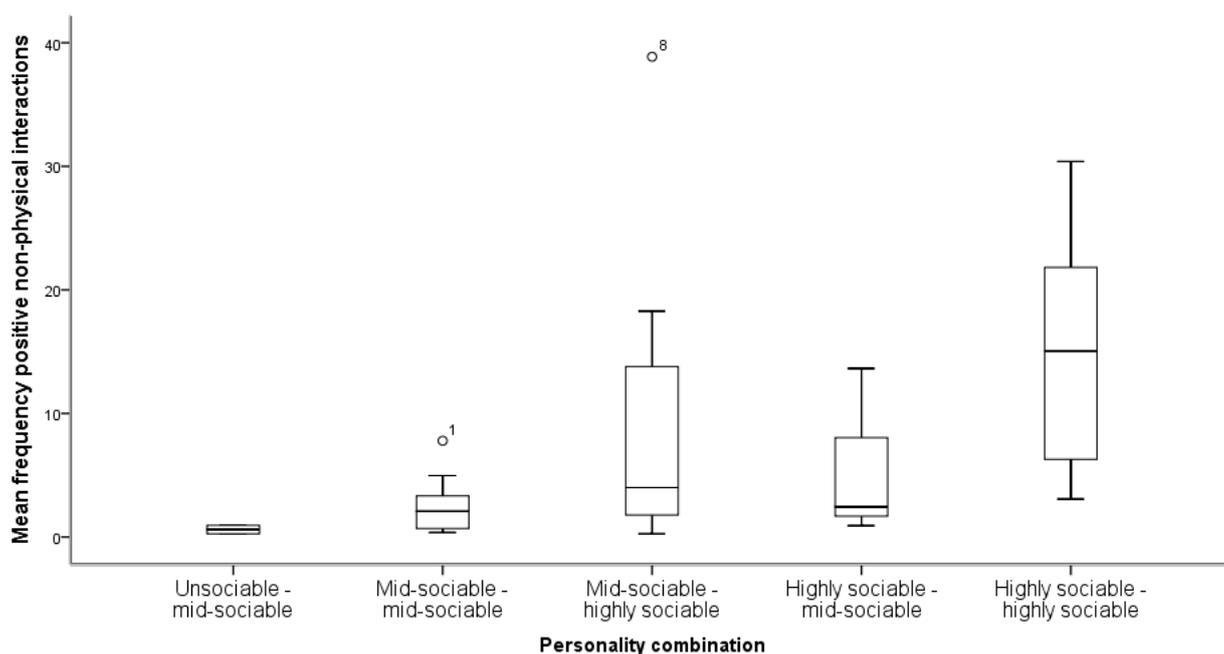


Figure 5.3. Mean frequency of positive non-physical interactions in relation to personality combinations. Elephants were grouped according to their level of sociability identified from the personality assessment [Unsociable: 0 – 3.3; Mid-sociable: 3.4 – 6.6, Highly sociable: 6.7 – 10]

5.3.3.3. Component 3 – Engaged with the environment

Individuals who scored higher on the ‘engaged with the environment’ component interacted negatively with more individuals within the herd than those who scored lower ($R_s=0.388$, $p<0.05$). There was no correlation between the ‘engaged with the environment’ score and the number of individuals interacted with in the herd in a positive way ($R_s=0.569$, $p>0.05$). There was a positive correlation between level of engagement with the environment and positive physical interactions ($R_s=0.392$, $p<0.05$). However, there was no significant correlation between the ‘engaged with the environment’ component score and frequency of positive non-physical interactions ($R_s=-0.119$, $p>0.05$) or negative physical ($R_s=0.222$, $p>0.05$) and non-physical interactions ($R_s=-0.143$, $p>0.05$) given by individual elephants. There was also no correlation between the ‘engaged with the environment’ component score and origin ($Z=-0.702$, $p>0.05$), sex (-0.580 , $p>0.05$), species ($Z=-0.462$, $p>0.05$), relatedness to others in the herd ($Z=-0.906$, $p>0.05$), age ($\chi^2(3)=3.628$, $p>0.05$) or number in the herd ($R_s=-0.144$, $p>0.05$).

5.4. Discussion

The objective of this chapter was to investigate whether keeper assessment of elephant personality in UK and Irish herds was related to social interactions and dyadic relationships. Reliability between keepers reached statistically acceptable thresholds and three personality factors were identified: ‘engaged with the environment’, ‘adaptable’ and ‘sociable’. Sociable personality component scores were not related to elephant origin, sex, species or relatedness to others, but they decreased as the age of the elephant increased. There was a positive correlation between combined sociable personality component scores in dyads and positive social interactions and a negative correlation with negative social interactions. Elephants considered to be more sociable by keepers interacted with more individuals in the herd than did less sociable elephants. Elephants considered highly sociable interacted with highly sociable elephants more than unsociable or mid-sociable elephants.

Personality assessment in humans and early personality assessment in animals used to focus on the five factor model of ‘neuroticism’, ‘extraversion’, ‘openness’, ‘agreeableness’ and ‘conscientiousness’ (McCrae & John, 1992). However, the inclusion of extra dimensions such as ‘dominance’ and ‘activity’ have been advocated (Gosling & John, 1999). Limitations of this fixed approach and problems associated with misinterpretation of the factors when it is being used in animal research and applied to animal personality types have been recognised (Gosling & John, 1999). It is instead advocated that researchers acknowledge that basic traits may exist within populations but that across species, different traits may be more or less important (Weiss, 2017). This chapter used a PCA to draw out specific components, rather than modelling the data on the more traditional five factor model. The three components identified in this study

aligned to findings from work undertaken by other researchers, who principally identified three to five components. This study indicates that keepers can reliably rate personality of their elephants, however level of expertise and time spent with the herd should be taken into account. Experience does not necessarily improve validity of ratings (Meagher, 2009) but as the ratings in this situation were based on knowledge of the elephants garnered over a period of time and across a range of situations, some experience (in this instance a minimum of three months) with the group was deemed necessary for an accurate assessment.

5.4.1. Relationship with social interactions and personality components

Makecha et al (2012) suggested that personality likely plays a critical role in frequency and types of social interactions in which elephants engage. This research supports that assertion. A relationship between frequency of social interactions and the components 'engaged with the environment' and 'sociable' was identified. There was no correlation with the 'adaptable' component. There was a positive correlation between 'engaged with the environment' and positive physical interactions, however elephants who scored higher on that component also interacted negatively with a greater number of individuals in the herd than those who scored lower. There is no clear reason for this finding. However, negative interactions included walking away from other elephants (see Ethogram, Table 4.2) and so it is possible that these elephants were avoiding some herd members, or being displaced by other higher ranking herd members. Playfulness and goal-directed behaviours are considered by the World Association of Zoos and Aquariums (WAZA) to be examples of positive experiences in terms of mental health for animals (Mellor et al., 2015). Elephants that were engaging negatively with a greater number of individuals in the herd were considered to be playful with objects. This is suggestive of positive welfare states and suggests some level of confidence in the environment. In order for zoo animals to experience good welfare they must be provided with environments that promote positive affective states (Mellor, 2016). Animals that are engaging with the environment are believed to be experiencing positive affective engagement which may contribute to positive welfare states (Mellor, 2015). Taken together these results suggest that the welfare of these individuals is not comprised; the relationship with positive social interactions, the occurrence of interaction with the environment and only low levels of negative social interactions suggest an overall positive affective state in relation to the environment. However, provision of environments which enable such individuals to avoid conspecifics when desired may be particularly important for their welfare.

The sociable personality component was the main area of focus for this chapter and so the majority of the analysis and the rest of the discussion focuses on the relationship between this personality component and social relationships in the study elephants. Individual sociability as perceived by keepers was not related to elephant origin, sex, species or relatedness to others in

the herd. This suggests that being born into a zoo, or being a member of a naturalistic herd did not have an impact on sociability of the study elephants. This finding is to be expected. Personality is believed to be shaped by past experiences and environmental variations (Sachser et al., 2013). Individuals may respond differently to the same environments but the behavioural changes should change in relation to others in the group (Gosling, 2001). Sociability score decreased as elephant age increased. This could be linked to development of young animals, settling into their adult personalities as they mature. The extent to which the zoo environment affects the development of personality is still an unknown area. Studies of laboratory rats have found that individual personality can be shaped by early environments (Rödel & Meyer, 2011). Powell and Gartner (2011) suggest that there is a need to assess the impact of physical and social rearing environments on personality developments, because there may be the potential to steer personality development. How the zoo environment shapes the personality of young elephants is an area for future consideration. African and Asian elephants are treated as one species in elephant management guidelines (Defra, 2017) despite distinct differences in their wild social structures (de Silva et al., 2011). There were no species level differences in sociability scores in the study elephants. There were no African elephant calves in the study herds so the lack of species level differences may be representative of this lack of African elephant calves or it may represent a genuine lack of difference between sociability in the two species. Future studies should seek to investigate species level differences in elephant personality at all age levels, to determine if there are significant differences in overarching 'species' personalities as opposed to within individuals only.

5.4.2. Analysis of dyadic relationships

Personality is individual and in chimpanzees, another highly social and intelligent species, friendships have shown homophily in personality types (Massen & Koski, 2014). It is therefore likely that in elephants, a highly social species who exhibit strong social bonds in wild populations, a relationship may exist between personality types within dyads. There was a positive correlation between the combined scores of individuals in dyads and non-physical positive social interactions and a negative correlation between the combined dyadic score and non-physical negative interactions. Elephants considered to be more sociable by keepers were therefore engaging in more positive interactions and less negative interactions than those considered less sociable. If keepers can reliably rate personality of their elephants then these findings are to be expected. Elephants are a social species and physical aggression in female wild elephant herds is minimal (Guthmann, 1970; Lee, 1987; Archie & Chiyo, 2012). Reports of the zoo elephant literature have documented aggression in elephant herds (Adams & Berg, 1980; Clubb & Mason, 2002; Wilson et al., 2006; Zoos Forum, 2010) but where details are provided the behaviours observed are those

which could be considered low levels of agonistic interactions, such as displacement (Adams & Berg, 1980; Wilson et al., 2006). Most reports in wild elephants of physical aggression are from bull elephants, during musth, a point of heightened sexual activity when elephants have elevated levels of testosterone (Lincoln & Ratnasooriya, 1996). None of the herds in this study housed more than one bull elephant. Bulls were housed with females, or with family groups including calves of both sexes.

It was hypothesised that there would be a link between sociability levels of social partners (e.g. individuals considered to be highly sociable would interact more with individuals who were also highly sociable). There was a relationship between sociable personality component scores in dyads but it was not linear. Elephants considered highly sociable engaged in positive non-physical interactions with other highly sociable elephants more frequently than they did with unsociable elephants. Mid-sociable elephants engaged most frequently with each other. These differences may be attributable to the relative hierarchical position of the individuals involved in the interaction or they may also represent a lack of options in terms of social level of herd mates. The largest herd size was seven and the smallest herd size was two. If all individuals in the group were considered to be of the same level of sociability there would not be the opportunity for individuals to engage in interactions with elephants of other levels. It could also reflect the effect of the hierarchy and position within the hierarchy on individual experiences. In the wild dominance interactions between African elephants were predominantly dyadic and were most frequent between group matriarchs (Wittemyer et al., 2007). Research into dolphins, another socially complex and therefore potentially comparative species, indicated that dolphin social rank was related to personality (Frick, 2016). However the level of correlation between social rank and personality was most apparent at extremes of the hierarchy; individuals at the extremes of the social hierarchy had a greater correlation between their personality and their social status (Frick, 2016).

Literature on the relationship between personality and social organisation is growing. It is recognised as an important field of research, especially when used in zoo animal welfare studies through identification of potentially more compatible social groups or appropriate partners for breeding (e.g. Carlstead et al., 1999b; Wielebnowski, 1999; Schel et al., 2013; Massen & Koski, 2014; Martin-Wintle et al., 2017). There is still a paucity of literature on the relationship between personality and social behaviour in zoo elephants, despite recognition of their complex social relationships and needs. For many species the relationship between personality and social relationships remains largely unclear, with a number of unanswered questions, including whether personality types are evenly distributed throughout groups or if groups are sorted according to personality (Webster & Ward, 2011). Personality and degree of sociability are believed to be inherently related, with one factor influencing the other. Horback et

al. (2013) suggested that zoo elephant personalities as rated by keepers with an extensive knowledge of the individuals concerned could be used as a proxy for long-term behavioural monitoring. A recent study published by Bonaparte-Saller and Mench (2018) was the first to use keeper surveys to try to assess social bond strength in zoo elephants. In their study they found that keepers could reliably rate elephant social bond strength (assessed using ICC scores) and ratings were related to proximity analyses of the study elephants. However, keeper assessment in that study, conducted across 23 herds in America, was not related to social interactions. Results of this chapter show that keeper ratings of personality are related to social interactions in the zoo herds. This supports the conclusion made by Bonaparte-Saller and Mench (2018), that elephant keepers can reliably rate the sociability of their animals. It also suggests that for UK and Irish herds, keeper ratings are significantly related to actual social relationships in zoo elephant herds and therefore could form a valid way of assessing zoo elephant relationships in the future.

The scan sampling technique utilised in this project to collect social interaction data may have led to an underrepresentation of actual interactions. Physical interactions accounted for a relatively small percentage of activity and so it is possible that association with others may reveal more information about the social preferences of these elephants. Researchers have found that keeper ratings of elephant personality can be representative of actual behaviour observed (Horback et al., 2013) but to the author's knowledge no research has investigated links between personality types and social interactions in UK and Irish zoo elephants. This work sought to fill that void. It is possible that the interactions observed in the current groups may be a result of the friendships and herd structures in the current elephant groups and that degree of sociability may change when put into other social groups. However, as has been detailed previously personality assessments have successfully been used in other species to predict mating success and compatibility of social groups (Massen & Koski, 2014; Martin-Wintle et al., 2017). The reliability of personality assessment as a predictive social compatibility tool, for example, when individuals are moved to other herds as part of routine population management or when group structure changes due to births or deaths, is an important area for future work.

5.5. Conclusion

The importance of consideration of personality has been highlighted in a number of species both in the wild and zoos. Engagement in positive social interactions is indicative of positive affective states in zoo animals. The results from this study show that elephants exhibit unique personalities and that individuals range in their level of sociability. Recognition of these differences is extremely important, and using a reliable assessment method which is unambiguous and repeatable is paramount for inclusion in welfare assessment. During this study keeper questionnaires were identified as a reliable means of assessing elephant personality. Keeper ratings of personality were related to frequency of social interactions. Individual differences in zoo animals have previously been related to: breeding success, resting behaviour and social compatibility. Keepers and researchers have highlighted the importance of caring for elephants on an individual basis and recent changes to elephant management guidelines have expressed this sentiment. Current guidelines state that UK and Irish zoos should be providing unique management plans for each animal and having a long-term management plan for each elephant exhibit, including behavioural profiles and details of herd compatibility. The ability to reliably document personality of zoo elephants is an important aspect to consider and include in individual management plans. There is the potential for a number of interacting factors which contribute to the success or failure of elephant social groups. Further work should build on the findings in this chapter, investigating whether personality plays a part in zoo elephant social hierarchies and exploring the potential for keeper ratings of personality as a predictive tool in elephant compatibility assessments. In order to fulfil the aim of this thesis and provide a fuller picture of factors affecting elephant social groups it is important to add to the information provided in this chapter by identifying whether herd demographics are related to elephant relationships and therefore potentially compatibility in zoo elephant herds.

5.6. Chapter summary

- Intra class correlation coefficients (demonstrating reliability between raters) were identified for nine of the personality adjectives included in the keeper assessment of personality questionnaire
- A principal components analysis reduced the nine adjectives into three personality components with good internal consistency: adaptable, sociable and engaged with the environment
- Elephants considered more 'sociable' by keepers interacted positively with a greater number of elephants in the herd than less 'sociable' elephants
- There was a negative correlation between the sociable personality component score and age of the study elephants
- Significant correlations were recorded between sociable personality component scores and social interactions
- Significant correlations were observed between combined sociable personality component scores in dyads and social interactions

During this chapter reliability between raters reached statistically acceptable thresholds for nine personality adjectives and three personality components were subsequently identified. The data presented in this chapter allowed the exploration of the relationship between elephant personality (as rated by elephant keepers) and frequency of social interactions in UK and Irish elephants thus answering Objective Three of this thesis, to identify whether a relationship exists between elephant personality and social interactions. This data feeds into the following chapter (Chapter Six) and is considered alongside a number of other herd demographics to see whether there is a relationship between a number of individual and zoo-level factors and social relationships in zoo elephant herds.

CHAPTER 6

Social group factors affecting interactions in zoo-housed elephants

6.1. Introduction

For the purposes of this research successful social groups have been defined as those where there is limited expression of behaviours indicative of stress or poor welfare (e.g. excessive aggression, performance of stereotypes), exhibition of behaviours indicative of positive welfare (e.g. positive social interactions) and successful reproduction (Inglett et al., 1989; Mellen, 1991; Lutz et al., 2003; Price & Stoinski, 2007). A range of factors can affect the success of social groups, especially when unfamiliar individuals are being introduced to one another (Brent et al., 2017). These have been reviewed in Chapter Two but they can be briefly considered to include opportunity for choice of social partners (Wielebnowski, 1999; Martin-Wintle et al., 2015), past individual experiences (Freeman & Ross, 2014; Prado-Oviedo et al., 2016), group sizes and compositions (Price & Stoinski, 2007), position in the social hierarchy (Sapolsky, 2005), individual compatibility (Carlstead et al., 1999b) and personality (Massen & Koski, 2014). Being able to understand details of interactions in social groups (Koene & Ipema, 2013) and how factors impact social relationships, has ramifications for animal welfare in zoos on both an individual and a group scale (Rose & Croft, 2015).

6.1.1. Background

A stable social group is thought to be a positive and 'comforting' influence on all of the group members (Williams et al., 2018a) but social compatibility is an area of concern for a number of species. Identification of appropriate social groups has the potential to impact on individual animal welfare in a number of ways. Social complexity, in terms of conspecific (group size and composition) or species (e.g. mixed species exhibits) composition, is an important area of enrichment (Carlstead & Shepherdson, 2000), and in elephants it has been recognised as the single most important thing to 'get right' for zoo animals (Rees, 2000). EAZA animal management guidelines advocate provision of social environments which reflect natural history in the wild (EAZA, 2014). However, the relationship between wild-type behaviour and enhanced welfare are considered by some to be correlational not causal (Veasey et al., 1996). There are indeed a number of examples where resemblance to wild-type social groups have led to successful social housing (detailed below), however there is controversy surrounding using the wild as an optimum standard (Veasey et al., 1996; Hutchins, 2006).

