

The social welfare of captive elephants

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy

Βу

Rutendo Mary-Ann Wazara September 2019

Table of Contents

Table of	Contents	2	
Acknow	ledgments	5	
Thesis A	bstract	7	
1 Genera	al Introduction	9	
1.1	Elephant Social Behaviour	9	
1.2	Elephants in Zoos	.15	
1.3 1.3. 1.3.	 Welfare Indices 1 Measures collected in captive elephants 2 Social behaviour and physiology 	. 17 .17 .18	
1.4	Thesis Aims and Hypotheses	.20	
Chapter	2: The social dynamics of captive Asian elephants (<i>Elephas maximus</i>)	25	
2.1		.25	
2.2	Abstract	.25	
2.3	Background	.26	
2.4	Methods	.29	
2.4.	1 Sample populations	.29	
2.4.	2 Data collection	.32	
2.4.	3 Measuring herd structure and individual sociality	.33	
2.4.	4 Associations over time	.36	
2.4.	5 Statistical analysis	.36	
2.5	Results	.38	
2.5.	1 Herd associations and structure	.38	
2.5.	2 Associations over time	.42	
2.6	Discussion	.46	
2.6.	1 Female associations and bond strength	.46	
2.6.	2 Node metrics and individual social position	.49	
2.6.	3 Methods for measuring bonds in captive elephants	.50	
2.7	Conclusions	.52	
 Chapter 3: Maternal care and allomothering in captive Asian elephants (<i>Elephas maximus</i>) 54 3.1 Abstract			

3.2	Background	55
3.3	Methods	58
3.3	.1 Sample Population	58
3.3	.2 Data Collection	59
3.3	.3 Measuring herd structure and dyad bond strength	61
3.3	.4 Statistical analysis	62
3.4	Results	65
3.4	.1 Maternal and allomaternal bond strengths	65
3.4	.2 Rate of maternal and allomaternal interactions	67
3.4	.3 Factors influencing allomother-calf bonds	72
3.5	Discussion	76
3.6	Conclusion	80
Chapte <i>maxim</i> u	r 4: The Night-time Networks of Captive Asian Elephants (<i>Ele</i> us) 82	phas?
4.1	Abstract	82
4.2	Background	83
4.3	Methods	87
4.3	.1 Sample Populations	87
4.3	.2 Social network analysis	92
4.3	.3 Statistical Analysis	93
4.4	Results	95
4.4	.1 Night-time sleeping networks	95
4.4	.2 Sleep networks over time	100
4.4	.3 Social position and sleep quality	103
4.5	Discussion	106
4.6	Conclusions	110
Chapte Asian e	r 5: Investigating the relationship between sociality and end lephants (<i>Elephas maximus</i>)	ocrinology in 112
5.1	Abstract	112
5.2	Background	
5.3	Materials and Methods	118
5.3	.1 Study animals and faecal sample collection	118
5.3	.2 Hormone Analysis	120
5.3	.3 Social Network Analysis	122
5.3	.4 Statistical Analysis	123

5.4 R	Results	126		
5.4.1	Longitudinal patterns of faecal glucocorticoids in captive Asian elepha 126	ants		
5.4.2	Social position, social events and individual endocrinology	131		
5.4.3	Sociality, adrenal activity and reproductive health	136		
5.5 C	Discussion	138		
5.6 C	Conclusions	143		
Chapter 6: The social history and reproductive rates of female Asian elephants (Elephas maximus) in the UK & European captive elephant population145				
6.1 A	\bstract	145		
6.2 B	Background	146		
6.3 N	Aethods	149		
6.3.1	Data Collection	149		
6.3.2	Data Analysis	150		
6.4 R	Results	151		
6.4.1	Herd stability and rearing success	151		
6.4.2	The effect of group composition on calf rearing success	153		
6.4.3	Inter-Zoo transfers and female longevity	153		
6.5 C	Discussion	157		
6.6 C	Conclusion	160		
Chapter 7	: General discussion	161		
Reference	95	170		
Appendix		188		

Acknowledgments

Firstly, I would like to thank my supervisors, Paula Stockley, Jane Hurst, and Lisa Holmes, for their expertise, wisdom, and support. Your constant guidance and knowledge during the course of this research have not only been invaluable but have also pushed me continue to strive be a well-rounded scientist. Paula, thank you for your constant encouragement and for believing in me and seeing my potential. Thank you to the members of the Mammalian Behaviour and Evolution groups. I have valued my time with everyone I worked with.

This study would not have been possible without the support of Sue Walker and the Chester Zoo Conservation Scholars & Fellows programme. Thank you to all members of the Chester Zoo the Science Team, thank you for sharing your knowledge, experience, and your space with me – I will always feel like part of the team. To Becky Mogey, thank you for guiding and teaching me all of the lab techniques I needed for my research – with great patience I must add! Thanks to Ronnie Cowl for showing even greater patience with my constant emails about permutations and SNA p-values, you are a wonderful teacher. I am also honoured and thankful that I had the opportunity to work with the exceptional Chester Zoo elephant management team: Andy McKenzie, Richard Fraser, James Edward, Alan Littlehales, and Emma Evison. Thank you for allowing me to be part of your team and to learn from such passionate and experienced people such as yourselves. And thank you for asking the questions that led to this research becoming a reality. I must also thank Dublin Zoo and their elephant keeping team; especially Gerry Creighton and Mel Sheridan – thank you both for carrying out data collection and contributing to this project. And thank you for being passionate about the potential of this work.

Thank you to my beautiful family and friends. To Rhiannon, thank you for your friendship, support and unconditional love for me, you are wonderful! Mom and

Dad, thank you for always believing in my dreams, even when I couldn't see them clearly for myself; and even if it meant letting me live on the other side of the world. Thank you for investing in me emotionally, spiritually, and financially. To my beautiful siblings, thank you for carrying me at my lowest points in this journey, and for cheering me on right to the end. Tashinga, Tadiwa, and Naledi – thank you for your constant messages of love and encouragement. Ishe and Izwi, thank you for taking care of your big sister and making sure I stayed well-fed and healthy even after late nights in the office. And Mbiri, thank you for promising to read all of my thesis because you love me.

I must also thank my husband, Will, and my parents-in-law, Dave and Suzy. Your home was a refuge when I needed it, and you always had time and space for me, thank you and I love you. Will, thank you for supporting my dream since the day we met in undergrad; I love you for that and I will never be able to fully express what you mean to me – that's a whole thesis in itself!

Finally, thank you God. In you, science and faith exist wholly, harmoniously, and beautifully. Thank you for letting me see creation as you do – good.

Thesis Abstract

The Social Welfare of Captive Elephants

Rutendo Wazara

The history of Asian elephants in Europe dates back as far as the 17th century, where they were part of the private menageries of royalty, and since then, the captive population of elephants in Europe has grown to several hundred individuals. Over time, great strides have been made in the improvement of their management and welfare, but institutions continue to seek ways to better manage elephants in captivity. As captive institutions continue to make great strides to improve zoo elephant management and welfare, evidence-based solutions are being sought in order to address the social needs of this species. The aim of this thesis is to provide evidence-based research to help institutions understand the social welfare of captive elephants. In this study, I aimed to quantify elephant sociality using well known social network methods. I characterised individual sociality, identified key group members and monitored changes in social structure over time. Results showed that calves and matriarchal females were the most central figures. Significant changes in herd structure were detected in response to birth events. Variation in bond strength over time was observed but significance varied. I also demonstrated that this methodology can be adapted to be utilised by animal caretakers as part of their daily husbandry and management routines.

Next, I aimed to observe the rate of maternal and allomaternal behaviours in a captive breeding herd to characterise the bonds and interactions of calves with nonmothers. In order to do this data were collected on touching, greeting, play and nursing interactions. My analysis showed significant variation in the types of allomaternal interactions in which females engaged. Calves interacted most often with their grandmothers and sisters; and most interactions were calf initiated. I also observed interesting allonursing behaviour initiated by one of three calves. Assessment of influences on allomaternal investment revealed that mother-allomother bond strength and number of years adult females spent as herd mates were significant influences.

As periodic recording of elephant night-time behaviour is becoming an increasingly common management tool for zoological institutions, I aimed to validate the reliability of these data for the assessment of herd cohesion and stability. My aims were to, explore the night-time network structure; investigated potential factors determining night-time associations; and investigate the stability of night-time networks over time and the relationship between social position and average amount of sleep per night. I was able to validate zoo management techniques, finding a strong correlation between day and night -time networks. Elephants were found to have significant preferred sleeping partners and calves were observed to be central within the sleeping networks. I observed monthly variation in sleep associations, however preferred partners remained consistent over time. A strong relationship was found between average hours of sleep per night and degree of sociality.

Strong bonds between individuals have been associated with a reduced glucocorticoid response to environmental and social stressors. I performed a longitudinal study of faecal glucocorticoid (fGCM) profiles of captive female Asian elephants to explore the relationship between an individual's fGCM concentrations and its social position. I assessed the impacts of season and major life events on secretion patterns. Spring, summer and winter were associated with significant increases in fGCM across all individuals. Birth and death events were also significantly associated with elevated fGCM concentrations. To determine the link between individual fGCM response and sociality, I assessed the magnitude of individual fGCM response and sociality in this study. Finally, I compared fGCM concentrations to those of faecal progesterone levels to explore relationships between social bond strength, adrenal activity and reproductive health. Although fGCM and fPGM concentrations appeared to have an inverse relationship, this present study found no evidence of a significant relationship.

Finally, using historic and current management data, I conducted an investigation on the impact social stability on the rearing success of captive Asian elephants in the broader UK and European zoo collection. I investigated how variation in herd stability and social structure impacted on the birth rate, calf rearing success and longevity of female elephants. I explored how herd stability and social structure were associated with variation in reproductive rate and calf survival. The presence of relatives, former herd mates, and larger herd sizes each appear to be beneficial effects for rearing success. Conversely, more frequent inter-zoo transfers were associated with evidence of negative effects on breeding success and may impact negatively on longevity.

This thesis aimed to use methods of monitoring animal behaviour and endocrinology already used by zoo institutions to demonstrate the power of combining these techniques to assess the welfare of captive elephant herds. The intention of this study was to spotlight the dynamics of captive elephant sociality and its impacts on factors such as calf rearing and individual endocrinology. It is my hope that such a study will add to the growing body of work focused on gaining a better understanding of the links between environmental, management and social factors and elephant survival *ex situ*.

1 General Introduction

The history of Asian elephants in Europe dates back as far as the 17th century, where they were part of the private menageries of royalty. Since then the captive population of elephants in Europe has grown to several hundred individuals (Clubb and Mason, 2002). Over time great strides have been made in the improvement of their management and welfare but institutions continue to seek ways to better manage elephants in captivity (Clubb and Mason, 2002; Harris et al., 2008; Rees, 2009). In the wild, elephants; Asian (*Elephas maximus*), African forest (*Loxodonta* africana cyclotis), and African savannah (Loxodonta africana africana) species live in complex family groups (Archie et al., 2006b; Moss et al., 2011; Raman Sukumar, 1989; Sukumar, 2003; T. N. C. Vidya and Sukumar, 2005). These groups begin with mothers and their offspring then extend to sisters, aunts, and grandmothers. By contrast captive elephants are often housed in smaller and less related groups and although regional zoo governing bodies have encouraged institutions to increase their herd sizes, housing space constraints and controlled breeding affect the number of elephants that zoos are able to house (Rees, 2009). This leads to questions concerning how best to address the social needs of the species (Harris et al., 2008; Rees, 2009). Social contact between conspecifics can be seen as 'social enrichment' and is important for the learning of normal species-specific behaviours (Clubb and Mason, 2002; Rees, 2009).

1.1 Elephant Social Behaviour

In the wild elephant species live in highly complex fission-fusion social groups, with the mother-calf dyad representing the most basic social unit (Daniel, 1998; Moss et al., 2011; Raman Sukumar, 1989; Sukumar, 2003). Family units containing related females and their offspring will remain together through their life time and seasonally multiple family units will fuse to form larger bond groups or subgroups containing hundreds of individuals (Archie et al., 2006b; Kurt and Garai, 2001; Wittemyer et al., 2007). In both the Asian and African species two or more associating mother-calf dyads are termed a family group and contain between 3 – 20 individuals (Archie et al., 2006b; Sukumar, 2006). Multiple associating family groups are known as a bond group, which can contain up to 40 members (Wittemyer et al., 2007). Larger herds, known as clans, are formed of many bond and family groups that share a similar dry season or home ranges (Archie et al., 2006b; Poole and Moss, 2008; R Sukumar, 1989; Sukumar, 2003; T. N.C. Vidya and Sukumar, 2005; Wittemyer et al., 2007). Wild Asian elephant clans, such as those in southern India, were observed to consist of 50 – 200 individuals (R Sukumar, 1989; Sukumar, 2003) and in wild African populations several hundred individuals can make up a single clan (Poole and Moss, 2008). These different tiers of elephant society have been observed in both Asian and African species and the fusion or fission of these tiers is determined by seasonal resource availability (Moss and Lee, 2011a; Raman Sukumar, 1989; Sukumar, 2003; Wittemyer et al., 2007; Wittemyer and Getz, 2007).

Although there are many similarities between elephant species, differences in herd structure and size exist. Due to extensive, long-term studies the African savannah elephant (*Loxodonta africana africana*) is known to have larger and very distinct multitiered family, bond and subgroups (de Silva and Wittemyer, 2012; Moss et al., 2011; Wittemyer et al., 2007). Analysis of African savannah elephant social groups have shown not only to contain a greater number of breeding females, but social network analysis shows this species to be highly gregarious with more and stronger direct connections with group members (de Silva and Wittemyer, 2012). In contrast, Asian elephants (*Elephas maximus*) are less gregarious with groups of fewer individuals and sparser networks compared to their African counterparts (de Silva and Wittemyer, 2012). Additionally, unlike the

African savannah species, Asian elephant societies show multilevel grouping but they do not have a strict hierarchical stratification in their groups (de Silva et al., 2017; de Silva and Wittemyer, 2012). In African elephants herds are led by an older and mature matriarch whose role is to share ecological, defensive and social knowledge with the herd (Mccomb et al., 2001; Schulte, 2000). In a comparison of the African and Asian species, De Silva et al (2017) observed that whilst African elephants benefited from a strict dominance hierarchy with a matriarchal lead, Asian elephants have a weaker hierarchy system as predation and resource scarcity are not a threat. Despite being less gregarious than their African counterparts, Asian elephants have still been documented to form strong bonds with closely related females (Silva et al., 2011a; T. N.C. Vidya and Sukumar, 2005). Vidya and Sukumar (2005b) demonstrated the degree of relatedness within Asian elephants in their study of family groups in southern India. Utilising nuclear microsatellite DNA their results showed that relatedness between adult females within groups was an average 0.37±0.159, reflecting relatedness as close as mother-daughters, full sisters or half-sisters (T. N.C. Vidya and Sukumar, 2005). The presence of closely related adult females within groups also suggests very low inter-group transfer within this southern India population (T. N.C. Vidya and Sukumar, 2005) which shows that, as found in African elephants, Asian elephant females will remain in their natal groups into their adulthood (Moss et al., 2011; Sukumar, 2006).

Cooperation to ensure the survival of kin and their offspring results in maximised inclusive fitness (Hamilton, 1963; Maynard Smith, 1964). For female elephants the benefits of helping kin include cooperative rearing and protection of young, sharing and defending resources and passing social and ecological knowledge from one generation to the next (Archie et al., 2006b; Lee, 1987; Mccomb et al., 2001). Juvenile females directly benefit from the experience they gain performing allomothering behaviours and similarly they guarantee that they will receive the same aid when they have young of their own (Lee, 1987; Moss and Lee, 2011a; Schulte, 2000; Whilde and Marples, 2012). It is also important to have

older and experienced females within the herd to pass down vital social and maternal skills. Ecological factors also shape the social structure and level of cooperation observed in an elephant herd (Raman Sukumar, 1989; Wittemyer et al., 2007). Elephant social dynamics are characterized as fission-fusion; a herd will consist of subgroups that will fuse together or separate from one another regularly (Wittemyer et al., 2007). In African savannah elephants fission-fusion structure allows for groups to separate during drier conditions when resources are scarce and then aggregate during wetter seasons when resources are abundant (Archie et al., 2006a; Nandini et al., 2017; Smith et al., 2011; Wittemyer and Getz, 2007). Wittemeyer *et al* (2007) found the sociality of African elephant groups was affected by seasonality. They observed that social cohesion at the "bond" and "clan" levels of the social system decreased during the dry season (Wittemyer et al., 2007). The tight ecological constraints of the dry period increase competition, resulting in individuals separating (Wittemyer et al., 2007). In contrast Wittemeyer et al (2005) observed that during wetter seasons, when resources were abundant, elephant subgroups were able to fuse into larger groups. The abundance in resources facilitated increased cooperative benefits (Wittemyer et al., 2007). In contrast Nandini et al (2017) observed that at the population level Asian elephants aggregated into larger groups during the dry season compared to the wet. They attribute this to patch density of resources in forest habitats; high group size when the patch density is high and clumped and low group size when resources are uniformly distributed and patch density is low (Nandini et al., 2017). Therefore, Nandini et al (2007) suggest that fission-fusion in Asian elephants is a means to associate with clan-mates whilst keeping their group sizes similar rather than changing social structures in size seasonally. This indicates that in the wild, kin selection benefits and ecological factors have played roles in shaping the elephant social system.

Elephants are sexually dimorphic and in the wild the two sexes live in very different social structures. Whilst female elephants remain in highly structured and complex social groups with their female relatives, males live in a more fluid social environment with fewer close associates and many weak associates (Chiyo et al., 2011; T. N. C. Vidya and Sukumar, 2005; T. N.C. Vidya and Sukumar, 2005). At puberty (9-18 years in African and 10-15 years in Asian elephants) male elephants undertake locational dispersal, becoming independent and moving away from their natal herd (Evans and Harris, 2008; T. N.C. Vidya and Sukumar, 2005). Studies on male elephant dispersal have shown that males spend their time asymmetrically between being in all-male groups, mixed-sex groups and alone (Chiyo et al., 2011; Evans and Harris, 2008). Observations on adolescent and adult male elephants have revealed that in early adolescence, between 10-20 years old, male elephants exhibit highly social behaviour with their agemates and congregate in larger allmale groups of 2-17 individuals (Chiyo et al., 2011; Evans and Harris, 2008). Although males have a more fluid social system compared to their female counterparts, age and relatedness are factors found to determine associations between males. Using nuclear microsatellite DNA in their study of Asian elephants in southern India, Vidya and Sukumar (2005b) found evidence that male dispersal in a location was non-random and that there was high relatedness between adult males within their study locations. Similarly, Chiyo et al (2011) found a weak but significant correlation between African male elephant associations and genetic relatedness. Whilst little is still known about the benefits of relatedness in malemale association of elephants this evidence adds to the hypothesis that relatedness to males in the same territory increases sparring safety and reduces conflict (Chiyo et al., 2011). Observations of the association of different male elephant age from early adolescence to late adulthood revealed that, unlike females, in general males have high associations with a few individuals and weak or random associations with many more individuals (Chiyo et al., 2011). However, adolescent males aged between 10 – 20 years old have been observed to be the most socially interactive age class, congregating in larger all-male groups (2-18 individuals) but this sociality

decreases with increased age (Evans and Harris, 2008). Both Chiyo *et al* (2011) and Evans and Harris (2008) documented that all male age classes had a high affinity towards older bull elephants (\geq 35 years old). It is believed that this level of sociality allows newly independent young bulls to gain crucial information from older bulls without posing a competitive threat (Evans and Harris, 2008).

Elephant social bonding is expressed through tactile communication, vocal communication, allomothering, and sharing novel resources (J H. Poole and Granli, 2011; T. N. C. Vidya and Sukumar, 2005). They are highly tactile and use this to express affiliation, reassurance, exploration, play and aggression (Gadgil and Nair, 1984; J H. Poole and Granli, 2011; T. N. C. Vidya and Sukumar, 2005). Greeting behaviour, for example, involves an individual placing its trunk in the mouth, face or genitals of another herd member – this can also be used for reassurance (T. N. C. Vidya and Sukumar, 2005). Acoustic signalling is used for long distance communication to express alarm, during conflict and threat displays and in greeting family members (Mccomb et al., 2001; T. N. C. Vidya and Sukumar, 2005). Their vocal communication ranges from loud, high frequency, calls to seismic, infrasonic communication (Hart et al., 2008). It is well documented that elephants are not only able to identify the vocal calls of their herd mates, but also unrelated individuals from other family groups which they may encounter when groups aggregate (Archie et al., 2006b; Hart et al., 2008; Mccomb et al., 2001). The intricacies of how sociality and relationship strength is expressed demonstrates its importance in elephant societies. An importance that has been proven to have both direct and indirect benefits for individuals of this species. Pinter-Wollman et al (2009) observed that in a group of translocated savannah elephants, the body condition of the translocated elephants positively correlated with the number of associates they had. Evidence has shown that social bonds with maternal relatives, in particular sisters and mothers, improves the annual and overall reproductive output of female elephants (Gobush et al., 2008a; Lynch et al., 2019). Moreover, evidence has shown that

females that are well connected and have relatives within their social group benefit from reduced levels of glucocorticoids (Foley et al., 2001; Gobush et al., 2008a). In fact, a study on the long term impacts of poaching on female African elephants revealed that whilst females in high-risk poaching areas had higher faecal glucocorticoid levels, this was reduced if their relatives or an older matriarch was present in their herd (Gobush et al., 2008a). Other studies in both elephants and other social species have also shown that the strength of relationships is associated with increased offspring survival and longevity (Silk et al., 2010a, 2003; Wittemyer et al., 2007).

1.2 Elephants in Zoos

Since they first made their appearance in the private menageries of nobility in the 17th century (Rothfels, 2008; Schulte, 2000), the captive elephant population in Europe has grown from just a handful of individuals to hundreds (Schmidt and Kappelhof, 2019). In that time large advances have been made in their management and welfare. However, studies argued that more attention must be paid to elephant social composition in zoos (Faust et al., 2006; Hutchins, 2006; Hutchins et al., 2008; Rees, 2009). Reports, in particular that by Harris *et al* (2008), on the welfare and husbandry of zoo elephants have noted that there must be focus on improving the social composition of captive herds due to its possible implications on individual health and herd sustainability. In the wild elephants live in large multi-tier groups (T. N. C. Vidya and Sukumar, 2005) and whilst zoos may try to mimic this social composition in captivity, most are unable due to spatial and management constraints (Clubb and Mason, 2002; Rees, 2009).

When compared to their wild counterparts zoo elephant herds differ, firstly, in group size. Traditionally most zoo facilities have housed elephants in either solitary conditions or in groups of no more than 3 individuals (Clubb and Mason, 2002; Harris et al., 2008; Rees, 2009). This is despite zoo governing bodies such as the American Zoo and Aquarium Association (AZA) giving recommendations to increase the number of individuals housed by zoo institutions to no less than 3 or 4 compatible females (AZA, 2001; BIAZA, 2010). Social enrichment through contact with individuals of the same species is important for the promotion of normal species-specific behaviours (Rees, 2009). Many normal behaviours in elephants are learnt, rather than innate, especially socio-sexual and maternal behaviours (Lee, 1987; Rees, 2009). It is for this reason that the British and Irish Association of Zoos and Aquariums (BIAZA) emphasize that maintaining an appropriate social group will "truly 'conserve' elephants in captivity as many naturally learnt behaviours and cultural elements should be maintained as possible," (BIAZA, 2010).

Secondly, whilst wild elephant herds contain multiple generations, the most common age class found in zoo herds is adult females between 27 and 36 years old (Clubb and Mason, 2002; Schmidt and Kappelhof, 2019; Schulte, 2000). Typically, infants are the most common class age (<1 - 3 years old) and make up a larger proportion of a wild herd (Clubb and Mason, 2002; Schulte, 2000). However, there are fewer infants in captive herds and some credit this to reproductively mature females not having opportunities to breed or exhibiting reproductive pathologies (Proctor et al., 2010a; Schmidt and Kappelhof, 2019; Schulte, 2000). Multigenerational groups are important for the development and stability of herds. The presence of infants encourages allomothering behaviour amongst nulliparous females (Lee, 1987; Schulte, 2000; Whilde and Marples, 2012). Although captive elephants may not need all of this knowledge, older females still have the potential to pass down crucial species-specific behaviour. This is also the case for the socialization of bull elephants (BIAZA, 2010; Chiyo et al., 2011; Evans and Harris, 2008; Slotow et al., 2000). Evans and Harris (2008) describe adolescence in male African elephants as a period of increased social learning during which they rely on mature bulls as social and ecological repositories of knowledge. When officials

struggled with antisocial and highly aggressive young bulls in Pilanesberg National Park, South Africa, older males were translocated into the park and their presence quickly calmed the young bulls (Slotow et al., 2000). Whether it is learning crucial mothering skills or reinforcing dominance hierarchies, a herd structure with overlapping generations enables the passing down of critical skills (Clubb and Mason, 2002; Veasey, 2006). The presence of older, experienced individuals within a herd is important for the social development, stability and behaviour of younger herd members (Chiyo et al., 2011; Slotow et al., 2000; Whilde and Marples, 2012).

Finally, elephants in zoos experience changes in group composition that are not experienced by wild herds. In naturally occurring herds female elephants will remain in their maternal groups into adulthood, whilst males disperse during adolescence (Evans and Harris, 2008; T. N. C. Vidya and Sukumar, 2005). In contrast, individuals in zoos are moved between institutions regularly. Whilst this may be for management or breeding purposes, such movement can be unusual when it involves the movement of young elephants between 3 and 8 years old from their natal herds and may have serious welfare implications (Clubb and Mason, 2002; Schmidt and Kappelhof, 2019). Clubb & Mason (2002) argue that the implications of movement between facilities may include the breaking of established bonds, the inhibition of social development and stress-related behaviours. The introduction of new individuals into a stable group also has the potential to disrupt the social structure and lead to changes in physiology and behaviour (Clubb and Mason, 2002).

1.3 Welfare Indices

1.3.1 Measures collected in captive elephants

Whilst animal welfare is often difficult to define (BIAZA, 2010; Broom, 1997), authors have related it to an animal's ability to cope with its environment (Broom, 1997) and its psychological wellbeing, which is a feeling-based state (Mason and Veasey, 2010; Veasey, 2006). Good welfare is considered to be when an animal is satisfied, in a state of relaxation, and experiences positive feelings (BIAZA, 2010; Broom, 1997; Mason and Veasey, 2010; Veasey, 2006). Whilst poor welfare is identified as when an animal's health or circumstances cause it pain, fear, anxiety or stress (Mason and Veasey, 2010). Since the feelings and individual experiences of an animal are immeasurable, welfare is measured indirectly using indicators (Mason and Veasey, 2010; Veasey, 2006). The welfare indicators used to measure the wellbeing of animals can be grouped broadly into physiological, behavioural and environmental influences (Veasey, 2006). Indicators that have been used to specifically measure elephant welfare in captivity have included reproductive status and output, adrenal activity, activity budgets, and stereotypical behaviours, to name a few (BIAZA, 2010; Carlstead et al., 2013; Hodges et al., 2010; Mason and Veasey, 2010) . Whilst some measures are fairly simple to collect others, such as those requiring biological samples, are more difficult to collect (Hodges, et al., 2010; Walter, 2010). However, a large body of work has found success in assessing elephant glucocorticoid and reproductive endocrinology non-invasively through the use of faecal samples (Brown et al., 1996; Edwards et al., 2016, 2014; Sanderson et al., 2015; Tingvold et al., 2013). Mason and Veasey (2010) assessed zoo elephant welfare using indicators they propose could be most effective indicators of wellbeing and they used protected wild populations as their "benchmarks" for these indicators. They suggested measuring fecundity rates, ovulation rates, still birth rates, infant mortality rates, overall survivorship and stereotypic behaviour (Mason & Veasey, 2010).