Resemblance to wild-type social groups in cotton-top tamarins led to increased breeding success; infant survival was high and incidences of abortion, stillbirth and parental neglect were low when individuals were housed in groups that replicate the wild (Price & McGrew, 1990). Moreover, providing chimpanzees with the opportunity to engage in fission-fusion dynamics akin to wild type interactions led to low aggression rates and reduced aggressive interactions over time (Schel et al., 2013). However, housing zoo animals in wild-type social groups is more difficult to do

in some species (Williams et al., 2018a). For example, in large species, such as elephants, replicating wild-type social groups can be physically difficult, and requirements are likely to vary according to individual circumstances (Zoos Forum, 2010). Therefore identifying the elements of the wild-type social group that animals require for good welfare within zoos is important for maintenance of optimum welfare.

Kinship predicts social compatibility in laboratory housed mice and primates (Olsson & Westlund, 2007) and it is an important predictor of social relationships in wild African elephants (Vance et al., 2009; Archie & Chiyo, 2012). However, kinship is not the sole driver in all social interaction networks, as unrelated individuals will still interact and form successful social groups in both *in-situ* and *ex-situ* environments. Agonistic social networks in ring tailed coatis are not affected by kinship (Hirsch et al., 2012) and female rhesus macaques maintain stable relationships with non-kin social partners (Massen & Sterck, 2013). In wild elephants relationships need not be based on kinship. Unrelated reintroduced elephants in Thailand formed successful social groups upon release (Thitaram et al., 2015), elephants from heavily poached areas join unrelated herds (Gobush et al., 2009) and a single orphaned female who was captive reared before being released successfully joined a wild herd upon release (Evans et al., 2013). Furthermore in zoo-housed Asian elephants unrelated individuals have developed 'special relationships' with others; indicated by spatial proximity, increased arousal behaviour when one member of the dyad is removed and omission of agonistic behaviour (Garai, 1992; Vanitha et al., 2010).

The value of kinship in zoo animal social groups and the negative effects of inappropriate social groups have been highlighted throughout this thesis but it is possible that there are a number of other factors contributing to the development of zoo animal relationships and social group success. In adult zoo chimpanzees, social relationships are affected by kinship, sex combinations, age differences, time spent together and personality (Fraser et al., 2008; Koski et al., 2012). Relationships between bottle-nose dolphin calves are also affected by multiple factors; choice of companions are driven more by calf age, personality and conspecific age than relatedness (Levengood & Dudzinski, 2016).

Despite understanding the importance of herd structure in wild elephants, only recently have researchers focussed on advancing knowledge of zoo elephant social relationships through analysis of social networks (e.g. Coleing, 2009; Bonaparte-Saller & Mench, 2018; Harvey et al., 2018). A large body of research and current elephant management guidelines suggest that, wherever possible, elephants should be housed in related, multigenerational family herds (Walter, 2010; AZA, 2011; Defra, 2012; Asher et al., 2015; Chadwick et al., 2017; Harvey et al., 2018). However, within the UK and Ireland there is a need to house a range of individuals who may not have relatives within the zoo population (reviewed in Chapter Three). Elephant keepers and researchers have highlighted the importance of providing elephants with

compatible groups, with a range of ages and access to others at night (Chadwick et al., 2017). However, to date, factors affecting social relationships in UK and Irish zoo elephants have not been investigated in any detail. Identifying social group factors that may help to predict individual compatibility within unrelated elephants is vital to their individual welfare. For example, utilising knowledge of factors most likely to increase the occurrence of positive social interactions in order to identify potentially socially compatible partners or group sizes/age compositions. Documentation of this information will feed directly into the individual elephant management plans as requested in the SSSMZP elephant management guidelines 2017 update (Defra, 2017).

It is theoretically possible to provide optimum welfare in zoos (due to, for example, provision of food stuffs and medical care, and a lack of predators) but it is important to develop biologically meaningful and realistic measures that reflect the quality of elephant care and welfare (Hutchins, 2006). Identification of an evolving 'gold standard', which epitomises optimal welfare in zoo elephants is important in helping to develop such measures. Understanding the effects of a range of social conditions on individual welfare is an area that should be explored further, to work towards such an over-arching goal, and assist in management decisions. Monitoring social behaviour of elephant dyads on a regular basis can provide valuable insight into group dynamics, and has the potential to be very important in management of zoo elephants (Harvey et al., 2018). This study goes one stage further, and investigates the relationship between a number of individual and zoo-level factors and social interactions in order to try to identify factors that may make elephant herds more or less likely to be socially compatible.

To the author's knowledge there has not been any identification of the relationship between demographic factors and zoo elephant social interactions and the exploration of personality and sociability has focused on association data rather than social interactions. Through completion of this project, information has been gathered which can help towards meeting the objectives of the BIAZA EWG by improving knowledge and contributing to a body of work designed to promote improved welfare in zoo elephants in the UK and Ireland. Understanding how individual personality and herd demographics are related to social interactions could prove essential in future management of elephant herds.

6.1.2. Aim and objectives

Despite knowledge of the level of sociality in wild elephants, and the recognition of the importance of compatibility in zoo herds, few researchers have investigated zoo elephant social relationships and none have identified demographic factors which may be affecting relationships. The majority of work undertaken looking at social interactions in zoo animals has focused on single groups, which prevents the opportunity to investigate social patterns among a species, as there can be much individual variation at the group (or establishment) level (Pacheco Pacheco, 2017). This chapter looks at a number of different social groups of mixed structures to establish whether there is a relationship between individual and zoo-level factors and elephant social behaviour in UK and Irish herds. The aim of this chapter is to build on research presented in Chapters Four and Five and identify what, if any, factors are related to frequency of social interactions (and therefore potentially social relationships), thus achieving Objective Four of the thesis. Wild elephants live in predominantly related matriarchal groups and reintroduced unrelated elephants bond best when calves are present. It is therefore hypothesised that the greatest frequency of positive interactions will be when elephants are related and when calves are present within the herd.

6.2. Methodology

6.2.1. Subjects and study sites

Details of the study elephants (n=32) and participating zoos (n=7) are provided in Chapter Four.

6.2.2. Data analysis

Data are expressed as a percentage of time elephants could have been observed for to prevent over-representation of sociability. Social interactions are expressed as a percentage of time spent giving social interactions (split into positive and negative physical and non-physical interactions) to other elephants. General linear models (GLMs) were used to investigate the influence of a number of individual and zoo-level factors on frequency of time individuals spent giving social interactions to the rest of the herd, and dyadic relationships. Assessed factors were: age of elephants, relatedness to others, species, origin, sex, study zoo and personality (see Chapter 5 for further details). Positive and negative physical interactions and positive and negative non-physical interactions were fitted as response variables, following quasibinomial error structures. Factors were fitted as separate fixed effects. Due to sample size limitations models were simplified and fixed effects were tested individually. All data analysis was undertaken in R (Version 1.1.383) using package lme4.

6.3. Results

Elephants were out of sight for a median of 30.54% (IQR: 20.11-35.49) of all observations. Results are reported as a percentage of all time they could have been observed for, in order to prevent over-representation of sociability in elephants who were out of sight for long periods of time. Feeding (median: 35.33% activity, IQR: 25.54 – 45.14) and resting (median: 14.79% activity, IQR: 7 – 19.38) were the most frequently observed behaviours. Social interactions were the next most frequently observed behaviour. Positive social interactions accounted for median 4.34% (IQR: 0.87 – 7.97) observations and negative social interactions represented median 0.14% (IQR: 0.07 – 0.33) observations (Figure 6.1).

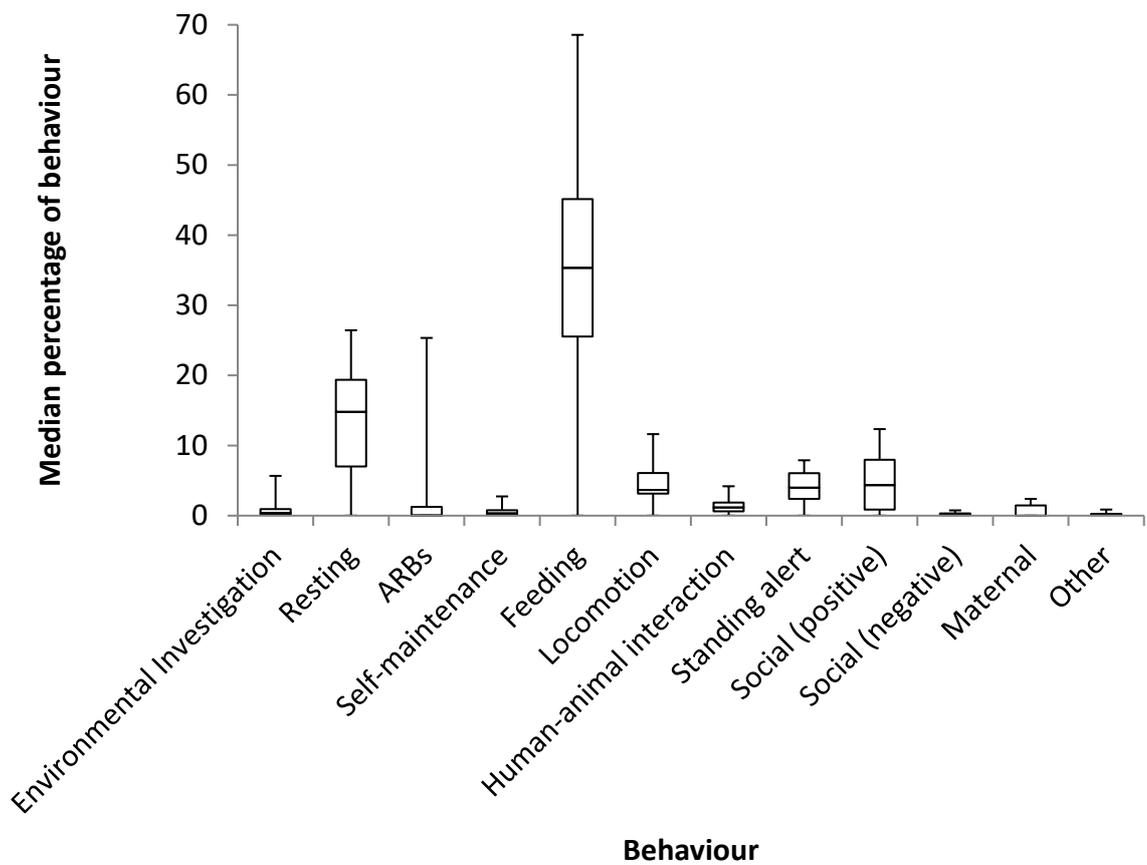


Figure 6.1. Median daily activity budget for the study elephants (n=32) at UK and Irish zoos (n=7). Elephants were out of sight for median 30.54% of time (IQR: 20.11-35.49)

6.3.1. Positive interactions

A breakdown of types of positive interactions is provided in Figure 6.2. Conspecific play, trunk to- and body to- were grouped as physical interactions. Trunk to- interactions were the most frequently occurring positive physical interactions, accounting for median 9.6% (IQR: 4.5 – 17.5%) of all positive interactions (range 0 – 75%). 88% of the study elephants engaged in positive trunk to- behaviours, whereas only 9% engaged in negative trunk to- behaviours.

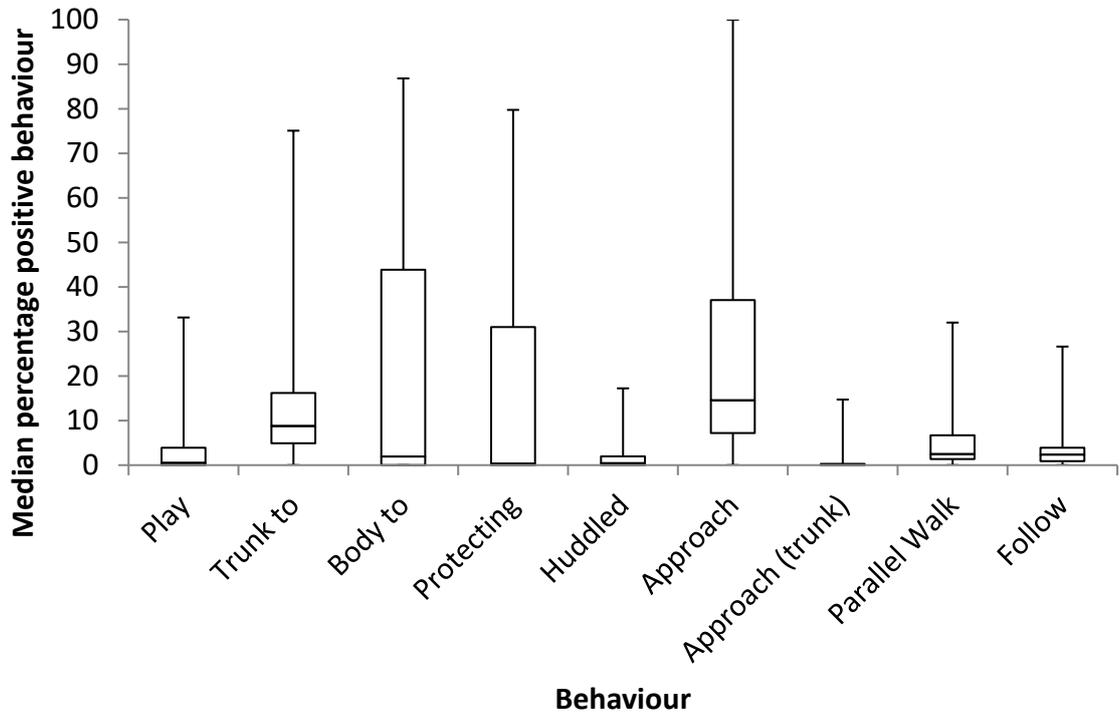


Figure 6.2. A breakdown of positive interactions observed. Conspecific play, trunk to- and body to- were grouped as physical interactions.

There was a positive correlation between frequency of positive physical social interactions and the extent to which elephants were considered to be sociable by keepers (0.41 ± 0.11 , $t=3.861$, $p<0.001$) (Figure 6.3). There was also a negative correlation between age and the sociable personality component score (-0.05 ± 0.02 , $t=-3.692$, $p<0.001$). There was a negative relationship between age (as assessed in age categories) and physical social interactions (-4.15 ± 0.29 , $t=-14.281$, $p<0.001$). Calves engaged in four times more positive physical social interactions than adults ($\chi^2=11.952$, $p<0.01$) (Table 6.1). There was no effect of relatedness to others, origin, zoo, sex, species, herd size or whether or not a calf was present in the herd on the frequency of positive physical social interactions.

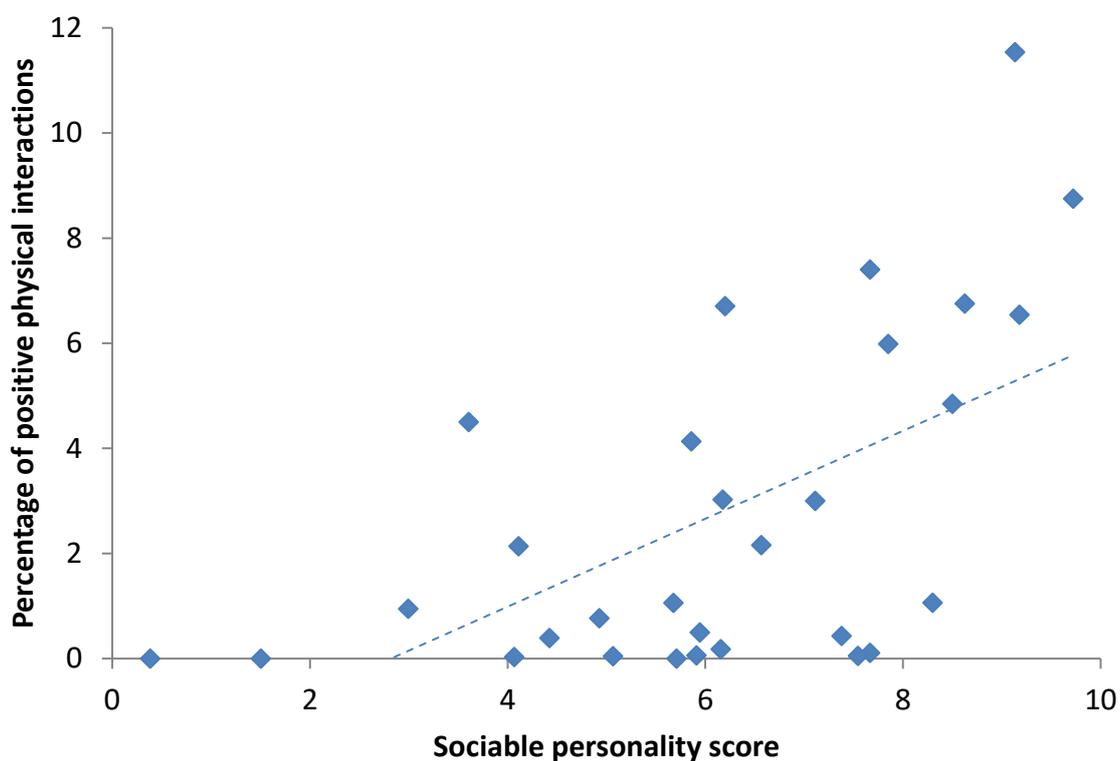


Figure 6.3. Relationship between sociable personality component score (assigned by keepers) and positive physical interactions given

Table 6.1. Median percent of social interactions for categorical variables assessed during analysis

Variable	Physical positive	Non-physical positive	Physical negative	Non-physical negative
Age category				
Adult	0.60*	1.57	0.02	0.12*
Sub-adult	0.50*	3.56	0.02	0.11*
Infant	5.99*	1.46	0.08	0.05*
Calf	7.40*	1.16	0.03	0.03*
Relatedness to others in herd				
Related	2.14	2.54*	0.04	0.07*
Unrelated	0.11	0.87*	0.01	0.17*
Species				
African	0.08	0.78*	0.01	0.13
Asian	2.15	1.77*	0.03	0.10
Calf presence				
Calf present	1.06	2.78*	0.03	0.11
Calf absent	0.11	0.87*	0.01	0.10

* indicates significant differences between the categories ($p < 0.05$)

There was a relationship between positive non-physical interactions and relatedness to others, species and the presence of a calf in the herd. Positive non-physical interactions were on average three times higher when elephants had a relative in the group than when they did not (1.08 ± 0.38 , $t = 2.803$, $p < 0.01$) and they were three times lower when no calves were present in the group (-1.29 ± 0.37 , $t = -3.488$, $p < 0.01$). Interactions between related individuals were on average three times more frequent than between unrelated individuals (Table 6.1). Positive non-physical interactions were higher in Asian herds than African herds (1.15 ± 0.45 , $t = 2.58$, $p < 0.05$). However, Asian elephants were held in, on average, larger and more related herds and so it is not possible to decipher from the data whether this finding is due to relatedness or to species. There was no relationship between the sociable personality component, elephant origin, zoo, age, sex or herd size and positive non-physical interactions.

6.3.2. Negative interactions

A breakdown of types of negative interactions is provided in Figure 6.4. Pushing/pulling and hitting/kicking were grouped as physical interactions. None of the investigated factors were correlated with negative physical interactions ($p > 0.05$). Negative non-physical interactions were affected by age of elephants (-2.27 ± 1.08 , $t = -2.105$, $p < 0.05$), calves engaged in ten times fewer negative physical interactions than adults ($\chi^2 = -16.800$, $p < 0.01$). There was also a negative correlation between herd size and negative non-physical interactions (-0.20 ± 0.08 , $t = 2.473$, $p < 0.05$) and the degree to which they were considered to be sociable by keepers (-0.25 ± 0.05 , $t = -4.664$, $p < 0.001$). Unrelated elephants engaged in three times more negative non-physical interactions than did related elephants (-0.77 ± 0.33 , $t = -2.313$, $p < 0.05$). There was no relationship between zoo, the presence of a calf, species, sex or origin.

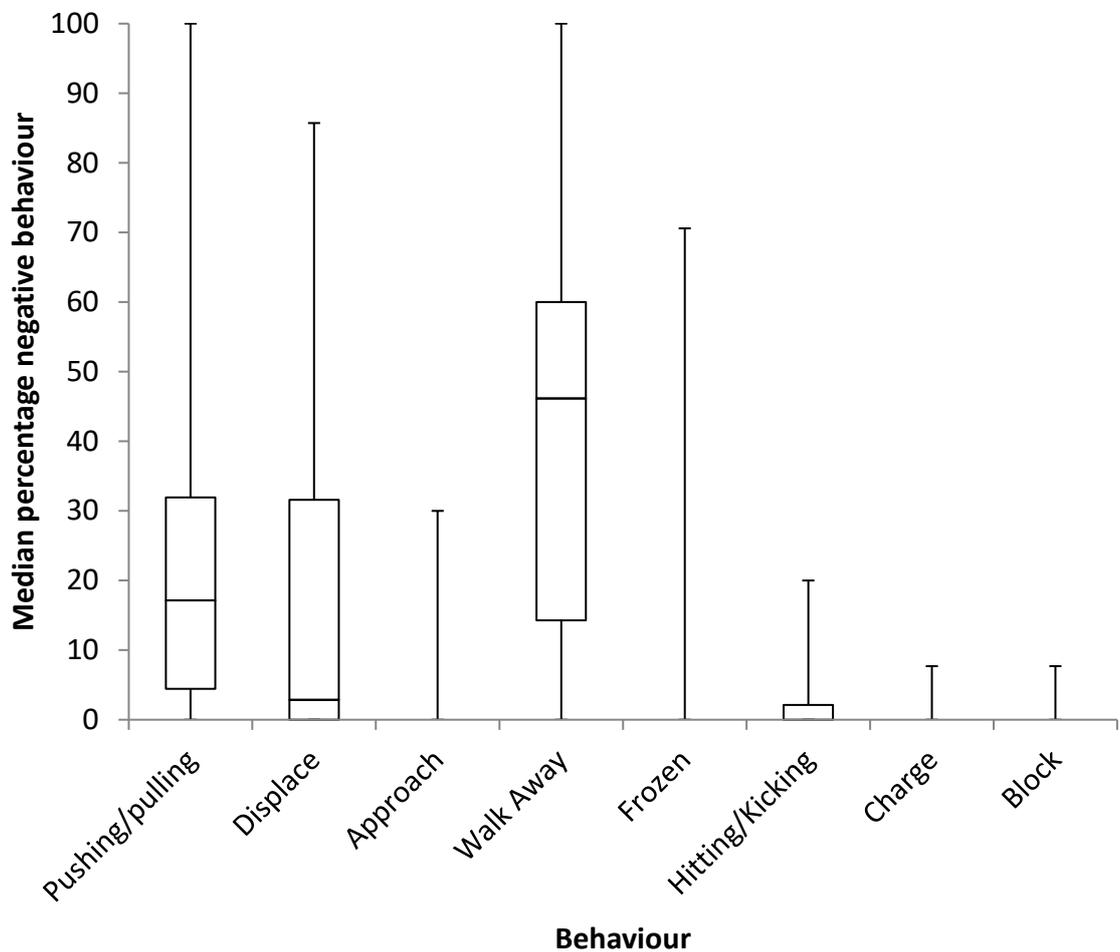


Figure 6.4. A breakdown of negative interactions observed. Pushing/pulling and hitting/kicking were grouped as physical interactions

6.4. Discussion

A number of individual and zoo-level factors affected social interactions in the observed herds. Positive physical interactions were affected by age (calves performed more than adults) and their personality (more sociable elephants engaged in more positive physical interactions). Positive non-physical interactions were affected by relatedness to others (greater frequency in elephants with relatives in the herd), species (higher in Asian elephants) and the presence of a calf in the group. Negative physical interactions were not significantly affected by any of the investigated factors, however this may be due to scarcity in performance of these behaviours. Negative non-physical interactions were related to age (adults engaged in more), personality (less sociable elephants engaged in more) and relatedness (frequency was higher in elephants that had no relatives in the group). It is potentially difficult to distinguish between some factors affecting interactions due to their overlapping nature and the relatively small sample size. This is an inherent problem in zoo research and so the reported results and accompanying discussion have been interpreted with this caveat in mind. These findings nevertheless contribute important knowledge to a currently relatively unknown subject area.

No overt aggression was observed during the study, with only minimal occurrences of 'correctional' behaviours such as trunk slap and kicking (Langbauer, 2000) recorded. This finding may be due to management of social incompatibilities by the study zoos. For example, at the onset of the study one herd was separated into two groups due to historic aggression between two females. The elephants still had the opportunity for tactile contact and so could still have engaged in agonistic interactions but the separation of these individuals and associated management was designed to minimise the occurrence of excessive aggression (Cairns pers. comm., 2016). Elephant keepers describe low levels of aggression as 'completely normal', however escalating aggression can be a cause for concern (Chadwick et al., 2017). Types of social behaviour recorded in this study, such as touching with the trunk, conspecific play, approaching conspecifics and displacement, were similar in nature to reports in other studies of zoo elephants (Adams & Berg, 1980; Brockett et al., 1999; Wilson et al., 2006; Freeman et al., 2010; Horback et al., 2013; Hacker et al., 2015; Bonaparte-Saller & Mench, 2018; Harvey et al., 2018).

6.4.1. Age and presence of calves

Positive physical interactions in this study were predominantly categorised as trunk to- (touching another elephant with the trunk in a non-aggressive manner) behaviours or social play. Trunk to- behaviours are a means of providing reassurance and comfort in elephants (Yasui & Idani, 2017). Positive physical interactions were not significantly affected by a calf in the herd, however positive non-physical interactions were greatest when calves were present, and on average calves engaged in four times more positive physical interactions than adults. Trunk to- behaviours were

the most frequently recorded positive physical interaction, and the occurrence of these behaviours decreased as the age of study elephants increased. Conspecific play was also related to age; the majority of conspecific play was observed at zoos which had calves in the herd and the highest frequency was recorded between bull elephant calves.

Care of offspring is a pivotal component in elephant social structure (Schulte, 2000) and reintroduced elephants form groups associated with the presence of an elephant calf, leading researchers to call for reintroductions to include groups of calves or adults with calves to increase the chance of successful group formation and long-term establishment of stable herds in the wild (Thitaram et al., 2015). The limited field of zoo research has also found that social interactions in zoo elephants are centralised around the presence of calves. When present, calves engage in most social interactions (Garai, 1992), connecting groups through initiation of social interactions (Coleing, 2009). Research in gorilla groups suggests that formation of new social groups is most likely to be successful when individuals are young (Stoinski et al., 2004). In wild African elephants the most frequent interaction type between immature elephants, especially young bulls, was social play (Lee, 1986).

The decrease in social interactions in older elephants is an interesting finding and one which could have a number of potential explanations. It could be that older elephants may have different backgrounds (e.g. wild caught) and they could have experienced different early management. Research has shown that elephants reared in social isolation may have impaired development (Kurt & Garai, 2001) and thus may not know how to interact socially, so if elephants have spent time in isolation in previous years this may have affected their social development. Or it could be that older elephants do not have such a great need to perform physical reassuring behaviours as frequently as calves. Elephant calves develop at a faster rate when they are exposed to physical contact (Moss, 1975). Furthermore, touch in elephant calves plays a role in normal development as well as enabling young elephants to test their strengths and capabilities with one another (Adams & Berg, 1980; Lee, 1987; Vidya & Sukumar, 2005). As has been noted above, calves are described as the herd nucleus in elephant groups (Gadgil & Vijayakumaran Nair, 1984; Coleing, 2009) and in the wild the allomothering of calves works to increase both calf survival and group stability (Lee, 1987). Touching (or trunk to-) behaviour could be a reinforcement of the social bond in the direction of older female to calf or it could be a result of a need for reassurance from the calf. Directionality of the interactions observed in this study is discussed in more detail in Chapter Four. Finally it could represent a change in social interactions as individuals age. Wild adult elephants do however engage in elaborate greeting rituals following separations, even if separation lasts for only a few minutes (Moss, 1981). However separations, especially for long periods of time, were not present in the study period. Further research should incorporate behavioural response to routine separation as a measure of social bond strength in adult elephants. The concept of social

behavioural change as individuals age has been reviewed in Krebs et al. (2018), however it is important to be able to separate a gradual change in social engagement as a result of natural aging from more serious health and therefore welfare problems.

Harris et al. (2008) advocated the need for herd structures with a range of ages, and these findings support this notion, but only for breeding herds, to provide companionship for youngest elephants and appropriate opportunities for social learning as they develop. However, it is not to say that an absence of calves in a herd leads to poor welfare. A lack of elephant calves did not necessarily lead to a lack of interaction within the study herds; adults did engage in positive physical interactions with one another when calves were not present. Investigating association rates in terms of proximity to others may be particularly important for herds with older members, where relationship strength may be better assessed using association data not just physical interactions.

6.4.2. Relatedness to others

Un-relatedness to other elephants in herds is one of many concerns for zoo elephant welfare, and researchers have suggested it can lead to aggressive behaviours (Clubb & Mason, 2002; Veasey, 2006). In this study, physical aggressive interactions were extremely rare and no overt aggression was observed. The most frequently observed physical negative interactions were pushing/pulling and hitting/kicking, which have been described as disciplinary behaviours (Langbauer, 2000). The occurrence of positive physical interactions were not affected by relatedness to others, but the frequency of positive non-physical interactions were higher and negative non-physical interactions were lower in elephants who had at least one relative in the herd. The lowest frequency of negative interactions was seen in the herd which most closely replicated a wild social group; a multi-generational group of related females and their offspring. However, the next two lowest frequency zoos comprised a herd with one unrelated individual and a completely unrelated herd (respectively). There was no significant difference in frequency of social interactions between the study zoos.

Historic reasons for limiting social choices and chaining/tethering elephants overnight were that there may be aggression between individuals (Wiedenmayer & Tanner, 1995; Brockett et al., 1999). The lack of overt aggression observed during this study suggests that this concern, in the UK and Ireland, is unfounded. Similar findings have been reported in other studies of zoo-elephant social behaviour, when physical aggression accounted for 0.5% or less of observed behaviour (Schmid, 1995; Gruber et al., 2000; Posta et al., 2013) and unrestricted access to others had no negative effects on behavioural profiles (Brockett et al. 1999). Low levels of aggression are described by keepers as 'normal', an integral part of maintaining the hierarchical herd structure (Chadwick et al., 2017). Zoo management guidelines suggest that, where possible elephants should

be kept in related, matriarchal family herds (Walter, 2010, AZA, 2011). However, there is a need to house a number of unrelated elephants within UK and Irish zoos and this trend is likely to continue whilst elephants are brought in from circuses or other zoos in Europe or are moved as part of zoo breeding programmes. Genetic relatedness predicts fission and fusion of social groups in wild African elephants, and associations between social groups persist long after original maternal kin have passed away (Archie et al., 2006). However, unrelated elephants successfully join wild social groups (Poole & Moss, 2008). In zoo-housed chimpanzees time spent together is one factor affecting social relationships between individuals (Fraser et al., 2008; Koski et al., 2012). It was not possible to look at years spent together in a measurable way as it was not always clear how long individuals had spent together prior to coming to the study zoos, for example, some had been housed together in previous collections. However, it could be possible that within zoo herds familiarity is as important as relatedness in individual compatibility and this is an area which should be investigated more thoroughly in the future.

6.4.3 Differences at the species level

Positive non-physical social interactions were more frequent in Asian elephants than African elephants, although there were no species level differences for positive physical, negative physical or negative non-physical interactions. The reason for these differences are unclear but it is possible that they are the result of a lack of equality in the observed social groups in terms of age structure and relatedness. Generally Asian elephants were kept in larger and more related groups than African elephants in the study, and none of the studied African elephant herds had calves in the groups. African and Asian elephants are presently treated as one species in terms of management guidelines (Defra, 2017). In the wild they have different social structures; African elephants predominantly live in larger and more complex social groups than Asian elephants (de Silva et al., 2011), although both African and Asian elephants have strong social bonds within their social groups (Moss & Poole, 1983; Chiyo et al., 2011; de Silva et al., 2011; Goldenberg et al., 2014). Differences in social structure in wild African and Asian elephants relate to the size and complexity of social groups; African elephant social groups are generally larger (de Silva & Wittemyer, 2012) and more connected than wild Asian elephant social groups (de Silva et al., 2011). These structural differences are likely an influence of their wild environments and thus may not be so prevalent in zoos. It is extremely important to consider species level differences in future studies of elephant social structures in zoos; if there are biologically relevant species-level differences in their social structures within zoos, which replicate wild-type differences, then consideration should be given to developing species specific guidelines, in order to ensure optimal welfare for all individuals. It may be that greater consideration should be given not just to species-level interactions, but also to group type, e.g. family group, bachelor herd or unrelated non-breeding females, to ensure all

individual needs are being met within the social group. An increased sample size may provide the opportunity to identify species level differences and so should be considered in future studies.

6.4.4. Personality

Personality (as identified using a keeper assessment of personality) (see Chapter Five) was related positively to frequency of positive physical interactions and negatively to frequency of negative non-physical interactions. Thus, keeper scores on sociability in elephants predict the amount of prosocial behaviour in which elephants engage. This is potentially extremely important in elephant management as it highlights the possibility of using keeper ratings as a proxy for behavioural observations. The findings also highlight the fact that elephants have unique personalities and that they range in their level of sociability. This may be a factor of their life experiences. Understanding more about the relationship between personality and friendship choices in elephants may be important for both current and future welfare of zoo elephants. If personality enables a means of assessing social compatibility in elephants it could help to predict the potential for social compatibility between elephants in future moves.

6.4.5. Factors not related to social interactions

Not all of the investigated factors were related to observed social interactions. There was no relationship between social interactions (physical or non-physical) and origin of elephants, which suggests that neither being born into a zoo nor coming from the wild predicts the ability of individuals to exist in a functional social group, a very important and promising finding for zoo elephants. It suggests that if provided with an appropriate social environment there is the potential to maintain good welfare for all zoo elephants, regardless of prior experiences. There was also no behavioural difference between male and female elephants although this finding could be due to the low number of adult bulls observed. In the wild there is a great deal of variation in terms of behavioural development in bulls and cows (Lee & Moss, 1999). Only two adult bulls were observed during the study and these were both only able to be recorded during daytime hours in outside enclosures. All other males in the observed herds were calves. The finding could also be due to redundancy of some behaviours in zoo populations (Mason, 2010), where social groups are more fixed and the opportunity to engage in some wild-type behaviours may not present itself. There was no relationship between positive physical interactions and relatedness to others, origin, zoo, sex, species, herd size or presence of calf, and no relationships were observed between negative physical interactions and any of the investigated factors. The lack of evidence to support a link between group size and positive social behaviour lends empirical evidence to support arguments made by elephant keepers and researchers that, within reason, compatibility of elephants is of greater importance than a minimum group size (Chadwick et al., 2017). These

findings may however be due to the low frequency of physical interactions recorded during the study. Further investigation of elephant sociability in terms of association data may reveal more relationships with the investigated factors, and lend further support to these findings.

It is highly likely that it is a combination of multiple, interacting factors that are affecting the success of elephant social groups, and it is important to recognise that the structure of social groups can change over time. This study was conducted over a 12 month period in order to minimise the effect of time of year. Social interactions were variable throughout the period of the year but there appeared to be no specific effect of seasonality across all of the study groups (Chapter Four). This work goes some way to identifying factors which may be influencing social relationships in zoo-housed elephants in the UK and Ireland, and lays down a reliable methodology for documenting and assessing elephant relationships. Knowing factors which may be influencing social relationships in zoo elephants will help to potentially predict social compatibility in zoo elephants, or at least to identify 'risk factors' which may reduce the likelihood of individuals being compatible. Future work should seek to investigate the relationship between physical interactions, proximity to other elephants and measures of a number of indicators of welfare, to attempt to document the relationship between physical interactions, proximity and physical and physiological welfare. The appropriateness of the use of social interaction rather than association to identify sociability in zoo elephants is debateable; however, no researchers have to date accurately identified the best way to assess this robustly.

This study has identified relationships between a number of factors and social interactions in the study elephants. However, these must be interpreted with caution. Frequency of social interactions, in particular physical negative interactions, accounted for a very small percentage of total time and thus whilst relationships were statistically significant they may not have biological relevance in terms of actual social group dynamics. Moreover, they may not currently be applicable to other zoo populations. Nevertheless, it is an important piece of work on which to build. Understanding that there could be factors which are affecting social relationships in zoo elephants is an important first step in being able to provide zoo elephants with appropriate environments which fulfil their complex social needs. Further research should be conducted to investigate whether the factors identified in this research affect other elephant groups in the same way as would be predicted following the outcome of this research, thus validating the findings of this work. In addition to this the relationship between the identified factors and welfare of individuals should be included as a point for further investigation, to determine the extent to which elephant social groups impact upon their wellbeing.

Tactile contact has been identified as being expressed less often than elephants may be proximate to herd mates, and it shows less consistency over time (Bonaparte-Saller & Mench, 2018). Prior to this study research has indicated that keeper

questionnaires may not be able to reliably predict interactions between elephants (Bonaparte-Saller & Mench, 2018). During this study changes in frequency of physical interactions in terms of number of interactions given did not show significant change over time, however overall herd networks did show some level of fluctuations (Chapter 4). Keeper ratings of elephant personality were related to actual observed social interactions and number of individuals interacted with in the herd (Chapter 5). Other researchers have identified tactile behaviours as an important component in elephant social interactions, recognising the importance of individual differences in the frequency and type of social interactions given (Makecha et al., 2012). It is clear from this project and other recent research (e.g. Chadwick et al. 2017; Bonaparte-Saller & Mench, 2018; Harvey et al., 2018) that this is an evolving and important field of research. Further understanding of factors which may affect zoo elephant social relationships and therefore potentially impact upon social well-being is paramount moving forwards. Establishing a greater understanding of herd dynamics leading to evidence-based social management decisions will help to provide optimum social groups. Furthermore, methodologies utilised in this study have applicability in other socially housed zoo species.