1.3.2 Social behaviour and physiology

A large body of work has been conducted in characterising and monitoring both reproductive (Brown, 2000a; Brown et al., 2007, 1999; Proctor et al., 2010a) and stress (Brown et al., 2010; Fanson et al., 2014; Foley et al., 2001; Gobush et al., 2008a; Menargues et al., 2012) hormone secretion in elephants (both captive and wild) under different conditions. Studies of captive elephants have shown different causes for stress, mainly focusing on the effects of changes in herd composition and management practices (Edwards et al., 2016; Menargues et al., 2008; Schmid et al., 2001; Wilson et al., 2004b). In general, research has found that elephants' basal cortisol levels have increased in response to perceived stressors However the individual variation and small sample sizes give inconsistent results between zoos (Edwards et al., 2016; Schmid et al., 2001; Wilson et al., 2004b). On the other hand, elephants display seasonal GC secretion, with concentrations elevating during dry seasons in African elephants (Foley et al., 2001; Gobush et al., 2008b) and the monsoon seasons in Asian populations (Mumby et al., 2015). Reported findings show that differences in age and sex exist, with younger animals secreting lower average concentrations than adults (Vijayakrishnan et al., 2018) . Males have been recorded to have higher GC concentrations on average and further elevations have been linked to musth and male-only group living (Kumar et al., 2014; Vijayakrishnan et al., 2018). The social structure of wild elephants has also been documented to be linked with their physiology. Interestingly, Foley et al 2000 found a significant relationship between group size and average cortisol concentrations. Lower ranking individuals in larger herds experienced higher levels of glucocorticoid levels (Foley et al., 2001). The presence of close kin within a herd has also been linked to reduced glucocorticoid secretion – even in times of high risk (Gobush et al., 2008a). Advances in zoo endocrinology techniques have led to the validation of many of these findings in captive elephants (Brown, 2000a; Brown et al., 2010; Grand et al., 2012; Menargues et al., 2008). Captive elephants have also shown diurnal and monthly variations in GC secretion, with studies on populations in the northern hemisphere reporting markedly elevated concentrations between May and October (Brown et al., 2010; Menargues et al., 2012). Investigations have also been conducted to link the correlation between individual personality ratings and cortisol secretions (Grand et al., 2012) and the effect of social rank and cortisol on female reproduction (Proctor et al., 2010b). However, during pregnancy, glucocorticoid secretion remains low whilst elevated progesterone levels maintain

the pregnancy (Fanson et al., 2014). Chronic elevated secretion of GC during pregnancy is of great concern in captive elephant breeding programs and the links between social stressors and reproductive health are needed (Brown, 2000a; Freeman et al., 2010).

1.4 Thesis Aims and Hypotheses

In order to investigate the significance of social behaviour for captive elephant welfare, the aim of this study is to quantify the social bonds of captive Asian elephants in UK zoos and to determine if there is a relationship between major social events - such as deaths, births, and the removal or introduction of individuals - and other welfare indicators, such as individual adrenal and reproductive endocrinology. Behavioural data collected during this study will be used to explore day and night-time social networks of zoo elephants. Behavioural data will also be used to investigate variation in social relationships over time and during specific life events and analysed in conjunction with elephant adrenal and reproductive endocrinology. I aim to use evidence-based research to help institutions understand the existing social bonds within their herds, and in response develop management practices that promote healthy social behaviour and a sustainable herd. This in turn will help institutions determine factors affecting optimal herd composition and stability. It is hoped that this project will reveal possible benefits of housing elephants in appropriate social groups. I hope that if benefits are identified, recommendations can then be made for institutions for how they manage and house elephant herds.

Chapter 2:

The purpose of this chapter is to test data collection methods of social behaviour for use in captive elephant management. Whilst simple methods are used for raw data collection, I use social network analyses to quantify bond strength and social position within two elephant groups. This study also tests a data collection protocol that is compatible with the management routine of an elephant keeper. The aims of Chapter 2 are therefore to:

- Use social network analysis to quantify and characterise zoo elephant social bonds. I will quantify social metrics of bond strength and centrality from simple observational data collections.
- Use social network analysis methods to characterise individual sociality and key members of the group. As found in the wild, I predict the strongest bonds will be between mother-calf dyads and related individuals
- 3. Monitor changes in social network structure over time and investigate responses to birth events. Whilst seasonal changes in sociality are well documented in elephants, these changes are linked to seasonality of food availability. Therefore, in the captive context where resources are consistent and abundant, I do not expect significant changes. I predict that in response to calf births, existing members will change their bonds in order to accommodate the infants.

Chapter 3:

The purpose of this chapter is to explore the interactions between calves and adult females to determine rates of allomothering behaviour present a captive breeding herd. I aim to:

- Observe the rate of maternal and allomaternal behaviours of an *ex situ* breeding elephant herd. Outside of the mother-calf dyad, I expect to find increased rates of allomaternal behaviours between calves and their adult relatives – especially sisters.
- 2. Characterise the bonds and interactions of calves with non-mothers in the herd, with the aim of identifying the individuals responsible for allomaternal

care. I expect that close relatives will interact more frequently with calves compared to non-relatives.

Determine the factors that influence female investment in alloparental care.
 I predict that degree of relatedness between calf and non-mother will be an important factor influencing alloparental care.

Chapter 4:

There have been a number of zoos that have commenced longitudinal studies on night-time behaviours of their elephant herds. This was initially to monitor sleep quality in response to improvements on enclosure design and management changes. Data has now been collected on the effect of social behaviour on sleep quality. The use of CCTV footage allows for keepers to store and revisit footage at convenient times that do not impede on their daily management schedules. Therefore, the aims of this study are to:

- Characterise and explore the night-time network structure of two zoo elephant herds using social network metrics.
- Investigate if degree of relatedness, age of difference between dyads, and number of years housed together, determine the strength of night-time associations. As observed in daytime bonds, I predict that relatedness will be a predictor of bond strength between sleeping partners
- Investigate the stability of night-time networks over time, looking at the monthly networks of each herd, in order to test if night-time social patterns are a reliable method for longitudinal monitoring.
- Investigate the relationship between social position and average amount of sleep per night.
- 5. Test whether night-time networks reflect day-time networks as a zoo management tool.

Chapter 5:

Using regularly collected faecal samples at Chester Zoo, this study aims to assess the relationship between elephant sociality and glucocorticoid secretion. In this chapter, I quantify individual faecal glucocorticoid secretion in response to social and management events. I also explore the relationship between sociality, adrenal activity and reproductive endocrinology. The aims of Chapter 5 are to:

- Explore the faecal glucocorticoid profiles of captive elephants and to investigate fluctuations in faecal corticosterone levels over time. I predict that longitudinal profiles of GC concentrations will have a seasonal pattern, and that longitudinal profiles of GC concentrations will show responses to particular social events that have occurred over time.
- Determine whether an individual's glucocorticoid levels reflect its bond strength and social position, by assessing the magnitude of individual GC secretion in response to social events. I predict that GC secretion will be significantly related to individual social position and bond strengths.
- 3. Finally, using faecal progesterone levels, I aim to explore relationships between social bond strength, adrenal activity and reproductive health.

Chapter 6:

The aim of this study is to conduct a broad investigation of how social bonds may impact on the welfare of captive Asian elephants in European zoos – in particular, calf rearing success. I used historical and current records from the Zoological Information Management Software (ZIMS) database to collect data on 93 breeding female elephants in European zoo collections. Data were collected on each female regarding it history of movement between institutions, calf rearing and herd mates. In this chapter I aim to:

- Quantify variation in the rearing success of zoo elephants in breeding groups, as it pertains to their sociality and herd stability. I predict that females that experience fewer management transfers and fewer movements between zoos will have better opportunities to rear calves successfully to over 3 years old.
- 2. Test for relationships between herd composition and rearing success for Asian elephants in UK and wider European zoological collections, using historic and current management data. I expect to find that females housed with family members and familiar herd mates have better rearing outcomes than those that are housed with unfamiliar individuals.
- 3. Assess the effect of having relatives present and the number of inter-zoo transfers on reproductive rate, calf rearing success and longevity of female Asian elephants. I expect reproductive rate to be reduced by increased inter-zoo transfers (this analysis is performed using only individuals where breeding bull presence within the herd is confirmed). I also predict that female rearing success and longevity will be greatly improved when housed with relatives or former herd mates.

Chapter 2: The social dynamics of captive Asian elephants (*Elephas maximus*)

2.1 Abstract

In the wild, elephants form strong bonds with maternal relatives, with the smallest family unit being the mother-calf dyad, and extending to sisters, aunts and grandmothers. Forming close bonds is also crucial for the social development and wellbeing of elephants. A report published on the welfare, housing and husbandry of elephants in UK zoos identified that the social dynamics of captive elephants may have important consequences for their overall welfare. Social network analysis methods are increasingly being used to visualise relationships within captive groups for research purposes, but the data may also prove useful in the management of zoo species. The aims of this study were 1) to use well known methods of social network analysis to quantify and characterise zoo elephant social bonds, 2) to use social network analysis methods to characterise individual sociality and key members of the group, and 3) to monitor changes in social network structure over time by investigating network changes in response to birth events and over months. Our results showed that similar to their wild counterparts, zoo elephants formed strong bonds with relatives. Older, matriarchal females and calves were the most central and were key figures in the zoo herd structure. However, strong bonds could also be formed between non-related individuals. Although association strengths varied over time, elephants preferred partners remained consistent. Furthermore, females experienced significant decrease in bond strength in response to birth events. This study successfully demonstrated that social network analysis can provide useful data for monitoring the wellbeing of captive herds of elephants and methodology can be adapted and utilised to fit the routines of keeping staff.

2.2 Background

The complexities and intricacies of animal social structure has been well documented in a range of species including non-human primates (Langergraber et al., 2009; Pepper et al., 1999; Silk et al., 2006a, 2006b), cetaceans (Whitehead and Arnbom, 1987), and social carnivores (De Villiers et al., 2003; Smith et al., 2011). Animal social structure can briefly be described as the interactions and the association between conspecifics (Whitehead, 2008a). Studies on social structure are able to capture information on the intricacies of individual behaviour, and how that shapes the wider population structure, whilst also considering the effects of factors such as ecology, sexual selection, and kin selection on social behaviour (Hamilton, 1963; Maynard Smith, 1964; Whitehead, 2008a). The social structure of wild elephants has been well documented in both the African and Asian species (Archie et al., 2006b; Moss et al., 2011; T. N. C. Vidya and Sukumar, 2005; Wittemyer et al., 2007; Wittemyer and Getz, 2007). Whilst there are subtle differences between the two species, both African and Asian elephant species are highly social, living in multigenerational complex social groups in the wild (Archie et al., 2006b; Sukumar, 2003; T. N. C. Vidya and Sukumar, 2005; Wittemyer et al., 2007). In these groups, females form long lasting bonds with their maternal relatives; bonds crucial not only for herd survival but also for an individual's social development and reproductive success (Archie et al., 2006b; Lee, 1987; McComb et al., 2006). The most basic social unit in the elephant social structure is the mothercalf dyad and core family groups contain 8 - 20 adult daughters, sisters and aunts, with the Asian species tending to have fewer group members than the African species (Moss et al., 2011; Sukumar, 2003). Elephant social structure follows a fission-fusion structure driven by seasonal availability of resources. The benefits of cooperation amongst a group of related female elephants include group rearing and protection of young, sharing and defence of resources, and the passing of social and ecological information to the next generation (Archie et al., 2006b; Lee, 1987; Mccomb et al., 2001; Schulte, 2000; Whilde and Marples, 2012). All of these

benefits have also been documented in other social mammals including non-human primates (Seyfarth et al., 2014; Silk et al., 2010b, 2010a, 2006a, 2003).

With respect to elephant conservation, it is becoming more apparent that the social needs of the species must be considered seriously, especially in zoos (Rees, 2003). Thus, it is important to understand and add to what has been previously documented on elephant social behaviour and herd structure. The purpose of measuring the bonds of captive elephants in this project is to understand both individual sociality and the stability of captive herds. Based on the known complexities of herds in the wild, zoo governing bodies are now raising questions as how to better address the social needs of captive elephants, and how social behaviour may be linked to the overall welfare of the species in captivity (Harris et al., 2008; Rees, 2003; Veasey, 2006). Captive herds most often differ from wild populations in size, age class, and herd stability. Zoos have also often only housed one elephant or groups of no more than three individuals (Clubb and Mason, 2002; Evans and Harris, 2008; Rees, 2009), whilst wild populations have a fission-fusion structure where multiple core family groups of tens of individuals congregate together and separate regularly (Smith et al., 2011; Wittemyer and Getz, 2007). On average, zoo herds consist of one or two age classes – usually adults as opposed to the multiple generations observed in wild populations (Clubb and Mason, 2002; Schulte, 2000). Although captive elephants may not require all the defensive and ecological knowledge that wild populations share, older females have the potential to pass down crucial species-specific behaviour. This is especially true for learned socio-sexual and maternal behaviours (Lee, 1987; Rees, 2009). A herd structure with overlapping generations promotes skills such as allomothering, maternal care, and group defence to be experienced and taught by all herd members (Lee, 1987; Lee and Moss, 2014; Mccomb et al., 2001). Finally, unlike their wild counterparts, captive elephants are frequently moved between institutions for management and breeding reasons. This type of movement is uncharacteristic for a herd and may have serious welfare consequences (Clubb and Mason, 2002; Lee,

1987; Schulte, 2000; Whilde and Marples, 2012). It has been argued that the impact of moving elephants between facilities may include breaking established bonds, disrupting social development, and increased expression of stress-related behaviours (Clubb and Mason, 2002). Introducing new individuals into a stable group may also have the potential to disrupt the existing social structure and lead to changes in physiology and behaviour (Clubb and Mason, 2002). Being able to monitor the quality of bonds the captive elephants make with their herd mates should therefore help to better understand the impacts of such changes on herd structure, physiology and overall welfare.

As zoos continue to increase the number of elephants they house, being able to monitor the sociality of their elephants and the stability of their herd in a measurable way will allow animal caretakers to ensure the social welfare of their animals is catered to. In this study the aim is to; 1) use a relatively simple method of quantifying the social bonds and herd structure of zoo elephants, 2) use social network analysis methods to characterise individual sociality and key members of the group, and 3) monitor potential changes in social network structure over time. The use of simple methods such as these could be developed for use as part of management practices by zoo staff in their regular monitoring of the elephants' welfare. The inclusion of the Dublin Zoo herd allows us to test this hypothesis by data collection being led by a member of the elephant keeping team. We predict that simple measures of association will reveal the most important bonds within zoo elephant herds are between family members, especially the mother-calf bond as found in wild populations (Archie et al., 2006b; Lee and Moss, 2014; T. N. C. Vidya and Sukumar, 2005). In the case of unrelated elephants in a herd, we predict that these individuals will bond with their age-mates or herd mates with whom they have been housed for the longest (Kurt and Mar, 1996).

2.3 Methods

2.3.1 Sample populations

Research was conducted on elephant herds at two members of the British and Irish Association of Zoos and Aquariums (BIAZA), Chester Zoo and Dublin Zoo (see Appendices 1.1 and 1.2). These zoos were selected for this study due to their similar management and husbandry methods. Both hold Asian elephants (Elephas maximus) and work using a protected-contact management strategy (BIAZA, 2010), to ensure the safety of both keeper and animal during husbandry and training. Both zoos hold breeding herds, with bull elephants that are mixed regularly during the daytime. At the beginning of this study, Chester Zoo (CZ) housed 6 Asian elephants: 4 related females, 1 unrelated female, and an adolescent bull elephant (Figure 2.3.1.1a). During this study, three additional calves were born, however data collected on these calves were not included in this study due too few data points. . All calves in this herd were fathered by the bull present in the herd. The elephants at Chester Zoo are housed in an enclosure that is divided into two outdoor paddocks – the Main paddock $(5,490m^2)$ and the Bull paddock $(530m^2)$; and two indoor pens – the Bull pen (415m²) and main house (985m²). The main paddock is a large outdoor area containing a pool (300m²), mud wallow, different feeding opportunities, and different environmental features and terrain all aimed at providing the herd with a naturalistic and stimulating habitat. Whilst keepers begin daily husbandry and management around 07:00, the herd, including the bull, is released into the main paddock around 10:00 at the zoo's opening time. From 10:00 until early afternoon the bull is mixed in the main paddock with the family group, and from early afternoon onwards, the bull is moved into the bull paddock. The elephants are brought back indoors at the zoo's closing time to receive routine health checks, after which they have access to both indoor and outdoor areas for the rest of night – the bull in the bull area and the family group in the main pen and

paddock (this part of the management routine was implemented in the summer of 2016).

At the time of data collection, Dublin Zoo (DZ) housed 12 Asian elephants: 1 breeding bull elephant and a breeding herd consisting of 11 related individuals of varying ages. Figure 2.3.1.1 (b) shows that the breeding herd contains two family groups that originate from two sisters that have both bred successfully at Dublin Zoo. During the course of the study period the bull was housed separately from the family group for reproductive management purposes and was therefore not included in this study. This bull was father to all calves present in the herd at the time of the study. The herd is housed in a habitat consisting of two large outdoor areas – main herd paddock (5000m²) and the bull paddock (2800m²). Similarly, to that of Chester Zoo, the Dublin Zoo main paddock is a large outdoor area containing a pool, mud wallow, different feeding opportunities, and different environmental features and terrain all aimed at providing the herd with a naturalistic and stimulating habitat. Although smaller, the bull paddock also included a pool and a variety of enrichment features. Indoors, the cow house includes an indoor section (425 m²) and an attached outdoor kraal (450m²). The bull house is separate from the cow house $(200m^2)$. The elephants have 24-hour access to their outdoor areas unless poor weather conditions or management requires that they be restricted to their indoor habitats. The Dublin Zoo elephant keeping team begin their daily husbandry and management routine from 08:30 onwards. The bull is released into the separate outdoor habitat at 09:30am, whilst the females and calves receive their footcare and elephant endotheliotropic herpes virus (EEHV) preventative training during this time. The females and calves are released into their outdoor area (weather dependent) from 10:30 – 15:00, during zoo opening times. Around 15:30, all animals are returned to indoors, and are given access to both indoor and outdoor areas overnight.



Figure2.3.1.1. The breeding herds of Chester Zoo (a) and Dublin Zoo (b). Both herds consist of adult cows and their offspring. Male offspring are indicated with a dark border, and females are indicated with no border. Both zoos hold breeding bulls that regularly mix with females and calves, however during the evening the bulls are housed separate from the rest of the herd.

2.3.2 Data collection

In order to measure and understand the strength and stability of elephant bonds in captivity, observational data were collected for two elephant herds from both Chester Zoo and Dublin Zoo (Appendix 1.1). Two years of data were collected on the herd housed at Chester Zoo, between February 2016 and March 2018. At Chester Zoo, observational data were collected from February 2016 to March 2018. The herd was observed on an average of 3 times a week, and observation periods were between 1 and 2 hours long, at varied times of the day during the zoo's opening hours (10:00 – 16:00 in the winter; 10:00 – 18:00 in the summer). Data collection during these times ensured that the animals' most natural associations were being recorded, as training and husbandry routine disturbance is minimised during zoo opening hours. Instantaneous scan sampling of the herd was performed at 10-minute intervals, in which the nearest neighbours of all herd members were recorded (Altmann, 1974; Martin and Bateson, 1993). Individuals considered to be an elephant's nearest neighbours and to be associating if they were within two body-lengths of one another (Appendix 1.3).

Observational data on the Dublin Zoo herd were collected for 14 weeks between 11 April and 26 August 2018. Data at this zoo were not collected by the primary researcher, but by the elephant keeping team. This decision was made with the intension of testing the validity of integrating data collection into daily keeper management and husbandry routines. Data collection methods were conducted similarly to those used on the Chester Zoo herd. Observations were also conducted on an average of three times per week. Adjustments were made to the method to take into account the daily management and husbandry schedule of the keeper; therefore, unlike Chester Zoo where data were collected during 1 to 2-hour sessions by the primary researcher, keepers at Dublin zoo collected data once an hour

throughout the course of the day. Using this method, at least 7 – 14 data points were recorded, equalling the same number of data points that would be collected in a 1 to 2-hour focal sampling observation period. Also taking into account an elephant keeper's daily workload, it was not practical to collect continuous data on social interactions between the elephants and therefore interactions during the day were not collected for this herd. To focus on the stability of the main breeding herd social network, bull elephants from both study groups were excluded from our data analysis. The calves born during this study period in the Chester Zoo herd were also excluded, and only the resident females CZHW1, CZHW2, CHW3, CZHW4 and CZM1 were included. All cows and calves in the Dublin Zoo herd were included in data analysis.

2.3.3 Measuring herd structure and individual sociality

To measure the sociality of each elephant and its position within its herd, we have used social network analysis techniques. In behavioural ecology, social network analysis is a common method to investigate the complex relationships and structures that arise due to individuals sharing the same ecological space and interacting with one another (Croft et al., 2008; Wey et al., 2008; Whitehead, 1997). Using complex social mechanisms such as mating, grooming, feeding and dominance behaviours, social network analysis provides thorough information on both individual social position and group structure (Croft et al., 2008; Whitehead, 2008a). This tool is not only able to quantify direct relationships between individuals, it also captures the interactions between social structure and biological factors such as information and gene flow, disease spread (VanderWaal et al., 2014), and ecological changes in dynamics (Silva et al., 2011b). In social networks, individuals are represented as nodes and their interactions with others are represented as ties – or edges – connecting them. The edges between nodes can either be binary or weighted. Weighted edges are used to indicate the strength of interaction or association between individuals. Association indices are used to

convert observed associations or interactions between group members into values that provide the weight to network edges.

In this study the simple ratio index (SRI) was used to quantify the bond strength between elephants and add weight to herd network edges. Association indices, such as the SRI, measure the frequency that two individuals are observed to be in close proximity of one another – essentially how often two individual associate (Bejder et al., 1998; Cairns and Schwager, 1987; Ginsberg and Young, 1992; Martin and Bateson, 1993). There are a variety of association indices that are used, but the Simple Ratio Index is most often used when monitoring animals in a captive setting (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Whitehead, 2008b). The Simple Ratio Index is calculated as:

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

Where , *x* represents the number of times individuals A and B are observed together; y_{AB} is the number of observation periods in which A and B are identified but are in different groups not associating with one another; y_A represents the number of observations in which only individual A is observed; and y_B is the number of observations periods where only individual B is observed (Cairns and Schwager, 1987; Ginsberg and Young, 1992). The values of the SRI range from $0 \rightarrow \infty$, with the higher values representing dyads that associate the most, and lower values representing dyads that associate the least. Whilst this index has been recommended for its simplicity and unbiased estimates of social bonds (Whitehead, 2008b), Ginsberg and Young (1992) note that it is rarely used because it can be time consuming when used on large data sets. De Silva *et al* (2011) used Simple Ratio Index values to study seasonal changes in the association patterns of wild Asian elephants. The simple ratio index (SRI) and other variations of this index have been used in studies of wild African and Asian elephants as a tool for constructing large

herd networks and to monitor seasonal changes in association over time (Silva et al., 2011a; Wittemyer et al., 2007).

The simple ratio index values were calculated to characterise the strength of association between dyads. Then, in order to understand individual, or node-level, position within the herd network we used three social network measures of social centrality. Firstly, to measure an individual's gregariousness – its tendency to form bonds with group members – the weighted degree was calculated for each herd member (Pepper et al., 1999; Whitehead, 2008b). The weighted degree is the total of all edge weights connected to as selected node (Croft et al., 2008; Whitehead, 2008b). Next, the weighted betweenness, which is the number of shortest paths that flow through a single individual (Farine and Whitehead, 2015a). This is a measure of an individual's tendency to move between subgroups. A high weighted betweenness indicates a high tendency to switch between subgroups, and conversely a low weighted betweenness reflects a higher likelihood of remaining in the same subgroup. An individual's weighted betweenness also measures how important that individual is in connecting different parts of the social network (Farine and Whitehead, 2015a; Whitehead, 2008a). The last centrality measure calculated was the eigenvector centrality: an individual's connectedness based on its neighbours' connectedness (Farine and Whitehead, 2015a; Newman, 2004). This measure represents the gregariousness of an individual's associates and a high value may be due to an individual having many connections or from being connected with a few individuals with a high degree, or a combination of the two (Farine and Whitehead, 2015a; Newman, 2004; Whitehead, 2008a). It is a useful measure for identifying potentially "key" members that serve as propagators of information and social hubs (Farine and Whitehead, 2015a). Due to the small group size of the Chester Zoo herd, eigenvector and betweenness centralities were not measured in addition to weighted degree; however, they were used on the larger Dublin Zoo herd network.

2.3.4 Associations over time

To investigate the impacts of major life events on the stability of the existing herd structure, as well as observing monthly patterns of association. Firstly, we used the CZ herd network to investigate the effect of birth events on herd stability. We conducted a comparison between the herd's social network 4 months before (September – December 2016) and 4 months after (January – April 2017) the calves were born: CZHW5 on 16 December 2016 and CZHW6 on 17 January 2017. The time period chosen represent periods where no birth-event management protocols were in place; mainly separating the unrelated female, CZM1, overnight from the rest of the herd for the safety of the calves. In order to investigate the significance of these birth events, the subsets of observations "Before" and "After" the birth events were created. To assess the effect of the birth event on resident female associations with one another, we excluded the new-born calves from the "Before" and "After" analyses. Next, CZ data were subset into 8 non-consecutive months across the year of 2016 (February – November) to observe monthly patterns of association. Similarly, the DZ herd data set was subset into 5 consecutive months from April to August 2018. To avoid any sampling bias in either observation period, the data were standardised ensuring that there was an equal number of data points in either time period. Data points were randomly removed from either time period to ensure that this was the case.

2.3.5 Statistical analysis

Herd networks from the data collected were generated and analysed using the R package *asnipe* (Farine, 2018). Using *asnipe* function "get_group_by_individual", the observed nearest-neighbour data were converted into a group by individual matrix which contains each herd member in the column and the association groups in which they were observed in the rows (Farine, 2013).
Once all observed associations were collated in the group by individual matrix, weighted social networks could be generated by using the "get network" function. Using this function, simple ratio index values could be calculated for each dyad so that a weighted social network of the herd was produced. To determine whether the observed herd network structures were significantly different from random, data stream permutations were performed following the method described by Farine (2013) using the *asnipe* function, "network permuation". The data stream permutation method performs swaps of individuals between groups, recalculating the network after each swap. This creates a set of randomised matrices - or null models – the number of which corresponds to the number of permutations performed; for this study permutations were performed 4000 times for each analysis (Bejder et al., 1998; Farine, 2013). In this study, since all individuals were part of one herd, the 'groups' individuals will be swapped between are observations of nearest neighbours. A P value was calculated by comparing the observed network coefficients to the distribution of network coefficients estimated from each of the 4000 permutations. Using this method, swaps could be restricted in the permutations to different time parameters, in days, to observe the stability of network structures over time. To test for non-randomness and avoid biases in further statistical analysis, all node-level metrics were compared to permuted networks. All node-level metrics were calculated using the sna package in R (Butts, 2016).

To test for effects of biological attributes including age, month and relatedness on the association patterns observed in the elephant herds, permuted Two-Sample t-tests and Mantel correlation tests were conducted. To compare weighted degree values before and after the CZ birth events, permuted t-tests were performed using the function "perm.test" from the R package, *browman* (Broman and Broman, 2019). The function "perm.test" performs a pairwise t-test was performed to obtain the *t* statistic from the observed data. The observed *t* statistic was then compared to *t* statistics obtained from 4000 permutations. A p-

value is obtained from this comparison, with significant p-values indicating that the observed t statistic was significantly greater than the permutations. The Mantel test is used especially to examine the correlation between two similarity or dissimilarity matrices (Croft et al., 2008; Mantel, 1967; Whitehead, 2008b). Calculated using the "mantel" function in the R package, vegan (Oksanen et al., 2018), matrices containing herd associations were compared with matrices containing herd relatedness coefficients (r), and a correlation coefficient r between the two matrices is calculated. The test randomizes the individuals in one matrix, calculating the correlation coefficient (r) for each permuted matrix. Statistical significance is determined by comparing the true value of r with the distribution of the set of permuted r values (Mantel, 1967; Whitehead, 2008a). If the Mantel correlation coefficient r > 0, this indicates a correlation between the two matrices; if r < 0 there is no correlation between the two matrices (Whitehead, 2008a). To assess monthly patterns of association and sociality, Mantel tests were used to test the similarity of SRI matrices between months. A linear mixed effects model was constructed using the *Ime4* package (Bates et al., 2015) to compare weighted degree measures over time, with the month as a fixed effect and elephant ID as the random effect: Imer(weighted degree ~ Month + (1|ID, = data). Statistical significance (*P_{rand}*) was determined by comparing the model coefficients fitted to the observed data with coefficients generated from 1000 network permutations.

2.4 Results

2.4.1 Herd associations and structure

First, association matrices were created for both herds, calculating the simple ratio index for all present dyads (Appendix 1.4). As predicted, in both herds the individuals that were observed most often together, and thus had the strongest bonds, were the mother-calf dyads as shown in Figures 2.4.1.1 and 2.4.1.2. As well as the mother-calf dyad, it can be seen in Figure 2.4.1.1 that associations in the CZ

herd were also strongest between family members (Mean SRI values: CZHW1 = 0.368, CZHW2 = 0.320, CZHW4 = 0.376). Despite this, the unrelated female CZM1 maintained moderate associations with the other females and shared a strong tie with the individual CZHW1 (SRI = 0.405). Similarly, mother-calf dyads also appeared to be the strongest ties in the DZ herd (Figure 2.4.1.2a). Although, interestingly, one mother-calf dyad in the herd shared an uncharacteristically weak bond compared to other similar dyads (DZB1-DZB4: SRI = 0.076). Amongst the adult females, the strongest bond was shared between the two oldest females in the herd, DZB1 and DZY1 (SRI = 0.272). It is important to note that these females are sisters. The weakest bond shared amongst the adult females was between DZB1 and DZY2, who were aunt and niece (SRI = 0.058).

Node metrics were calculated and used to determine whether the observed networks were significantly different from random. After comparison to the distribution of permuted networks, all measures of centrality were found to be significantly different from random (p < 0.001(Appendix 1.5). First, we calculated the weighted degree to investigate individual gregariousness and tendency to associated with herd mates (See Appendix 1.6 for a measures). Looking at the CZ herd first, we found that the calf had the highest weighted degree ($S_1 = 1.884$) and thus the highest tendency to form associations, followed by its mother and sister. Contrastingly, the female CZHW3 was found to have the lowest weighted degree in $(S_1 = 1.18)$, suggesting that it was less gregarious than its relatives. In the larger DZ herd, calves, especially those younger than 3 years old, had the highest weighted degree values (average S_i = 1.542), whilst adult females had lower values. Amongst the adult females, the two matriarchal females were more gregarious (DZB1: S_i = 1.412; DZY1: $S_i = 1.646$). Next, focusing on the DZ group, the weighted betweenness and eigenvector centralities were measured. In this herd, the highest betweenness centrality scores were held by two infant calves (DZY2b = 10; DZY4= 9), indicating that these two individuals were the intermediates of the most paths within the herd (Figure 2.4.1.1b). The lowest betweenness were scores were found between an

adult female (DZB2) and two calves (DZB4 and DZY2a); they all measured a betweenness of 0. High scores of eigenvector centrality were also held by DZY4 ($e_i = 0.354$) and DZY2b ($e_i = 0.326$), as well as one of the older females (DZY1: $e_i = 0.351$).

Relatedness did not correlate significantly with bond strength amongst the females in the CZ herd (Mantel test based on Spearman's rank: r = 0.302, p = 0.233, permutations = 4000). Conversely, in the DZ herd a positive correlation was found between an elephant's bond strength and relatedness with each of its herd mates (Mantel test based on Spearman's rank: r = 0.361, p = 0.009, permutations = 4000), indicating that stronger bonds were found between elephants that were closely related, whereas weaker bonds were found between elephants more distantly related to each other. However, two females DZY2 and DZB2, shared one of the strongest bonds amongst the adult females (SRI = 0.092) although they were more distantly related. The weaker bonds within the herd were found between females that were distantly related.



Figure 2.4.1.1 The social network of the Chester Zoo elephant herd. These weighted networks were calculated using the simple ratio index. The thickness of the edges (lines) indicate the strength of association between two individuals. Thicker lines represent stronger bonds and thinner lines are weaker bonds. Each node (circles) represent individual herd members, and the colours of each node indicate the adults (orange), juveniles (3 - 5 years old; yellow). The network illustrates that whilst all individuals in the group are connected, the strongest bonds were found between mother-calf dyads.



Figure 2.4.1.2. Social networks of the Dublin Zoo elephant herds. These weighted networks were calculated using the simple ratio index. The thickness of the edges (lines) indicate the strength of association between two individuals. Thicker lines represent stronger bonds and thinner lines are weaker bonds. Each node (circles) represent individual herd members, and the colours of each node indicate the adults (orange), juveniles (3 - 5 years old; yellow), and infants (0-3 years old; blue). Although all individuals in the group are connected, the strongest bonds were found between mother-calf dyads (A). The sparsified network (B) highlights the two individuals with the highest weighted betweenness measures withing the herd.

2.4.2 Associations over time

Chester Zoo

Once individual position in the herd was established, the next step was to understand herd stability and the stability of individuals' bonds over time, investigating the impacts of major life events on the stability of the existing herd structure, as well as the impacts of environmental changes experiences during the seasons. Firstly, changes in bond strength and network metrics "Before" and "After" two birth events were investigated on the Chester Zoo herd. As shown in Figure 2.4.2.1, there was a weakening of existing herd ties after CZHW5 and CZHW6 were born. The birth events proved to decrease in the weighted degree of the resident females significantly (Permuted paired t-test: t (4) = 4.98, p = 0.006). Secondly, we investigated the effect of monthly changes on the associations of the CZ group. To do this, all associations between February and November 2016 were subset per month. Simple ratio measures between herd mates in the February herd network were found to correlate with SRI measures in the July (r = 0.584, p = 0.033), August (r = 0.538, p =0.05) networks (see Appendix 1.7 for full summary). Significant correlations in dyad bond strengths were also found between the April and July networks and September and October networks (Table 2.4.2.1). As illustrated in Figure 2.4.2.2a, variation was found in the individual weighted degree measures. Average weighted degree measures were found to be similar between February (mean S_i = 1.642), May (mean S_i = 1.542) and July (mean S_i = 1.643). Average weighted degree measures in the later months began to decrease with October having the lowest average (mean $S_i = 0.9$). Although some variation was observed, LMM results were not found to be statistically significant (Appendix 1.8).



Figure 2.4.2.1 The social network of Chester Zoo's resident female elephants before two calves (CZHW5, CZHW6) were born (1 September – 14 December 2016), and after the two calves were born (18 January – 19 April 2017). The network edges indicate that after the birth events, the strength of bonds amongst the resident females weakened. A comparison of the individual weighted degree between the two time periods show a significant decrease in the individual weighted degree after the birth of the calves (Paired t-test: t (4) = 4.98, p = 0.006).



Figure 2.4.2.2 Social position patterns were monitored monthly to observe the impact of time and season on herd stability. Monthly measurements of weighted degree CZ data were subset into months between February and November 2016 (A), whilst DZ data were subset between April and August 2018. Weekly measurements of the Weighted Degree, Betweenness Centrality, Eigenvector Centrality and Average Simple Ratio Index score for each elephant.

Table 2.4.2.1 Analysis of captive elephant social bonds overtime to determine the stability of elephant bonds over time, monthly networks calculated using the simple ratio index were correlated with one another using the Mantel test. Significant correlations between monthly networks (in bold) indicate similarity. Correlation coefficient (r) and significance (p < 0.05; based on 1000 network permutations) are provided.

	r	p
Chester Zoo		
February x July	0.584	0.033
February x August	0.538	0.05
April x July	0.438	0.050
September x October	0.575	0.042
Dublin Zoo		
April x May	0.872	0.001
April x June	0.811	0.001
April x July	0.749	0.001
April x August	0.890	0.001
May x June	0.855	0.001
May x July	0.803	0.001
May x August	0.884	0.001
June x July	0.830	0.001
June x August	0.887	0.001
July x August	0.807	0.001

<u>Dublin Zoo</u>

Analysis of social bonds and weighted degree over months was also conducted on the DZ data (Figure 2.4.2.2). Data were subset into 5 consecutive months from April to August 2018. Comparisons between monthly networks found that all monthly networks were positively correlated with one another (Table 2.4.2.1). The weighted degree measured over time shows that whilst there was variation in values each month, particular individuals had consistently high values, whilst others have consistently low weighted degree values. The youngest calves, DZY2B and DZY4, had the highest measures weighted degree for the greatest number of months – 3 out 5 months. Amongst the adults, DZY1 had the highest weighted degree for 4 months. These 3 individuals have the strongest weighted degree in the social network. The individual with the lowest weighted degree for the greatest number of months was the adult female, DZB2; followed by the adult DZB2 and DZB1, DZY2a (1 out of 5 months). The mean weighted degree measures were greatest in April (S_i = 1.67) and June (S_i = 1.57). Then measures declined in July (S_i = 1.27) and August (S_i = 1.29 Again, despite the observed variation, LMM results were not found to be statistically significant (Appendix 1.8).

2.5 Discussion

2.5.1 Female associations and bond strength

A key aim of this study was to apply widely used social network analysis methods to characterize and monitor the social networks of captive elephants. As we predicted, bonds amongst female elephants were strongest with their infant calves, followed by their close maternal relatives, reflecting what has been documented and characterized in wild Asian and African elephant herds (Archie et al., 2006b; Moss et al., 2011; T. N. C. Vidya and Sukumar, 2005; Wittemyer et al., 2007; Wittemyer and Getz, 2007). Observations of wild

family herds report that immature calves under the age of 5 years old remained in close proximity to their mothers (Lee, 1987); similarly we observed that the strongest bonds were between females and their calves aged below 3 years old. Amongst adult females, we found interesting, group-specific patterns in associations. In both herds, adult females had strong ties with individuals most closely related to them. In the DZ herd, there was a significant positive correlation between dyad bond strength (SRI) and maternal relatedness, indicating that bonds were strongest between more related elephants and were weaker as relatedness became more distant. Where all individuals were related, females shared the strongest bonds with those that were most closely related to them, i.e. mothers and siblings, and weaker bonds with individuals less closely related, i.e. cousins, grandmothers, and great relatives. However, in the CZ herd, relatedness was not a statistically significant driver of the observed association patterns. This was mainly due to the herd including an unrelated female, CZM1, that was well integrated in the group. Archie et al (2011) note that although their findings supported that a female elephant's closest relationships were formed with kin, relatedness is not the only determining factor. In fact, if a female is in a group without close kin, they are still able to have close relationships and engage in affiliative and cooperative behaviours with herd mates (Archie et al., 2011). With this in mind, Archie et al (2011) argue that the amount of time individuals spent within 5m proximity of each other was a better predictor of social affiliation and cooperation between individuals. Therefore, the strong bond that CZM1 shared with CZHW1 despite not being related can be attributed to the length of time these females have lived in the same herd (27 years). Thus, whilst we expected herd members to have preferably stronger bonds with their maternal kin (Archie et al., 2006b; Moss et al., 2011; Silk et al., 2010a, 2006a), it is important to consider that for elephants in zoological collections that hold herds containing a mixture of related and non-related females, time spent with conspecifics can be a key driver for developing strong bonds (Gobush et al., 2009; Kurt and Mar, 1996).

It was also important to understand the impact of major life events, such as birth events, on herd stability. Herd stability was assessed before and after two birth events in the Chester Zoo herd, as well as stability over months in a single-year period. Focusing on

the resident females, a significant decrease in association behaviour after the birth of two calves in December 2016 and January 2017 was found. The decrease in association is to be expected as females shifted their time in maternal care and allomaternal care of the new infants. In other words, female bonds weakened as they spent time building bonds with the new calves. Next, the females' bonds were observed monthly – from February to November 2016. Bond strengths appeared to increase during the warmer months (May, July and August), then began to decrease from September to November as temperatures cooled. In the wild, African elephant family units have been known to aggregate during wet seasons and to fission during dryer seasons when resources are scarce (Moss and Lee, 2011a). In contrast, observations of wild Asian elephants have found that during dry periods, family units congregate around common water sources, but disperse into the jungle once the rains come and water is more abundant (Raman Sukumar, 1989; Sukumar, 2003). Although exsitu elephant populations do not have the same seasonal ecological pressures as their wild counterparts, it appears that association rates vary seasonally. With association rates being higher during warmer months and lower during colder months. Such associations could be attributed to extended daylight hours in the summer or shorter daylight hours in the winter. Another factor may be seasonal management practices such as increased time outdoors during the summer, or earlier facility closures during the winter months.

Analysis of the Dublin Zoo herd network over time also showed that bonds correlated with on another across months. This correlation indicated that individuals maintained the same main partners over months (Silva et al., 2011a). When looking at an elephant's top 3 social partners, an elephant's strongest bond generally remained the same for all 5 months, whilst the other 2 positions were held by different individuals over the weeks. Archie *et al* (2006) and Moss and Lee (2011) observed that fission-fusion behaviour between elephant family groups can occur within time scales spanning as hours, days, and weeks, indicating that within long-term associations of a herd of elephants, variations on a daily and weekly scale can be just as important as variations on a monthly or yearly scale. Average associations were highest during April and June and lowest during July and August. Unlike Chester Zoo observations, a decrease in associations were observed during the

warmer months in the Dublin Zoo herd. It is unclear whether this decrease was due to environmental factors or management factors that occurred during this period.

2.5.2 Node metrics and individual social position

In order to characterize an individual's sociality within its respective herd, measures of centrality were used to quantify social position. Initially, each elephant's weighted degree was calculated; this is a measurement of an elephant's tendency to associate, or in other words its gregariousness. In both herds young animals (< 5 years old) had the highest tendency to associate with other herd members. Observations of both wild African and Asian elephants reveal that calves have higher frequency association and frequency rates than adult females (Lee, 1987; Lee and Moss, 2011; Sukumar, 2003). Wild calves and juveniles have also been found to always be in close proximity to their mothers or other family members, especially when very young, making them "firmly embedded in the family social context," (Lee and Moss, 2011). Amongst the adult females, older, matriarchal individuals were most gregarious (CZ: CZHW1, DZ: DZY1, DZB1). Additionally, when the DZ herd is divided into family units - DZB1 with offspring and DZY1 with offspring -the DZY family generally had higher weighted degree values than the DZB family, indicating that as well as being able to characterise individual gregariousness, gregariousness between different families in larger herds could be compared. The betweenness centrality identified how key an elephant was in connecting subgroups and how likely they would move between subgroups. In the larger Dublin herd, the betweenness centrality varied between individuals. Two young calves had the highest betweenness scores (betweenness = 9 - 10), reflecting that the most association paths went through these individuals. The scores reflect that social cohesion was mainly dependent on the presence of the two calves DZY4 and DZY2b. Their dependency on their mothers and allomothers for care and protection also makes them central within the herd (Lee and Moss, 2011). The matriarchal females of the DZ herd, were also responsible for cohesion in the herd, however not to the extent of the calves. Based on the number of neighbours an individual had and the strength of their

associations with those neighbours, the eigenvector centrality scores reflected a similar centrality pattern as betweenness. The same individuals that had high betweenness scores were also found to have high eigenvector centrality scores. These individuals were not only connected to other highly central individuals, but they were also connected to individuals that were less likely to associate with each other. More simply put, gregarious individuals encouraged social cohesion between less gregarious herd mates, highlighting the key role that calves and older females play in encouraging social cohesion and association between other group members. In larger herds such as the one at Dublin Zoo, measuring weighted betweenness can identify individuals that play a key role in maintaining group cohesion (Brent, 2015; Snijders et al., 2017; Wey et al., 2008). Especially in decisions regarding the removal of an individual from a herd, betweenness scores can help predict whether this removal would lead to lower association rates between remaining group members, or have no effect at all (Lusseau and Newman, 2004; Snijders et al., 2017; Wey et al., 2008). Whilst eigenvector centrality scores can tell us whether individuals are central or peripheral based on connectedness of their partners. In Chiyo et al.'s (2011) study of wild male elephant sociality, high eigenvector centralities positively correlated with age, suggesting that older bulls were influential members of the herd as they were connected to both younger individuals and other old bulls. In our study, one adult female (DZY1) and two calves held the highest scores; it is possible this adult female represented an influential figure for social information within the herd. However, unlike the observations in Chiyo et al. (2011), the impacts of such individuals on herd survival and repositories of social information in captive herds is still to be clearly defined.

2.5.3 Methods for measuring bonds in captive elephants

A key aim of this study was to use existing social network analysis tools used in wild elephant populations to quantify captive elephant networks (Archie et al., 2006b; Chiyo et al., 2011; Evans and Harris, 2008; Nandini et al., 2017; Pinter-Wollman et al., 2009; Silva et al., 2011a). When simple observational data collection methods are used over long periods of time, robust analyses can be conducted to quantify and characterize captive herd social

networks. Data could be captured to measure group cohesion, herd stability over time and individual social position. Association index measures of wild elephants have ranged from 0.011 – 0.017 in large population analyses (Nandini et al., 2017; Silva et al., 2011a) and 0.028 – 0.993 in small core group analyses (Archie et al., 2006b; Chiyo et al., 2011; Evans and Harris, 2008). In this study mean SRI values were within the range of values found amongst core groups of 1-17 individuals (Chester Zoo SRI: 0.237 - 0.376; Dublin Zoo SRI: 0.108 - 0.149) (Archie et al., 2011; Chiyo et al., 2011; Evans and Harris, 2008). In captivity, association indices such as the SRI can help inform animal caretakers of each animal's close partners and whether these relationships persist over time or are temporary (Rose and Croft, 2015). Weighted degree, betweenness, and eigenvector centrality have also been used to determine the importance of individuals within wild elephant societies and changes in metrics over time have also been studied (Chiyo et al., 2011; Goldenberg et al., 2014; Pinter-Wollman et al., 2009). Individual weighted degree was calculated for both herds, however due to the small size of the Chester Zoo herd, betweenness and eigenvector centralities were not appropriate. On the other hand, in the larger Dublin Zoo herd, wellconnected and central individuals could be identified using all three metrics. Thus, it is important to consider the effect of group size on metric selection in captive zoo populations. In larger groups, more detailed metrics may be used, whilst smaller groups the use of only one centrality metrics may be enough (Webber et al., 2020). Alternatively, other metrics such as lagged rate of association and time ordered networks would prove to be more valuable to monitor the persistence of bonds over time (Blonder et al., 2012; Whitehead, 2008a, 1995). Although comparing social networks of different populations can pose a challenge and are often incomparable (Castles et al., 2014; Croft et al., 2008), we aimed used replicable and modifiable methods to collect data on two captive elephant groups that had similar husbandry and welfare practices. Simple techniques such as these can be adopted by elephant management teams to monitor herd stability over time and observe effects of herd composition and management changes on all or specific individuals. In the case of data collection at Dublin Zoo, the aim was to test the "user-friendliness" of collecting regular association data for animal caretakers. Although modifications of the methods were made to suit the keeper's management schedule, the networks produced

was still found to be significantly different from random upon analysis, and temporal patterns could be observed. However, we acknowledge that it is important to further develop these techniques until methods are standardised, in order to compare networks between zoo collections (Castles et al., 2014; Rose and Croft, 2015).

2.6 Conclusions

In our study we found that although elephants preferred to have strong relationships with close relatives, when kin are not present females are capable of forming strong and stable bonds with non-relatives. However, non-relatives require time to form stable and long-lasting bonds (Gobush et al., 2008b; Kurt and Mar, 1996). In the *ex-situ* context, where elephants are often housed with non-relatives and age mates, it is important to know that strong bonds can develop between non-related individuals. In these situations, the key for success is ample time for individuals to familiarize, associate and form bonds with one another. Calves were the most social individuals in both herds; this is attributed to calves being at a crucial stage in their exploratory and social learning (Lee and Moss, 2011). The presence of calves within a herd also changes how females associate with one another. As found in the Chester Zoo herd, the birth events led to females redirecting their associations with one another toward the new calves. Cooperation between mothers and allomothers in the care of young elephants increases cooperation and cohesion between herd members, as well as increases the survival of young (Lee, 1987; Lee and Moss, 2011).

Other key herd members were the eldest related females in each herd. Matriarchal females in elephant societies are known to be repositories of social and ecological knowledge, and have experience navigating social complexities such as infant care and protection (Lee and Moss, 2011; Mccomb et al., 2001). The presence of older related females not only means that younger elephants have a reference point for social learning, but they also have an experienced leader that will maintain group cooperation and share specific skills such as maternal care and group defence (McComb *et al.*, 2001). For

conservation purposes, it is important for such females to be present in the herd for successful social development and reproductive success. Gobush *et al* (2008) noted that the absence of older experienced females can lead to the breakdown of a herd's ability to defend itself, find crucial food resources and cooperatively rear young. If elephant herds are to thrive in *ex-situ* or managed *in-situ* facilities, it is imperative that these herds be multigenerational to ensure that members that are important to social development and cohesion are present to encourage associations between more peripheral individuals. Moreover, although the bull males were not the main focus of this study, the social development and exposure to male-male bonds must also be considered. Although the bonds of bull elephants with females are casual (Sukumar, 2003), they form bonds with other bulls with who they associate frequently (Chiyo et al., 2011; Evans and Harris, 2008). Older bulls also play an important role in teaching young males male-specific socio-sexual behaviours crucial to healthy male development (Chiyo et al., 2011; Slotow et al., 2000). Therefore, studies such as this one should also be conducted on all-male ex-situ herds to ensure the rearing and management of healthy bulls.

A look at the elephants' associations over time showed us that captive elephants may also have a cyclic pattern to their associations as found in their wild counterparts, although they may not have the same ecological pressures driving this cyclicity. We also found that associations varied from week to week, thus echoing what was described by Lee and Moss's (2011) findings in wild African elephants. Even in *ex-situ* facilities, elephants appear to be socially flexible, varying their rates of association weekly, to monthly to seasonally. And whilst they are flexible, they still maintain strong bonds with select individuals within in their herd. Understanding the flexibility and consistency of elephant associations is therefore another important key to maintaining high management and welfare standards in *ex-situ* conservation programs.

Chapter 3: Maternal care and allomothering in captive Asian elephants (*Elephas maximus*)

3.1 Abstract

Assistance in care and protection of infants from allomothers has been shown to reduce pressure on mothers and increase the survival of young. Elephants (Loxodonta spp., Elephas spp.) are communal breeders and live in groups of related females that share in the responsibility of rearing and protecting each other's offspring. It is believed that the presence of calves encourages cooperative relationships amongst females in a family group and enhances calf survivorship. In our study of a captive breeding herd our aims are to: 1) observe the rate of maternal and allomaternal behaviours of an ex situ breeding elephant herd, 2) characterise the bonds and interactions of calves with nonmothers in the herd, with the goal of identifying the individuals responsible for allomaternal care, and 3) determine the factors that influence female investment in alloparental care. Our results showed that after interaction between mothers and calves, the highest interactions occurred between calves and their sisters and grandmothers. These individuals were identified to be key allomothering figures. In this herd we found that the determining factor of a female's rate of allomothering was the strength of its bond with the calf's mother, and years spent as herd mates with the calf's mother.

3.2 Background

Allomothering – the care and protection of young by non-mothers, has been found to be beneficial to the survival of offspring of many social mammals. Communal rearing and allomaternal behaviours are found in diverse mammalian species including non-human primates, carnivores, and rodents (Briga et al., 2012; Kohda, 1985; König, 1997). Alloparental care in many non-human primate species is expressed as helpers assisting in the carrying of infants, grooming, play, babysitting, and occasionally suckling (Kohda, 1985; O'Brien and Robinson, 1991). In a review of these, Bales et al. (2000) found that survivorship of callitrichid primate infants is positively correlated with the number of male helpers in the group, rather than the number of females. Wedge-capped capuchin (Cebus olivaceus) and vervet monkey (Cercopithecus aethiops sabaeus) allomothers give mothers the opportunity to leave their infants in order to forage, and guarantee that their young are not left alone (Fairbanks, 1990; O'Brien and Robinson, 1991). In the Rodrigues fruit bat (Pteropus rodricensis), assistance to mothers by helpers has been observed during birth events (Kunz et al., 1994). Kunz et al (1994) observed female Rodrigues fruit bats receive assistance from other females during parturition. These helpers appeared to help stimulate the progress of labour through physical contact with the mother, and also helped prevent the mother and emerging infant from falling (Kunz et al., 1994). In small rodents, allomaternal care can be expressed through nest guarding, grooming, retrieval of young and huddling with pups (Schubert et al., 2009; Stone et al., 2010). Highly social carnivores such as lions (Panthera leo), African painted dogs (Lycaon pitcus), and hyenas (Hyaena brunnea, *Crocuta crocuta*) communally rear the offspring of either the dominant pair or all breeding individuals in the group (Riedman, 1982). Alloparental care in these groups includes allonursing, carrying, sharing food, grooming and protection of young (Riedman, 1982).

Alloparents, often nulliparous or juvenile individuals, may provide care almost equivalent to that of the mother to young that are not their own genetically (König, 1997). Infant care can be costly to a mother by reducing her foraging time, as well as the increases

in energetic output needed to nurse offspring (Moss and Lee, 2011b; Rosenbaum and Gettler, 2018). Assistance in care and protection of infants from non-mothers has been shown to reduce this pressure on mothers and increase the survival of young (Lee and Moss, 2011; O'Brien and Robinson, 1991). Female vervet monkeys ate more food per handful when they allowed allomothers to hold their offspring (Stanford, 1992). With help from allomothers, mothers may minimise the costs of lost foraging time and high lactation demands (Lee and Moss, 2011; Stanford, 1992), and ensure the care and protection of their offspring longer after their infant becomes independent of them (König, 1997; O'Brien and Robinson, 1991), thus increasing offspring survival. The benefits to allomothers have been hypothesised to be increased experience in caring and rearing young, inclusive fitness, and reciprocated care for their own offspring. Prairie voles (*Microtus ochrogaster*) have a higher rate of offspring survival if they have had previous experience alloparenting younger siblings (Stone et al., 2010). Alloparental care is strongly associated with relatedness in many species, and it is thought that this is driven by the indirect benefits of ensuring the survival of kin (Briga et al., 2012; Hawkes, 2004; Maynard Smith, 1964). Stanford (1992) found that female capped langurs (*Presbytis pileate*) were selective in their allomother choice. They observed that mothers often chose to care for each other's young because this allowed them to alternate opportunities to forage without disturbance from their offspring (Stanford, 1992).