6.5. Conclusion

Appropriate social groups comprising compatible individuals can be one of the hardest things to provide social species in zoos, especially an animal with needs as complex as an elephant. Historically researchers looked to wild elephant social groups to predict zoo elephant social wants and needs, but the zoo environment is artificial and social groups are more fixed than in the wild. Furthermore, the pressures driving social group formation and existence are not present within zoos, and so factors driving social group success in zoos may be different to the wild. The occurrence of positive social interactions has been identified as an important yet understudied indicator of welfare in zoo elephant social groups. Recent research has begun to focus more on social interactions in zoo elephants and current guidelines recognise the importance of individual compatibility. It is likely that a number of factors may affect zoo elephant social relationships and identification of these is important for future welfare. The results from this study show that elephant relationships (as measured through frequency of social interactions) are related to age, personality, presence of calves in a herd, relatedness to others in the herd and species. Whilst it is important to recognise that these factors may be to some extent overlapping, this study has made important first steps to identify things that may be affecting the success of zoo elephant relationships. These results must however be interpreted with some caution. Whilst significant differences were identified the frequency of social interactions was relatively low in the study herds, and so the impact of the differences between the factors investigated may need further research in a wider range of institutions before extrapolations can be made from the dataset and

inferences relating to welfare are made. The most interconnected group was the largest group with the greatest number of calves, however elephants held in smaller groups also engaged in a range of positive social behaviours. The lack of a significant link between elephant herd size and positive social behaviour lends evidence to support suggestions by elephant keepers that the recommended minimum group size of four individuals (currently a criterion in the SSSMZP elephant management guidelines) may not be as important as compatibility for individual welfare. It is clear from the results of this study that elephants need social companions but the degree to which they require or seek out social interactions may differ between individuals. Being able to predict factors that may contribute to the success of social groups is important for both individual and whole group welfare. Further work is needed to investigate the relationship between the factors identified and individual elephant welfare, to document whether or not there is a direct link between the occurrence of positive or negative social interactions and individual elephant welfare. Taking into account individual life histories and social needs at different life stages is also an important area for consideration. This work takes the first important steps in a long research road to identify how the zoo environment is affecting elephant social groups and to ensure individual and group needs are being met within collections.

6.6. Chapter summary

- Positive non-physical interactions were greatest when calves were present
- Positive non-physical interactions were higher and negative non-physical interactions were lower when elephants had at least one relative in the herd
- Positive physical interactions were related positively to sociable personality types whilst negative non-physical interactions were negatively related to personality

This chapter identified individual and zoo-level factors affecting performance of positive and negative social interactions in zoo elephants. The data presented in the chapter combined frequency of social interactions (Chapter Four), personality ratings undertaken by elephant keepers (Chapter Five) and other factors to produce an overall assessment of factors which may be related to elephant social relationships. Key factors that may contribute to the success of elephant social groups were identified. This research has contributed to an evidence-base on the social needs of elephants, by identifying key factors related to elephant social interactions. It can be used to help develop individual long-term management plans and support evidence-based social management decisions. This study is thus contributing knowledge which will help to identify optimum social groups for zoo elephants in the future.

CHAPTER 7

Discussion & Conclusions

7.1. Overview of thesis

Social structures are a defining characteristic of species (Brando & Buchanan-Smith, 2017), and social animals live in a wide range of group types with varying levels of change and complexity, from virtually static to fission-fusion. Within zoos, catering for social needs of animals has been identified as a difficult task, especially for socially complex or intelligent species (Brando & Buchanan-Smith, 2017). Researchers suggested that the welfare of elephants in zoos could not be maintained to an optimum standard, and social needs were highlighted as an area of major welfare concern (Clubb & Mason, 2002; Harris et al., 2008). Elephants are housed in zoos throughout the world, in a range of size and composition of groups (Van Wees & Belterman, 2011; Schwammer & Fruehwirth, 2012), with varying levels of management (Stroud, 2007; Meehan et al., 2016a). Previous research on social relationships in zoo elephants is limited (but see Coleing 2009, Bonaparte-Saller & Mench, 2018; Harvey et al., 2018), which is surprising given the importance wild elephants place on social companionship, and the recognition of the inability to care for elephant welfare to a satisfactory standard within zoos throughout Europe and America (Clubb & Mason, 2002; Kiiru, 2007). The presence of affiliative social interactions in zoo animal herds is indicative of positive affective states (Mellor, 2015).

This study aimed to increase the current knowledge base on social relationships in elephants housed within UK and Irish zoos. Measureable improvements have been seen in elephant keeping in the UK and Ireland since concerns were first raised in 2002, and elephant management guidelines have changed (reviewed in Chapter Three). UK and Irish zoos do to some extent manage their social groups, but largely elephants are given opportunity to freely interact with conspecifics in the herd. This makes them an interesting study population. A multi-faceted approach was used throughout this thesis in order to determine individual and zoo-level factors which are affecting social relationships and herd structures in UK and Irish zoo elephants (incorporating extensive behavioural observations, keeper questionnaires and social network analysis). Social network analysis was used to answer Objective Two (Chapter Four), to determine if elephant social relationships are stable over time. Four principle social interaction networks were identified: (i) positive physical interactions, (ii) positive non-physical interactions, (iii) negative physical interactions and (iv) negative non-physical interactions. Relationships varied across zoos and between the interaction networks created. Positive social networks included all members of the social group, whereas negative interactions were restricted to specific individuals or a subset of individuals within the herds. Stability of the herds differed between zoos and balance of interactions differed between dyads. The thesis then investigated elephant personality, through the use of a keeper assessment of personality questionnaire (Chapter Five). Nine personality adjectives were reliably rated by elephant keepers which were reduced down using a PCA to three personality components: 'adaptable', 'sociable' and 'engaged with the environment'. Elephants

considered to be more sociable by keepers interacted with a greater number of individuals in the herd than did less sociable elephants and there was a positive correlation between sociable personality component scores and physical positive interactions and a negative correlation with non-physical negative interactions. Chapter Five contributed to Objective Three, to identify whether a relationship exists between elephant personality and social relationships. Finally, the thesis explored the potential herd demographics affecting social interactions in zoo-housed elephants in the UK and Ireland (Chapter Six), and in doing so answered Objective Four, to identify whether there is a relationship between individual and zoo-level factors and elephant social relationships. Positive physical interactions were affected by age and personality. Positive non-physical interactions were affected by relatedness to others, species and the presence of a calf in the group. Negative physical interactions were not affected by any of the investigated factors. Negative non-physical interactions were related to age, personality and relatedness. Findings were discussed in depth within the respective chapters. The wider implications of the study including the relationships between social interactions and elephant welfare, study limitations and areas for future research are considered here.

7.2. Social interactions and elephant welfare

Support from conspecifics is important for good welfare in social species (Rault, 2012). The expression of affiliative interactions can lead to positive affective states and is therefore indicative of good welfare (Mellor, 2015). Elephants are one of few social species to still be held in social groups that may not be reflective of their natural social groups (Bonaparte-Saller & Mench, 2018; Williams et al., 2018a), due to their size and the complicated nature of their wild social groups. In the wild they are principally found in related matriarchal herds. These herds undergo fission-fusion dynamics to some extent throughout the year and so the range of social partners and group size is variable (Wittemyer et al., 2005; de Silva et al., 2011). In UK and Irish zoos there is a need to cater for unrelated elephants in relatively static social groups. Social groups are relatively static due to logistical challenges encountered when moving such large animals (Stevenson & Walter, 2006), and short-term welfare implications of moving elephants to new herds (Schmid et al., 2001; Laws et al., 2007). Group size may also be limited by enclosure capacity (Defra, 2012; EAZA, 2014).

There is a lack of information about social relationships within zoo elephants (Bonaparte-Saller & Mench, 2018). The occurrence of positive social interactions is considered to be an indicator of good welfare in zoo elephants (Chadwick et al., 2017; Williams et al., 2018b) and researchers have suggested that social factors can be more important than space in elephant welfare (Meehan et al., 2016a). Overt aggression was not seen in the study zoos, which is likely a product of the active drive by zoos to prevent escalated aggression in herds, by providing animals with stimulating environments which occupy their time, and giving opportunities to decide when to

associate with and when to avoid conspecifics (e.g. Tresz & Wright, 2006). Male and female African and Asian elephants in the wild engage in different social behaviours and have different social requirements (Vance et al., 2009; Chiyo et al., 2011; Goldenberg et al., 2014), yet they all require social companions for good welfare in zoos (reviewed in Chapter 2). Research investigating social relationships in zoo elephants has principally focused on assessment of association data rather than physical interactions (Coleing, 2009; Harvey et al., 2018). Bonaparte-Saller and Mench (2018) found that elephant keepers could reliably rate the associations in their elephant herds but not interactions.

Social interactions are not an overtly common behaviour but the importance of tactile contact in elephants is widely understood (Langbauer, 2000; Makecha et al., 2012). It has been suggested that tactile contact plays a more limited role in elephant social bonds than proximity (Bonaparte-Saller & Mench, 2018), however this point is unproven, and research of wild Asian elephants suggests that elephants use tactile contact as a means of providing reassurance to others in times of distress (Plotnik & de Waal, 2014). Furthermore, the social significance of tactile contact has been documented (Yasui & Idani, 2017). Social interactions were thus used as a means of investigating social relationships in the study herds. Adams and Berg (1980) suggested that elephants have a need for bodily contact and physical interaction with other members of their species. Frequency of positive physical and non-physical and negative non-physical social interactions differed significantly between zoos however in all instances positive interactions were more frequent than negative interactions. Aggression in zoo elephants is often subtle (Harris et al., 2008). In 2002 it was claimed that aggression in zoo elephants was 'relatively common' (Clubb & Mason, 2002) although this was not quantified with reference to time spent engaged in aggressive behaviours. The majority of negative interactions recorded in this study were non-contact aggression, and they occurred at a very low level. Some low lying levels of aggression are normal and their presence is important for maintenance of hierarchical structures in social groups (Chadwick et al., 2017). Other studies have reported agonistic behaviours in elephants although all have been at relatively low levels, and in lower frequencies than positive interactions (Adams & Berg, 1980; Wilson et al., 2006; Harris et al., 2008). Allowing elephants sufficient space for avoidance is thought to be key to reducing conflict (de Silva et al., 2017; Williams et al., 2018a). Elephant keeping has changed markedly over time and thus the results highlighted in this study could reflect appropriate management at an individual herd level and the recognition of need for appropriate space for elephants in zoos. Maintaining individual social bonds is necessary to preserve and promote stable and compatible social groups (Wilson et al., 2006) and it is clear from consultation with keepers that this is very much at the forefront of their minds (Chadwick et al., 2017).

Understanding herd structure has important implications for the long-term welfare of both individual elephants and herds. There is a need to move elephants between herds as part of breeding programmes, and also to meet individual needs, e.g. providing appropriate breeding opportunities. There is also a finite space in which to house elephants and so as herds expand there may be a need to move groups of individuals to set up new herds. Preservation of certain key individuals may be essential in maintaining group cohesion in social animals (Lusseau & Newman, 2004). Knowledge of close social bonds and key individuals within social networks is essential to enable evidence-based management decisions to be made. The results of this study indicated that there was rarely a single 'key' individual that was responsible for linking the rest of the herd, more often there were either a number of equally important individuals making up a 'social' sub-group with a small number of individuals sitting on the periphery of the herd or all individuals interacted relatively equally within the network. Positive networks were far more interlinked in all study zoos than were negative social networks. Not all individuals engaged in agonistic interactions. It is therefore important to look at an individual's position within a network prior to undertaking irreversible or long-term management decisions.

Despite relative equality in terms of numbers of partners interacted with the majority of interactions recorded within dyads were not balanced. Within each pair one individual usually either gave or received more interactions. These findings replicate the linear dominance hierarchies observed in wild African elephants (Wittemyer & Getz, 2007). The imbalance of interactions within zoo elephants has the potential to be stressful for the individual receiving the majority of the interactions, if they were not comfortable with the situation. However, when personality of elephants in dyads was investigated it was found that highly sociable elephants were engaging in more non-physical positive interactions with other highly sociable elephants than with unsociable elephants, suggesting that the effect of 'enforced' social interaction was relatively low. The low frequency of negative interactions also supports this claim.

7.3. Factors affecting social interactions

Wild elephants have been the subject of extensive studies, trying to identify factors which are driving their extremely complex and interesting social interactions. In the wild elephants gain direct benefits from sociality (Pinter-Wollman et al., 2009) and kinship has been identified as a predictor in elephant relationships (Archie & Chiyo, 2012). However other research has indicated that wild (Vance et al., 2009), reintroduced (Thitaram et al., 2015) and zoo (Garai, 1992) elephants can bond successfully with unrelated individuals where advantages gained from enhancing fitness of kin are not present. Individual differences in amount of tactile behaviour and social partner preferences have been reported in the literature (Adams & Berg, 1980; Garai, 1992; Makecha et al., 2012) and this notion was supported by this study. A number of factors were related to the

frequency of social interactions, within dyads and on an individual elephant level. Interactions were related to age, relatedness to others, species, the presence of a calf in the group and individual personality.

Calves played an important role in the relationships observed in the study herds. Calves were central to social interactions in many of the herds, interacting positively with all members of the group and they also engaged in more physical interactions than older elephants. This may be demonstrative of their need for reassurance through tactile contact. Wild elephant behaviour is focused around calf care (Lee, 1987), and they have been described as the binding agent in reintroduced elephant social groups (Thitaram et al., 2015). Appropriate social groups are considered one of the best forms of enrichment for social species in zoos (Rees, 2009). The presence of calves in the study groups may have provided enrichment for older herd members whilst satisfying their own need for physical stimulation and allowing them to learn. Older elephants engaged in less tactile contact than younger elephants, which may reflect the lack of need to reinforce social bonds through touch in adults. However, a lack of positive physical interactions does not necessitate poor welfare in a herd. Elephants in zoos are in permanent closer proximity to other elephants than their wild counterparts, so the more extravagant greeting rituals observed in wild elephants (Poole & Moss, 2008) may be lost within zoos, where conspecifics are more constant. In groups of wild male African elephants older individuals had high centrality and strength scores within their social networks and they predominantly associated with others of a similar age (Chiyo et al., 2011). Interactions specific to bull elephants could not be thoroughly investigated due to a lack of bull elephants in the study. However a close relationship was observed between bull elephant calves in one zoo. For adult elephants use of nearest-neighbour analysis to assess period of time spent 'within' a social group may provide more detailed information about relationships than interactions alone. It would be interesting to investigate behavioural repertoire of individuals when herd members undergo short-term separation (e.g. for health care or individual training sessions) as a potential measure of relationship strength.

Wild elephant social groups are typically related, multigenerational herds with a range of ages from calves through to adults (Moss & Poole, 1983; Vidya & Sukumar, 2005a). Elephant management guidelines and researchers highlight multigenerational matriarchal herds with a wide range of ages as the gold standard in zoo elephant management (Veasey, 2006; AZA, 2011; Defra, 2017; Harvey et al., 2018). However, within the UK and Ireland, and indeed throughout the world there may still be a need to house unrelated individuals. Some of these may have no known relatives within the zoo population. Within this research, origin of elephants was not related to social interactions which suggests that the unique pasts experienced by some elephants was not a confounding factor in building relationships, but elephants housed with at least one relative did engage in fewer negative interactions than unrelated elephants. This finding supports research by

Harvey et al. (2018) who found higher levels of affiliation in a related elephant herd, and also lends extra scientific evidence in support of the current management guidelines (Defra, 2017). The fact that origin was not related to social interactions however is important to note. Taken together these findings both support the current literature which indicates that elephants can form successful social bonds with unrelated and unfamiliar individuals and provides scientific evidence that indicates that there is the potential to house a number of types of elephants successfully in UK and Irish zoos. They suggest that elephants, especially female, should not be removed from kin groups, but unrelated elephants can still form social relationships and so can be a functioning member of a social group, both within completely unrelated herds or with family groups.

Personality can shape how animals perceive zoo environments and subsequently their experiences (Horback et al., 2014; Watters et al., 2017). Personality assessment is increasingly being incorporated into zoo animal welfare studies (Tetley & O'Hara, 2012; Watters & Powell, 2012). Providing animals with appropriate social groups is integral to welfare and the recent recognition that each animal will experience the social environment differently within a group has been important for improving animal welfare (Watters & Powell, 2012). It has been assumed that personality ratings should be related to behaviour patterns but this need not always be the case (Kuhar et al., 2006). Elephant keepers can reliably rate the personality of elephants with whom they are primary caretakers and are familiar, and these personality ratings have been related to association patterns of elephants (Bonaparte-Saller & Mench, 2018), resting behaviour (Williams et al., 2015) and levels of cortisol (Grand et al., 2012). The importance of incorporating expert opinion in welfare assessment has been highlighted in the elephant welfare assessment literature (Chadwick et al., 2017) and it is again highlighted throughout this thesis. Within zoos there may be a need to house a range of individuals, some more disparate than others. As is detailed above, personality can be shaped by past experiences and it has the potential to affect individual compatibility. To the author's knowledge no other researchers have investigated the relationship between personality and social interactions in zoo elephants however information gathered from the wild elephant literature (Wittemyer et al., 2007) and from investigation of social networks in dolphins suggests that personality may be related to (or influence) social rank (Frick, 2016). Social rank was not investigated during this study due to the potential for fluctuations in social rank position (McKenzie pers. comm., 2015) and the inability to accurately rate this in a time efficient and comparable manner. It is possible that social rank is interacting with personality and/or social interactions to produce the reported outcome. At two of the study zoos an elephant did not engage in any physical social interactions. In both instances they were considered to be the lowest ranking individual within the herd. The presence of less social animals within the herd may not always lead to compatibility issues but monitoring interactions to ensure excessive aggression

or other behavioural indicators of poor welfare are not occurring is important for individual welfare.

Provision of areas for animals to associate with or be separate from the rest of the social group could also help to increase the likelihood of compatibility. Space has been identified as a potential stressor for socially housed zoo species (Price & Stoinski, 2007; Williams et al., 2018a) and the importance of providing open ecosystems for the social and spatial organisation of wild African elephants has been recognised (Wittemyer et al., 2007). This thesis has shown interesting results which have practical application in the zoo industry. Current SSSMZP elephant management guidelines state that UK and Irish zoos should be providing unique management plans for each animal and having a long-term management plan for each elephant exhibit, including behavioural profiles and details of herd compatibility (Defra, 2017). The ability to reliably document personality of zoo elephants is an important aspect to consider in such individual management plans. Future work should seek to build on assessments undertaken here to investigate the potential for keeper ratings of sociability as a predictive tool in elephant compatibility assessments. This is not the first-time personality has been advocated for inclusion in welfare assessments but it is the first time such a technique has been suggested for inclusion in the long-term management plans of elephant herds and it deserves considerably more thought and discussion moving forwards.

Beyond the factors detailed in this discussion there could also be a number of physiological factors which influence levels of sociability in zoo-housed elephants, such as reproductive condition in females or musth in males. It was beyond the scope of this research to directly assess these factors, however the long-term nature of data collection should have helped to limit the impact these may have had. Nevertheless, it is important to recognise that there may be a multitude of factors in addition to those assessed in the thesis.