Elephants (*Loxodonta spp., Elephas spp.*) are communal breeders and live in groups in which all females give birth and share in the responsibility of rearing and protecting the young in the herd (Lee, 1987; Lee and Moss, 2011; Sukumar, 2003). Allomothering behaviour has been observed to include affiliative, play, comforting and allosuckling behaviours, performed most often by female relatives, nulliparous adolescent females, and occasionally juveniles and unrelated females (Lee, 1987). Maternal and allomothering behaviours are critical skills that female elephants learn from their herd mates through practice and watching older herd members (McComb *et al.*, 2001; Archie, Moss and Alberts, 2006). It is believed that the presence of calves encourages cooperative relationships

amongst females in a family group and enhances calf survivorship (Lee, 1987; Schulte, 2000; Whilde and Marples, 2012). The presence of allomothers in the herd gives mothers the opportunity to forage for longer and at longer distances away from the herd (Lee and Moss, 2011). Moreover, because female elephants develop their mothering skills through experience, the presence of allomothering and maternal behaviours should be an important consideration for a sustainable captive breeding herd. The presence of older maternal and allomaternal figures in the herd can positively affect the reproductive success of a herd, both in the wild and in captivity (Kurt and Mar, 1996; Mccomb et al., 2001). In Kurt and Mar's (1996) assessment of neonate mortality in captive Asian elephants (*Elephas* maximus), they found that females that had not experienced maternal or allomaternal care as juveniles were unable to give similar care to their own young, resulting in poor infant mortality. They found significant improvement in maternal care in adult females that had been cared for by an older female when younger (Kurt and Mar, 1996). Conversely, in the zoo setting, Hartley and Stanley (2016) found that female elephants successfully reared young when they had had direct past experience with calves; either their own or of other herd members. This is an indication that sustainable and successful reproduction of elephants in captivity relies on individuals experiencing care from their own mothers or other females in the group, in order for them to successfully rear their own young. Here, we aim to: 1) observe the rate of maternal and allomaternal behaviours of an ex situ breeding elephant herd, 2) characterise the bonds and rates of interaction of calves with nonmothers in the herd, with the goal of identifying the individuals responsible for allomaternal care, and 3) determine the social factors that influence female investment in alloparental care. Specifically, we investigate the strength of relationship between mother-allomother and allomother-calf dyads, the degree of relatedness between mother-allomother and allomother-calf dyads, and the number of years that mothers and allomothers spent together as herd mates.

3.3 Methods

3.3.1 Sample Population

Research was conducted on a breeding Asian elephant herd at Chester Zoo, UK. Chester Zoo work using a protected-contact management strategy, to ensure the safety of both keeper and animal during husbandry and training. The zoo houses breeding females and their offspring, as well as a bull elephant that is mixed with the females regularly. The elephants at Chester Zoo are housed in an enclosure that is divided into two outdoor paddocks: The Main paddock (5490m²) and the Bull paddock (530m²), and two indoor pens: The Bull pen $(415m^2)$ and main house $(985m^2)$. The main paddock is a large outdoor area containing a pool, mud wallow, different feeding opportunities, and different environmental features and terrain, all aimed at providing the herd with a naturalistic and stimulating habitat. Whilst keepers begin daily husbandry and management around 07:00, the herd, including the bull, is released into the main paddock around 10:00 at the zoo's opening time. From 10:00 until early afternoon the bull is mixed in the main paddock with the family group, and from early afternoon onwards, the bull is moved into the bull paddock. The elephants are brought back indoors at the zoo's closing time to receive any health checks, after which they have access to both indoor and outdoor areas for the rest of night – the bull in the bull area and the family group in the main pen and paddock. At the beginning of this study, Chester Zoo housed 6 elephants: 3 related breeding cows (CZHW1, CZHW2, CZHW3), 1 unrelated cow (CZM1), 1 female calf (CZHW4) and a young breeding bull elephant (not included in this study) (Figure 3.3.1.1). The oldest calf (CZHW4), already present in the herd when data collection began, is the offspring of CZHW1 and was born on 20 August 2015. During this study, three more calves were born: on 16 December 2016 CZHW3 gave birth to a female calf, CZHW5; the following month CZHW2 gave birth to a male calf, CZHW6 on 17 January 2017; and finally, CZHW1 gave birth to a second calf, a male, on 17 May 2018. Following their births, CZHW5 and CZHW6 were included in this study; 45 days and 35 days of data, respectively, on these calves were included. However, the male calf born on 17 May 2018 was not included in this study as it was born after the data collection period.

3.3.2 Data Collection

Data were collected from February 2016 to March 2018 (Appendix 1.1). The herd was observed on average 3 times a week, and observation periods were between 1 and 2 hours, at varied times of the day during the zoo's opening hours (10:00 – 16:00 in the winter; 10:00 – 18:00 in the summer). Data collection during these times ensured that the animals' most natural associations were being recorded, as opening times were when the least training and husbandry occurred. Scan sampling was conducted to record the nearest neighbours for all individuals, both adults and calves, every 10 minutes (Altmann, 1974; Martin and Bateson, 1993). Nearest neighbours were considered to be individuals within 2 body-lengths of one another; thus, they were considered to be associating. Using an ethogram of elephant social behaviours developed for this study (Appendix 1.3), continuous sampling of both affiliative and agonistic social interactions between the elephants was conducted during the observation period.

Maternal and allomothering behaviour was investigated using the data already being collected on the associations and interactions of the elephants in the Chester Zoo herd. Based on other literature on observed allomothering behaviour in Asian and African elephants (Gadgil and Nair, 1984; Lee, 1987; Joyce H. Poole and Granli, 2011; Posta et al., 2013; Rapaport and Haight, 1987) the defined allomothering behaviours used in this study were "touching": the use of trunk or body mass to gently brush, rub, caress or lean up against another for a prolonged period (> 2 seconds); "greeting": trunk tip placed in mouth, on temporal gland or between leg or conspecific; "nursing": milk suckled from mother or lactating non-mother; and "play": trunk twining, pursuit, mounting, gentle pushes that occur between conspecifics (Appendix 1.3. Agonistic behaviours were also recorded,

including slapping, kicking, pushing, displacements, rejection of affiliative interactions and rejection of nursing solicitations (Appendix 1.3).



Figure 3.3.1.1 Chester Zoo Breeding Herd Composition. The herd consisted of 3 related breeding females and their calves, the CZHW family. The herd also had 1 unrelated non-breeding adult female, CZM1.

3.3.3 Measuring herd structure and dyad bond strength

Association indices were calculated to characterise the strength of association between dyads. Association indices measure the frequency that two individuals are observed to be in close proximity of one another – essentially how often two individuals associate (Bejder et al., 1998; Cairns and Schwager, 1987; Ginsberg and Young, 1992; Martin and Bateson, 1993). There are a variety of association indices that are used, but the Simple Ratio Index is most often used when monitoring animals in a captive setting (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Whitehead, 2008b). The Simple Ratio Index is calculated as:

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

Where , *x* represents the number of times individuals A and B are observed together; y_{AB} is the number of observation periods in which A and B are identified but are in different groups not associating with one another; y_A represents the number of observations in which only individual A is observed; and y_B is the number of observations periods where only individual B is observed (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Silva et al., 2011a). This index has been recommended in the past for its simplicity and unbiased estimates of social bonds, especially when all subject individuals are easily identifiable (Ginsberg and Young, 1992; Whitehead, 2008b). De Silva *et al* (2011) used Simple Ratio Index values to study seasonal changes in the association patterns of wild Asian elephants.

Similar to the Simple Ratio Index (SRI), the Composite Sociality Index (CSI) measures bond strength, however it was developed to measure bond strength based on affiliative interactions rather than spatial proximity (Silk et al., 2013, 2010b, 2010a, 2006b). By using the frequency of interaction between two individuals to measure bond strength, the CSI not only gives information regarding association frequency but it also characterises the relationship between individuals as affiliative (Silk et al., 2013). It is calculated as:

$$CSI_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{f_i}}{d},$$

where *d* is the number of behaviours that contribute to the index; f_{ixy} is the rate of behaviour *i* for dyad *xy*; and f_i represents the mean rate *i* across all dyads in the study sample (Silk, et al., 2013). Other studies have calculated the composite sociality index and identified an individual's preferred partners using grooming interactions and proximity (Silk et al., 2010b, 2009, 2006b). Here we have used touching and greeting interactions between herd members to determine CSI values for each dyad. The values of both the simple ratio and composite sociality indices range from $0 \rightarrow \infty$. Higher values indicate dyads that associate frequently and have more frequent affiliative interactions. By contrast, dyads with lower values associate less frequently and have fewer affiliating interactions (Martin and Bateson, 1993; Silk et al., 2013; Whitehead, 2008a).

3.3.4 Statistical analysis

Social network analysis is a common method used by behavioural ecologists to investigate the complex relationships and structures that arise due to individuals sharing the same ecological space and interacting with one another (Croft et al., 2008; Wey et al., 2008; Whitehead, 1997). Using complex social mechanisms such as mating, grooming, feeding and dominance behaviours, social network analysis provides thorough information on both individual social position and group structure (Croft et al., 2008; Whitehead, 2008a). This tool is not only able to quantify direct relationships between individuals, but it also captures the interactions between social structure of ecological and biological factors such as information and gene flow, disease spread (VanderWaal et al., 2014), and seasonal changes in dynamics (Silva et al., 2011b). In social networks, individuals are represented as nodes and their interactions with others are represented as ties – or edges – connecting them (Figure 3.4.1). The edges between nodes are defined as either binary or weighted. Weighted edges are used to indicate the strength of interaction or association between individuals. To investigate the sociality of each elephant and its position within the herd, social network analysis methods were used to calculate node and dyadic-level metrics. Association indices are used to convert observed associations or interactions between group members into values that provide the weight to network edges.

In this study, the herd structure and dyadic-level metrics were generated and analysed in R (R Core Team, 2017), using the packages asnipe (Farine, 2018) and sna (Butts, 2016). Using *asnipe* function "get_group_by_individual", the observed nearest-neighbour data were converted into a group by an individual matrix which contains each herd member in the column and the association groups in which they were observed in the rows (Farine, 2013). Once all observed associations were collated in the group by individual matrix, weighted social networks could be generated by using the "get network" function; specifying that edged weights be calculated using the simple ratio index. Then, in order to understand individual, or node-level, position within the herd network we used the weighted degree as a measure of an elephant's social centrality. The weighted degree is a measures of an individual's gregariousness – its tendency to form bonds with group members (Pepper et al., 1999; Whitehead, 2008b). The weighted degree is the total of all edge weights connected to a selected node (Croft et al., 2008; Whitehead, 2008b). This was calculated using the *sna* package. To determine whether the observed herd network structure was stable and significantly different from random, they were compared to null models produced by data stream permutations that were performed 4000 times (Farine, 2013; Farine and Whitehead, 2015b). The data stream permutation method performs swaps of individuals between groups, recalculating the network after each swap. This creates a set of matrices, the number of which corresponds to the number of permutations performed (Bejder et al., 1998; Farine, 2013). All permutations were performed using the R package, asnipe (Farine, 2018), following the method described by Farine (2013). A P value was calculated by comparing the observed network coefficients to the distribution of network coefficients estimated from each of the 4000 permutations. This is a test for nonrandomness and avoids biases in further statistical analysis due to the non-independent

nature of social network data. Whilst the edge weights calculated using the simple ratio index were symmetrical (undirected), we also created directed networks with the *igraph* package (Csardi and Nepusz, 2006) to demonstrate initiator and recipient strength using total interaction frequency as edge weights. The directed networks give an indication of the main initiator and recipient of interactions (Croft et al., 2008).

To test whether relatedness was a significant driver for the association patterns observed between calves, mothers and allomothers, Mantel tests were conducted (Farine, 2013; Whitehead, 2008b). This test was also used to test the relationship between dyadic associations (SRI) and affiliative interactions (CSI). The Mantel test is used to examine the correlation between two similarity or dissimilarity matrices (Croft et al., 2008; Whitehead, 2008b). The test randomizes the individuals in one matrix, calculating the correlation coefficient for each permuted matrix. Statistical significance is determined by comparing the true value of r with the distribution of the set of permuted r values (Whitehead, 2008a). If the Mantel correlation coefficient r > 0, this indicates a correlation between the two matrices; if r < 0 there is no correlation between the two matrices (Whitehead, 2008a). Using "mantel" in the vegan library in R (Oksanen et al., 2018) set to 4000 permutations, matrices containing herd bond strengths (SRI) were first compared with herd interactions (CSI) and then to relatedness matrices, and for each comparison a correlation coefficient rbetween the two matrices was calculated. Spearman rank correlations were performed to investigate other possible drivers of allomothering behaviour in this group, including allomother-mother bond strength, calf-allomother degree of relatedness, and motherallomother degree of relatedness.

3.4 Results

3.4.1 Maternal and allomaternal bond strengths

The first aim of this study was to observe the bonds between females and calves present in the herd, as well as the rate of maternal and allomothering behaviour. At the start of this study in 2016, only one calf was present in the herd, CZHW4, the youngest offspring of the matriarch CZHW1 (Figure 3.4.1.1). During this time this calf's bond with its mother was found to be the strongest within the herd structure (SRI = 0.766), followed by its relationship with its sister, CZHW2 (SRI = 0.5), and with the unrelated adult CZM1 (SRI = 0.404). The weakest bond that the calf shared was with its sister's adult offspring, CZHW3 (SRI = 0.320). When individual network metrics were measured, the calf was also found to have the highest weighted degree of all individuals (S_i = 1.992), indicating its high tendency to associate with other herd members, and once again its mother (CZHW1, $S_i = 1.935$) and sister (CZHW2, $S_i = 1.700$). With the addition of two more calves to the herd we could investigate the effects of such social change to the herd's stability, and more specifically the females' associations with not just one, but now 3 calves (Figure 3.4.1.1). As expected, all mother-calf dyads represented the strongest bonds in the herd (Figure 3.4.1.1). The strongest of these bonds was between CZHW3 and its new infant CZHW5 (SRI = 0.773); followed by CZHW1 and CZHW4 (SRI = 0.633) and CZHW2 and its calf CZHW6 (S_i = 0.544). Interestingly, the male calf CZHW6 had a strong bond with its grandmother (SRI = 0.6) – a bond that was stronger than its bond with its mother. After the calves were born the weighted degree of all individuals related to the calves increased, including that of the individual that previously had the lowest weighted degree, CZHW3 (S_I = 2.232). All three calves, CZHW4, CZHW5, and CZHW6, had the highest weighted degree values (respectively: S_1 = 2.808, S_1 = 2.570, S_1 = 2.743). Whilst the matriarch of the family group (CZHW1) had a relatively high weighted degree (S₁ = 2.676), the unrelated female (CZM1) had the lowest weighted degree value after the birth of the calves ($S_1 = 1.928$).



Figure 3.4.1.1 Social Network of Chester Zoo Herd. Edges (lines) between each individual are given a weighting (thickness) based on the bond strength shared between a dyad. The bond strengths each elephant shares with its herd mates are calculated using the Simple Ratio Index (SRI). The colour of the nodes corresponds with adults (tan) and calves (green) present in the herd. At the beginning of the study (A), the calf's (CZHW4) strongest bonds were found to be with its mother (CZHW1), sister (CZHW2) and unrelated herd member (CZM1). After two birth events in the herd (B), the 3 mother-calf dyads present in the herd structure represented the strongest bonds (highlighted).

3.4.2 Rate of maternal and allomaternal interactions

Using "touch", "greeting", "nursing", and "play" interactions, the mean interaction frequencies per hour were calculated for each calf-female dyad (Figure 3.4.2.1). We found that interaction frequencies significantly varied between the calf CZHW4 and the different adults in the herd, as well as differing for each behaviour type (X^2 = 128.84, df = 9, p < 0.001). As expected, mean touching (2.7/h) and nursing (1.9/h) frequency occurred most often between the calf (CZHW4) and its mother (CZHW1). Outside of interactions with its mother, the calf had high frequencies of touching with the unrelated female, CZM1 (2.1/h), and its sister, CZHW2, (1.9/h). Whilst the calf mainly nursed from its mother (1.9/h), it was also observed to nurse from its sister, CZHW2, and its relative, CZHW3, at almost equal rates, 1.4/h and 1.5/h respectively. When this is broken down further, the calf had a total of 28 nursing interactions with CZHW2 and 22 nursing interactions with CZHW3. By contrast, nursing interactions were not observed between the calf and the unrelated female, CZM1. Frequency of play occurred more often between the CZHW4 and its sister, CZHW2 (2.9/h) and its relative, CZHW3 (1.2/h), compared to between CZHW1 and its mother or the unrelated female. Interestingly, greeting frequency was observed to be highest between the calf and unrelated female (1.9/h). The calf appeared to engage in play interactions with all of the adults in the herd, however its most frequent rates of play occurred with its sister, CZHW2 (2.9/h, n = 33).

The females' investment in maternal and allomothering interactions increased with the arrival of the new calves, CZHW5 and CZHW6 (Figure 3.4.2.1b). The group grew from consisting of 10 dyads to 21 dyads (Appendix 2.1). New bonding types were also formed, between grandmothers and calves, and between the three calves. With this increase in group members and dyads, we found an increase in herd interactions, especially between CZHW4 and the new calves CZHW5 and CZHW6. Within this group of dyads, the highest frequency of play was observed (CZHW4-CZHW5: 3.3/h; CZHW4-CZHW5: 4.14/h). After interactions with one another, calves interacted most often with their mothers. As expected, the new-born calves nursed almost exclusively from their mothers (n = 107).

However, we observed that the oldest calf, CZHW4, nursed less from its mother (CZHW1: 1.55/h) and relatives (CZHW2: 1/h; CZHW3: 1.14/h) after the arrival of the new calves. Outside of interactions with their mothers, the new-born calves interacted frequently with their grandmothers, as well as their sisters. The grandmother-calf pair, CZHW1 and CZHW6, that were found to share a very strong bond, were also found to have high touching (2.09/h) and greeting (2.6/h) rates, with the calf's touching and greeting rates being higher with its grandmother than with its mother. Greeting behaviours appeared to be the most frequent type of interaction that calves exhibited with all of their relatives.



Figure 3.4.2.1. The frequency of "touching", "greeting", "nursing", and "play" interactions between adult female Asian elephants and calves in Chester Zoo. The mean rate of interaction between each female and 1 calf present in the herd (A) and 3 calves present in the herd (B).



Figure 3.4.2.2. Directed network of interactions between members of the Chester Zoo elephant herd with one calf present (A) and when 3 calves were present (B) in the herd. The thickness of edges indicates the frequency of interaction between two nodes, and the arrows indicate the direction of initiation of interactions. Calves (tan) were observed to be the main initiators of interactions with adults (green).

Figure 3.4.2.2 illustrates the initiators and recipients of affiliative interactions between the calves and their adult herd mates. Out-strength measures indicate that all three calves initiated most interactions (CZHW5: 300; CZHW6: 344), with the oldest calf, CZHW4, having the highest measures when she was the only calf (out-strength = 555) and when all 3 calves were present (out-strength: 351). Similarly, all 3 calves had the highest instrength measure in the network with the youngest calf, CZHW6 scoring highest (in-strength = 244), followed by CZHW5 (in-strength = 230) and finally the oldest calf, CZHW4 (instrength = 203). To explore calf-initiated interactions, we next calculated the proportion of these interactions that were accepted or rejected by members of the group. Figure 3.4.2.3 shows the number of calf-initiated interactions accepted and rejected by each adult. To begin with, calf-initiated interactions were most often accepted by their mothers (CZHW4 -CZHW1 =37.8%, n = 312; CHW5 - CHW3 = 67.4%, n = 116; CZHW6 - CZHW2 = 40.58%, n = 84). For calf-initiated interactions with non-mothers, interactions from CZHW5 were accepted most by its grandmother (CZHW2 = 15.11%, n = 26); from CZHW6 its grandmother (CZHW1 = 33.81%, n = 70). Interestingly, when CZHW4 was the sole calf in the herd, its initiated interactions were accepted most often by its sister, CZHW2 (22.52%, n = 136). However, with the two other calves present, its initiated interactions were most often accepted by relative CZHW3 (28%, n = 62). On average, 1.82% of calf-initiated interactions were rejected by adult females. Out of all 3 calves, the oldest calf, CZHW4, experienced the highest number of rejections (CZHW2: n = 20; CZHW3 = 34).

To further explore female responses to calf soliciting, we focused on the acceptance and rejection of nursing solicitation. Both CZHW5 and CZHW6 suckled mainly from their mothers, CZHW3 (95.52%) and CZHW2 (53.42%) respectively, with both of them experiencing no rejection. The acceptance of nursing soliciting by CZHW4 toward its mother decreased from 100% acceptance (n = 102) when it was sole calf, to 41.25% (n= 33) when all 3 calves were present in the herd. This calf's suckling solicitation also decreased from 170 attempts to 80 attempts. When all 3 calves were present, CZHW4 allonursed from CZHW2 (2.5%, n = 2) and CZHW3 (38.75%, n = 31). CZHW5 suckled exclusively from its mother but

was observed attempting to suckle from the older calf (CZHW4) on one occasion. CZHW6 was observed suckling from its grandmother CZHW1 (30.14%, n = 22). Whilst the average calf suckling bout from mothers ranged between 01:19 – 01:21 (mm: ss), mean suckling bouts from non-mothers were shorter for CZHW6 (01:14). Interestingly, CZHW4 had a higher average suckling bout from CZHW3 (01:28) when compared to suckling with its mother. No calves in the herd attempted to suckle from non-relative CZM1. Figure 3.4.2.4shows the aggression network of the herd. In general, low levels of aggression from the adults were directed toward the calves. However, the older calf, CZHW4, was the recipient of the most agonistic interactions (CZM1: n = 28; CZHW2: n = 18; CZHW3: n = 29.

3.4.3 Factors influencing allomother-calf bonds

To investigate possible factors driving allomothering behaviours between females and calves (Table 3.4.3.1), we first performed a correlation test between an allomother's bond strength with a calf's mother and its bond with the calf, for which we found a significant positive correlation (Spearman's rank correlation: r = 0.835, p = 0.005) (Figure 3.4.3.1b). A positive correlation was also found between the number of years a mother and potential allomother had been housed together in the same zoo facility (Spearman's rank correlation: r = 0.670, p = 0.047) (Figure 3.4.3.1a). However, other possible factors such as mother-allomother degree of relatedness (Spearman's rank correlation: r = 0.401, p = 0.285) and calf-allomother degree of relatedness (Spearman's rank correlation: r = 0.401, p = 0.285)


Figure 3.4.2.3. The total number of interactions initiated by calves CZHW4, CZHW5, CZHW6 that were accepted (A) and rejected (B) by adult females. Calf-initiated interactions were most often accepted by their mothers. For calf-initiated interactions with non-mothers, interactions from CZHW5 were accepted most by its grandmother (CZHW2 = 15.11%, n = 26); from CZHW6 its grandmother (CZHW1 = 33.81%, n = 70). On average, 1.82% of calf-initiated interactions were rejected by adult females. Out of all 3 calves, the oldest calf, CZHW4, experienced the highest number of rejections (CZHW2: n = 20; CZHW3 = 34).



Figure 3.4.2.4. Directed network of agonistic behaviours between calves and adult females. The thickness of the edges reflects total number of agonistic interactions, whilst the arrows are directed from initiator toward recipient of the interaction.

Table 3.4.3.1. Factors influencing calf-allomother bonds. The association (SRI) and interactions (CSI) strengths, and degree of relatedness between mothers, allomothers and calves.

 The years that mothers and allomothers spent together as herd mates was also recorded.

Calf	Mother	Allomother	Calf- Allomother SRI	Allomother- Mother SRI	Calf- Allomother CSI	Allomother- Mother CSI	Calf- Allomother Relatedness	Allomother- Mother Relatedness	Mother- Allomother Years as herd mates
CZHW4	CZHW1	CZHW2	0.480	0.465	1.200	0.777	0.250	0.500	19
		CZHW3	0.335	0.268	0.938	0.270	0.125	0.250	12
		CZM1	0.361	0.380	0.715	0.265	0.000	0.000	27
CZHW5	CZHW3	CZHW1	0.330	0.268	0.487	0.270	0.125	0.250	12
		CZHW2	0.352	0.310	0.732	0.881	0.250	0.500	12
		CZM1	0.280	0.246	0.279	0.315	0.000	0.000	12
CZHW6	CZHW2	CZHW1	0.601	0.465	2.122	0.777	0.250	0.500	19
		CZHW3	0.299	0.310	0.807	0.881	0.250	0.500	12
		CZM1	0.334	0.328	0.535	0.334	0.000	0.000	19



Figure 3.4.3.1. Significant correlations were found between A) the number of years a mother and potential allomother had been housed together in the same zoo facility (Spearman's rank correlation: r = 0.670, p = 0.047), and b) the bond strength between the allomother and the calf's mother, and the allomother's bond with the calf (Spearman's rank correlation: r = 0.835, p-value = 0.005).

3.5 Discussion

An aim of this of this study was to observe the rate of maternal and allomaternal behaviours of an ex situ breeding elephant herd. Common social network analysis techniques were used to quantify raw data and to monitor changes in the herd's associations and behaviours. Firstly, as expected, the strongest bonds within the herd were between the mother-calf dyads, reflecting that female elephants spent most of their time associating with their offspring. This finding was expected, as this has been observed in both captive and wild elephants (Lee and Moss, 2011; Whilde and Marples, 2012), as well as other mammal species including giraffes (Langman, 1977; Nakamichi et al., 2015; Pratt and Anderson, 1979), primates (Maestripieri, 1994), cetaceans (Taber and Thomas, 1982; Thomas and Taber, 1984), and ungulates (Ralls et al., 1986). Mother-calf interactions were amongst the highest in the group – especially touching, greeting and nursing behaviours. In both wild Asian and African elephants, calves less than 6 months old were observed to be in closest contact with their mothers for over 50% of the observed time (Gadgil and Nair, 1984; Lee and Moss, 2011). Interactions between wild mother-calf elephant dyads were also found to be strong and primarily initiated by the calves, whilst mothers touched their calves to reassure them of their presence and to keep the calves within close proximity of them (Gadgil and Nair, 1984; Lee, 1987; Lee and Moss, 2011). Whilst they had strong bonds with their mothers, all three calves in the present study were the main initiators of interactions within all dyads that they were part of. The younger calves received fewer rejections when initiating interactions, however interactions initiated by the older calf (CZHW4) were rejected more often. As described by Lee and Moss (2011), very low levels of aggression from mothers or allomothers toward calves between 0 to 24 months is expected. Nursing interactions were observed to occur between a mother and its calf almost exclusively. Interestingly, we observed that the eldest calf, CZHW4, allonursed from its sister (CZHW2) and adult relative (CZHW3), who were both lactating. Most notably, we observed that after the two birth events, CZHW4 suckled from its mother less, and allonursing from CZHW2 reduced greatly, but continued to allonurse from its relative (CZHW3). These instances of allonursing

were observed to only occur when CZHW3 was nursing its own calf; therefore, it is possible that the calf's (CZHW4) allonursing was opportunistic, only suckling when its relative was already standing to nurse its own calf. Interestingly, neither CZHW2 nor CZHW3 allonursed on another's calves, but CZHW1 allonursed CZHW2's calf (CZHW6). Lee's (1987) observations of wild African elephants revealed over 90% of nursing bouts occurred between mother and calf and in this particular group of elephants, allonursing bouts were infrequent, only constituting 3.7% of nursing observations. In contrast, allonursing has been more commonly observed in both zoo (Rapaport and Haight, 1987) and free ranging (Gadgil and Nair, 1984) captive Asian elephants. In this study, allonursing bouts constituted 30% of total observed nursing bouts Although other studies have noted that most females reject suckling attempts from calves that are not their own, they observed that allomothers were usually females that had weaned off their own calves or were close relatives of the allonursing calf (Gadgil and Nair, 1984; Rapaport and Haight, 1987; Sukumar, 2003). In this study, the presence of younger calves appears to have shifted the herd's attention to fully caring for these new additions, making the older 3-year-old calf more independent of its mother. Weaning in elephants can occur between 26 and 113 months, and spatial independence from their mothers increases as calves age (Lee, 1987; Lee and Moss, 2011; Sukumar, 2003). So, whilst allonursing may not be nutritionally vital to the healthy 3-year-old calf in this herd, as Sukumar (2003) notes, it may serve as a comfort mechanism as the calf adjusts to the introduction of its new siblings.

Next, our aim was to identify key individuals involved in cooperatively rearing the calves with the mothers. Although the young calves were almost always in close proximity with their mothers, our results show that a calf's sister, grandmother, and relatives play key roles giving allomaternal support. When there was only one calf present in the herd (CZHW4), the calf shared high interaction rates with its sister (CZHW2), and when there were more calves present in the herd, calves shared high interaction rates with their grandmothers and sisters. Wild studies have recorded that key allomothers in elephant societies tend to be

nulliparous adolescent females related to the calf - usually a calf's older sisters (Lee, 1987; Lee and Moss, 2011); however, the presence of calves triggers cooperation between all related herd members (Gadgil and Nair, 1984; Kurt and Mar, 1996; Rapaport and Haight, 1987; Schulte, 2000; Whilde and Marples, 2012). Although these two groups of females were identified as allomothers in this present study, we found that there was variation in the types of interactions exhibited between these females and the calves. A majority of interactions between calves and these allomothers were greeting interactions. As well as elephants, greeting interactions in social species such as lions and hyaenas have been highlighted as methods of bond strengthening and reinforcement (Matoba et al., 2013; Smith et al., 2011). With this understanding, the greeting interactions observed in this study between allomothers and calves can be seen as instances of bonds being established and reinforced between the calves and their adult relatives. Grandmothers were involved higher rates of touching with the calves than the other allomother groups. The support of grandmothers in elephant calf rearing is crucial because the maternal experience and knowledge they carry is important for calf survival (Hawkes, 2004; Mccomb et al., 2001; Moss and Lee, 2011b; Schulte, 2000). Lee and Moss (2011) note that grandmothers can assist in the care of their grand offspring through allonursing and allomothering interactions; however, we did not see allomothering investment in the form of play or allonursing by this group. Some play and allonursing interactions were observed between calves and their adult sisters, however at a low frequency. Lee and Moss (2011) noted that the presence of a calf's sisters in a herd can increase its survival just as much as the presence of grandmothers. When away from their mothers, Lee (1987) noted that a calf's nearest neighbours were often adolescent or nulliparous females that were responsible for ensuring that the calf remained well integrated and close to the group. Although in the presence of relatives the unrelated female was not a key allomother, this female still engaged in touching and greeting behaviours with the calves.

With this study, we also aimed to determine whether the degree of relatedness and bond strength between a mother and her herd mates affected the investment in allomother care that females are willing to give to a calf. Elephant societies are known for their preferential cooperation with close relatives, with their core groups consisting of related females and offspring (Archie et al., 2006b). Archie et al 's (2006) studies on elephant social structure and relatedness showed that the high relatedness structure of elephant social dynamics causes a bias in cooperation towards an individual's closest relatives. Such a bias would allow the females to maximize the indirect benefits of inclusive fitness, through caring for and protecting their relatives' offspring (Archie et al., 2006b; Hamilton, 1963). We found that in the presence of both related and unrelated females, the factors that correlated with the relationship (SRI) between allomothers and calves was the bond strength between an allomother and the calf's mother, and the number of years that adult females spent as herd mates. Kurt and Mar (1998) and Schulte (2000) note that years spent as herd mates is a possible driver for cooperation between female elephants in *ex situ* facilities instead of relatedness. Most often zoo elephant herds consist of unrelated individuals, and it is possible that the time females spend together and the relationships they establish with one another is what drives them to cooperate when rearing calves (Kurt and Mar, 1996; Schulte, 2000). Further studies are needed to test this relationship among captive breeding herds consisting of multiple unrelated females, to compare rates of allomothering and the number of years that unrelated females have been housed together.

During this study, we found that both adult-calf interactions and calf-calf interactions were high. The presence of three calves was notably marked by the very high rate of play amongst them. The high rates of play and tactile interactions between calves and their age-mates matches other findings that describe young elephant play as being intense, especially with relatives and age-mates (Lee, 1987; Lee and Moss, 2014, 2011). Like other animals, play in young elephants is linked to the development of social skills, understanding social etiquette, and development of socio-sexual behaviours (Chiyo et al., 2011; Lee and Moss, 2014, 2011; Nunes et

al., 2015). Whilst young calves are capable of lone play and playing with adult herd members, the intensity of play that they engage in with their age-mates is much higher (Lee and Moss, 2014). Therefore, the addition of two more calves is a beneficial source of social enrichment for the older calf, CZHW4. The presence of younger siblings also allowed the calf, CZHW4, to begin developing allomaternal skills, both by watching the adults care for their calves and by babysitting. Young nulliparous females learn maternal skills through allomothering opportunities, and studies have shown that a female's past experience with calf care can affect her reproductive success (Moss and Lee, 2011b). Therefore, the presence of younger siblings will benefit this young female's reproductive success in the future.

In general, we found that the presence of calves encouraged females to engage in a variety of interactions that are specific to maternal and allomaternal care – most interestingly allonursing. It also allowed for young calves to experience interactions with adults and calves that are crucial to their development as socially integrated individuals and as future mothers. Allomothering behaviours can involve a variety of different behaviours, though we may not have observed all in this study group; however we acknowledge that herd size and number of calves in an *ex situ* elephant herd could possibly explain why some interactions were not observed (Schulte, 2000).

3.6 Conclusion

In wild elephants, the communal rearing of calves increases cooperation between adult females. This cooperation between the adults leads to an increase in reproductive success and calf survivorship. Studies have shown that relatedness, group size and the presence of multiple generations increases calf survivorship and reproductive success. Our study showed that the presence of calves in a captive herd encouraged interactions that would otherwise not be observed amongst adult zoo elephants – especially the interesting behaviour of allonursing. This is especially key when considering that elephants need to experience birth events and maternal interactions early on in life in order to be reproductively successful in the future (Hartley and Stanley, 2016). However, unlike wild elephant family groups, captive elephants are not always surrounded by relatives; therefore, it is important to understand that successful calf rearing between unrelated females stems from females having prolonged relationships with one another. An understanding of this will improve the *ex situ* efforts to manage a sustainable and genetically viable elephant population.

Chapter 4: The Night-time Networks of Captive Asian Elephants (*Elephas maximus*)

4.1 Abstract

The strength of mammal social relationships is commonly measured through observations of interactions between individuals during natural waking hours, however in group living species, night-time associations can be just as informative. Preferred social partners are more likely to sleep in close proximity to one another to provide protection, care of offspring and social comfort. Sleep plays an important role in the health and wellbeing of animals and therefore any disturbance can be physiologically detrimental to individuals. The periodic recording of elephant night-time and sleeping behaviour is increasingly becoming a common management practice of keeping staff at many zoological institutions as a measure of wellbeing. A goal of this study is to validate the use of night-time social patterns as a reliable method of assessing herd cohesion and stability. Therefore, the aims of this study are to: 1) characterise and explore the night-time network structure of two zoo elephant herds using social network metrics; 2) investigate if degree of relatedness, age of difference between dyads, and number of years housed together determine the strength of night-time associations; 3) investigate the stability of night-time networks over time, looking at the monthly networks of each herd, in order to test if night-time social patterns are a reliable method for longitudinal monitoring; 4) investigate the relationship between social position and average amount of sleep per night, and 5) test whether night-time networks reflect day-time networks as a zoo management tool. Our results show that elephants have strong stable night-time networks in which they have preferred sleeping partners. Calves are central within sleeping networks, choosing to sleep with their mothers or other age-mates. Comparisons between monthly bond strength and weighted degree measures produced varied results. The comparison between daytime associations and night-time sleeping associations produced varying results and therefore warrants further comparison on larger, longitudinal data sets. A strong relationship was found between average hours of sleep per night and degree of sociality.

4.2 Background

The structure and benefits of social living and bonding have been widely studied in a range of social mammals (Clutton-Brock, 2009; Hamilton, 1964). Cooperation and bond reinforcement between group members is thought to be maintained through social interactions between conspecifics, as found with the greeting behaviour of spotted hyenas (Smith et al., 2011), and licking and head rubbing in African lions (Matoba et al., 2013). In non-human primates, having longlasting stable bonds with a select few partners within the group has been suggested to enhance an individual's longevity, buffering the effects of social stress (Silk et al., 2010b). Studies on the relationships between females report that well integrated females are more successful at rearing young, as they profit from receiving assistance from allomothers in the group; they also have better access to shared resources, and lower exposure to male harassment and predation risks (Cameron et al., 2009; Fairbanks, 1990; Hawkes, 2004; Silk et al., 2010a, 2009, 2003). The maintenance of strong social bonds has also been suggested to act as a buffer to the possible effects that social stress may have on an individual's physiology (Carter et al., 2008; Grippo et al., 2007; Silk et al., 2009; Taylor et al., 2000). Whilst many of these studies explore the role of daytime social bonds, social behaviour and interactions continue through the night, determining activities such as feeding, nesting and sleeping behaviours. Observations of night-time behaviour of social animals can often be challenging for investigators due to the difficulty of locating and observing individuals in low light or darkness (Noser et al., 2003; Tobler and Schwierin, 1996), however researchers have been able to conduct such studies both in the wild and in captive settings, especially in non-human primate species. In captivity, observations of chimpanzee sleeping and nesting behaviour have revealed that not only do individuals have preferred sleeping sites, but they also have preferred sleeping partners (Lock and Anderson, 2013; Riss and Goodall, 1976). In in these groups, relatedness was not found to drive sleeping partner preference, but instead preferred sleeping site and early rearing history were drivers of a chimpanzee's sleeping partner choice (Lock and Anderson, 2013; Riss and Goodall, 1976). Noser et al (2003) observed that in a captive group of gelada

baboons, group members slept in two distinct clusters, and the onset of sleep only occurred when all members were present in their respective clusters. They noted that sleep within these groups was fragmented due to disturbances caused by group members waking and causing the rest of the group to wake, before returning back to sleep (Noser et al., 2003). Additionally, sleep latency was not influenced by social rank; however, more dominant individuals were found to be more alert during the night, seemingly in order to respond to nocturnal dangers more quickly (Noser et al., 2003). Sleeping group size is generally species and season-dependent, but primate social groups tend to associate more closely at sleeping sites with basic sleeping units consisting of mother-infant dyads, which adapt as the infant becomes more independent (Anderson, 2000). In wild primates, sleeping partner preferences have been observed to reflect daytime associations and are influenced by mate choice and dominance rank (Anderson, 2000). By comparison, findings on sleeping partner preference in captive non-human primates have been variable (Noser et al., 2003; Riss and Goodall, 1976).

With limited published research on nocturnal social behaviour of other mammal species, the existing work on the social behaviour of non-human primates at night can serve as an informative foundation on social sleep behaviour. Understanding how highly social species maintain associations and remain cohesive through the night, can serve as a key indicator of individual welfare, as social dynamics can potentially affect quality of sleep and in turn other aspects of individual health. In studies of non-human primates in zoological collections, nighttime observations can inform researchers and animal managers of an individual's total sleep time, preferred sleeping partners, preferred sleeping sites, as well as group cohesion compared to daytime observations (Noser et al., 2003; Riss and Goodall, 1976). Similarly, the nocturnal behaviour of some large mammal species has also been investigated in the zoo setting, including the Asian and African elephant. Elephants are diurnal, and similar to other large herbivores, sleep for relatively short periods during the night, with an average of 4 hours per night in captivity (Tobler, 1992; Walsh, 2017) and an average of 2 hours in the wild (Gravett

et al., 2017). Elephants have two states of rest – standing rest and recumbent (or lying) rest. Standing rest is characterised with reduced movements in the trunk and body, and this is often followed by recumbent rest (Holdgate et al., 2016; Tobler, 1992). Tobler (1992) noted that when an elephant was recumbent on its side with legs stretched straight out, the onset of sleep commences quickly, with eyes being visibly closed and the occurrence of muscle twitching and occasional audible snoring. In a study on the recumbence behaviour of zoo elephants, Holdgate *et al* (2016) reported species differences with Asian elephants displaying higher rates than African elephants. Seasonal differences in sleep duration also occur, with elephants sleeping earlier and longer during the winter compared to other seasons (Tobler, 1992). Housing substrate has long been seen as a factor impacting quality of sleep in elephants as hard, concrete floors are result in infrequent recumbent rest compared to sand-like substrates (Holdgate et al., 2016). This finding was used as direct evidence for improving welfare standards for zoo elephants as part of a DEFRA ten year review in the UK (BIAZA, 2010).

The homeostatic nature of sleep means that if deprivation occurs, it can be recovered through more intense and longer sleep (Siegel, 2005; Zepelin et al., 2005). Disturbances to the quality of sleep can be affected by many factors, in particular the social environment of the individual (Kent et al., 2015). In both humans and non-human primates, social dynamics and bonds impact the quality and duration of sleep of an individual (Kent et al., 2015; Mochida and Nishikawa, 2014). Humans are more likely to have better quality sleep with a greater number of supportive ties compared to aversive ties and the relationship with family members has a significant positive impact on quality of sleep (Kent et al., 2015). In Mochida and Nishikawa's (2014) study of wild Japanese macaques, small sleeping clusters and clusters containing natal individuals. Conversely, they observed synchronization of wakefulness in non-natal clusters, greater than in natal clusters (Mochida and Nishikawa, 2014). Synchronisations of recumbence and wakefulness have also been observed in zoo elephants, indicating that group sleeping is highly

social for group-living species (Holdgate et al., 2016). In a longitudinal study of sleep behaviour in the elephant herd at Dublin Zoo, Walsh (2017) explored potential factors affecting individual sleep quantity: age, social interactions and the presence of new-born calves. After the birth of calves, Walsh (2017) observed a reduction in sleep amongst all herd members, attributing this to cooperative vigilance and calf protection, but also increased waking amongst members. Mochida and Nishikawa (2014) concluded that an individual's sleep duration at night is affected by the quality of relationships with its sleep partners, either through familiarity or frequent daytime associations and affiliative integrations. In the same way flooring substrate has been found to impact the sleep quality of zoo elephants (Holdgate et al., 2016), further understanding should be gained on the impact of herd social dynamics on an individual's quality of sleep at night. In Walsh's 2017 study, a female elephant had a period of reduced sleep which was attributed to conflict with a herd mate; whilst the presence of a female in oestrus caused the bull elephant to also sleep less (Walsh, 2017). Consistent sleep disruption or sleep deprivation have been shown to affect the circadian cycle of sleep and wakefulness (Berger and Phillips, 1995), reduced or impaired cognitive performance (Cirelli and Tononi, 2008), acute and chronic inflammation (Faraut et al., 2012; Opp and Krueger, 2015), increased cortisol levels (Wright et al., 2015), and cardiovascular and metabolic disease (Tobaldini et al., 2017). In social mammals where sleep can be disrupted by group members, it is important to understand how cohesive elephant herds are at night to reduce the more adverse effects of disrupted sleep.

As the periodic recording of elephant night-time and sleeping behaviour is becoming an increasingly common management practice of keeping staff at many zoological institutions (Evison et al., 2020; Holdgate et al., 2016; Tobler, 1992; Walsh, 2017), this study will serve to validate the use of night time social patterns as a reliable method of herd cohesion and stability through correlations with daytime associations. The principle aims are to: 1) characterise and explore the night-time network structure of two zoo elephant herds using social network metrics; 2) investigate if degree of relatedness, age difference between dyads, and number of years housed together determine the strength of night-time associations; 3) investigate the stability of night-time networks over time, looking at the monthly networks of each herd, in order to test if night-time social patterns are a reliable method for longitudinal monitoring; 4) investigate the relationship between social position and average amount of sleep per night, and 5) test whether night-time networks reflect day-time networks as a zoo management tool. This comparison will tell us whether an elephant's preferred night-time partners are consistent with its preferred daytime partners.

4.3 Methods

4.3.1 Sample Populations

Data were collected at two BIAZA affiliated zoological collections housing Asian elephant (*Elephas maximus*) breeding herds, Chester Zoo (CZ) and Dublin Zoo (DZ). Chester Zoo housed 6 Asian elephants: 3 related breeding females, 1 juvenile calf, 1 unrelated non-breeding female, and an adolescent bull elephant (Figure 4.3.1.1a). Dublin Zoo housed 12 Asian elephants: 1 breeding bull elephant and a breeding herd consisting of 3 related breeding females and their offspring of varying ages (Figure 4.3.1.1b). During this study, three additional calves were born at Chester Zoo, however data on the calves was not included in this study as there were not enough data points to make meaningful analyses. These zoos were selected for this study due to their similar management and husbandry methods. Both zoos manage their herds using a protected-contact management strategy, to ensure the safety of both keeper and animal during husbandry and training. Both herds consist of breeding cows and their offspring, as well as bull elephants that are mixed regularly. At both institutions the elephant keeping teams' daily management routine begins between 07:00am and 08:30, firstly performing health checks on each individual elephant, followed by training exercises. Between 09:30 and 10:00am, the herds are moved to their outdoor paddocks for the day

(coinciding with the open hours of the zoos); during this time keepers are able to clean out the indoor paddocks, re-stock feeders, and conduct other administrative duties while elephants are given access to their outdoor paddocks (E Evison 2015, personal communication; G Creighton 2018, personal communication). The elephants return indoors between 16:00 and 17:00, depending on season, allowing keepers to perform final health checks and training before the end of the working day. At both zoos, the herds are given access to their outdoor and indoor paddock areas overnight, except during periods of extreme weather or intense cold. Figure 4.3.1.2 shows the area of indoor housing for each herd. Overnight, the elephants at Chester Zoo are housed in three areas – the Bull pen (415m²) and main house (985m²) which can be partitioned into 2 pens (Pen 1 and Pen 3) by inter-pen gates when management requires it. The Dublin Zoo indoor enclosure contains the cow house, which is divided into an indoor section (425 m²) and an attached outdoor kraal (450m²). Here, bull house is separate from the cow house (200m²). Both zoos house the females and calves separately from the bulls overnight for reproductive management and safety of individual elephants. Thus, the focus of the paper is on the sleeping associations of the adult females and their calves since they were housed together, whilst the bulls spent the evenings alone in their pens. Data of sleeping associations were collected by analysing Closed Circuit Television (CCTV) footage of the females and calves over the same period as when the day-time observations were conducted. Footage was collected every other day from Chester Zoo during months of February, April, May, October and December 2016 and January and February 2017; and from Dublin Zoo from April 2018 to August 2018. The data collection protocol used in this study was adapted from methods employed by the Chester Zoo elephant keeping team (Evison et al., 2020). Each video was reviewed using continuous sampling methods over a 12-hour period between 19:00 and 07:00 (Chester Zoo) or a randomly selected 2-hour period between 19:00 and 07:00 (Dublin Zoo) two to three times per week (Appendix 1.1). During video analysis, all observed bouts of sleep for all herd members were recorded. The start of a sleeping bout was defined as when the elephant was completely recumbent on its side, with its head and all four legs parallel to the ground. The end of a sleeping bout was defined as when the elephant returned to a

standing position on all four feet. Sleeping associations were defined if the sleeping animals was within two body-lengths of another individual. If any part of an elephant's body was in direct physical contact with another elephant this was noted to be a touching interaction. When an elephant was observed sleeping, the start time of sleep and the time of wake up were recorded, as well as the individuals that were in close proximity to them as they slept.



Figure 4.3.1.2 The breeding herd of Chester Zoo (A) and Dublin Zoo (B). Both herds consist of adult cows and their offspring. Male offspring are indicated with a dark border, and females are indicated with no border. Whilst both zoos also hold breeding bull elephants that regularly mix with the calves and females, during the evening the bulls sleep separately from the rest of the herd. Therefore, this study focuses on the adult females and their offspring.



Figure 4.3.1.2 The floor plan of indoor housing facilities of A) Chester Zoo (©Chester Zoo) which consists of 3 areas: The Bull pen (415m2) and main house (985m2) which can be partitioned into 2 pens (Pen 1 and Pen 3). The Dublin Zoo enclosure B) contains the cow house, which is divided into an indoor section (425 m2) and an attached outdoor kraal (450m2). Here, the bull house is separate from the cow house (200m2) (© Dublin Zoo). Both zoos house the females and calves separately from the bulls overnight.

4.3.2 Social network analysis

Association and sociality indices were used to determine the herd's nocturnal social network with preferred sleeping partners. The indices measured the relationship between an elephant and each of its herd mates. A Simple Ratio Index (SRI) was used to measure the frequency that two individuals were observed to be in close proximity of one another (Bejder et al., 1998; Cairns and Schwager, 1987; Ginsberg and Young, 1992; Martin and Bateson, 1993) and is commonly used when monitoring animals in a captive setting (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Whitehead, 2008b).

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

In this calculation x represents the number of times individuals A and B are observed together; y_{AB} is the number of observation periods in which A and B are identified but are in different groups not associating with one another; y_A represents the number of observations in which only individual A is observed; and y_B is the number of observations periods where only individual B is observed (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Silva et al., 2011b). Whilst it has not been used to analyse night-time behaviour in elephants, De Silva et al (2011) used Simple Ratio Index values to study seasonal changes in the day-time association patterns of wild Asian elephants. SRI values were then used as edge weights in the night-time sleeping networks to reflect the strength of association between herd members. To understand the dynamics of sleeping networks, three centrality metrics were used to investigate how individual sleeping interactions influenced the elephants' overall night-time sleeping network. First, the weighted degree: the total of the weights on the edges connected to the node (Croft et al., 2008; Whitehead, 2008b). Weighted degree reflects individual gregariousness - its tendency to associate with group members (Croft et al., 2008; Pepper et al., 1999; Whitehead, 2008b, 2008a). Second, weighted betweenness: the number of shortest paths that flow through a single individual (Farine and Whitehead, 2015a). This highlights an individual's tendency to change between subgroups. Individuals with high betweenness will tend to switch between subgroups, whilst individuals

with low betweenness will remain in the same group. Third, eigenvector centrality: an individual's connectedness based on its neighbours' connectedness (Farine and Whitehead, 2015a). This therefore shows the gregariousness of an individual's associates.

4.3.3 Statistical Analysis

Due to the differing group size (Chester, n = 7; Dublin, n = 11), statistical comparisons cannot be made between these two herd networks (Castles et al., 2014; Farine and Whitehead, 2015a). However, in order to make descriptive comparisons between the Chester and Dublin elephant networks, the dataset for each group was standardised so that all matrices and metrics calculated for each network were derived from an equal number of data points for each herd. Nighttime sleeping networks were calculated and generated using *asnipe* (Farine, 2018) and sna (Butts, 2016) packages in R (R Core Team, 2017). Following methods described by Farine (2013), "get group by individual" in asnipe was used to convert the observed sleeping associations into a group by individual matrices containing each herd member in the column and the sleeping groups in which they were observed overnight. Once all observed associations were collated in the group by individual matrices, the "get network" function could be used to generate weighted social networks calculated specifically using the simple ratio index. Next, we used "network permutation" to determine if the observed sleeping networks were significantly different from random by comparing the coefficients of 4000 permuted networks fitted to those of our observed data (Farine, 2013; Farine and Whitehead, 2015b). The data stream permutation method performs swaps of individuals between groups, recalculating the network after each swap. This creates a set of matrices, the number of which corresponds to the number of permutations performed (Bejder et al., 1998; Farine, 2013). Node-level metrics were then calculated for each herd network. Due to its small size, only the weighted degree could be calculated from the Chester Zoo network using *sna* (Butts, 2016). However, as well as weighted degree, eigenvector centrality and weighted

betweenness measures were calculated for the larger Dublin Zoo network using *tnet* (Opshal, 2009). To test for non-randomness and avoid biases in further statistical analysis, all node-level metrics underwent the same permutation process.

Permuted t-tests were performed to conduct within-herd comparisons of node metrics using "perm.test" from the *broman* library in R (Broman and Broman, 2019). Permutations for "perm.test" are specified to 4000. To test sleeping association patterns over time, data were subset into months for both herds. The Dublin Zoo data was subset into 5 consecutive months from April to August 2018. However, during the time of study technical changes occurred to the facility's CCTV storage system, meaning consecutive months could not be collected for the Chester Zoo dataset. To explore whether there were significant changes in the herd networks between months, linear mixed models were used to compare node-level metrics between each month using "Imer" in Ime4 in R (Bates et al., 2015). Each model contained the node metric as the response variable and month as the fixed effect, and individual ID as the random effect: Imer(Degree~Month + (1|ID). Linear models were used to investigate the effect of social position on average amounts of sleep per night using "Im" from in the R base library (R Core Team, 2017): $Im(Degree \sim SleepTime)$. Significance (P_{rand}) for all models was calculated by first building the models with the observed data, comparing the coefficient of the magnitude of the slope from the observed data with the coefficient estimates from 4000 permuted networks. A one tailed significance was then calculated by comparing where the observed estimate fell relative to the permuted estimates (Bejder et al., 1998; Farine, 2013). Mantel tests were used to test the correlations between day and night-time social networks for each herd (Mantel, 1967). They were also used to investigate whether age, relatedness or years spent as herd mates were significant drivers of night-time sleeping associations. The Mantel test is used to examine the correlation between two similarity or dissimilarity matrices (Croft et al., 2008; Mantel, 1967; Whitehead, 2008b). Using "mantel" in the R package vegan (Oksanen et al., 2018), matrices containing herd night-time sleep associations were compared with matrices containing day-time associations, and a correlation coefficient r between the two matrices was calculated. Similarly, night-

time sleep matrices were compared to relatedness coefficient matrices, and the resulting correlation *r* coefficient was calculated. Both calculations were specified to employ 4000 permutations.

4.4 Results

4.4.1 Night-time sleeping networks

The night-time sleeping networks generated for both herds showed that at night all individuals were well connected (Figure 4.4.1.1). More specifically, in the CZ herd, night-time sleeping networks indicated that the strongest sleeping associations occurred between the mother-calf dyad (CZHW1-CZHW4) and the weakest being dyads that contained CZHW3 (Figure 4.4.1.1). However, when many calves were present, as in the DZ herd, the strongest sleeping associations were between the calves (Figure 4.4.1.1). Both mother-calf dyads and calf-calf dyads shared SRI values of \geq 0.5. Within the Chester Zoo network, high SRI bonds occurred between the related individuals CZHW1, CZHW2 and CZHW4 (SRI \geq 0.5); and with the unrelated female, CZM1. Despite being a related member of the group, CZHW3 had the lowest SRI values in the group.

To further identify the individuals that were the most central in elephant sleeping networks, measures of centrality were calculated for all members in both herds (Appendix 3.1). All observed measures of centrality were found to be significantly different from random (<0.001), with the exception of DZ eigenvector centrality values (Table 4.4.1.1). The weighted degree was then used to determine an individual's tendency to associate, and thus its tendency to sleep near its herd mates. DZ's calves were found to have significantly higher weighted degree scores than the adult herd members (two sample t-test: t= -9.534, p = 0.007, permutations = 4000) (Figure 4.4.1.2). This indicated that calves had a higher tendency to sleep with other individuals. However, this was not the case in in the CZ herd. Despite having the highest weighted degree value compared to adults, the presence of only one calf (CZHW4) in the CZ herd meant that statistical analyses were unable to be

performed between calves and adults. All elephants in the DZ herd had a betweenness of 0 and eigenvector centrality were not found to be statistically significant from random (Table 4.4.1.1).