7.4. Implications for management of zoo elephants

The wild is not always the optimum standard (Wolfensohn et al., 2018) and wild elephant social behaviour is driven by seasonal ecological factors, where resource availability limits group size and composition (Wittemyer et al., 2005; Pinter-Wollman et al., 2009). Yet despite this, the wild is still used as a benchmark from which recommendations on how to keep elephants in zoos are made, with this information being fed directly into elephant management guidelines. This thesis aimed to bring to light new information about how elephants were interacting within zoos, and to identify relationships between individual and zoo-level factors and elephant social interactions. A thorough review of the literature has highlighted the importance of social interactions in zoo elephants, and the need to provide elephants with appropriate social groups and space in which to interact in a species-typical and peaceful manner with conspecifics. The importance of facilitating appropriate social interactions has been voiced by elephant keepers

(Chadwick et al., 2017). Acknowledging the potential for fluidity in social dynamics should be both recognised and utilised in elephant management programmes. Recent updates to elephant management guidelines highlight the importance of regularly monitoring social welfare of individual elephants (Defra, 2017). Elephant keepers suggest that low levels of aggression are normal but extreme aggression may be a cause for concern (Chadwick et al., 2017). Implementing regular monitoring will help to identify potential areas for concern in elephant herds before aggression escalates to unacceptable levels. Engaging with preventative and proactive management practices is important for animal welfare and ensuring positive affective states. Repeatable methodologies for capturing social interactions within elephant herds are important to help to monitor relationship change over time and detect subtle changes in group dynamics. Understanding expected levels of sociability from individuals at different life stages and being able to predict relationships are important first steps in incorporating such measures in routine welfare assessment. This study provides a baseline for such data.

7.5. Is there a future for elephants in zoos?

The research conducted for this doctorate has shown marked changes in elephant keeping since initial concerns were raised in 2002. It was recognised by the European Elephant Group (Endres et al., 2003) and other researchers (Rees, 2003b, 2009) that the data presented by Clubb and Mason (2002) was lacking and partially invalid. The results from this study lend support to these claims and suggest that in 2002 the social groups of UK and Irish zoo elephants were not as poor as first believed. Critically this thesis has demonstrated that some of the early welfare concerns may not have been as valid as first thought but perhaps more crucially it has shown through reviews of the literature and elephant management guidelines that the attitudes towards elephant keeping are positive. Great importance is placed on evidence-based research and management practices in order to improve zoo elephant welfare. Practically elephants are difficult to house in zoos, but results obtained during this study have indicated that zoo elephant populations are for the time-being self-sustainable and well-managed for individual animal needs. This is highlighted by the occurrence of young individuals in the herd and the expression of positive social interactions and lack of overt aggression. Recommendations for elephant care and social needs have been voiced by elephant keepers (Chadwick et al., 2017) and guidelines have changed in light of such research (Defra, 2017).

Social interactions were found to be variable; all elephants engaged in positive non-physical interactions and the majority engaged in positive physical interactions. Less elephants engaged in negative interactions and physical negative interactions were rarely observed. Compatibility changed over time and fluidity was observed in the four identified social networks. This is important to take into account when looking at the success of elephant social groups. It is

also important to understand more about why some elephants do not engage in positive physical interactions, and to assess whether their welfare is compromised as a result of the lack of physical interaction. Gaining more knowledge on the time elephants spend in proximity to one another will also help to understand the state and importance of their social relationships. Changes to elephant management guidelines are fuelled by evidence-based research, which is helping to identify ways in which we can better provide for elephants. Routine assessments are in place to continue to monitor and improve zoo elephant welfare through both behavioural and physical assessments of health (BIAZA Elephant Welfare Group, 2016). Continuing to monitor relationships as elephants age and develop is important for individual welfare, and this should be garnered during such assessments. It is beyond the scope of this study to make recommendations as to whether or not we can now adequately provide for elephants in zoos, but the study does highlight the need to understand more about compatibility and what may be causing changes in compatibility in zoo elephants. The results from this work, do however show promise, the presence of positive interactions are indicative of positive affect in the study elephants and the clearer guidelines which include monitoring welfare over time are an important part of optimising elephant welfare in the long-term.

7.6. Study limitations

The methods used to address the study objectives were appropriate for the research area, but they are not without limitations due to the applied and real-life nature of the project. The research was carried out over the period of a year and produced a relatively large data set but it only utilised one potential measure of sociability. Elephants are socially complex and can communicate in a range of ways (not all audible to humans) (Langbauer, 2000), and social affiliation may not be the only indicator of communication (Sumpter et al., 2008). The use of interaction over association data has been discussed in more detail in this thesis, but it is worth reiterating that there is the potential for different social relationships to be observed amongst elephants if a different measure of sociability is used. This study assessed frequency of social interactions but it did not assess welfare of individual elephants, nor did it attempt to further validate social interactions as an indicator of welfare in elephants. Social interactions, especially physical negative interactions, were extremely low in frequency which means that although significant differences were seen for some of the investigated factors they may not necessarily correspond to biologically relevant relationship differences in the herds. Future research should seek either to find a reliable means of using continuous sampling to record social interactions or to utilise proximity to other elephants as an additional means of assessing sociability in elephants, with the recognition that physical social partners may differ from nearest neighbours. Without

validation of the use of nearest neighbour as a proxy for social partners it must be borne in mind that these could represent different types of social relationships.

Positive social interactions have been advocated as a positive indicator of welfare, but they should be considered in conjunction with other, validated indicators (Williams et al., 2018). The low frequency of negative interactions within the study herds is indicative of positive welfare (Chadwick et al., 2017) however there were individuals in some of the study herds who did not engage in any physical interactions with other elephants. A reduction in frequency of positive social interaction from a sociable elephant to one which is not engaging in any social interactions would be indicative of a welfare problem for the individual and prompt further assessment, however it is not clear whether an absence of physical interactions is indicative of a good or poor welfare state, or whether that is dependent upon personality of the individual elephant. Further research should be undertaken, especially in individuals that were not engaging in physical interactions with other elephants, to determine their welfare state, and validate social interactions as an indicator of welfare in its own right. Validation could include a comparison of social interactions with other robustly-validated indicators such as stereotypies or faecal glucocorticoids and incorporation of qualitative behavioural assessment (QBA) to determine the emotional valence of the individual.

There are a number of other factors which could impact on herd dynamics, including enclosure size and complexity and management style. Elephants in UK and Irish zoos are handled in both free contact (where elephants and handlers share the same space) and protected contact (where there is a physical barrier between handlers and elephants). The majority of collections in this study held their animals in protected contact. Because of the small number of participating zoos (n=7), the lack of difference in contact systems and no extremes in terms of enclosure size or complexity, it was impossible to incorporate these extra factors when assessing the impact of social groups on social interactions. Moreover, there were no bachelor herds included in this study and so one 'group type' in terms of social housing could not be assessed during this study. It was also difficult to fully investigate some of the factors identified. For example, it was hard to explore species level differences. There were no African elephant calves in the study herds and Asian elephants were generally kept in more related groups than African elephants, which means that some species level differences could have been masked by the presence or absence of younger herd members. There was also a skew towards adults in the study population which reduced the opportunity to fully investigate age profiles within the study herds. It is suggested that future research should encompass a far wider range of zoos including European establishments, with more extensive variation in enclosures (in terms of size and design) and husbandry methods. A full spectrum of types of herd should be included: breeding herds, female only herds and bachelor groups, of varying ages and relationships. This would add to the findings produced from this study, increasing knowledge and potentially further validate factors affecting social relationships in zoo

elephants. Further work such as this would also increase the opportunity to extrapolate these preliminary findings to inform wider population management.

Due to unforeseen technical problems with recording equipment and occasional lack of compatibility with zoo CCTV systems it was not possible to gather the same amount of data from each study zoo nor for camera coverage to incorporate the same percentage of the enclosures. There was also a variation between enclosure size and content at the study zoos. The frequency of hours of data collected varied across the data collection points for some of the study zoos and elephants may not have been recorded for 100% of observations. Recording frequencies of observations could thus be an underrepresentation of actual levels social interactions in the groups. The use of scan sampling may also have led to an underrepresentation of actual interactions. However, due to the nature of elephant social interactions these recording and sampling methods were considered the most appropriate for this data set. Elephant interactions can be very complex and it can be hard to distinguish one from another, especially on video footage. The use of scan sampling with a short inter-scan interval allowed correct identification of individuals and enabled the context of the interaction to be identified. This ensured increased accuracy and thus could be considered a reliable representation of observed interactions. One of the technical difficulties encountered was to do with using batteries to power the cameras. In future it is recommended that wherever possible cameras be powered by mains power, although this may not always be practical.

Finally, 'key' individuals were identified using betweenness as the measure of connectedness. There are a number of different measures of connectedness with respective limitations (see Chapter Four) however for the purposes of this study this measure was considered most appropriate. Betweenness is a measure of centrality and connectedness, and it is considered a measure of how information spreads within a network (Newman, 2005). Betweenness centrality can pick out individuals who play the role of 'brokers' between animal communities, identifying important individuals (Lusseau & Newman, 2004). Preservation of key individuals may be key to maintaining group cohesion (Lusseau & Newman, 2004) and the use of betweenness as a measure of centrality allows identification of such individuals. Betweenness was thus used as a measure of connectedness in this instance in order to identify which elephants had most importance in terms of interactions given/received with the rest of the herd.

7.7. Areas for future research

Areas of future research are summarised as (i) identification of a way for keepers to routinely capture social interaction data in a meaningful, repeatable and time-efficient manner, (ii) identification of whether there is a relationship between physical proximity and social interactions in zoo elephants, (iii) assessment of the reliability of personality assessment as a

predictive social compatibility tool and (iv) incorporation of behavioural synchrony into welfare assessment. These points are discussed in further detail below.

Assessment of behaviour is a straight forward way in which to gather important information on zoo elephant welfare (Asher et al., 2015). Indeed, monitoring behaviour as part of routine welfare assessment is a stipulation in recent elephant management guidelines (Defra, 2017). Requirements for monitoring herd compatibility is also included in the guidelines, however assessment of this needs further refinement. Elephant relationships can change over time and data collected at one time point may not represent long-term social preferences. This study identified a detailed data collection method. Identifying a simplistic method to routinely capture social interaction data in a meaningful and repeatable manner is an important next step for inclusion in long-term welfare assessment and welfare improvement plans for all elephants in the UK and Ireland. Methods must be time efficient to enable keepers to incorporate them into other behavioural and health assessments. Social compatibility is extremely important to welfare of all social species and creation of a process to monitor social relationships in a quick and easy fashion would have applicability across many zoo-housed species.

Whether or not physical proximity to another individual can be used as a proxy for physical interactions in group living animals has been a cause of some debate in the scientific literature; with some researchers suggesting that there is a correlation between the position of an individual in a proximity network and an interaction network (Farine, 2015) whilst others suggest that they should not be used as a proxy for one another (Castles et al., 2014). Whether or not this assumption can be played out across all species remains unclear. This is a very important area for future research. Researchers looking at elephant social interactions in US zoos (Bonaparte-Saller & Mench, 2018) found that social relationships as assumed from social interactions were not related to keeper assessments of social bonds but affiliative partners assessed through associations could be. Furthermore, they found that associations were more stable over time than interactions. This thesis highlights consistency in social interactions over time and correlations between interactions and keeper ratings of personality. Future research should look to identify if there is a relationship between proximity and social interaction in zoo elephants, and to identify the extent to which one can be considered a proxy for the other, if at all. Association data can be more difficult to capture objectively and accurately within some zoo environments, and this must be considered in interpretation of such data. Enforced proximity within inside enclosures or restricted spaces may lead to false definitions of social relationships (Harvey et al., 2018). Clear definitions of criteria which must be met in order for an animal to be considered 'in group' must be created, based on the size and design of a number of different elephant enclosures, in order to make the metrics repeatable in other collections, and therefore useful moving forwards.

The third area for future work arising from this thesis is an assessment of the reliability of personality assessment as a predictive social compatibility tool. Research in other species has advocated the use of personality assessment in successful social management (e.g. Tetley & O'Hara, 2012; Martin-Wintle et al., 2017; Gartner & Weiss, 2018). Moving elephants to new social groups is not without risk and it can have some short-term effects on individual welfare (Schmid et al., 2001; Laws et al., 2007). This research indicated that UK and Irish zoo elephant keepers could reliably rate personality in their elephant herds and that it was related to observed social interactions. Being able to predict and therefore improve likelihood of success of social groups has important ramifications for elephant welfare. Future work should therefore seek to apply these assessments when individuals are moved to other herds as part of management programmes or when social group structure changes following births or deaths.

A final area for future consideration is the incorporation of measurements of behavioural synchrony into welfare assessment. Behavioural synchrony has been defined simply as meaning the behaviour of several individuals is related in time; displaying the same behaviour at the same time (Engel & Lamprecht, 1997). Behavioural synchrony has been identified as a positive welfare indicator in cattle (Napolitano et al., 2009). Whilst to date there are no known studies investigating the occurrence of behavioural synchrony in zoo elephants it has been suggested that behavioural synchrony and evidence of individuals 'banding together' in times of stress is an indicator of good welfare (Chadwick et al., 2017). It was beyond the scope of this study to investigate thoroughly behavioural synchrony within elephant herds, however it is an area of future research which is very important in zoo elephant welfare studies. Capturing this data in a meaningful and repeatable manner would be an important next step in enhancing the knowledge of social relationship structures in zoo elephants and would contribute to the ongoing goal of improving zoo elephant welfare.

7.8. Conclusion

Elephants are adaptable; studies of wild elephants following large scale elephant culls and reintroduced populations suggest that elephants can cope with a range of social conditions. Elephants in the wild have very complex social relationships which are affected by a number of different factors, and historic research has highlighted difficulties in caring for elephant social needs within zoos. Elephant keeping and elephant management guidelines have developed markedly over time yet until recently information on zoo-elephant social interactions was lacking. Researchers in the US recently found links between social variables and more traditional indicators of welfare (e.g. stereotypies). Elephant keepers have also suggested that social compatibility is paramount in the welfare of social groups. Indeed, research has suggested that appropriate social groups can be more important than space available to elephants. In order to make evidence-based

recommendations to social grouping aspects of elephant management guidelines it is important to first discover how the restrictions of the zoo environment and herd demographics are related to social interactions in zoo elephants. There is a lack of work in this study area and so this thesis sought to fill that void. The overarching aim of this thesis was to find out more information about social interactions, herd structures and dyadic interactions in UK and Irish zoo elephants under current management.

Zoo elephants exhibit flexibility in social relationships but interactions appear to be driven less by seasonality and more by personality, age of individuals, and the overall structure of the herd in terms of age composition and relatedness. Four interaction networks were observed: physical and non-physical positive networks and physical and non-physical negative networks. Physical negative interactions were rare, accounting for a very small portion of daily elephant activity. Positive social networks were far more interconnected than negative social networks, which reflect the strong affiliative social bonds observed in wild elephants. The agonistic interactions observed were predominantly what may be described as 'corrective' behaviours, with no extreme aggression (e.g. sparring) observed during the entire study.

These findings have important implications in welfare assessment of zoo elephants going forwards. The occurrence of positive interactions and interconnected positive social networks suggests UK and Irish zoo elephants are housed in successful social groups and individuals are in positive affective states and therefore experiencing positive welfare. The results have uncovered some key demographic factors which could be affecting social interactions and relationships in zoo elephants and therefore contributing to cohesive and successful social groups. Furthermore, the findings have begun to provide evidence for complex herd structures which may not be entirely static over time. However, there is still a considerable amount of work to be undertaken in this area before the social wants and needs of zoo elephants can be truly identified, and an objective assessment of whether these needs can be met in zoos can be undertaken. Elephant management can vary between collections and it is clear from the literature that it is different between countries. There is not a one size fits all model which will be appropriate for all zoo elephants, however the way in which management is affecting social relationships in elephant herds must be considered. Of particular importance is the knowledge that interactions are flexible over time, and this should be borne in mind when considering long-term welfare assessment and compatibility plans. It is recommended that social networks in zoo elephant herds are monitored prior to a known change in the group structure (such as an impending birth or an elephant move) to ensure minimum impact on the social structure of the herd. The potential for inclusion of keeper ratings of personality in assessing compatibility between individuals in current groups and in predicting potentially compatible partners or social groups for elephants to be moved to is an important avenue for investigation. Consideration of compatibility of group members, along with daily

behavioural observations and anecdotal welfare assessments have been undertaken by elephant keepers for many years, however it is important to develop objective, repeatable approaches which can be documented and stored on elephant records. Recent updates to elephant management guidelines advocate the importance of individual welfare assessment plans, an objective keeper assessment of personality questionnaire such as that developed during this study is important for inclusion in such an assessment. Further studies should now be undertaken which consider the proximity of elephants to other individuals in the herd, to investigate how this is related to social interactions, in order to provide a fuller picture. Long-term research should focus on identifying a means of quickly assessing social compatibility in order for them to be included in long-term welfare assessment. This study has made the first step towards identifying how herd demographics are affecting social interactions in zoo-housed elephants and has created an opening for more research to further advance this knowledge and enhance long-term zoo-elephant welfare.

7.9 Recommendations

The following recommendations for changes to practice and areas of future research have arisen from this research:

- The way in which management regimes are affecting social relationships in zoo elephants should be factored into decision making. To develop a greater understanding and shape decision-making moving forwards, elephant keepers should maintain information on social relationships within herds in order to document the effect of management changes on these relationships. For example, if animals are being separated (either into smaller groups or having an individual removed from the group) for routine veterinary treatment or overnight it is important to understand the impact that may have on the herd. Understanding more about social interactions and herd structures will enable mitigation strategies to be put in place if required to ensure elephant welfare is being maintained at an optimum standard (e.g. allowing two individuals to stay together, if it is safe to do so, if one needs to be separated for veterinary treatment).
- Zoo elephant social networks should be monitored before and after known changes to group structures, such as impending births, euthanasia of an elephant or an elephant move to ensure impacts on herd social structure are minimal. Previous research has indicated that changes to herd structures can affect overall social relationships. Understanding key relationships in the network and how they change in response to changes in herd structure is important to help identify situations which have the potential to exert pressure on social relationships in zoo elephants.
- Zoos should incorporate personality assessments into behavioural profiles of elephants. Keeper knowledge (as used in personality assessments) should then be captured and utilised when planned changes are being made to elephant herds. Based on personality assessments, predictions should be made as to the likely success of elephants being moved to new herds. The prediction can then be compared with actual relationship development between individuals post move. This will, over time, enable the investigation of the reliability of keeper ratings of personality as a predictive tool in elephant compatibility assessment, thus validating such an assessment and providing a management tool.
- Future research should focus on an assessment of how proximity to other elephants is related to social interactions, to provide a fuller picture of social bonds and enhance understanding of elephant social relationships
- Long-term research should focus on identifying means of quickly assessing social compatibility between individuals, to facilitate inclusion of such a measure in long-term welfare assessment. Being able to gather data in a snapshot fashion is important if assessment of social

relationships are to be incorporated into regular monitoring. Measures used to assess social relationships must be workable in a zoo setting and time-efficient.

References

- Adams J & Berg JK. 1980. Behaviour of female African elephants (*Loxodonta africana*) in captivity. *Applied Animal Ethology*, 6: 257–276
- Ahloy-Dallaire J, Espinosa J & Mason GM. 2017. Play and optimal welfare: Does play indicate the presence of positive affective states? *Behavioural Processes*, 156: 3-15
- Alexander BK & Roth EM. 1971. The effects of acute crowding on aggressive behaviour of Japanese monkeys. *Behaviour*, 39: 73-90
- Alford PL, Bloomsmith MA, Keeling ME & Beck TF. 1995. Wounding aggression during the formation and maintenance of captive, multimale chimpanzee groups. *Zoo Biology*, 14: 347-359
- Altmann J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour*. 49: 227-267
- Amrein M, Heistermann M & Weingrill T. 2014. The Effect of Fission-Fusion Zoo Housing on Hormonal and Behavioral Indicators of Stress in Bornean Orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, 35: 509–528
- Anderson CE. 2005. *Exploring behaviour and social relationships of a captive group of chimpanzees (Pan troglodytes)*. University of Tennessee, Knoxville.
- Archie EA & Chiyo PI. 2012. Elephant behaviour and conservation: Social relationships, the effects of poaching, and genetic tools for management. *Molecular Ecology*, 21: 765-778
- Archie EA, Moss CJ & Alberts SC. 2006. The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B: Biological Sciences*, 273: 513–522
- Armstrong S. 2015. *The effects of the death of an elephant on social and physical behaviours of the remaining members of a captive herd of African elephants, Loxodonta africana*. University of Leeds.
- Asa CS, Traylor-Holzer K & Lacy RC. 2011. Can conservation-breeding programmes be improved by incorporating mate choice? *International Zoo Yearbook*, 45: 203-212
- Asher L, Williams E & Yon L. 2015. Developing behavioural indicators , as part of a wider set of indicators , to assess the welfare of elephants in UK zoos. *Defra Project WC1081*. UK: Defra
- Aureli F et al. 2008. Fission-Fusion Dynamics. *Current Anthropology*, 49: 627–654
- AZA. 2011. *AZA Standards for Elephant Management and Care*. AZA
- Barber JCE. 2009. Programmatic approaches to assessing and improving animal welfare in zoos and aquariums. *Zoo Biology*, 28: 519-530
- Barnes R, Greene K, Holland J & Lamm M. 2002. Management and husbandry of duikers at the Los Angeles Zoo. *Zoo Biology*, 21: 107-121
- Bates LA et al. 2010. Why do african elephants (*loxodonta africana*) simulate oestrus? an analysis of

- longitudinal data. *PLoS ONE*, 5: e0010052
- Beisner BA & Isbell LA. 2008. Ground substrate affects activity budgets and hair loss in outdoor captive groups of rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, 70: 1160–1168.
- BIAZA. 2018a. *Elephant care and welfare* [online]. Available at: <https://biaza.org.uk/elephant-welfare-group> [Accessed on 26 September 2018]
- BIAZA. 2018b. *Our vision and mission* [online]. Available at: <https://biaza.org.uk/elephant-welfare-group> [Accessed on 21 September 2018]
- BIAZA Elephant Welfare Group. 2016. *5 Year Report: British & Irish Association of Zoos & Aquariums Elephant Welfare Group*. BIAZA
- Birkett LP & Newton-Fisher NE. 2011. How abnormal is the behaviour of captive, zoo-living chimpanzees? *PLoS ONE*, 6: e0020101
- Blackett TA, McKenna C, Kavanagh L & Morgan DR. 2017. The welfare of wild animals in zoological institutions: are we meeting our duty of care? *International Zoo Yearbook*, 51: 187–202
- Blaine S & Winkler R. 2019. What is a mahout? The human side of elephant husbandry [online]. Available at: <https://horizontravelpress.com/guides/elephants-in-asia-ethically-014/what-is-a-mahout> [Accessed on 01 February 2019]
- Blanc J. 2008. *Loxodonta africana*. The IUCN Red List of Threatened Species 2008. [online] Available at: <https://www.iucnredlist.org/species/12392/3339343> Accessed on 17 January 2019
- Bloomsmith MA & Lambeth SP. 1995. Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. *Applied Animal Behaviour Science*, 44: 65–74
- Blumstein DT et al. 2010. Towards an integrative understanding of social behavior: new models and new opportunities. *Frontiers in Behavioral Neuroscience*, 4: 34
- Bonaparte-Saller M & Mench JA. 2018. Assessing the dyadic social relationships of female african (*Loxodonta africana*) and asian (*Elephas maximus*) zoo elephants using proximity, tactile contact, and keeper surveys. *Applied Animal Behaviour Science*, 199: 45–51
- Bond M & Watts E. 1997. Recommendations for infant social environment. In: Sodara C (Ed.), *Orangutan Species Survival Plan Husbandry Manual*. Chicago: Chicago Zoological Park.
- Borgatti SP. 2002. NetDraw Software for Network Visualization. Lexington, KY: Analytic Technologies.
- Borgatti SP, Everett MG & Freeman LC. 2002. Ucinet 6 for Windows: Software for Social Network Analysis. Harvard, MA: Analytic Technologies.
- Borrego N & Gaines M. 2016. Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour*, 114: 21–26
- Brambell FWR. 1965. *Report of the Technical Committee to Enquire Into the Welfare of Animals Kept Under Intensive Livestock Husbandry Systems*. London: HM Stationery Office

- Brando S & Buchanan-Smith HM. 2017. The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, 156: 83-95
- Bremner-Harrison S, Prodohl PA & Elwood RW. 2004. Behavioural trait assessment as a release criterion: Boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation*, 7: 313–320
- Brent L, Kessel A & Barrera H. 1997. Evaluation of introduction procedures in captive chimpanzees. *Zoo Biology*, 16: 335-342
- Brockett R et al. 1999. Nocturnal behavior in a group of unchained female African elephants. *Zoo Biology*, 18: 101–109
- Broom DM. 1986. Indicators of poor welfare. *British Veterinary Journal*, 142: 524–526
- Broom DM. 1991. Animal welfare: concepts and measurement. *Journal of Animal Science*, 69: 4167-4175
- Brown JL, Walker SL & Moeller T. 2004a. Comparative endocrinology of cycling and non-cycling Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. *General and Comparative Endocrinology*, 136: 360–370
- Brown JL, Olson D, Keele M & Freeman EW. 2004b. Survey of the reproductive cyclicity status of Asian and African elephants in North America. *Zoo Biology*, 23: 309 - 321
- Bryan K, Bremner-Harrison S, Price E & Wormell D. 2017. The impact of exhibit type on behaviour of caged and free-ranging tamarins. *Applied Animal Behaviour Science*, 193: 77-86
- Byrne RW, Bates LA & Moss CJ. 2009. Elephant cognition in primate perspective. *Comparative Cognition & Behavior Reviews*, 4: 65-79
- Carenzi C & Verga M. 2009. Animal welfare: review of the scientific concept and definition. *Italian Journal of Animal Science*, 8(sup1): 21–30
- Carlstead K et al. 1992. Urinary monitoring of adrenal responses to psychological stressors in domestic and nondomestic felids. *Zoo Biology*, 11: 165–176
- Carlstead K, Fraser J, Bennett C & Kleiman DG. 1999a. Black rhinoceros (*Diceros bicornis*) in U.S. Zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. *Zoo Biology*, 18: 35–52
- Carlstead K, Mellen J & Kleiman DG. 1999b. Black Rhinoceros (*Diceros bicornis*) in U. S. Zoos: I. Individual Behavior Profiles and Their Relationship to Breeding Success. *Zoo Biology*, 18: 17–34
- Carlstead K & Shepherdson DJ. 1994. Effects of environmental enrichment on reproduction. *Zoo Biology*, 13: 447-458
- Carlstead K & Shepherdson DJ. 2000. Alleviating stress in zoo animals with environmental enrichment. In: Moberg GP & Mench JA (eds) *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare*. USA: CABI Publishing

- Caro T. 1993. Behavioral solutions to breeding cheetahs in captivity: Insights from the wild. *Zoo Biology*, 12: 19–30
- Castles M et al. 2014. Social networks created with different techniques are not comparable. *Animal Behaviour*, 96: 59-67
- Chadwick CL. 2014. *Social behaviour and personality assessment as a tool for improving the management of cheetahs (Acinonyx Jubatus) in captivity*. PhD thesis, University of Salford
- Chadwick CL, Williams E, Asher L & Yon L. 2017. Incorporating stakeholder perspectives into the assessment and provision of captive elephant welfare. *Animal Welfare*, 26: 461–472
- Charif RA et al. 2005. Spatial relationships and matrilineal kinship in African savanna elephant (*Loxodonta africana*) clans. *Behavioral Ecology and Sociobiology*, 57: 327-338
- Chiyo PI et al. 2011. Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. *Animal Behaviour*, 81: 1093-1099
- Choo Y, Todd PA & Li D. 2011. Visitor effects on zoo orangutans in two novel, naturalistic enclosures. *Applied Animal Behaviour Science*, 133: 78–86
- Choudhury A et al. 2008. *Elephas maximus*. The IUCN Red List of Threatened Species [online]. Available at: <https://www.iucnredlist.org/species/7140/12828813> [Accessed on: 17 January 2019]
- Christensen JW, Søndergaard E, Thodberg K & Halekoh U. 2011. Effects of repeated regrouping on horse behaviour and injuries. *Applied Animal Behaviour Science*, 133: 199-206
- Cinini SM et al. 2014. Social isolation disrupts hippocampal neurogenesis in young non-human primates. *Frontiers in Neuroscience*, 8: 1-9
- Clark FE. 2011. Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, 73: 748–757
- Clubb R & Mason GM. 2002. A review of the welfare of zoo elephants in Europe. A report commissioned by the RSPCA. Oxford UK: University of Oxford
- Clubb R et al. 2008. Compromised survivorship in zoo elephants. *Science*. 322: 1649
- Coleing A. 2009. The application of social network theory to animal behaviour. *Bioscience Horizons*, 2: 32–43
- Coleman K et al. 2012. Behavioral Management, Enrichment, and Psychological Well-being of Laboratory Nonhuman Primates. In: Abee CR, Mansfield K, Tardif SD & Morris T (Eds). *Nonhuman Primates in Biomedical Research*, Elsevier Inc
- Cooper MA & Bernstein IS. 2000. Social grooming in Assamese macaques (*Macaca assamensis*). *American Journal of Primatology*, 50: 77-85
- Coussi-Korbel S & Frigaszy D. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, 50: 1441–1453
- Couzin ID. 2006. Behavioral ecology: social organization in fission–fusion societies. *Current Biology*,

16: 169–171

- Croft DP, James R & Krause J. 2008. *Exploring Animal Social Networks*. Princeton and Oxford: Princeton University Press.
- Dathe HH, Kuckelkorn B & Minnemann D. 1992. Salivary cortisol assessment for stress detection in the Asian elephant (*Elephas maximus*): A pilot study. *Zoo Biology*, 11: 285–289
- Dawkins MS. 2008. The science of animal suffering. *Ethology*, 114: 937–945
- Dawkins MS. 2017. Animal welfare with and without consciousness. *Journal of Zoology*, 301: 1-10
- de Rouck M, Kitchener AC, Law G & Nelissen M. 2005. A comparative study of the influence of social housing conditions on the behaviour of captive tigers (*Panthera tigris*). *Animal Welfare*, 14: 229-238
- de Silva S, Ranjeewa ADG & Kryazhimskiy S. 2011. The dynamics of social networks among female Asian elephants. *BMC Ecology*, 11: 17
- de Silva S, Schmid V & Wittemyer G. 2017. Fission–fusion processes weaken dominance networks of female Asian elephants in a productive habitat. *Behavioral Ecology*, 28: 243–252
- de Silva S & Wittemyer G. 2012. A Comparison of Social Organization in Asian Elephants and African Savannah Elephants. *International Journal of Primatology*, 33: 1125–1141
- de Waal FBM. 1989. The myth of a simple relation between space and aggression in captive primates. *Zoo Biology*, 8(S1): 141-148
- Defra. 2012. *Secretary of State’s Standards of Modern Zoo Practice*. UK: Defra
- Defra. 2017. *Secretary of State’s Standards of Modern Zoo Practice Appendix 8 – Specialist exhibits, Elephants*. UK: Defra
- Dembiec DP, Snider RJ & Zanella AJ. 2004. The effects of transport stress on tiger physiology and behavior. *Zoo Biology*, 23: 335–346
- Dudzinski KM & Ribic CA. 2017. Pectoral fin contact as a mechanism for social bonding among dolphins. *Animal behaviour and cognition*, 4: 30-48
- Dunbar RIM & Shultz S. 2010. Bondedness and sociality. *Behaviour*, 147: 775–803
- EAZA. 2012. *EAZA Population Management Manual*. EAZA
- EAZA. 2014. *EAZA Standards for the Accommodation and Care of Animals in Zoos and Aquaria*. EAZA
- EAZA. 2018. *EAZA Breeding Programme Overview October 2018*. EAZA
- EAZA. 2019. *EAZA Specialist Programmes* [online]. Available at: <https://www.eaza.net/conservation/programmes/> [Accessed on 30 January 2019]
- EAZA & BIAZA. 2017. *Joint response from the European Association of Zoos and Aquaria and the British and Irish Association of Zoos and Aquariums to the release of the Born Free Foundation’s ‘Beyond the Bars’ report on wild animal welfare in the United Kingdom* [Press release] March 2017

- Elephant Voices. 2018. *Elephant Voices on Elephants in Captivity* [online]. Available at: <https://www.elephantvoices.org/elephants-in-captivity-7/-in-zoos.html> [Accessed on 27 September 2018]
- Endres J et al. 2003. *Dokumentation 2002 - Elephants in European Zoos and Safari Parks*. Munich: European Elephant Group.
- Endres J et al. 2006. *Survey 2006 - Elephants in European Zoos and Safari Parks*. European Elephant Group
- Engel J & Lamprecht J. 1997. Doing what everybody does? A procedure for investigating behavioural synchronization. *Journal of Theoretical Biology*, 185: 255–262
- European Commission. 2015. *EU Zoos Directive. Good Practices Document*. European Commission
- Evans SJ. 2014. Elephants REALLY never forget: How freed circus animals Shirley and Jenny locked trunks, hugged and played when they met for the first time in TWENTY years [online]. Available at: <https://www.dailymail.co.uk/news/article-2579045/Elephants-REALLY-never-forget-How-freed-circus-animals-Shirley-Jenny-locked-trunks-hugged-played-met-time-20-years.html> [Accessed on 19 January 2019]
- Evans KE & Harris S. 2008. Adolescence in male African elephants, *Loxodonta africana*, and the importance of sociality. *Animal Behaviour*, 76: 779–787
- Evans K, Moore RJ & Harris S. 2013. The release of a captive-raised female African elephant (*Loxodonta africana*) in the Okavango Delta, Botswana. *Animals*. 3: 370-385
- Farine DR. 2015. Proximity as a proxy for interactions: Issues of scale in social network analysis. *Animal Behaviour*, 104: 1-5
- Farine DR & Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84: 1144-1163
- Farm Animal Welfare Council. 2012. *Five Freedoms* [online]. Available at: <http://webarchive.nationalarchives.gov.uk/20121010012427/http://www.fawc.org.uk/freedoms.htm> [Accessed on 12 December 2018]
- Finnegan R. 2005. Tactile Communication. In: Classen C (Ed), *The book of touch*. New York: Berg
- Fishlock V & Lee PC. 2013. Forest elephants: Fission-fusion and social arenas. *Animal Behaviour*, 85: 357–363
- Fox RA & Millam JR. 2014. Personality traits of pair members predict pair compatibility and reproductive success in a socially monogamous parrot breeding in captivity. *Zoo Biology*, 33: 166–172
- Fraser ON, Schino G & Aureli F. 2008. Components of relationship quality in chimpanzees. *Ethology*, 114: 834-843
- Freeman HD & Gosling SD. 2010. Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology*, 72: 653–671

- Freeman HD & Ross SR. 2014. The impact of atypical early histories on pet or performer chimpanzees. *PeerJ*, 2:e579
- Freeman EW, Schulte BA & Brown JL. 2010. Using behavioral observations and keeper questionnaires to assess social relationships among captive female African elephants. *Zoo Biology*, 29: 140–153
- Frick EE. 2016. *Establishing a link between personality and social rank in a group of bottlenose dolphins (Tursiops truncatus)* [Masters thesis]. The University of Southern Mississippi
- Fureix C et al. 2012. Exploring aggression regulation in managed groups of horses *Equus caballus*. *Applied Animal Behaviour Science*, 138: 216–228
- Gadgil M & Vijayakumaran Nair P. 1984. Observations on the social behaviour of free ranging groups of tame Asiatic elephant (*Elephas maximus* Linn). *Proceedings: Animal Sciences*, 93: 225–233
- Galef BG. 2003. Animal social learning. In: Nadel L (Ed) *Encyclopedia of cognitive sciences (Vol 4)*. Macmillan
- Galef BG & Laland KN. 2005. Social Learning in Animals: Empirical Studies and Theoretical Models. *BioScience*, 55: 489 - 499
- Garai ME. 1992. Special Relationships between Female Asian Elephants (*Elephas maximus*) in Zoological Gardens. *Ethology*, 90: 187-205
- Gartner MC, Powell DM & Weiss A. 2016. Comparison of Subjective Well-Being and Personality Assessments in the Clouded Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera leo*). *Journal of Applied Animal Welfare Science*, 19: 294-302
- Gartner MC & Weiss A. 2018. Studying primate personality in zoos: implications for the management, welfare and conservation of great apes. *International Zoo Yearbook*, 52: 79-91
- Gittleman JL & McMillan G. 1996. Conservation of endangered species in captivity. In: Gibbons E, Durrant B & Demarest J (Eds), *Conservation of Endangered Species in Captivity*. Albany: New York Press
- Glatston AR, Geilvoet-Soeteman E, Hora-Pecek E & Van Hooff JARAM. 1984. The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Saguinus oedipus oedipus*. *Zoo Biology*, 3: 241–253
- Gobush KS, Kerr B & Wasser SK. 2009. Genetic relatedness and disrupted social structure in a poached population of African elephants. *Molecular Ecology*, 18: 722–734
- Gobush KS & Wasser SK. 2009. Behavioural correlates of low relatedness in African elephant core groups of a poached population. *Animal Behaviour*, 78: 1079–1086
- Goldenberg SZ et al. 2014. Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*. *Animal Behaviour*, 95: 111-119
- Gosling SD. 2001. From mice to men: What can we learn about personality from animal research?