Comparisons of the CZ and DZ sleeping networks in Figure 4.4.1.3 show group-specific metric differences. Elephants in the DZ network herd were found to have greater weighted degree scores (mean $S_I = 4.401$) compared to their CZ counter parts. Conversely, the CZ herd was observed to have greater SRI scores (mean SRI = 0.488). When testing possible factors affecting association strength between individuals, degree of relatedness was not found to be significantly correlated in the CZ herd network (Mantel test: r = 0.491, p = 0.2). Moreover, although all individuals in the DZ herd were related, no statistically significant correlation was found between relatedness and bond strength (Mantel test: r = -0.184, p = 0.892). In fact, neither the age difference between herd members (Mantel test, (CZ): r = 0.2, p = 0.317; (DZ): r = -0.5, p = 0.97) nor the number of years housed together (Mantel test, (CZ): r = -0.247, p = 0.7; (DZ): r = -0.455, p = 0.99) were significantly correlated to herd associations.



Figure 4.4.1.1 Night-time association networks of Chester Zoo (A) and Dublin Zoo (B) breeding herds. Nodes represent individuals in each herd, and the thickness of the edges connecting the nodes represents the strength of association between individuals. Edge thickness is calculated using the Simple Ratio Index; and thicker lines representing strong bonds and vice versa. In both networks, node colour indicates animal age: adult (brown), juvenile (pink), calf (yellow)



Figure 4.4.1.2 Weighted degree of herd member of the Chester Zoo (A) and Dublin Zoo (B) groups. Comparisons between adult and weighted degree scores revealed that calves in the DZ herd had significantly higher scores compared to adult members (t-test: t = -9.534, p = 0.007). Although the single calf in the Chester Zoo herd did have the highest weighted degree, this could not be analysed statistically.

Table 4.4.1.1 Comparison of the night-time network sociality metrics of CZ (n = 7) and DZ (n = 11) zoo elephant herds. The significance of each metric was determined by the comparison of the standard deviation (SD) of the observed social networks, and the mean standard deviation of permuted networks (4000 permutations). Significance was determined by examining the proportion of observed standard deviations that were greater or less than the standard deviations of the permuted networks. P_{rand} values of < 0.05 indicated that the observed network was more structured than the random networks.

		Observed		Permuted	
Network	Node Metric	Mean	SD	Mean SD	P _{rand}
CZ network	Simple Ratio Index	0.488	0.278	0.240	0.00
	Weighted Degree (Si)	2.442	0.34	0.272	0.00
DZ network	Simple Ratio Index	0.440	0.179	0.179	0.00
	Weighted Degree (Si)	4.401	0.806	0.806	0.00
	Eigenvector Centrality (ei)	0.297	0.053	0.053	0.235
	Weighted Betweenness	0	0	0	0.00



Figure 4.4.1.3 Comparison of sleeping network metrics between Chester (n = 7) and Dublin Zoo (n = 11) herds. The Dublin herd was found to have greater weighted degree scores compared to the Chester herd. However, the Chester herd was observed to have greater average bond strength scores.

4.4.2 Sleep networks over time

To further understand the night-time association patterns of elephants in ex situ facilities, network metrics were compared over time. Data collected from the CZ herd was subset into four non-consecutive months in 2016: February, April, May, and December; to view the effect of change in season on night-time associations (Figure 4.4.2.1). Observations show that SRI and weighted degree values increased from February to April, but a decrease was also observed in May and December. Comparisons of monthly SRI values for each herd revealed that CZ bond strengths were positively correlated between February and April (Mantel test: r = 0.889, p = 0.008), February and May (Mantel test: r = 0.681, p = 0.041), and May and December (Mantel test: r = 0.0.7471, p = 0.008) (see Appendix 3.2), indicating that night-time bond strengths between dyads in April and May were similar to those in February. However, no significant correlations were found between nighttime bond strengths in February and December, April and May, or May and December. Table 4.4.2.1 shows the results of the LMMs investigating the effect of time on node metrics. Despite the observed changes in individual weighted degree in the CZ herd, these changes between months were not found to be statistically significant (Table 4.4.2.1). Similarly, data collected from the DZ herd were subset into consecutive months from April to August 2018 and comparisons of bond strengths and node metrics over this time were performed (Figure 4.4.2.2). The same comparison of DZ monthly SRI values showed that bonds across all months were significantly correlated with one another (p < 0.001) indicating that bonds between all dyads remained similar over the 5 months (Appendix 3.2). Comparisons of node metric measurements between April and August (see Appendix 3.3 for full results) showed firstly that although a gradual decrease in weighted degree was observed between April and July (Figure 4.4.2.2), no significant change was found. However, the increase in weighted degree measures observed in August was found to be significant compared to all other months (Table 4.4.2.1).



Figure 4.4.2.1 Changes in night-time node-level metrics over different seasons in Chester Zoo herd. To observe the effect of time on the stability of night-time herd network dynamics, data were subset into 4 non-consecutive months in 2016: February, April, May and December.



Figure 4.4.2.2 Dublin Zoo associations patterns and sociality metrics over 5 consecutive months. To observe the effect of time on herd network dynamics, data were subset into 5 consecutive months in 2018: April, May, June, July, August. weeks. Individual (node-level) sociality metrics were calculated for each month.

Table 4.4.2.1 The effect of time on sleeping network structure. Results of Linear mixed effects models (LMM) comparing weighted degree over non-consecutive months in 2016 (Chester Zoo) and 5 consecutive months in 2018 (Dublin Zoo). Due to the non-independent nature of observed network metrics, significance of the model (P_{rand}) was calculated by 1) calculating the model using the observed networks, 2) comparing the coefficients from the model to coefficients calculated using 4000 permutations of the network, 3) calculating one tailed significance (P_{rand}) by comparing the where the observed estimate fell relative to the permuted estimates. Model estimates, standard error, *t* value and P_{rand} are presented.

			Estimate	s.e.	t	P _{rand}
CZ network						
Degree	February	April	0.31	0.045	6.817	0.113
		May	-0.116	0.1022	-1.41	0.576
		December	-0.615	0.238	-2.577	0.931
	April	May	-0.4270	0.146	-2.915	0.897
		December	-0.926	0.28	-3.3017	0.978
	May	December	-0.498	0.171	-2.910	0.921
DZ network						
Degree	April	August	1.4669	0.2487	5.899	0.0334
	May	August	1.6342	0.2487	6.571	0.0376
	June	August	2.1007	0.2487	8.447	0.001
	July	August	2.2525	0.2487	9.058	0.0588

4.4.3 Social position and sleep quality

Calculations of hours slept per night showed that in both herds, the youngest group members had most amount of sleep per night on average (CZ = 05:04:36; DZ = 04:06:12), and conversely the eldest individuals in the herd had fewer hours of sleep per night (Figure 4.4.3.1). Table 4.4.3.1 presents the LMM results investigating the relationship between average sleep time per night and weighted degree. Model results for both the CZ and DZ herd showed a significant relationship between an elephant's average sleep time per night and the corresponding weighted degree measurement (Table 4.4.3.1). A Mantel test revealed a significant correlation between the day and night-time networks of the CZ herd (Mantel test: r = 0.89, p = 0.016). Similarly, the day and night-time networks of the DZ herd were also positively correlated with one another (Mantel test: r = 0.405, p = <0.001). This indicates that in both herds, an individual's sleeping partners was also more likely to be the same individual they spend time with during the day.



Figure 4.4.3.1 The average sleep per night of elephants in the CZ (A) and DZ (B) herds. The average minutes of sleep per night was calculated for each elephant, with younger herd members having higher amounts of sleep per night compared to older herd members (C).

Table 4.4.3.1 The relationship between average sleep per night and gregariousness. The amounts of sleep per night were compared to individual measures of weighted degree (C). Higher weighted degree measures were significantly associated with high amounts of sleep per night in the DZ herd. However, this association was not found in the CZ herd. Model coefficients, standard error, *t* value, *p* and P_{rand} are presented.

		Estimate	s.e.	t	p	Prand
CZ herd						
Degree	Intercept	2.142	1.047	2.045	0.133	0.259
	Average Sleep per Night	0.0012	0.004	0.291	0.790	0.015
DZ herd						
Degree	Intercept	1.776	0.637	2.787	0.021	<0.001
	Average Sleep per Night	0.011	0.003	3.715	0.004	<0.001

4.5 Discussion

The aim of this study was to use simple measures of association to characterise and explore the night-time network structure of captive elephants. Using night-time CCTV footage of two captive elephant herds, data were collected on the sleeping partners of each herd member. These observations were then used to calculate the herd network and individual sociality of herd members at night. In previous nocturnal studies of captive elephants, researchers have observed the subjects in person using methods that caused as little disturbance as possible (Brockett et al., 1999; Wilson et al., 2006). Recently, however, the use of infrared video cameras has allowed researchers to observe captive herds over night without worry of disturbing the animals' sleep (Tobler, 1992). Additionally, the use of CCTV footage allows for recordings to be stored and viewed at the convenience of elephant management teams. Our findings showed that elephants had preferred sleeping partners that they frequently slept near overnight. In this study, higher Simple Ratio Index values (SRI) between dyads represented individuals that were observed to sleep near one another most often, and lower SRI values represented dyads that were least likely to be observed sleeping near one another. Comparisons to random networks showed that these associations formed a network that was significantly different from random. Despite finding that the elephants had preferred sleeping partners, relatedness was not found to drive the observed association trend in either group of elephants. It is possible that this is also due to the nature of the sample animals. In one group (CZ) there was only one completely unrelated individual, and in the other group (DZ) all individuals were related. Therefore, further exploration of this relationship would require a larger variation in relatedness amongst herd members. In their study of captive chimpanzees, Riss and Goodall (1976) noted that unlike wild chimpanzees, sleeping partner preference in captive groups was peer-dependent, and mainly driven by early rearing experiences. They noted that the long standing partner preferences within their study group were directly related to the group management of the chimpanzees when they were first brought to the facility as juveniles (Riss and Goodall, 1976). Similarly, it is possible that although both elephant herds consisted

of related individuals, partner preference may also be peer-dependent, either based on age between peers or years spent housed together. Despite these findings, comparisons between age difference of herd members and sleep association, and number of years housed together, and sleep associations were not found to be statistically significant in this study. Within the indoor enclosures it was observed that zoo keeping staff created "beds" of raised sand to improve elephant sleep comfort and to ease the transition between standing and recumbency for older herd members. These beds were in specific sites, and it is possible that this management routine is driving the close proximity of the sleeping elephants. Especially in instances when elephants have the freedom to move their indoor and outdoor areas overnight. Preferred or managed sleeping sites could therefore be another potential driver of night-time associations and should be explored in future studies, as previously observed in captive primates (Lock and Anderson, 2013; Riss and Goodall, 1976).

Node-level metrics showed that calves in the Dublin Zoo herd had significantly higher weighted degree scores than the adult females, indicating that calves were more gregarious and therefore more likely to have a sleeping partner than the older herd members. Previous findings on sleep in captive infant and juvenile calves have shown that elephant calves had shorter but more frequent sleeping bouts overnight (Tobler, 1992; Walsh, 2017). Socially, wild elephant calves are known to be highly social, initiating most interactions with other herd members, especially age-mates (Lee, 1987; Lee and Moss, 2014, 2011), and it appears that they maintain this close proximity to herd members over night as well (Stokes, 2017). This difference between adult and calf gregariousness was not found to be significant within the Chester Zoo herd, due to two of the calves being new-born and having fewer observations that included them, unlike the older calf in this herd. However, all three calves present in this herd were observed always sleeping in close proximity to their mothers. At night, calves remain central and in close proximity within the herd to sleep with their mothers or age-mates, similar to that observed in daytime studies of elephant groups (Lee, 1987; Lee and Moss,

2014). On comparing the node-level metrics between the studied herds, it was found that elephants in the Dublin Zoo herd had greater weighted degree scores than their Chester Zoo counterparts. The difference in weighted degree scores reflects the difference in herd size (Chester Zoo n = 7; Dublin Zoo n = 11); Dublin Zoo has more individuals, and therefore more associates for a herd member. Conversely, we found that members of the Chester Zoo herd had higher bond strength averages. In their study of the social dynamics of wild female African elephants (*Loxodonta africana*), Moss and Lee (2011) discuss the determining factors of cohesion in family groups. Based on their findings, they explain that associations and cohesiveness were very strong amongst individuals in smaller groups, but as groups size increased, associations became more fluid and group coordination was more difficult to maintain (Moss and Lee, 2011a). Whilst this may be the case in wild studies, it is unclear if our findings are biologically meaningful or a result of having differing group sizes. A further comparative study of captive herd social structures of similar sizes is needed to explore this.

Elephant associations are known to be flexible and dynamic, changing over days, weeks, and months, as well as seasonally (Moss and Lee, 2011a; T. N. C. Vidya and Sukumar, 2005; Wittemyer and Getz, 2007). Wild elephant dynamics follow a fission-fusion structure that is influenced by seasons of food abundance or shortage; during short drier seasons, herds break down into smaller subgroups, and fuse together into larger herds during rainy seasons (Sukumar, 2003; Wittemyer et al., 2007; Wittemyer and Getz, 2007). Sleep associations of the Chester Zoo herd were compared over four months (February, April, May and December 2016), and revealed a gradual increase in node-level metrics across months. Correlations performed between each monthly network showed that whilst February and April bond strengths correlated, no correlations were found between the other months, indicating that sleep association strengths between females were dissimilar in the other months. There are two possible reasons for this increase; firstly, the increase in weighted degree and average bond strength observed in April may be driven by an increase in sleeping bouts during this period of the year. However, if this was
solely the case, a similar increase in weighted degree and bond strength would have been observed during the first winter period. Alternatively, this increase can be explained by the addition of calves to the herd, thus increasing the number of sleeping partners that individuals could associate with. When new-borns are present, mothers are known to reduce their sleep in order to care for their infants (Siegel, 2008) and zoo elephants have been observed to reduce their sleep in order to collectively care for new calves (Walsh, 2017). It is possible that females increasing their associations to integrate the new calves into the group is a better explanation for higher bond strength measures. However further data must be collected to gain understanding on whether patterns of sleep associations of captive elephants are driven by seasonal changes as found in wild herds, despite having consistent resources present. The changes in weighted degree across months was not found to be statistically significant. It is possible that although bond strengths changed over time, social position did not. In the 5 consecutive months of data from the Dublin Zoo herd (April to August 2018), analysis revealed that SRI values between all dyads across all months were significantly correlated, meaning that in this larger herd, individuals maintained the same and main associates remained similar across over time (Silva et al., 2011a). In this herd, the individual weighted degree and bond strength scores gradually decreased with July and August having the lower values. The changes in weighted degree values were statistically significant. Lower sleeping associations during these periods may be connected to the combination of the longer summertime days and the elephants having access to the outdoor paddock for feeding, thus fewer sleeping associations are occurring during this time. In previous studies captive elephants have also been observed to have lower sleeping during the summer months compared to the winter periods (Tobler, 1992). Tobler (1992) suggests that this seasonality may be driven more by keeper activity during the seasons rather than endogenous seasonality of the elephants.

To investigate the relationship between social position and sleep quality, a linear model was performed to compare individual weighted degree and average

sleep per night. In both herds, this relationship was found to be statistically significant – more gregarious herd members had higher averages of sleep per night. Since the most central herd members were calves, this result was to be expected as young mammals exhibited higher bouts of sleep than adults (Walsh, 2017; Wilson et al., 2006; Zepelin et al., 2005). Whilst weighted degree values reflected the most social sleepers with the herd, eigenvector centrality reflected an individual's connectedness to other well-connected sleepers. This suggests that when central individuals sleep well, those that are connected to these individuals will also benefit from good sleep (Brent, 2015). Conversely, it is possible that disturbances in the sleep of central individuals may also have an impact on the sleep of their neighbours. Finally, we compared night-time associations with daytime observations collected during the same study period. Similar methods were used to calculate bond strength and construct daytime social networks for each herd. In both herds, day and night-time bonds were significantly correlated, indicating that at night individuals preferred to sleep near the same herd mates they spent the most time with during the day.

4.6 Conclusions

Captive elephants appear to have preferred sleeping partners, although this was not found to be driven by relatedness. Calves were found to be the most central individuals in the sleeping networks, choosing to sleep near their mothers or other calves. Despite observed fluctuations in the weight of individual metrics over time, main sleeping partners remained consistent. However, further longitudinal study of night-time social networks is still required to determine whether this seasonality is due to seasonality of management routines, environmental temperature or length of daylight hours. Frequent and consistent study of nighttime elephant bonds from a weekly to a yearly basis will allow elephant managers to understand not only sleep association patterns over time, but also to identify an individual's most consistent and key relationships. It will also allow facilities to monitor the effects of different factors on herd night-time social dynamics, and how these factors could potentially improve or disrupt social ties and ultimately individual sleep patterns. The study of night-time elephant social networks is also a better alternative for monitoring herd dynamics for elephant keeping teams as data can be extracted from recorded video footage that can be stored and used when it suits keepers. This is most often a better alternative for keepers, as it offers little disruption to their daily management and husbandry routines. In this study, day and night-time associations correlated with one another; a larger data set is needed to further validate this finding and to identify instances when no correlation is found and what potential factors may be the cause. Understanding and knowing an individual's preferred sleeping partner(s) would be a beneficial addition to the monitoring already conducted on the quality of sleep of captive elephants and provide evidence for herd cohesion in the management of the species.

Chapter 5: Investigating the relationship between sociality and endocrinology in Asian elephants (*Elephas maximus*)

5.1 Abstract

Glucocorticoids (especially cortisol) are often associated with stress in relation to captive animal welfare. However, they have also been associated with social behaviours, and individuals with strong and stable social bonds may experience reduced effects of environmental and physiological stress. In this study we quantified the faecal glucocorticoid (fGCM) profiles of captive female Asian elephants over time, to explore if an individual's faecal glucocorticoid concentrations reflect its sociality and social position, and to test how significant social events may influence individual endocrinology. Therefore, the aims of this study were to: 1) explore the longitudinal faecal glucocorticoid profiles of captive elephants and to investigate fluctuations in faecal corticosterone levels over time; 2) determine whether an individual's glucocorticoid levels reflect its bond strength and social position, by assessing the magnitude of individual GC secretion in response to social events; and 3) use faecal progesterone levels to explore relationships between social bond strength, adrenal activity and reproductive health. We found that the spring, summer and winter periods were associated with high fGCM concentrations. Significant elevations in fGCM secretion were also coincided with birth and death events . Although no significant relationship was found between social position and magnitude of fGCM secretion, strong bonds appeared to be associated with improved recovery to baseline fGCM levels after birth events. However, in this present study we found no evidence for significant relationships between social bond strength, adrenal activity and reproductive health.

5.2 Background

Most often, in studies of captive animal welfare, glucocorticoids (especially cortisol) are discussed in relation to the adverse effects of chronic stress on animal physiology. Whilst such discussions are still very relevant to captive animal welfare, it is important to distinguish between the normal mechanisms of the biological stress response, and prolonged chronic response. When faced with a particular stressor, the vertebrate body response is to release glucocorticoid (GC) steroid hormones (Munck et al., 1984; Sapolsky, 2002). In mammals, the main glucocorticoid steroid released is cortisol, whilst in reptiles, birds and rodents, corticosterone is the dominant GC. The release of this steroid serves three functions: to direct stimulation of physiological processes in responding to the stressor successfully, to maximise the performance of other stress response mechanisms in the body, and to return processes to normal once the perceived stressor is no longer present (Romero, 2004; Sapolsky, 2002). Regulation of GC release is controlled by a negative feedback system between the hypothalamic – pituitary – adrenal axis (HPA). When a stress is perceived by the brain cortex, neuronal signals are sent to the hypothalamus, which produces corticotropinreleasing hormone (CRH) (Munck et al., 1984; Sapolsky, 2002). CRH from the hypothalamus is stimulates the release of adrenocorticotropic hormone (ACTH) from the anterior lobe of the pituitary gland to the adrenal glands (Munck et al., 1984; Sapolsky, 2002). In the adrenal glands, ACTH promotes the production and release of cortisol, corticosterone and other GCs to reach different effector sites within the body (Munck et al., 1984; Sapolsky, 2002). Once the perceived stress ceases, GCs act as a feedback loop to the brain, stopping CRH and ACTH production. During an acute stress response, GC effects on the body include the release of energy stores into the blood stream, increased blood flow and pressure to circulate oxygen and glucose faster – all to prepare the individual for either confrontation or quick escape from the stressor (Romero, 2004; Sapolsky, 2002). In

the normal context, the stress response is intended to aid an animal in coping with and responding to a perceived stressor effectively, and return the body to the normal state as quickly as possible (Romero, 2004; Sapolsky, 2002). However, if the stressor persists, and the GC secretion remains elevated, its adaptive effects on the body gradually become detrimental (Romero, 2004; Sapolsky, 2002; Sapolsky et al., 1997). Consequences of a prolonged stress response include hypertension, ulceration, anovulation, growth deficiencies, impotency, and impaired disease resistance (Sapolsky, 1999, 1997).

Most often, when considering the relationship between GC release and social behaviour, associations are made with social rank, social approach and inhibition motivation (Koren et al., 2008; Mehta and Josephs, 2010). Studies have also found glucocorticoids such as cortisol to contribute to fearful and social avoidance behaviours (Mehta and Josephs, 2011; Raulo and Dantzer, 2018). Such behaviours can be related to the personality of an individual. However, in natural populations, links between social behaviour and physiological benefits have been made in some species, including non-human primates. Silk et al. (2003; 2009; 2010) found that social integration had positive effects on the reproductive performance, offspring survival and longevity of female baboons. Their data showed that fully socially integrated females were more likely to successfully rear offspring (Silk et al., 2003). Similarly they proposed that females with strong social bonds increased the survival of their offspring as they were less vulnerable to predation, shielded from social conflict, and maternal stress was lower (Silk et al., 2009). Young et al (2014) demonstrated the strong bonds between male macaques (*Macaca sylvanus*) reduced the physiological stress response to high rates of aggression from group mates. In fact, their findings also showed that these strong bonds proved an important buffer to both social and environmental stressors (Young et al., 2014). Furthermore, Wittig *et al.* (2016) reported that the social bond partners of chimpanzees (Pan troglodytes schweinfurthii) had a significant effect on the down regulation of the HPA-axis during both intense stressor encounters and everyday affiliative interactions. In fact, it is possible that in the absence of its bond partner,

an individual may in fact experience an increase the HPA-axis response to stressors (Wittig et al., 2016; Zayan, 1991).

A large body of work has been conducted in characterising and monitoring both reproductive (Brown, 2000a; Brown et al., 2007, 1999; Proctor et al., 2010a) and stress (Brown et al., 2010; Fanson et al., 2014; Foley et al., 2001; Gobush et al., 2008a; Menargues et al., 2012) hormone secretion in elephants (both captive and wild) under different conditions. In the wild, elephants have been found to have seasonal GC secretion, with concentrations elevating during dry seasons in African elephants (Foley et al., 2001; Gobush et al., 2008b), and during the monsoon seasons in Asian populations (Mumby et al., 2015). Captive elephants have also shown monthly variations in GC secretion, with studies on populations in the northern hemisphere reporting markedly elevated concentrations between May and October (Menargues et al., 2012), and January and August (Brown et al., 2010). Brown et al (2010) also successfully characterised the diurnal pattern of captive elephant cortisol secretion, reporting that concentrations were highest in the early morning hours and gradually decreased over the course of the day. Differences in GC secretion between sex and age have also been found. Older animals have been found to secrete higher average GC concentrations compared to younger elephants; however younger animals exhibited greater increases in response to specific stressors (Vijayakrishnan et al., 2018) . Males have been recorded to have higher GC concentrations on average than females, as well as higher concentrations during acute stress responses (Kumar et al., 2014; Vijayakrishnan et al., 2018). Interestingly, Tingvold et al. (2013) found opposite results in African bull elephants, reporting that bulls had lower concentrations compared to females.

Elephants are highly social mammals, and the hierarchical structure and the strength of bonds has been well documented (de Silva et al., 2017; de Silva and Wittemyer, 2012; T. N.C. Vidya and Sukumar, 2005; Wittemyer et al., 2007). Studies assessing the relationship between elephant sociality and glucocorticoid secretion

in wild populations has had interesting results. Foley *et al.* (2000) found a significant relationship between group size and average cortisol concentrations. In larger group sizes (16 members), cortisol levels were significantly elevated among the lowest ranking individuals but this was not the case in smaller groups (Foley et al., 2001). Tingvold *et al.* (2013) reported a more general pattern, stating that larger family groups had higher GC concentrations compared to groups of 2-5 individuals. In a study of the long-term effects of poaching activity in African elephants, Gobush *et al.* (2008) reported that females had significantly lower GC concentrations when close kin or adult matriarch were present, and higher GC levels when they had weak bonds with no family members present in their herd. Most interestingly, Gobush *et al.* (2008) also found that despite being in a high poaching region, females with strong bonds with close kin had relatively low GC secretion compared to those in protected areas.

In the captive environment, different causes for stress in captive elephants have been studied, mainly focusing on the effects of changes in herd composition, and management practices (Edwards et al., 2016; Menargues et al., 2008; Schmid et al., 2001; Wilson et al., 2004b). In general, studies have found that elephants' basal cortisol levels have increased in response to perceived stressors, however they also found variation in individual responses to stress – some elephants had better coping mechanisms than others in certain social contexts (Edwards et al., 2016; Schmid et al., 2001; Wilson et al., 2004b). In captive African elephants, Grand et al. (2012) investigated the correlation between individual personality ratings and cortisol, to observe individual differences. They found that individuals with fearful personalities had higher cortisol levels, whilst individuals with more sociable, aggressive, or equable personalities had lower cortisol levels (Grand et al., 2012). Links between captive management and physiology, especially chronic stress, have been thoroughly investigated (Edwards et al., 2016; Morfeld et al., 2016; Schmid et al., 2001; Wilson et al., 2004a). These effects are of most concern when the social development, reproductive health, and sustainability of captive elephants is considered (Brown et al., 2016; Edwards et al., 2016; Kurt and Garai, 2001; Proctor

et al., 2010b). In the normal elephant endocrinology, the glucocorticoid and oestrogen cycles have an inverse relationship (Fanson et al., 2014). Over the course of the oestrus cycle, hormone levels of one hormone will peak whilst the other troughs. However, during pregnancy, glucocorticoid secretion remains low whilst elevated progesterone levels maintain the pregnancy (Fanson et al., 2014). Chronic elevated secretion of GC during pregnancy is of great concern in captive elephant breeding programs, and a better understanding of the links between social stressors and reproductive health is needed (Brown, 2000a; Freeman et al., 2010).

The extensive literature on GC concentration in both captive and wild populations has shown that a large array of knowledge can be attained from longitudinal collection of GC hormone concentrations. It is possible that as well as giving information about group and individual variation in secretion, analysis of such hormones coupled with data on social bonds and position will also provide information on individual sensitivity and resilience to different stressors. Variation in responses to stress, coupled with information on an individual's social bonds, will help us understand the impacts of not only management practices to a female's physiology but also how changes to her social life might affect her health. It may help us understand whether a female elephant is more likely to isolate herself during stressful situations, or if she is more likely to reinforce her existing bonds with members of her herd. Using faecal samples collected longitudinally, the aim of this study is to: 1) explore the faecal glucocorticoid profiles of captive elephants and to investigate fluctuations in faecal corticosterone levels over time, 2) determine whether an individual's glucocorticoid levels reflect its bond strength and social position, by assessing the magnitude of individual GC secretion in response to social events, and 3) use faecal progesterone levels to explore relationships between social bond strength, adrenal activity and reproductive health.

5.3 Materials and Methods

5.3.1 Study animals and faecal sample collection

Faecal samples for this study were collected from 5 female Asian elephants (Elephas maximus) housed at Chester Zoo, UK: CZM1, CZHW1, CZHW2, CZHW3, CZHW4 (Figure 5.3.1). At the beginning of this study, Chester Zoo housed 6 Asian elephants: 3 related breeding females, 1 juvenile and 1 unrelated female. During this study, three additional calves were born, but faecal samples were not collected for these individuals. As part of routine reproductive monitoring at the zoo, regular faecal samples are collected and stored for the 3 breeding females (CZHW1, CZHW2, CZHW4) every other day and are analysed for faecal progestogen metabolite concentrations (fPGM). Faecal samples are collected between 07:00 and 09:00 by the elephant keepers every other day for all subject animals and immediately frozen. For the purposes of this study, faecal samples were also collected in the same manner from the unrelated female (CZM1) and the juvenile female (CZHW4) and were analysed for both faecal glucocorticoid (fGCM) and faecal progestogen (fPGM) metabolites. Samples used were collected between February 2016 and December 2018 (n = 1636; Appendix 4.1). Chester Zoo currently stores faecal samples for all the elephants that it has housed over the past ten years, and staff collect faecal samples from their current herd regularly. Samples are mainly analysed for reproductive health purposes, however other analyses have been conducted on these samples (Edwards et al., 2016).



Figure 5.3.1. Herd members of Chester Zoo elephant herd. All individuals included in this study are females ranging between 3 and 46 years old. The group consists of four related females and one unrelated female. Three females, (CZHW1, CZHW2, and CZHW3) were pregnant from at the start of this study, and subsequently gave birth during the study period.

5.3.2 Hormone Analysis

The methods used for faecal sample extraction and hormone analysis are those routinely employed by the endocrinologists at Chester Zoo. Faecal samples were collected between 07:00 and 09:00 by the elephant keepers every other day for all subject animals. Each sample was placed in a labelled re-sealable zipper plastic bag which was immediately frozen at -20°C. Samples were extracted using the wet-weight extraction technique adapted from Walker et al. (2002) and described elsewhere (Edwards et al., 2014; Watson et al., 2013), whereby 0.5 g of faecal matter was extracted with 5 ml of 90% methanol, shaken overnight, dried and reconstituted in 1 ml of 100% methanol, and stored at-20°C until being analysed with an enzyme immunoassay (EIA) (CJM006; supplied by Coralie Munro, University of California Davis, CA, USA). Extracted samples were then used in faecal glucocorticoid (fGCM) EIA analysis. The variability in optical density across EIA plates was determined using the following standard competitive EIA protocol, adapted from Munro and Stabenfeldt (1984). In the analysis of fGCM concentrations, each well contained either the same concentration of synthetic corticosterone standard or Asian elephant faecal extract. The polyclonal antibody CJM006 was diluted (1:15,000) in coating buffer (0.05 M NaHCO3, pH 9.6), loaded 50 ul/well on a 96-well Nunc-Immuno MaxiSorp microtitre plate (Thermo-Fisher Scientific, UK), covered with a microplate sealer and incubated overnight at 4°C. Plates were washed five times (0.15 M NaCl, 0.05% Tween 20), and the entire plate loaded with 50 ul/well of corticosterone standard (1.25 ng/ml; C2505 Sigma-Aldrich, Dorset, UK) in EIA buffer (0.1 M NaPO4, 0.149 M NaCl, 0.1% bovine serum albumin, pH 7.0), or Asian elephant faecal extract (diluted 1:10 in EIA buffer) immediately followed by 50 µl /well of horseradish peroxidase conjugate (diluted at 1:70,000 in EIA buffer). Following incubation in darkness, for 2h at room temperature, plates were washed 5 times and incubated with 100 ul/well substrate (0.4 mM 2,20-azino-di-(3-ethylbenzthiazoline sulfonic acid) diammonium salt (ABTS), 1.6 mM H2O 2, 0.05 M citrate, pH 4.0), in darkness, until average optical

density (OD) reached 0.8 to 1.0. The resulting OD of all individual wells was then measured at 405 nm.

The faecal progestogen (fPGM) samples included in this study were analysed from the same faecal samples used for the fGCM analysis. Using near similar methods to that of fGCM EIA analysis, the fPGM EIA the polyclonal antibody CL425 (supplied by Coralie Munro, University of California Davis, CA, USA) was diluted (1:10,000) in coating buffer (0.05 M NaHCO3, pH 9.6), loaded 50 ul/well on a 96well Nunc-Immuno MaxiSorp microtitre plate (Thermo-Fisher Scientific, UK), covered with a microplate sealer and incubated overnight at 4°C. The same plate washing protocol was conducted the next day, and the entire plate loaded with 50 μ /well of progesterone standard (0.156 – 0.78 pg/well) in EIA buffer (0.1 M NaPO4, 0.149 M NaCl, 0.1% bovine serum albumin, pH 7.0). The faecal extract was diluted in EIA buffer immediately (1:40), followed by 50 ul/well of horseradish peroxidase conjugate (diluted at 1:35,000 in EIA buffer). Following protocols for this assay, the plate is incubated in constant light for 2h at room temperature, and then washed 5 times and incubated with 100 ul/well substrate [0.4 mM 2,20-azino-di-(3ethylbenzthiazoline sulfonic acid) diammonium salt (ABTS), 1.6 mM H2O 2, 0.05 M citrate, pH 4.0), in constant light and the resulting OD of all individual wells was then measured at 405 nm.

The assay has been biologically and biochemically validated, with corticosterone antiserum CJM006 cross-reactivities published for use in Asian elephants (Watson et al., 2013). Intra- and inter-assay coefficients of variation (CVs) were <10% and <15%, respectively for high- and low-binding synthetic and biological controls. EIAs were biochemically validated for measuring corticosteronereactive metabolites in female Asian elephant faecal extracts through parallelism (R²=0.99, F_{1,7}=1145.11. P <0.001) and matrix interference assessment (R²=0.90, F_{1,7}=64.70. P <0.001). Intra- and Inter-assay coefficients of variation (CVs) were <10% and <15%, respectively for high- and low-binding synthetic and biological controls (Watson et al., 2013). Samples for the majority of EIA analyses conducted for fGCM was conducted by the author, and when this was not possible, by Chester

Zoo Laboratory Coordinator, Rebecca Mogey (Appendix 4.1). Whilst the main author performed fGCM EIA analyses, fPGM analyses were conducted exclusively by the Chester Zoo Science staff, as part of routine pregnancy monitoring.

5.3.3 Social Network Analysis

To determine the herd's daytime social network and individual sociality, two measures of association were used to quantify the strength of relationship an elephant had with each of its herd mates. First, we used the Simple Ratio Index (SRI) to measure the frequency that two individuals are observed to be in close proximity of one another (Bejder et al., 1998; Cairns and Schwager, 1987; Ginsberg and Young, 1992; Martin and Bateson, 1993). The Simple Ratio Index is most often used when monitoring animals in a captive setting (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Whitehead, 2008b). This particular association Index is calculated as:

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

In this calculation, x represents the number of times individuals A and B are observed together; y_{AB} is the number of observation periods in which A and B are identified but are in different groups not associating with one another; y_A represents the number of observations in which only individual A is observed, and y_B is the number of observations periods where only individual B is observed (Cairns and Schwager, 1987; Croft et al., 2008; Ginsberg and Young, 1992). Values calculated from this index can be between $0 \rightarrow \infty$, with higher values representing stronger bonds, and lower values representing weaker bonds. These values provide the edge weights in the herd networks.

Once the measures of association were calculated, these values were used as edge weights in the herd social networks and thus reflected the strength of association between herd members. Once the herd social network was constructed, measures of centrality were calculated to determine the social position of each elephant within the network. In social network analysis, the weighted degree is defined as the total of the weights on the edges connected to the node (Croft et al., 2008; Whitehead, 2008b). Weighted degree reflects individual gregariousness – its tendency to associate with group members (Croft et al., 2008; Pepper et al., 1999; Whitehead, 2008b, 2008a). Statistical significance from random of the weighted degree was calculated by comparing the coefficients of null models fitted to our observed data, using coefficients calculated on 4000 data stream permutations (Farine, 2013; Farine and Whitehead, 2015b). The data stream permutation method performs swaps of individuals between groups, recalculating the network after each swap. This creates a set of matrices, the number of which corresponds to the number of permutations performed (Bejder et al., 1998; Farine, 2013). To test for non-randomness and avoid biases in further statistical analysis, all node-level metrics were permuted.

5.3.4 Statistical Analysis

Statistical analyses in this study were performed using R (R Core Team, 2017). Calculations of and permutations for the elephant social networks were performed using the *asnipe* package (Farine, 2018). After simple ratio index (SRI) was calculated for all dyads, the top 3 bond strengths were averaged for each female and used as each female's SRI values for all analyses. Individual weighted degree measures were then calculated with the *sna* package (Butts, 2016). First, daily faecal hormone metabolite readings from February 2016 to December 2018 were used to determine baseline faecal glucocorticoid levels for each elephant. This initial analysis of both faecal corticosterone and faecal progesterone metabolite concentrations was conducted using the package *hormLong* (Fanson and Fanson, 2014). Following methods by Edwards *et al.* (2016) and Fanson *et al.* (2014), all concentration values were log₁₀-transformed to normalise data for analysis. Using "hormBaseline" in the *hormLong* library, baseline values for both faecal

corticosterone (fGCM) and faecal progestogen (fPGM) metabolite were calculated employing an iterative process described by Brown *et al* (1996). This method calculates baseline hormone values by systematically removing all concentration values that exceeded the mean plus 1.5 standard deviations (*mean* + 1.5*SD*). Once all values exceeding this were removed, the remaining values were considered to be the baseline hormone range of an individual (Brown et al., 1996). From this calculation, samples within an elephant's baseline range and those exceeding its baseline range – i.e. peaks – can be distinguished.

Analyses of the relationships between corticosterone, progesterone and measures of sociality, we constructed generalised linear mixed effects models (GLMMs) using the package *lme4* (Bates et al., 2015). To explore longitudinal patterns in fGCM secretion in the subject individuals, a generalised linear mixed effects model was used to determine the relationship between daily fGCM secretion and season (spring, summer, autumn, winter) and major social events. Season and major events were fixed effects, whilst elephant ID was controlled for: glmer(fGCM \sim season * events + (1|ID), family = "gaussian"). Major social events that occurred during this study were defined as births, deaths, and temporary separation of herd members (CZM1) during birth events. During this study period, individuals CZHW3, CZHW2, and CZHW1 each gave birth on 16 December 2016, 17 January 2017 and 17 May 2018 respectively. For the safety of the new-born calves, the female CZM1 was separated from the herd over-night close to each expected due date, and then reintegrated with the rest of the herd after each calf was born. The death events included in this study were that of the adult female CZHW2 (September 2018), and calves CZHW4 and CZHW6 (October 2018), after contracting elephant endotheliotropic herpes virus (EEHV).

To investigate the relationship between social position and variation in the magnitude of individual fGCM secretion data were subset between February 2017 and March 2018. Monthly averages of corticosterone concentrations, corresponding monthly SRI and weighted degree were then computed for this period. We calculated the area under the curve (AUC) of all data points that

exceeded an elephant's baseline fGCM values; these were known as "peaks". The function "hormArea" from hormLong was employed to calculate the area under the curve for each peak using the trapezoid method with respect to the baseline cut-off value (Cockrem and Silverin, 2002; Fekedulgen et al., 2007; Littin and Cockrem, 2001). Calculation of the area under the curve gave the magnitude and time taken (in days) for a female's fGCM concentrations to return to baseline range; knowns as "peak recovery time". First, we investigated the relationship between social position and fGCM secretion using a GLMM where the response variable was monthly weighted degree, and the fixed effects were the mean area under the curve, total number of peaks above baseline, and mean concentration of peaks; controlling for elephant ID: glmer(Degree ~ Cort + TotalPeaks + MeanPeaks + MeanAUC + (1|Month) + (1|ID), family = gaussian(link = "log")). Due to the nonindependent nature of network metrics, statistical significance for each fixed effect was obtained by comparing observed coefficients of the model to coefficients of 1000 permuted networks (Farine, 2017). If the observed model coefficients were greater than those generated by the permutations, they were considered to be statistically significant. Furthermore, we analysed the magnitude of female fGCM concentrations in response to the birth events in December 2016 and January 2017 to assess the effects of bond strength (SRI), social position (weighted degree) and recovery time from the peak in fGCM back to baseline range around each event. A linear mixed effects model (LMM) was used to investigate this relationship with the area under the curve as the response variable, weighted degree, major social events, average SRI, recovery from a peak were random effects; and controlling for individual ID: Imer(peak AUC ~ SRI * W.Deg * peak time.dys * Event * (1|Elephant.ID), data=birth1.5.auc peaks,REML = FALSE).

Finally, we constructed an GLMM model to explore the relationship between daily faecal glucocorticoid and progestogen concentrations and social position in 3 cycling females (CZHW1, CZHW2, CZHW3). The response variable was Daily faecal glucocorticoid concentrations; with daily faecal progestogen concentrations (collected on the same day), SRI and weighted degree measures as random effects. Individual ID was controlled for in this model: glmer(Corticosterone

Progesterone + SRI + Weighted degree + (1|ID)),family = gaussian(link = "log")).
First, we conducted the analysis on samples collected before CZHW2 and CZHW3
gave birth; then, the analysis was repeated afterward both females gave birth.

5.4 Results

5.4.1 Longitudinal patterns of faecal glucocorticoids in captive Asian elephants

Faecal corticosterone levels (fGCM) including baseline values were calculated for all 5 elephants included in this study (Table 5.4.1.1). Initial analysis indicated that fGCM levels amongst the females ranged between 2.645 ng/g and 148.636 ng/g, with a mean baseline of 16.561 ng/g. Individual fGCM levels indicate variation between females, with the youngest female, CZHW4 having the highest baseline mean of fGCM concentrations (19.714 ng/g) and the adult female CZHW3 the lowest fGCM concentrations (14.591 ng/g) (Figure 5.4.1.1). Investigation of the herd network showed that the mother and calf dyad in the herd had the higher average association strength and weighted degree scores within the herd (CZHW1: SRI_{avg}= 1.246, weighted degree = 2.433; CZHW4: SRI_{avg}= 1.323, weighted degree = 2.568). These two individuals represented the most gregarious and central individuals in the herd. The unrelated adult female in the group had the lowest average association strength and weighted degree scores (SRI_{avg} = 0.667, weighted degree = 1.695).

To explore the longitudinal fGCM patterns among herd members, we constructed a generalised linear mixed model to investigate the relationship between elephant fGCM concentrations, season and major social events (Table 5.4.1.2). Figure 5.4.1.1 shows the daily fGCM (A), monthly (B) and seasonal (C) concentrations between February 2016 and December 2018. Faecal corticosterone concentrations appeared to be higher during Spring (estimate \pm s.e. = 0.093 \pm 0.011, *t* = 8.651, *p* = < 0.001), Summer (estimate \pm s.e. = 0.063 \pm 0.011, *t* = 5.63, *p* = < 0.001) and Winter (estimate \pm s.e. = 0.076 \pm 0.010, *t* = 7.408 *p* = < 0.001) seasons.

As part of our analysis of elephant faecal corticosterone levels over time, we assessed the effects of major life events on faecal corticosterone secretion. The timescale of this analysis is expressed as days, with Day 1 being first day of sample collection, and data being collected every other day onwards. Along with fGCM samples and observational data, major life events were also recorded over time (Figure 5.4.1.1). A sharp increase and decrease in individual fGCM concentrations were observed during the first birth events (16 December 2016 and 17 February 2017) but no statistical significance was detected (Table 5.4.1.2). Comparatively, a larger peak in fGCM concentrations was observed around the time of the third birth that occurred in the summer (17 May 2018) (estimate \pm s.e. = 0.188 \pm 0.024, *t* = 7.408 *p* = < 0.001). No statistically significant changes in fGCM secretion were detected surrounding the partitioning of CZM1 prior to a birth event or its return to the herd after a birth event (Table 5.4.1.2). Closer to the end of the study period, 3 herd members (CZHW2, CZHW4, CZHW6) died, and after these 3 events an increase in fGCM was detected (estimate \pm s.e. = 0.083 \pm 0.023, t = 3.689 p = < 0.001).

Table 5.4.1.1. The social and faecal corticosterone profiles of the female elephants of Chester Zoo. The age and reproductive status of each female is detailed below. Bond strength values for each female are expressed as the Simple Ratio Index (SRI). For each elephant an SRI value is calculated using an elephant's frequency of association with each of its herd mates, and the sum of its top 3 relationships is used. The cut-off is the threshold value for peaks above the calculated baseline (mean + (1.5*SD)); points below the cut-off are considered to be baseline, and those above are considered to be peaks. Base mean is the average of all points determined to be baseline; peak mean is the average of all points classified as peaks. Finally, peak base is the ratio of peak-to-baseline, calculated as peak mean.

Elephant ID	Age (years)	Parous/Nulliparous	SRI value (from top 3 associations)	Weighted Degree	Faecal Corticosterone (ng/g)						
					min	mean	max	sd	cut-off	base	peak
										mean	mean
CZHW1	36	Parous	1.246	2.433	2.752	17.727	62.052	7.485	28.056	16.44	34.581
CZHW2	21	Parous	0.949	2.212	2.645	15.408	48.806	6.598	21.558	13.39	27.556
CZHW3	14	Parous	0.911	2.0244	3.862	14.591	148.636	10.43	19.995	12.012	28.4
CZHW4	3	Nulliparous	1.323	2.568	4.437	19.714	99.168	9.956	30.324	17.785	40.799
CZM1	46	Nulliparous	0.667	1.695	8.247	18.157	43.165	7.213	23.802	15.93	33.218



Figure 5.4.1.1 Elephant faecal corticosterone levels over time. Hormone samples were collected for 5 captive female Asian elephants (4 adults and 1 juvenile) covered a period of over 1000 days from February 2016 and December 2018. Major life events were also recorded over this time period to assess individual response to possible disruptions to the herd network (A). Daily fGCM concentrations patterns were then subset into average concentrations per month (B) and also analysed per season (C).

Table 5.4.1.2 The effect of season and major life events on daily faecal corticosterone concentrations of female Asian elephants at Chester Zoo. Results are shown for a linear mixed effects model comparing the effect of birth events, herd member deaths, pre-birth partitioning of CZM1, and post-birth re-join of CZM1. The Spring, Winter, and Summer seasons were associated with significantly higher fGCM concentrations. Herd member deaths, and the summertime birth event (May 2018) also marked periods of increased fGCM concentrations.

Fixed effects	Estimate	s.e.	t	Р
Intercept	0.136	0.022	6.198	<0.001
Spring	0.093	0.011	8.651	<0.001
Summer	0.063	0.011	5.636	<0.001
Winter	0.076	0.010	7.408	<0.001
Birth events	-0.025	0.017	-1.492	0.136
CZM1 pre-birth partitioning	0.012	0.057	0.204	0.839
CZM1 post-birth reintroduction	-0.061	0.056	-1.081	0.280
Herd member death	0.083	0.023	3.689	<0.001
Summer * Birth events	0.188	0.024	7.839	<0.001
Random Effect	Variance	SD		
Elephant ID	0.0003	0.0182		

5.4.2 Social position, social events and individual endocrinology

A subset of the data was used to compare individual measures of weighted degree to fGCM secretion. For each female, baseline fGCM range, total number of peaks above the baseline, and mean area under the curve were calculated (Table 5.4.2.1). CZHW1 and CZM1 were found to have the greatest number of peaks above their baseline fGCM range, each having 17 peaks; whereas the calf, CZHW4, had the fewest (n = 8). Despite exhibiting fewer peaks about its baseline range, CZHW4 had higher mean peak fGCM concentrations (30.602ng/g). In terms of magnitude of peaks with respect to the baseline cut-off, the female CZHW4 exhibited the largest AUC value (AUC = 2120.5); in fact, this female displayed a higher AUC average compared to its herd mates (AUC = 260.25). Analysis of the relationship between social position and fGCM response using GLMM found no statistically significant relationship between individual weighted degree and corticosterone, mean AUC, number of peaks above baseline or their mean value (Table 5.4.2.2).

Elephant.ID	Weighted Degree	Baseline cut- off (ng/g)	Mean Area Under the Curve	Total Peaks above cut-off	Peak mean (ng/g)
CZHW1	2.013	10.39	92.51	17	16.226
CZHW2	1.88	16.679	21.835	17	19.891
CZHW3	1.54	9.723	260.25	10	18.79
CZHW4	1.7	25.55	11.557	8	30.602
CZM1	2.06	14.51	84.05	16	21.117

Table 5.4.2.1. Quantifying the magnitude of faecal corticosterone secretion of the female elephants of Chester Zoo. For each elephant the baseline cut-off value, mean area under the curve, total peaks in fGCM secretion above the cut-off value, and mean concentration value of peaks were calculated.

Table 5.4.2.2. Results of generalised linear mixed effects model testing the relationship between individual social position and faecal glucocorticoid secretion. The effect of the fixed effects: average monthly corticosterone concentrations, the total number of peaks above baseline concentrations; mean peak concentrations; and mean area under the curve were assessed on the response variable: monthly weighted degree. Individual identity was specified as the random term. The estimate, standard error, *t* value, *P* and *P*_{rand} (calculated from 1000 permutations) are presented.

	Estimate	s.e.	t	Р	Prand
Intercept	1.910	0.724	2.637	0.008	0.120
Corticosterone	0.266	0.169	1.575	0.115	0.558
Total Peaks (n)	-0.045	0.021	-2.142	0.032	0.622
Mean Peaks	-0.039	0.018	-2.117	0.034	0.667
Mean AUC	-0.002	0.001	-2.399	0.016	0.721

As birth events appeared to have a significant effect on the individual fGCM concentrations, we focused on two of the birth events that occurred in December 2016 and January 2017 to investigate the individual corticosterone response to social events. Using all fGCM points that exceeded the baseline cut-off, we once again calculated the area under the curve (AUC) to study each elephant's response to birth events. For this analysis only the females CZHW1, CZHW2 and CZHW3 were included because data were collected consistently throughout the observed period for these three individuals (Figure 5.4.2.1). Our observations revealed that between November 2016 and February 2017, the female CZHW2 experienced fewer peaks (n = 4) in fGCM levels compared to the other two females. CZHW2 also had the largest variation in corticosterone responses (AUC range = 4.815 – 254.95) during this time, however the female CZHW3 had the largest single fGCM response (AUC = 351.619) between all three females. Subsequent to this, it took 41 days for this female's fGCM concentrations to return to baseline range. The oldest of the 3 females, CZHW1, did not have such high AUC values; yet, this female experienced more peaks above the baseline cut-off value over this period (n = 12). Average recovery time from peak concentrations back to baseline ranges also varied between individuals. Despite experiencing the least number of peaks in fGCM concentrations, CZHW2 had a recovery time of 11.7 days. CZHW3 had an average recovery time of 8 days. Interestingly, although it experienced the greatest number of peaks, CZHW1 had an average recovery time of 2.33 days. A linear mixed effects model (Table 5.4.2.3) showed that event type and peak recovery time had a significant effect on the size of the area under the curve during this period, with an increase in AUC magnitude during birth events (estimate \pm s.e. = 1884.37 \pm 637.729, t = 2.932, p = <0.01). Although neither the simple ratio index nor weighted degree measures had a significant effect on the AUC, interactions between these factors and peak time and events were significant. The interaction between association strength (SRI) and peak recovery time was associated with smaller AUC by $23.303 \pm$ 11.80 (estimate \pm s.e); however, the interaction between weighted degree and peak time were associated with a larger AUC (estimate \pm s.e. = 31.64 \pm 12.76, t = 2.481, $p = \langle 0.01 \rangle$. We also found the that partitioning of CZM1 from the herd prior to the birth events also had a significant association with AUC magnitude.



Figure 5.4.2.1 Elephant faecal corticosterone secretion during two birth events. Focusing on the 3 parous females (CZHW1 = red; CZHW2 = green; CZHW3 = yellow) in the herd, we investigated individual fGCM secretion in response to birth events (blue lines) on day 320 and 352. A female's response to each birth event was calculated using area under the curve with respect to the baseline cut-off (black line) and the number of days taken for fGCM levels to return to below the baseline cut-off.

Table 5.4.2.3 Results of linear mixed effects model testing the factors affecting the area under the curve of individual corticosterone response during two birth events. Factors include measures of association, the Simple Ratio Index and Composite Sociality Index; peak time, which is the time it takes (in days) for a peak in corticosterone to return to baseline values; and life events, which include birth, routine, and partitioning events. All statistically significant (<0.05) factors and interactions are highlighted in bold lettering.

Fixed effects	Estimate ± s.e.	df	t	Р
Intercept	126.89 ± 69.88	23	1.816	0.0824
SRI	136.30 ± 73.67	23	1.85	0.0772
Weighted degree	-123.56 ± 64.73	23	-1.909	0.0688
Peak recovery time (days)	-37.74 ± 17.61	23	-2.143	0.043
Birth events	1884.37 ± 642.75	23	2.932	0.007
CZM1 pre-birth partitioning (C)	133.70 ± 12.79	23	10.454	<0.001
SRI * Peak recovery time (days)	-26.30 ± 11.80	23	-2.229	0.036
Weighted degree * Peak recovery time (days)	31.64 ± 12.76	23	2.481	0.021
SRI * Birth events	799.50 ± 325.82	23	2.454	0.022
Weighted degree * Birth event	-1164.96 ± 429.55	23	-2.712	0.012

5.4.3 Sociality, adrenal activity and reproductive health

We investigated the relationship between sociality, adrenal activity and reproductive hormones. Again, we focused on the three individuals for which faecal corticosterone and progesterone results were consistently recorded, CZHW1, CZHW2 and CZHW3. Before CZHW2 and CZHW3 gave birth, no relationship was found between fGCM and fPGM concentrations; but one was found between fGCM concentration and weighted degree (Table 5.4.3.1). Analysis conducted on hormone concentrations after CZHW2 and CZHW3 gave birth also found no relationship between progesterone and corticosterone concentrations in these individuals. Again, weighted degree and additionally SRI were observed to significantly associate with fGCM concentrations. Nonetheless, Figure 5.4.3.1 shows that corticosterone and progesterone levels appear to have an inverse relationship.

Table 5.4.3.1 Results of generalised linear mixed effects model investigating the relationship between adrenal activity, reproductive endocrinology and sociality of 3 captive female elephants. Daily faecal glucocorticoid concentrations (response variable) were compared with corresponding daily faecal progestogen concentrations, SRI and weighted degree measures (random effects); whilst individual ID was controlled for. Analysis was conducted before CZHW2 and CZHW3 gave birth (a), and afterward. Model estimates, standard errors, *t* and *P* values are presented. All statistically significant (<0.05) factors and interactions are highlighted in bold.

		Estimate	s.e.	t	Р
a) Pre – births	Intercept	-0.019	0.098	-0.195	0.846
	Progesterone	-0.030	0.022	-1.359	0.174
	SRI	-0.122	0.100	-1.224	0.221
	Weighted degree	0.158	0.077	2.057	0.040
b) Post – births	Intercept	-0.113	0.130	-0.872	0.383
	Progesterone	0.025	0.032	0.797	0.425
	SRI	-0.243	0.117	-2.073	0.038
	Weighted degree	0.223	0.106	2.103	0.036



Figure 5.4.3.1 The interaction between faecal progesterone and faecal corticosterone of 3 parous female Asian elephants. From the start of the study period, progesterone levels remained elevated in all three females during their pregnancy and shortly after giving birth (a). During this time, corticosterone levels were observed to be supressed. After each female gives birth (b), its progesterone levels begin to decrease over time, and it appears that when corticosterone concentrations are elevated, progesterone levels are low, and vice versa.