- Psychological Bulletin*, 127: 45–86
- Gosling SD & John OP. 1999. Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8: 69–75
- Grand AP et al. 2012. Using personality ratings and cortisol to characterize individual differences in African Elephants (*Loxodonta africana*). *Applied Animal Behaviour Science*, 142: 69–75
- Greco BJ et al. 2013. Social learning in captive African elephants (*Loxodonta africana africana*). *Animal Cognition*, 16: 459–469
- Greco BJ et al. 2016a. The days and nights of zoo elephants: Using epidemiology to better understand stereotypic behavior of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. *PLoS ONE*, 11: e0144276
- Greco BJ et al. 2016b. Elephant management in North American zoos: Environmental enrichment, feeding, exercise, and training. *PLoS ONE*, 11: e0152490
- Greco BJ, Meehan CL, Heinsius JL & Mench JA. 2017. Why pace? The influence of social, housing, management, life history, and demographic characteristics on locomotor stereotypy in zoo elephants. *Applied Animal Behaviour Science*, 194: 104–111
- Gruber TM et al. 2000. Variation in stereotypic behavior related to restraint in circus elephants. *Zoo Biology*, 19: 209–221
- Guinet C & Bouvier J. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, 73: 27–33
- Gurusamy V, Tribe A & Phillips CJC. 2014. Identification of major welfare issues for captive elephant husbandry by stakeholders. *Animal Welfare*, 23: 11–24
- Guthmann A. 1970. Effects of Group Size and Composition on Interactive Behaviors of Wild African Elephants in Tarangire National Park. *Mjur*, 65–78
- Hacker CE, Horback KM & Miller LJ. 2015. GPS technology as a proxy tool for determining relationships in social animals: An example with African elephants. *Applied Animal Behaviour Science*, 163: 175–182
- Hancocks D. 1980. Bringing nature into the zoo: Inexpensive solutions for zoo environments. *International Journal for the Study of Animal Problems*, 1: 170–177
- Harris M, Sherwin C & Harris S. 2008. *The Welfare, Housing and Husbandry of Elephants in UK Zoos*, Defra WC05007, UK: Defra
- Hartley M & Stanley CR. 2016. Survey of reproduction and calf rearing in Asian and African elephants in European zoos. *Journal of Zoo and Aquarium Research*, 4: 1–8
- Harvey N et al. 2018. Social Interactions in Two Groups of Zoo-Housed Adult Female Asian Elephants (*Elephas maximus*) that Differ in Relatedness. *Animals*, 8: e132
- Heintz et al. 2017. The relationship between social play and developmental milestones in wild chimpanzees (*Pan troglodytes schweinfurthii*). *American Journal of Primatology*, 79: e22716

- Herrelko ES, Buchanan-Smith HM & Vick SJ. 2015. Perception of available space during chimpanzee introductions: Number of accessible areas is more important than enclosure size. *Zoo Biology*, 34: 397–405
- Highfill LE et al. 2010. Rating vs. coding in animal personality research. *Zoo Biology*, 29: 509-516
- Hill SP & Broom DM. 2009. Measuring zoo animal welfare: Theory and practice. *Zoo Biology*, 28: 531-544
- Hirsch BT, Stanton MA & Maldonado JE. 2012. Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. *PLoS ONE*, 7: e37301
- Horback KM, Miller LJ, Andrews JRM & Kuczaj SA. 2014. Diurnal and nocturnal activity budgets of zoo elephants in an outdoor facility. *Zoo Biology*, 33: 403–410
- Horback KM, Miller LJ & Kuczaj SA. 2013. Personality assessment in African elephants (*Loxodonta africana*): Comparing the temporal stability of ethological coding versus trait rating. *Applied Animal Behaviour Science*, 149: 55–62
- Hosey G, Melfi V & Pankhurst S. 2013. *Zoo Animals: Behaviour, Management, and Welfare*. Oxford: Oxford University Press
- Hutchins M. 2006. Variation in nature: Its implications for zoo elephant management. *Zoo Biology*, 25: 161-171
- Inglett BJ, French JA, Simmons LG & Vires KW. 1989. Dynamics of intra-family aggression and social reintroduction in lion tamarins. *Zoo Biology*, 78: 1–27
- Jacobson SL, Freeman HD, Santymire RM & Ross SR. 2017. Atypical experiences of captive chimpanzees (*Pan troglodytes*) are associated with higher hair cortisol concentrations as adults. *Royal Society Open Science*, 4:170932
- Jones RB & Williams JB. 1992. Responses of pair-housed male and female domestic chicks to the removal of a companion. *Applied Animal Behaviour Science*, 32: 375-380
- Judge PG & De Waal FBM. 1993. Conflict avoidance among rhesus monkeys: Coping with short-term crowding. *Animal Behaviour*, 46: 221-232
- Kagan R, Carter S & Allard S. 2015. A Universal Animal Welfare Framework for Zoos. *Journal of Applied Animal Welfare Science*, 18(sup 1): S1-S10
- Kiiru W. 2007. *The sad state of captive elephants in Canada*, Canada: Zoo Check Canada
- Kleiman DG. 1994. Mammalian sociobiology and zoo breeding programs. *Zoo Biology*, 13: 423-432
- Koene P & Ipema B. 2013. Social networks and welfare in future animal management. *Animals*, 4: 93–118
- Koontz FW & Roush RS. 1997. Communication and social behaviour. In: Kleiman DG, Allen ME, Thompson KV & Lumpkin S (Eds), *Wild mammals in captivity : principles and techniques*. The University of Chicago Press.
- Koski SE, de Vries H, van de Kraats A & Sterck EHM. 2012. Stability and change of social relationship

- quality in captive chimpanzees (*Pan troglodytes*). *International journal of primatology*, 33: 905-921
- Krause J, Lusseau D & James R. 2009. Animal social networks: an introduction. *Behavioral Ecology and Sociobiology*, 63: 967-973
- Krebs BL et al. 2018. Managing aged animals in zoos to promote positive welfare: A review and future directions. *Animals*, 8: e116
- Krueger K, Flauger B, Farmer K & Hemelrijk C. 2014. Movement initiation in groups of feral horses. *Behavioural Processes*, 103: 91-101
- Kuhar CW et al. 2003. Factors affecting reproduction in zoo-housed geoffroy's tamarins (*Saguinus geoffroyi*). *Zoo Biology*, 22: 545-559
- Kuhar CW, Stoinski TS, Lukas KE & Maple TL. 2006. Gorilla Behavior Index revisited: Age, housing and behavior. *Applied Animal Behaviour Science*, 96: 315–326
- Kummer H. 1971. *Primate societies: group techniques of ecological adaptation*. New York: Routledge
- Kurt F. 2005. Behaviour and ecology of wild and captive Asian elephants. In: *First European Elephant Management School*. Hamburg.
- Kurt F & Garai M. 2001. Stereotypies in captive Asian Elephants: a symptom of social isolation. In: Schwammer HM, Foose TJ, Fouraker M & Olson D (Eds), *A Research Update on Elephants and Rhinos*. Münster, Germany: Schöling Verlag.
- Lacy RC. 2009. Stopping evolution: genetic management of captive populations. In: Amato G, DeSalle R, Ryder OA and Rosenbaum HC (Eds), *Conservation genetics in age of genomics*. New York: Columbia University Press
- Langbauer WR. 2000. Elephant communication. *Zoo Biology*, 19: 425–445
- Latham NR & Mason G. 2008. Maternal deprivation and the development of stereotypic behaviour. *Applied Animal Behaviour Science*, 110: 84–108
- Laws N et al. 2007. A case study: Fecal corticosteroid and behavior as indicators of welfare during relocation of an Asian elephant. *Journal of Applied Animal Welfare Science*, 10: 349–358
- Lee PC. 1986. Early social development among African elephant calves. *National Geographic Research*, 2: 388–401
- Lee PC. 1987. Allomothering among African Elephants. *Animal Behaviour*, 35, 278–291
- Lee PC, Poole JH & Moss CJ. 2011. Male social dynamics: independence and beyond. In: Moss CJ & Croze H (Eds), *The Amboseli elephants: a long term perspective on a long-lived mammal*. Chicago: University of Chicago Press
- Lee PC et al. 2013. Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (*Loxodonta africana*). *Biology Letters*, 9: 20130011
- Lee PC & Moss CJ. 1999. The social context for learning and behavioural development among wild

- African elephants. In: Box HO & Gibson KR (Eds), *Mammalian Social Learning: Comparative and Ecological Perspective*. Cambridge University Press.
- Lee PC & Moss CJ. 2012. Wild female African elephants (*Loxodonta africana*) exhibit personality traits of leadership and social integration. *Journal of Comparative Psychology*, 126: 224–232.
- Lee PC & Moss CJ. 2014. African Elephant Play, Competence and Social Complexity. *Animal Behavior and Cognition*, 2: 144 - 156
- Lehmann J & Boesch C. 2004. To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, 56: 207–216.
- Levengood AL & Dudzinski KM. 2016. Is blood thicker than water? The role of kin and non-kin in non-mother-calf associations of captive bottlenose dolphins (*Tursiops truncatus*). *Behavioural processes*, 124: 52-59
- Lewis MH et al. 2000. Early social deprivation in nonhuman primates: Long-term effects on survival and cell-mediated immunity. *Biological Psychiatry*, 47: 119-126
- Lewis KD et al. 2010. A survey of elephant husbandry and foot health in North American zoos. *Zoo Biology*, 29: 221–236
- Li C, Jiang Z, Tang S & Zeng Y. 2007. Influence of enclosure size and animal density on fecal cortisol concentration and aggression in Père David's deer stags. *General and Comparative Endocrinology*, 151: 202-209
- Lincoln GA & Ratnasooriya WD. 1996. Testosterone secretion, musth behaviour and social dominance in captive male Asian elephants living near the equator. *Journal of Reproduction and Fertility*, 108: 107–113
- Ljungberg T & Westlund K. 2000. Impaired reconciliation in rhesus macaques with a history of early weaning and disturbed socialization. *Primates*, 41: 79-88
- Lusseau D & Newman MEJ. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B: Biological Sciences*, 271(Suppl 6): S477-S481
- Lusseau D et al. 2003. The bottlenose dolphin community of doubtful sound features a large proportion of long-lasting associations: Can geographic isolation explain this unique trait? *Behavioral Ecology and Sociobiology*, 54: 396–405
- Lutz C, Well & Novak M. 2003. Stereotypic and self-injurious behavior in rhesus macaques: A survey and retrospective analysis of environment and early experience. *American Journal of Primatology*, 60: 1–15
- MacKay JRD & Haskell MJ. 2015. Consistent individual behavioral variation: The difference between temperament, personality and behavioral syndromes. *Animals*, 5: 455-478
- Makecha R, Fad O & Kuczaj SA. 2012. The Role of Touch in the Social Interactions of Asian Elephants (*Elephas maximus*). *International Journal of Comparative Psychology*, 25: 60–82
- Mallapur A, Waran N & Sinha A. 2005. Factors influencing the behaviour and welfare of captive

- lion-tailed macaques in Indian zoos. *Applied Animal Behaviour Science*, 91: 337–353
- Maple TL & Bloomsmith MA. 2017. Introduction: The science and practice of optimal animal welfare. *Behavioural Processes*, 156: 1-2
- Maple TL, Bloomsmith MA & Martin A. 2008. Primates and pachyderms: a primate model of zoo elephant welfare. In: Forthman D (Ed), *An elephant in the room: the science and well-being of elephants in captivity*. North Grafton: Tufts University Cummings School of Veterinary Medicine/Center for Animals and Public Policy.
- Marker L & O'Brien SJ. 1989. Captive breeding of the cheetah (*Acinonyx jubatus*) in North American zoos (1871–1986). *Zoo Biology*, 8: 3–16
- Martin-Wintle MS et al. 2015. Free mate choice enhances conservation breeding in the endangered giant panda. *Nature Communications*, 6: 10125
- Martin-Wintle MS et al. 2017. Do opposites attract? Effects of personality matching in breeding pairs of captive giant pandas on reproductive success. *Biological Conservation*, 207: 27–37
- Martin P & Bateson P. 1993. *Measuring Behavior: An introductory guide*. Cambridge University Press.
- Mason GJ. 2010. Species differences in responses to captivity: Stress, welfare and the comparative method. *Trends in Ecology and Evolution*, 25: 713–721.
- Mason GJ et al. 2013. Plastic animals in cages: Behavioural flexibility and responses to captivity. *Animal Behaviour*, 85: 1113–1126
- Mason GJ & Veasey JS. 2010a. How should the psychological well-being of zoo elephants be objectively investigated? *Zoo Biology*, 29: 237–255
- Mason GJ & Veasey JS. 2010b. What do population-level welfare indices suggest about the well-being of zoo elephants? *Zoo Biology*, 29: 256–273
- Massen JJM & Koski SE. 2014. Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35: 1–8
- Massen JJM & Sterck EHM. 2013. Stability and Durability of Intra- and Intersex Social Bonds of Captive Rhesus Macaques (*Macaca mulatta*). *International Journal of Primatology*, 34: 770-791
- Massen JJM, Sterck EHM & de Vos H. 2010. Close social associations in animals and humans: Functions and mechanisms of friendship. *Behaviour*, 147(911): 1379-1412
- Matoba T, Kutsukake N & Hasegawa T. 2013. Head Rubbing and Licking Reinforce Social Bonds in a Group of Captive African Lions, *Panthera leo*. *PLoS ONE*, 8: e73044
- McCarthy M. 2001. *The last menageries* [online]. Available from: <https://www.independent.co.uk/environment/the-last-menageries-9130278.html> [Accessed on 17 January 2019]
- McComb K et al. 2001. Matriarchs act as repositories of social knowledge in African elephants.

Science, 292: 491–494

- McCowan B, Anderson K, Heagarty A & Cameron A. 2008. Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behaviour Science*, 109: 396–405
- McCrae RR & John OP. 1992. An Introduction to the Five-Factor Model and Its Applications. *Journal of Personality*, 60: 175–215
- McDougall PT, Reale D, Sol D & Reader SM. 2005. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced and wild populations. *Animal Conservation*, 9: 39-48
- McKnight BL. 2015. Relationship between group dynamics and spatial distribution of African elephants in a semi-arid environment. *African Journal of Ecology*, 53: 439–446
- McPhee ME & Carlstead K. 2010. The importance of maintaining natural behaviors in captive mammals. In: Kleiman DG, Allen ME, Thompson KV & Lumpkin S (Eds), *Wild mammals in captivity : principles and techniques*. The University of Chicago Press.
- Meagher RK. 2009. Observer ratings: Validity and value as a tool for animal welfare research. *Applied Animal Behaviour Science*, 119: 1–14
- Meehan CL, Hogan JN, Bonaparte-Saller M & Mench JA. 2016. Housing and social environments of African (*Loxodonta africana*) and asian (*elephas maximus*) elephants in North American Zoos. *PLoS ONE*, 11: e0146703
- Meehan CL, Mench JA, Carlstead K & Hogan JN. 2016. Determining connections between the daily lives of zoo elephants and their welfare: An epidemiological approach. *PLoS ONE*, 11: e0158124
- Mellen JD. 1991. Factors influencing reproductive success in small captive exotic felids (*Felis* spp.): A multiple regression analysis. *Zoo Biology*, 10: 95–110
- Mellen JD, Hayes MP & Shepherdson DJ. 1998. Captive environments for small felids. In: Shepherdson DJ, Mellen JD & Hutchins JDM (Eds), *Second nature: environmental enrichment for captive animals*. Washington: Smithsonian Institution Press
- Mellor DJ. 2015. Positive animal welfare states and encouraging environment-focused and animal-to-animal interactive behaviours. *New Zealand Veterinary Journal*, 63: 9-16
- Mellor DJ. 2016. Updating Animal Welfare Thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living". *Animals*, 6: 21
- Mellor DJ, Hunt S & Gusset M. 2015. *Caring for Wildlife - The World Zoo and Aquarium Animal Welfare Strategy*. WAZA
- Mench J. 1998. Why it is important to understand animal behavior. *ILAR Journal*, 39: 20-26
- Millspaugh JJ et al. 2007. Stress Response of Working African Elephants to Transportation and Safari Adventures. *Journal of Wildlife Management*, 71: 1257–1260

- Molvar EM & Bowyer RT. 1994. Costs and Benefits of Group Living in a Recently Social Ungulate: The Alaskan Moose. *Journal of Mammalogy*, 75: 621–630
- Morgan KN & Tromborg CT. 2007. Sources of stress in captivity. *Applied Animal Behaviour Science*, 102: 262–302
- Morris-Drake A & Mumby HS. 2018. Social associations and vocal communication in wild and captive savannah elephants *Loxodonta africana*. *Mammal Review*, 48: 24-36
- Moss CJ & Poole JH. 1983. Relationships and social structure in african elephants. In: Hinde RA (Ed), *Primate social relationships: an integrated approach*. Oxford: Blackwell Scientific Publications
- Mueller JE et al. 2013. Seasonal and Diurnal Variations in African Elephant (*Loxodonta africana*) and Black Rhinoceros (*Diceros bicornis*) Behavior in a Northern Climate Zoo. *International Journal of Comparative Psychology*, 26: 304-323
- Napolitano F, Knierim U, Grass F & de Rosa G. 2009. Positive indicators of cattle welfare and their applicability to on-farm protocols. *Italian Journal of Animal Science*, 8(sup 1): 355-365
- Newman MEJ. 2004. Analysis of weighted networks. *Physical Review E*, 70: 056131
- Newman MEJ. 2005. A measure of betweenness centrality based on random walks. *Social Networks*, 27: 39-54
- Novak M, Tiefenbacher S, Lutz C & Meyer J. 2006. Deprived environments and stereotypes: insights from primatology. In: Mason G & Rushen J (Eds), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. Wallingford, Oxford: CABI.
- Nowak MA. 2006. Five rules for the evolution of cooperation. *Science*, 314: 1560-1563
- Nyakaana S, Abe EI, Arctander P & Siegismund HR. 2001. DNA evidence for elephant social behaviour breakdown in Queen Elizabeth National Park, Uganda. *Animal Conservation*, 4: 231-237
- O’Connell-Rodwell et al. 2011. Male African elephants (*Loxodonta africana*) queue when the stakes are high. *Ethology Ecology and Evolution*, 23: 388-397
- Olson D. 2004. *Elephant husbandry resource guide*. Lawrence, KS: Allen Press
- Olson D & Wiese RJ. 2000. State of the North American African elephant population and projections for the future. *Zoo Biology*, 19: 311-320
- Olsson IAS & Westlund K. 2007. More than numbers matter: The effect of social factors on behaviour and welfare of laboratory rodents and non-human primates. *Applied Animal Behaviour Science*, 103: 229-254
- O'Regan HJ & Kitchener AC. 2005. The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review*, 35: 215-230
- Ortega J & Eggert LS. 2004. The Living Elephants: Evolutionary Ecology, Behavior, and Conservation. *Journal of Mammalogy*, 85: 582–582
- Owen MA, Swaisgood RR, Czekala NM & Lindburg DG. 2005. Enclosure choice and well-being in

- Giant Pandas: Is it all about control? *Zoo Biology*, 24: 475–481
- Pacheco Pacheco MX. 2017. *Social network structure and personality in captive meerkat, *Suricata suricatta*, populations: assessment, comparison between wild and captive meerkat populations and captive management implications* (PhD thesis). University of Exeter
- Palme R, Robia C, Baumgartner W & Möstl E. 2000. Transport stress in cattle as reflected by an increase in faecal cortisol metabolite concentrations. *Veterinary Record*, 146: 108-109
- Pinter-Wollman N, Isbell LA & Hart LA. 2009. The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proceedings of the Royal Society B: Biological Sciences*, 276: 1009–1014
- Plotnik JM & de Waal FBM. 2014. Asian elephants (*Elephas maximus*) reassure others in distress. *PeerJ*, 2: e278
- Poddar-Sarkar M & Brahmachary RL. 2014. Chapter 15 Pheromones of Tiger and Other Big Cats. In: Mucignat-Caretta C (Ed), *Neurobiology of Chemical Communication*, Boca Raton (FL): CRC Press/Taylor & Francis
- Poole JH. 1994. Sex differences in the behaviour of African elephants. In: Short R & Lynch P (Eds), *The differences between the sexes*. Cambridge: Cambridge University Press
- Poole J & Granli P. 2008. Mind and movement: meeting the interests of elephants. In: Forthman D, Kane L, Hancocks D & Waldau P (Eds). *An elephant in the room: the science and well-being of elephants in captivity*. Hannover (NH): Tufts University Press
- Poole JH & Moss CJ. 1981. Musth in the African elephant, *Loxodonta africana*. *Nature*. 292: 830-831
- Poole JH & Moss CJ. 2008. Elephant sociality and complexity: the scientific evidence. In: Wemmer C & Christen K (Eds), *Elephants and ethics: towards a morality of coexistence*. Baltim: John Hopkins University Press
- Posta B, Huber R & Moore DE. 2013. The Effects of Housing on Zoo Elephant Behavior : A Quantitative Case Study of Diurnal and Seasonal Variation. *International Journal of Comparative Psychology*, 26: 37–52
- Powell DM & Gartner MC. 2011. Applications of Personality to the Management and Conservation of Nonhuman Animals. In: Inoue-Murayama M, Kawamura S, Weiss A (Eds), *From Genes to Animal Behavior*. Japan: Springer
- Prado-Oviedo NA et al. 2016. Evaluation of demographics and social life events of Asian (*Elephas maximus*) and African elephants (*Loxodonta Africana*) in North American zoos. *PLoS ONE*, 11: e0154750
- Price E & McGrew WC. 1990. Cotton-top tamarins (*Saguinus oedipus*) in a semi-naturalistic captive colony. *American Journal of Primatology*, 20: 1–12
- Price E & Stoinski TS. 2007. Group size: Determinants in the wild and implications for the captive

- housing of wild mammals in zoos. *Applied Animal Behaviour Science*, 103: 255–264
- Racevska E & Hill CM. 2017. Personality and social dynamics of zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Journal of Zoo and Aquarium Research*, 5: 116-122
- Rault JL. 2012. Friends with benefits: Social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science*, 136: 1-14
- Réale D, Gallant BY, Leblanc M & Festa-Bianchet M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, 60: 589-597
- Rees PA. 2000. Are Elephants Enrichment Studies Missing the Point? *Ratel*, 27: 230–232
- Rees PA. 2003a. Asian elephants in zoos face global extinction: Should zoos accept the inevitable? *Oryx*, 37): 20-22
- Rees PA. 2003b. RSPCA elephant welfare recommendations would compromise zoo breeding programmes. *International Zoo News*, 50: 86-90
- Rees PA. 2004. Some preliminary evidence of the social facilitation of mounting behavior in a juvenile bull asian elephant (*Elephas maximus*). *Journal of Applied Animal Welfare Science*, 7: 49–58
- Rees PA. 2009. The sizes of elephant groups in zoos: Implications for elephant welfare. *Journal of Applied Animal Welfare Science*, 12: 44–60
- Renner MJ & Kelly AL. 2006. Behavioral decisions for managing social distance and aggression in captive polar bears (*Ursus maritimus*). *Journal of Applied Animal Welfare Science*, 9: 233-239
- Rödel HG & Meyer S. 2011. Early development influences ontogeny of personality types in young laboratory rats. *Developmental Psychobiology*, 53: 601–613
- Rohland N et al. 2010. Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. *PLoS Biology*, 8: e1000564
- Rommeck I et al. 2009. Risk factors and remediation of self-injurious and self-abuse behavior in Rhesus Macaques. *Journal of Applied Animal Welfare Science*, 12: 61–72
- Rose PE & Croft DP. 2015. The potential of social network analysis as a tool for the management of zoo animals. *Animal Welfare*, 24: 123–138
- Rose PE & Croft DP. 2017. Social bonds in a flock bird: Species differences and seasonality in social structure in captive flamingo flocks over a 12-month period. *Applied Animal Behaviour Science*, 193: 87–97
- RSPCA. 2002. *Live hard, die young: how elephants suffer in zoos*. Horsham, UK.
- Rubenstein DI et al. 2015. Similar but different: Dynamic social network analysis highlights fundamental differences between the fission-fusion societies of two equid species, the onager and Grevy's zebra. *PLoS ONE*, 10: e0138645
- Sachser N, Kaiser S & Hennessy MB. 2013. Behavioural profiles are shaped by social experience: When, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368: 20120344

- Salas M et al. 2016. Aggressive behavior and hair cortisol levels in captive Dorcas gazelles (*Gazella dorcas*) as animal-based welfare indicators. *Zoo Biology*, 35: 467–473
- Sapolsky RM. 2005. The influence of social hierarchy on primate health. *Science*, 308: 648–652
- Schel AM et al. 2013. Network Analysis of Social Changes in a Captive Chimpanzee Community Following the Successful Integration of Two Adult Groups. *American Journal of Primatology*, 75: 254–266
- Schmid J. 1995. Keeping circus elephants temporarily in paddocks - the effects on their behaviour. *Animal Welfare*, 4: 87–101
- Schmid J, Heistermann M, Gansloßer U & Hodges JK. 2001. Introduction of foreign female Asian elephants (*Elephas Maximus*) into an existing group: Behavioural reactions and changes in cortisol levels. *Animal Welfare*, 10: 357–372
- Schulte BA. 2000. Social structure and helping behaviour in captive elephants. *Zoo Biology*, 19: 447–459
- Schulte-Hostedde AI & Mastromonaco GF. 2015. Integrating evolution in the management of captive zoo populations. *Evolutionary applications*, 8: 413–422
- Schuttler SG, Whittaker A, Jeffery KJ & Eggert LS. 2014. African forest elephant social networks: Fission-fusion dynamics, but fewer associations. *Endangered Species Research*, 25: 165–173
- Schwammer HM & Fruehwirth S. 2012. *African Elephant EEP European Studbook 2012*. Austria: Vienna Zoo
- Sejian V, Lakritz J, Ezeji T & Lal R. 2010. Assessment methods and indicators of animal welfare. *Asian Journal of Animal and Veterinary Advances*, 6: 301–315
- Seltmann MW et al. 2018. Evaluating the personality structure of semi-captive asian elephants living in their natural habitat. *Royal Society Open Science*, 5: 172026
- Shier D. 2000. Effects of familiarity on Social Behavior. In: Yoerg SI & Shier DM. *Captive breeding and anti-predator behaviour of the Heermann's kangaroo rat (Dipodomys heermanni)*. University of California
- Shoshani J & Tassep P. 1996. Summary, conclusions and a glimpse into the future. In: Shoshani J & Tassep P (Eds), *The Proboscidea: Evolution and Paleoecology of Elephants and their Relatives*. Oxford: Oxford University Press.
- Shrout PE, Fleiss JL. 1979. Intraclass correlations-uses in assessing rater reliability. *Psychological Bulletin*, 86: 420–428
- Silk JB. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 362: 539–559
- Silk JB, Cheney D & Seyfarth R. 2013. A practical guide to the study of social relationships. *Evolutionary Anthropology*, 22: 213–225
- Snijders L, Blumstein DT, Stanley CR & Franks DW. 2017. Animal Social Network Theory Can Help

- Wildlife Conservation. *Trends in Ecology and Evolution*, 32: 567-577
- Stevenson M. 2002. *Management Guidelines for the Welfare of Zoo Animals: Elephants *Loxodonta africana* and *Elephas maximus*. 1st Edition*. BIAZA.
- Stevenson M & Walter O. 2006. *Management Guidelines for the Welfare of Zoo Animals: Elephants *Loxodonta africana* and *Elephas maximus*. 2nd Edition*. BIAZA.
- Stoeger AS & Baotic A. 2016. Information content and acoustic structure of male African elephant social rumbles. *Scientific Reports*, 6: 27585
- Stoinski TS, Daniel E & Maple TL. 2000. A preliminary study of the behavioral effects of feeding enrichment on African elephants. *Zoo Biology*, 19: 485–493
- Stoinski TS, Lukas KE, Kuhar CW & Maple TL. 2004. Factors influencing the formation and maintenance of all-male gorilla groups in captivity. *Zoo Biology*, 23: 189-203
- Stroud P. 2007. Defining issues of space in zoos. *Journal of Veterinary Behavior: Clinical Applications and Research*, 2: 219–222
- Sukumar R. 1994. *Elephant days and nights: ten years with the Indian elephant*. Oxford University Press
- Sukumar R. 2003. *The Living Elephants: Evolutionary Ecology, Behavior, and Conservation*. Oxford University Press
- Sukumar R. 2006. A brief review of the status, distribution and biology of wild Asian elephants *Elephas maximus*. *International Zoo Yearbook*, 40: 1–8
- Sumpter D, Buhl J, Biro D & Couzin ID. 2008. Information transfer in moving animal groups. *Theory in Biosciences*, 127: 177-186
- Sunquist ME. 1981. The Social Organization of Tigers (*Panthera Tigris*) in Royal Chitawan National Park, Nepal. *Smithsonian Contributions to Zoology*, 336: 1–98
- Swaigood RR & Schulte BA. 2010. Applying knowledge of mammalian social organization, mating systems and communication to management. In: Kleiman DG, Allen ME, Thompson KV & Lumpkin S (Eds), *Wild mammals in captivity : principles and techniques*. The University of Chicago Press.
- Swaigood RR & Shepherdson DJ. 2006. Environmental enrichment as a strategy for mitigating stereotypies in zoo animals: a literature review and meta-analysis. In: Mason GJ & Rushen J (Eds). *Stereotypic animal behaviour: fundamentals and applications to welfare*. 2nd edition. Wallingford, UK: CAB International
- Tarou LR, Bashaw MJ & Maple TL. 2000. Social attachment in giraffe: Response to social separation. *Zoo Biology*, 19: 41-51
- Tennessen T. 1989. Coping with confinement - Features of the environment that influence animals' ability to adapt. *Applied Animal Behaviour Science*, 22: 139–149
- Tetley CL & O'Hara SJ. 2012. Ratings of animal personality as a tool for improving the breeding,

- management and welfare of zoo mammals. *Animal Welfare*, 21: 463–476
- Theil JH, Beisner BA, Hill AE & McCowan B. 2017. Effects of Human Management Events on Conspecific Aggression in Captive Rhesus Macaques (*Macaca mulatta*). *Journal for the American Association for Laboratory Animal Science*, 56: 122-130
- Thitaram C et al. 2015. Social group formation and genetic relatedness in reintroduced Asian elephants (*Elephas maximus*) in Thailand. *Applied Animal Behaviour Science*, 172: 52–57
- Thornton A & Clutton-Brock TH. 2011. Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366: 978–987
- Tresz H & Wright H. 2006. Let them be elephants! How Phoenix Zoo integrated three “problem” animals. *International Zoo News*, 53: 154–160
- Twycross Zoo (2018). *Our elephants have moved home* [online] Available at: <https://twycrosszoo.org/animals/asian-elephants/> [Accessed on 17 January 2019]
- UNEP, CITES, IUCN & TRAFFIC. 2013. *Elephants in the Dust - The African Elephant Crisis*. Norway: United Nations Environment Programme, GRID-Adrenal.
- van Schaik CP et al. 2003. Orangutan cultures and the evolution of material culture. *Science*, 299(5603): 102-105
- van Schaik CP & Burkart JM. 2011. Social learning and evolution: The cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366: 1008-1016
- van Wees M & Belterman R. 2011. *Europe Regional EAZA - EEP Asian Elephant Studbook Elephas maximus*. Netherlands: Rotterdam Zoo.
- Vance EA, Archie EA & Moss CJ. 2009. Social networks in African elephants. *Computational and Mathematical Organization Theory*, 15: 273–293
- Vanitha V, Thiyagesan K & Baskaran N. 2010. Daily routine of captive Asian elephants (*Elephas maximus*) in three management systems of Tamil Nadu, India and its implications for elephant welfare. *Journal of Science, Transformation, Environment, and Technology*, 3: 116–122
- Vaz J et al. 2017. Prevalence and determinants of stereotypic behaviours and physiological stress among tigers and leopards in Indian zoos. *PLoS ONE*, 12: e0174711
- Veasey JS. 2006. Concepts in the care and welfare of captive elephants. *International Zoo Yearbook*, 40: 63–79
- Veasey JS. 2017. In pursuit of peak animal welfare; the need to prioritize the meaningful over the measurable. *Zoo Biology*, 36: 413–425
- Veasey JS, Waran NK & Young RJ. 1996. On Comparing the Behaviour of Zoo Housed Animals With Wild Conspecifics As a Welfare Indicator. *Animal Welfare*, 5: 13-24

- Videan EN & Fritz J. 2007. Effects of short- and long-term changes in spatial density on the social behavior of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, 102: 95–105
- Vidya TNC & Sukumar R. 2005a. Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *Journal of Ethology*, 23: 205-210
- Vidya TNC & Sukumar R. 2005b. Social and reproductive behaviour in elephants. *Current Science*, 89: 1200–1207
- Walter O. 2010. *Management Guidelines for the Welfare of Zoo Animals: Elephants *Loxodonta africana* and *Elephas maximus**. 3rd Edition. BIAZA.
- Waples KA & Gales NJ. 2002. Evaluating and minimising social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). *Zoo Biology*, 21: 5–26
- Wasserman S & Faust K. 1994. *Social network analysis: Methods and applications*. Cambridge: Cambridge University Press
- Watters JV, Bremner-Harrison S & Powell DM. 2017. Phenotype management: an inclusive framework for supporting individuals' contributions to conservation populations. In: Vonk J, Weiss A & Kuczaj SA (Eds). *Personality in Nonhuman Animals*. Springer.
- Watters JV & Powell DM. 2012. Measuring Animal Personality for Use in Population Management in Zoos: Suggested Methods and Rationale. *Zoo Biology*, 31: 1–12
- Webster MM & Ward AJW. 2011. Personality and social context. *Biological Reviews*, 86: 759–773
- Weiss A. 2017. A human model for primate personality. *Proceedings of the Royal Society B: Biological Sciences*, 284: 20171129
- Wells DL. 2005. A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, 93: 13–17
- Wells DL & Irwin R. 2008. Auditory stimulation as enrichment for zoo-housed Asian elephants (*Elephas maximus*). *Animal Welfare*, 17: 335–340
- Wey TW & Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, 79: 1343-1352
- Wey TW, Blumstein DT, Shen W & Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, 75: 333–344
- Whilde J & Marples N. 2012. Effect of a birth on the behavior of a family group of Asian elephants (*Elephas maximus*) at Dublin Zoo. *Zoo Biology*, 31: 442–452
- Whiten A et al. 1999. Cultures in chimpanzees. *Nature*, 399: 682-685
- Whitham JC & Wielebnowski N. 2013. New directions for zoo animal welfare science. *Applied Animal Behaviour Science*, 147: 247–260
- Widowski T. 2015. Chapter 15: Why are behavioural needs important? In: Grandin T (Ed), *Improving animal welfare: a practical approach*. USA: CABI.

- Wiedenmayer C & Tanner R. 1995. Untethered housing of Asian elephants *Elephas maximus* at Zurich Zoo. *International Zoo Yearbook*, 34: 200–205
- Wielebnowski NC. 1999. Behavioral differences as predictors of breeding status in captive cheetah. *Zoo Biology*, 18: 335–349.
- Wielebnowski NC et al. 2002. Impact of social management on reproductive, adrenal and behavioural activity in the cheetah (*Acinonyx jubatus*). *Animal Conservation*, 5: 291–301
- Wiese RJ. 2000. Asian elephants are not self-sustaining in North America. *Zoo Biology*, 19: 299–309
- Williams E et al. 2015. An investigation into resting behavior in Asian elephants in UK Zoos. *Zoo Biology*, 34: 406–417
- Williams E, Bremner-Harrison S & Ward SJ. 2018a. Can we meet the needs of social species in zoos? An overview of the impact of group housing on welfare in socially housed zoo mammals. In: Berger M & Corbett S (Eds). *Zoo Animals: Husbandry, Welfare and Public Interactions*. Hauppauge, New York: Nova Science Publishers.
- Williams E, Chadwick CL, Yon L & Asher L. 2018b. A review of current indicators of welfare in captive elephants (*Loxodonta africana* and *Elephas maximus*). *Animal Welfare*, 27, 235–249
- Wilson ML et al. 2006. Nocturnal behavior in a group of female African elephants. *Zoo Biology*, 25: 173–186
- Wittemyer G, Douglas-Hamilton I & Getz WM. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, 69: 1357–1371
- Wittemyer G & Getz WM. 2007. Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Animal Behaviour*, 73: 671–681
- Wittemyer G, Getz WM, Vollrath F & Douglas-Hamilton I. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: A contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, 61: 1919–1931
- Wolfensohn S et al. 2018. Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals*, 8: 110
- Worlein JM et al. 2017. Socialization in pigtailed macaques (*Macaca nemestrina*). *American Journal of Primatology*, 79: 1–12
- Yasui S & Idani G. 2017. Social significance of trunk use in captive Asian elephants. *Ethology Ecology and Evolution*, 29: 330–350
- Yasui S et al. 2013. Personality Assessment and Its Association With Genetic Factors in Captive Asian and African Elephants. *Zoo Biology*, 32: 70–78
- Yon L, Williams E, Harvey N & Asher L. 2019. Development of a Behavioural Welfare Assessment Tool for Routine Use with Captive Elephants. *PLoS ONE*, 14: e0210783.
- Young RJ. 2003. Environmental Enrichment: an Historical Perspective. In: Young RJ (Ed). *Environmental enrichment for captive animals*. UFAW

- Ziegler TE & Crockford C. 2017. Neuroendocrine control in social relationships in non-human primates: Field based evidence. *Hormones and Behavior*, 91: 107-121
- ZIMS. 2017. Species 360 Zoological Information Management System (ZIMS). Retrieved from: zims.species360.org
- Zoo Licensing Act. 1981. *Zoo Licensing Act (Amendment) 1981* [online]. Available at: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/69595/zoo-licensing-act-guide.pdf [Accessed on 22 February 2019]
- Zoos Forum. 2010. *Elephants in UK Zoos: Zoos Forum review of issues in elephant husbandry in UK zoos in the light of the Report by Harris et al (2008)*. Defra.