5.5 Discussion

The aim of this study was to investigate how social factors influence the faecal glucocorticoid profiles of captive Asian elephants, using samples collected

longitudinally. Our findings showed variability in fGCM concentrations between individuals. The calf CZHW4 was found to have the highest mean baseline fGCM concentrations, whilst the female CZHW3 had the lowest mean fGCM concentrations. A similar pattern to what was found in Kumar *et al.*'s (2014) results of age differences between female GC secretion. Although individual variation in baseline fGCM concentration amongst elephants is to be expected, this finding is contrary to what has been observed. Vijakrishnan et al. (2018) observed the opposite pattern. In their study, older females exhibited higher mean GC concentrations than younger elephants. Amongst the adults however, we observed that the older females, CZM1 and CZHW1, had higher mean baseline concentrations compared to the younger adult females, CZHW2 and CZHW3. Exploration of long-term fluctuations in faecal corticosterone concentrations showed that season had a significant effect on fGCM concentrations. Patterns in faecal corticosterone concentrations showed that average monthly concentrations were significantly higher during spring, summer and winter. Concentrations were found to be slightly higher in the summer and spring months than in the winter months. Similar patterns have been recorded in the seasonal patterns of zoo elephant salivary cortisol (Menargues et al., 2012). It is possible that this is due to an increase in the herd's activity as they spent more time outdoors and had increased enrichment within their paddock. Mumby et al. (2015) found that in semi-captive elephants in Myanmar, glucocorticoid concentrations were highest just before the monsoon months (June, July, August), which also marked the end of their rest period and resuming of their work in timber camps. Increases in glucocorticoid concentrations during the colder winter period are also to be expected in captive Asian elephants (Brown et al., 2010) and more specifically to this herd, increases in fGCM concentration also corresponded with the planned births that occurred in this time.

Our study of longitudinal hormone patterns also included observing the effect of elephant life events on individual endocrinology. These major events included birth events, separations, group re-joining events, and deaths. Although the effect of the first two birth events were not found to be statistically significant,

the birth event in May 2018, CZHW1 giving birth to a calf, and the death of CZHW2 and CZHW4 had significant effects on individual fGCM secretion. In the females that gave birth during this study (CZHW1, CZHW2 and CZHW3), elevated glucocorticoids such as cortisol mark the onset of parturition (Brown, 2000b; Fanson et al., 2014), although the first two birth events were not found to have a significant effect. In these females, this increase was followed by a steep post-partum decline in fGCM concentrations. The elevated corticosterone levels in the other herd members present during these birth events may have been in response to the females' behaviour upon the onset of parturition. During birth events, female elephants have been observed to be excitable, vocalise and surround the herd that is giving birth (Daniel, 1998; Moss et al., 2011). Historically, new-born calves have been injured in the past and it is now part of the zoo's management protocol to house the unrelated female, CZM1, separately in an adjacent section overnight leading up to the due date. Once the calf is born this female is reunited with the rest of the herd as soon as possible. Although the partitioning and reintroduction of CZM1 during birth events did not have a significant effect on elephant fGCM secretion, their return back into the group after the birth event was associated with a significant decrease in fGCM secretion; this decrease in fGCM secretion might actually be in response to the end of the birth event as opposed to CZM1 re-joining the group. Data collection was inconsistent for this female meaning that we did not have fGCM data covering the time of initial separation. However, due to the unexpected nature of the birth of the third calf in May 2018, CZM1 was not separated from the herd, and fGCM concentrations appeared to match the characteristic increase pre-parturition and decrease post-partum observed in the other herd members.

To determine the effect of social events on individual faecal corticosterone secretion, we focused on the females' response time by calculating the area under the curve with respect to maximum baseline values. Our observations revealed that the oldest of the 3 females, CZHW1, experienced the most peaks above the baseline cut-off value over this period, but also had the lowest peak recovery time.

This suggests that although this female had a higher sensitivity to external stressors than its herd mates, it was able to recover from the stressor relatively quickly. Similarly, wild adult female Asian elephants were observed to have generally higher GC concentrations, however the magnitude of their response to intense anthropogenic stressors was relatively low (Vijayakrishnan et al., 2018). It was suggested that this finding reflected the females' habituation to the known stressors within their environment (Vijayakrishnan et al., 2018). It is possible that CZHW1 has also become habituated to common stressors within its zoo environment, leading to quicker recovery back to baseline concentrations after encountering a stressor. It must also be noted that this female was being treated for chronic arthritis, which could also have contributed to its increased number of fGCM peaks. Whilst CZHW1 had the largest variation in corticosterone responses during this time, the female CZHW3 had the largest single response that overlapped the first birth event. It appears that fGCM concentrations in this female remained elevated until parturition. The area under each peak correlated significantly with the number of days it took for an individual's fGCM levels to return to below the baseline cut-off value after a peak. None of these females had showed significant peaks above baseline at the time of the second birth event. This suggests that the elevated fGCM levels observed during the first birth were in response to the novelty of the event; but there was less novelty to the second birth event. The variation in the magnitude and time taken for fGCM concentrations to return to baseline are important indicators to describing fGCM secretion (Cockrem and Silverin, 2002; Littin and Cockrem, 2001). Whilst fluctuations in fGCM secretion can be expected, understanding how long the stress response takes to return to baseline levels can help determine what different individuals perceive as stressful. No significant relationship was found between weighted degree, mean magnitude of fGCM response (AUC) or peaks about baseline ranges. Despite this, significant links between bond strength, sociality and the stress response have been found in elephants and other mammalian, bird and reptile species (Beery and Kaufer, 2015; Gobush et al., 2008b; Hennessy et al., 2008; Wittig et al., 2016; Young et al., 2014). Koren et al., (2008) observed that dominant rock hyrax males (Procavia capensis) most often had higher GC concentrations compared to subordinate males.

Oppositely, Foley et al. (2000) observed that in large African elephant female groups, GC concentrations were highest among lower ranking individuals. We did, however, find that the interaction between higher SRI, weighted degree values and peak recovery time had lower fGCM responses during birth events. This suggests that although that birth events were a source of social excitement for the herd, well connected individuals were better able to recover from the event. Affiliative bonding and the presence of social partners has been shown to reduce individual fGCM response to novel or intense stressors (Hennessy et al., 2008; Wittig et al., 2016; Young et al., 2014). Female Guinea pigs (*Cavia porcellus*) were observed to have a reduced plasma cortisol response to a novel cage when a female or male partner was present (Hennessy et al., 2008). In both chimpanzees and wild macaques, the presence of preferred partners attenuated individual responses to daily and intense social stressors (Wittig et al., 2016; Young et al., 2014). The presence of related and older individuals improves calf survivorship and female longevity in Asian elephants (Hawkes, 2004; Lee and Moss, 2011; Lynch et al., 2019). It is possible that the experience of individuals present during births may also be a factor for reduced fGCM levels during this type of event.

Finally, we assessed the relationship between corticosterone and progesterone concentrations. In their study, Fanson *et al* (2014) found a significant inverse correlation between cortisol and progesterone. They found that during periods of elevated progesterone, cortisol was low and *vice versa* (Fanson et al., 2014). Meyer *et al.*, (2004) also reported that cortisol remained stable over the course of gestation. Although there appeared to be a similar interaction between corticosterone and progesterone concentrations in this study, no statistical significance was found. This may be due to our small sample of individuals. Samples from the three individuals used to make this comparison covered a period when all three females were pregnant, thus their progesterone levels were persistently high for most of the observation period, until the onset of parturition. Fanson *et al* (2014) highlight that the agonistic and antagonistic effects of cortisol are key to the timing of important events in the oestrus cycle – especially ovulation. Additionally,

unlike these three females, analysis of reproductive hormones is not routinely conducted on the adult female CZM1 and the calf CZHW4. CZM1 was not included in the reproductive monitoring of the herd due to evidence of non-cycling, however Fanson *et al* (2014) predict that in non-cycling elephants, pre-ovulatory cortisol concentrations may be lower than expected normally and therefore inhibit ovulation. Whilst faecal glucocorticoids are not direct predictors of reproductive function (Brown, 2000b), the role that they play in normal reproductive function must be investigated in all female elephants (Fanson et al., 2014; Meyer et al., 2004).

5.6 Conclusions

A key aim of this study was to investigate the effect of social bonds and social position on the endocrinology of captive Asian elephants. We found that higher bond strengths were associated with higher faecal corticosteroid concentrations. The variability we observed in these findings, however, indicate that extremes are more magnified in smaller herds, and suggest that studies of larger herds are necessary to test the robustness of our findings. Birth events were found to be significant social stressors for the group. Whilst daily responses to management and day-to-day herd interactions may be difficult to detect (Menargues et al., 2012), distinguishing events that illicit a group response versus an individual response are important in herd management. With that being said, individual variation in fGCM secretion can be characterised by the magnitude and time it takes for individuals' responses to return to baseline values. Although zoo facilities monitor the cyclicity of their breeding elephants regularly, many individuals – including non-cycling and young females – are excluded. Data from Fanson et al (2014) shows that glucocorticoids have a key role in the timing of reproductive mechanisms, and their work supports the need for both progesterone and glucocorticoids to be analysed by for all captive female elephants as a method of monitoring reproductive health.
Chapter 6: The social history and reproductive rates of female Asian elephants (Elephas maximus) in the UK & European captive elephant population

6.1 Abstract

The aim of this study is to conduct a broad investigation of how social bonds may impact on the welfare of captive Asian elephants in European zoos. Using historic and current management data, we investigate how variation in herd stability and social structure may impact on the birth rate, calf-rearing success and longevity of female elephants in zoos with an active breeding programme. Factors used to assess herd stability and social structure include the number of inter-zoo transfers experienced by female elephants, and the presence of relatives and former herd mates. We use these factors to test if herd stability and social structure is associated with variation in reproductive rate and calf survival. We find that the presence of relatives or former herd mates, and larger herd sizes, each appear to have beneficial effects for breeding success. Conversely, more frequent inter-zoo transfers were associated with evidence of negative effects on breeding success and may impact negatively on female longevity. Our findings thus add to growing evidence that the social environment and life events experienced by elephants in captivity contribute significantly to their reproductive success and social and physical development.

6.2 Background

The purpose of the modern zoo is to act as a centre for *ex situ* conservation efforts including breeding programmes, research centres and stores of genetic diversity. Although many zoos hold collections with hundreds of species, a main challenge is the survival of these species outside of their natural habitats (Tidière et al., 2016). Many zoos aim to become genetic reservoirs of biodiversity and in doing so are driven to conserve sustainable, genetically varied populations (Lees and Wilcken, 2009). A sustainable population is one that has all of its resources available and can persist without external supplementation (Lacy, 2013; Lees and Wilcken, 2009). In the zoo setting, one translation of a sustainable *ex situ* species population would be one where all resources and enrichment required were provided internally, where growth rates were being met and where no supplementation of external individuals or resources was required (Lees and Wilcken, 2009). However, achieving these goals has been challenging for many zoos as it is difficult to control for factors such sex ratio skews, inbreeding, high death rates and low birth rates (Lees and Wilcken, 2009).

Survivorship of individuals in zoos has been more difficult to control in some species than others. A comparative analysis of longevity and senescence in mammals by Tidière *et al.* (2016) explored whether animals lived longer in zoos. They found that 84% of the species in their study had higher survivorship in captivity than in the wild, and this was especially true for shorter-lived mammals (Tidière et al., 2016). In zoos, shorter lived mammals benefitted from reduced environmental pressures that drives mortality in these species (Tidière et al., 2016). By contrast, larger species, that have longer life cycles and mature at slower rates, did not have increased survivorship in captivity (Tidière et al., 2016). The authors suggest that this is due to the early onset of reproductive maturity and breeding that these individuals experience under zoo conditions. Thus, they emphasize that more needs to be done in the management of long-lived animals if survivorship is to improve (Tidière et al., 2016). Whilst zoos struggle to sustain captive population numbers in some species, they have success in others. Survivorship in orangutans

(*Pongo spp*) has been observed to be significantly higher in wild individuals compared to *ex situ* orangutan populations (Wich et al., 2009). Survivorship of young individuals has been especially difficult in captive populations (Wich et al., 2009). On the other hand, reindeer (*Rangifer tarandus*) and red deer (*Cervus spp*.) were observed to have increased survivorship in captivity compared to wild populations (Müller et al., 2010). Roe deer (*Capreolus capreolus*) only had increased in survivorship in zoos when they were intensively managed, otherwise they had significantly lower survivorship to compared to wild roe deer (Müller et al., 2010).

The viability of the captive elephant population has been met with criticism and doubt over the years. Low reproductive rates, high mortality, poor body condition and irregular social groups have been identified as factors affecting the survivorship in both African (*Loxodonta africana*) and Asian (*Elephas maximus*) captive elephants (Clubb et al., 2009; Clubb and Mason, 2002; Rees, 2003). Although in most recent years, elephant reproduction in zoos has increased in UK and European collections (Schmidt and Kappelhof, 2019), elephant survivorship in zoos is still noted to be lower than in wild populations (Clubb et al., 2009). A comparison between wild and captive individuals shows that wild individuals survive an average age of 56 years in African elephants, and 47 years in Asian elephants (Moss et al., 2011; Sukumar, 2003). Their captive counterparts, however, have reduced average life spans of 12 and 18 years respectively (Clubb et al., 2008). Furthermore, fecundity is low in captive elephants, with most females of reproductive age not being bred or suffering from reproductive pathologies (Brown et al., 2016; Clubb et al., 2009; Faust et al., 2006). Also, more females are aging, reducing the number of reproductively active individuals, while the number of males is increasing (Faust et al., 2006; Wiese, 2000). Population modellers have predicted that these factors have made the captive elephant populations in North America and Europe unsustainable, and likely to go extinct in the next 30 years (Faust et al., 2006; Wiese, 2000; Wiese and Willis, 2004). In the model developed by Faust *et al* (2006), the captive elephant population declined by 2% every year for the next 30 years. Whilst their predictions suggested that zoos would be unable to stop this decline in elephant numbers, a combination of different strategies could

help slow down this trend (Faust et al., 2006). They suggest that in order to improve population viability, annual birth rate must drastically increase (Faust et al., 2006). Wiese (2000) also discusses the need for increased birth rates in North American zoos in order to produce self-sustaining populations. They report that in addition to reducing mortality rates, zoos must double the number of births per year to take into account a skew in the sex ratio of calves (Wiese, 2000).

Since the publishing of these reports, there has been an improvement in the reproductive rates of captive elephants in the UK and Europe (Schmidt and Kappelhof, 2019). A 76% increase in calf births in recent years has been attributed to more zoos choosing to keep their elephants in maternal herd structures similar to those of their wild counterparts (Schmidt and Kappelhof, 2019). Both the Asian and African elephant species cooperatively rear their offspring in groups of maternal relatives (Lee, 1987; Moss and Lee, 2011b; T. N. C. Vidya and Sukumar, 2005). Within these herds of related individuals females gain maternal experience through participation in allomothering behaviours, act as buffers to alleviate social stress on pregnant females, invest in their inclusive fitness and are guaranteed reciprocated care of their own offspring by fellow herd mates (Moss and Lee, 2011b). Recently, studies have shown that the presence of sisters increases a female elephant's reproduction rate per year (Lynch et al., 2019). The aim of this study is to conduct a broad investigation of how social bonds may impact on the welfare of captive Asian elephants in European zoos. Whilst studies have already been conducted on the survivorship and welfare of elephants in European zoos (Clubb & Mason, 2002), this study will aim to look at the birth rate, rearing success and longevity of zoo elephants in breeding groups, as it pertains to their sociality and herd stability. Studies conducted by authors such as Kurt and Mar (1996), Prado-Oviedo et al. (2011), and Hartley and Stanley (2016), have highlighted that the social environments and life events experienced by elephants in captivity all contribute to their reproductive success and social and physical development. The present study complements these previous investigations by testing for relationships between herd composition and breeding success for Asian elephants in UK and wider European zoological collections, using historic and current

management data. This will also allow us to assess the effect of having relatives present and the number of inter-zoo transfers on reproductive rate, calf rearing success and longevity of female Asian elephants.

6.3 Methods

6.3.1 Data Collection

Data for this study were collected using the Zoological Information Management Software (ZIMS) database (Species360, 2019). ZIMS is a global webbased database utilised by zoological collections to store information regarding the management, movement, husbandry and veterinary care of all individual animals and species populations in their care (Species360, 2019). The robustness of the software allows for zoo collections to record daily, real-time data about their animals, as well as track each animal's life history over time (Species 360, 2019). ZIMS is used by more than 40 member institutions and other conservations bodies globally (Species360, 2019). Data were collected for 93 female Asian elephants (Elephas maximus) from 13 different UK and European zoos. For the purposes of this study, the females included were of breeding age ranging from 8 to 59 years old. The ZIMS database provides historical and current data on the movements, health and reproduction for each individual recorded on the database. In the current study, data collected for each elephant included: current age or age at death; number of offspring and descendants; parent IDs; siblings (from maternal lineage); wild caught or captive born; transfers between collections; and time spent in each collection (see Appendix 5.1 for full list of factors). Data were also collected on each female elephant's current status (dead or alive), number of inter-zoo transfers, number of management transfers experienced, its age upon arrival to a new zoo, herd size, the number of calves a female gave birth to at each zoo, and the presence or absence of family members. All females included in this study had some exposure to a breeding bull during their reproductive years in captivity. However, whether this exposure was in the form of a bull being a resident within

the female's herd or through temporary transfers for mating was not always clear. Therefore, for calculations of mean birth rate per zoo (number of calves/years housed at a zoo), the data were subset to only include females the were known to be housed with resident bulls. For this study, family members were defined as mothers and adult sisters from the maternal lineage. Relatedness was determined by using the "Pedigree" tool within the ZIMS database. This tool tracks the descendants, parents and siblings (maternal and paternal) of specified individuals. To track a female's rearing success, the total number of offspring produced was recorded and subset by whether the offspring died before or survived past 3 years old, and whether surviving offspring lived into adulthood (> 8 years old).

6.3.2 Data Analysis

Linear mixed effects models (LMMs) were used to explore factors explaining variation in the rearing success of female Asian elephants in European. Models were first conducted to determine whether the number of times female elephants were transferred between institutions predicted their calf rearing success. For this model the dependent variable was the total number of calves alive, with fixed effect being total zoo transfers, total residencies and birth type of an individuals, whilst controlling for elephant ID and elephant age: Imer(total alive ~ total transfers + total zoos + birth type + (1|ID) + (1|Age). Secondly, a model was performed to determine the effect of female elephants being housed with other related adult females on calf survival. Total offspring produced by a female, the birth rate per zoo, and offspring alive over 3 years old and over 8 years old were fixed factors. The presence of relative, former herd mates and average herd size were all fixed effects, with elephant age and zoo ID as random effects: $Imer(x \sim relatives present$ + former herd mates present + average herd size + (1|Age) + (1|Zoo ID). Finally, we assessed the relationship between the number of transfers a female experienced and individual longevity. This was conducted by comparing age of female to total zoo transfers, birth type, status at time of study (dead or alive), and average herd size: Imer(age ~ total zoos + birth type + longest residency + status + average herd

size + (1|elephant ID). All data analyses were conducted using *lme4* package in R (R Core Team, 2017).

6.4 Results

Based on our data, the average herd size of our sample population was 5 elephants in a group and the average age of our sample population was 35 years old (wild-born: 39.4 y; captive-born: 33.4y) (Table 6.4.1). Based on birth type, 46.2% of breeding females were wild caught, 42 % were captive born and 11% had unknown origins according to ZIMS. Females included in this study gave birth to a total of 114 calves (both living and deceased at time of study). Twenty-three percent of females were housed with adult relatives, whilst approximately 70% of females lived in groups where no relatives were present. Most females did not encounter former herd mates (57%) and 37.6% were housed with former herd mates.

6.4.1 Herd stability and rearing success

First, we tested if the number of times female elephants were transferred between institutions predicted their calf rearing success. Of the offspring recorded (n = 114), 47.3% (n = 56) were found to still be alive at the time of data collection. Of these 56 offspring, 47 were recorded to be above the age of 3 years old (4 + years old), and 22 (12 + years old) had survived to adulthood. Additionally, we examined the relationship between herd demographics and the proportion of calves that died. Fifty percent of the females (n=46) included in this study gave birth to calves (n=106). Of these females, 69.5% experienced the death of at least one calf. The results in Table 6.4.1.1 shows that the total number of living offspring a female had was negatively affected by increased movement between zoos. Whereas more long-term zoo residencies were associated with having more living offspring. **Table 6.4.1** Summary of Asian elephant demographics in UK and European herds. The summary included the number of elephants (N) and distribution of age, birth type, total number of offspring produced in a female's lifetime, and whether a female was housed with family member or former herd mates. The range, mean and standard deviation are presented for each category.

		Ν	Range	Mean	Standard Deviation
Zoo elephant Age (years)	Captive-born	39	8 - 54	33	12.68
	Wild	43	8 - 59	35.5	13.25
	Unknown origin	11	58	39.75	13.23
Number of		68			
Zoo		(institutions	0-11	3.130	2.05
Transfers		included)			
Number of Offspring	Captive-born	74	0-8	1.897	1.77
	Wild-born	32	0 - 5	0.76	1.84
	Unknown origin	8	0-3	0.72	1.77
Number of Relatives Present	Yes	22			
	No	65			
Presence of Former Herd mates	Yes	35			
	No	53			

Table 6.4.1.1 A summary of the parameters from linear mixed effects model exploring the relationship between herd stability and female calf rearing success. A female's total number of offspring alive at the time of this study were compared with the total number of zoo transfers, total zoo residencies and the birth type of a female; controlling for elephant ID and age. Parameters of the model include, estimate ± standard error, degrees of freedom, t value, and p value. Significant effects are highlighted in bold font.

		Estimate ± s.e.	df	t	Р
Total calves alive	Intercept	0.77 ± 0.253	88	3.036	0.003
	Total Zoo Transfers	-0.238 ± 0.114	88	-2.083	0.0401
	Total Zoo Residencies	0.309 ± 0.152	88	2.026	0.0458
	Unknown Birth Type	-0.561 ± 0.352	88	-1.595	0.114
	Wild-Born	-0.425 ± 0.248	88	-1.703	0.092

6.4.2 The effect of group composition on calf rearing success

Next, we investigated the effect of female elephants being housed with other related adult females or female herd mates on calf rearing success. Twentytwo percent of breeding females in this population were housed with family members and 35% of females were housed with former non-related herd members. The presence of relatives and former herd mates was found to be positively related to the total number of calves a female gave birth to (Table 6.4.2.1). Average herd size and the presence of former herd mates also had a significant positive effect on calves surviving over 3 years old. However, only average herd size appeared to have a significant relationship with offspring surviving to over 8 years old (Table 6.4.2.1). We found no significant effect of the presence of former herd mates or relatives on the birth rate of females per zoo.

6.4.3 Inter-Zoo transfers and female longevity

We assessed the relationship between the number of transfers a female experienced and individual longevity. We found a significant relationship between the average residency of an elephant and its age (Figure 6.4.3.1). As may be expected, older females were more likely to have been transferred between multiple zoos; however, there was also positive relationship between age at the time of data collection and the maximum duration of residency at a single zoo (Table 6.4.3.1a). To explore this relationship further we focused on females that are now deceased (n =36). Again, we found that long-lived females had longer residencies in a single zoo than short-lived females (Table 6.4.3.1b). We also found that in both living and deceased females, older females were more likely to be wildborn or of unknown origin. As a way of measuring the longevity of a female's genetic line, we also looked at the longevity of its offspring past the age of 3 years old (Table 6.4.2.1). **Table 6.4.2.1** Result of full LMMs exploring the effect of the presence of family members or former herd mates on a) the total number of offspring a female produced, b) a female's mean birth rate a female per zoo (number of calves birthed/years spent at a zoo), c) the number of calves reared to over 3 years old, and d) the number of offspring that survive to adulthood. Family members are defined as adult maternal relatives of the breeding females, and former herd mates are defined as non-relative females that a particular female was housed with at a previous zoo. Parameters of the model include, estimate ± standard error, degrees of freedom, t value, and p value. Significant effects are highlighted in bold font.

	Fixed effects	Estimate ± s.e.	df	t	Р
a) Total number of offspring	Intercept	-0.266 ± 0.455	42.2	-0.585	0.561
	Relatives Present	0.991 ± 0.422	78.66	2.347	0.021
	Former herd mates present	0.557 ± 0.368	69.014	1.512	0.135
	Average Herd Size	0.178 ± 0.059	56.52	3.207	0.003
b) Mean birth rate per zoo	Intercept	0.0002 ± 0.066	53.135	0.004	0.997
	Relatives Present	0.224 ± 0.155	65.42	1.566	0.123
	Former herd mates present	-0.0002 ± 0.147	63.53	-0.002	0.999
c) Calf reared to over 3 years old	Intercept	-0.186 ± 0.252	45.05	-0.739	0.463
	Average Herd Size	0.069 ± 0.033	60.338	2.117	0.038
	Relatives Present	0.363 ±0.233	78.862	1.561	0.122
	Former herd mates present	0.493 ± 0.204	69.591	2.419	0.018
d) Calf surviving to over 8 years old	Intercept	-0.273 ± 0.165	78	-1.655	0.101
	Average Herd Size	0.066 ± 0.021	62.163	3.158	0.002
	Relatives Present	0.181 ± 0.156	79.232	1.154	0.252
	Former herd mates present	0194 ± 0.133	67.808	1.460	0.148



Figure 6.4.3.1 The relationship between average residency (in years) at a zoo and age of a female. Older females were found to spend significantly more time at a zoo compared to younger females. This significance was found both for females that were already deceased (estimate \pm s.e. = 0.715 \pm 0.150, df = 29, t = 4.767, p < 0.001) and for those that were still alive (estimate \pm s.e. = 0.778 \pm 0.091, df = 66.996, t = 8.565, p < 0.001).

Table 6.4.3.1 Results of full LMMs exploring the effect inter-zoo movement and female longevity. To assess this relationship, the response variables were a) age of all females sampled at the time of the study and b) age of females that were deceased at the time of study. Models included Zoo ID as random effects, and fixed effects included birth type, total zoos moved to, longest zoo residency and average herd size. Parameters of the model include, estimate ± standard error, degrees of freedom, *t* and *p* values. Significant effects are highlighted in bold.

		Estimate ± s.e.	df	t	Р
a) Age of female	Intercept	2.323 ± 3.621	70.79	0.642	0.523
	Total zoos	4.108 ± 0.669	78.856	6.143	<0.001
	Unknown birth type	12.740 ±2.915	78.929	4.371	<0.001
	Wild-born	12.684 ± 2.092	75.335	6.063	<0.001
	Dead	-4.361 ± 2.070	69.150	-2.107	<0.001
	Longest zoo residency	0.778 ± 0.091	66.996	8.565	<0.001
	Average herd size	0.302 ± 0.312	74.452	0.967	0.3369
b) Age of deceased females	Intercept	4.847 ± 8.893	29	0.545	0.589
	Total zoos	2.486 ± 1.409	29	1.764	0.088
	Unknown birth type	11.087 ± 6.009	29	2.164	0.075
	Wild-born	11.098 ± 5.128	29	2.164	0.038
	Longest zoo residency	0.715 ± 0.150	29	4.767	<0.001
	Average herd size	0.291 ± 0.865	29	0.336	0.739

6.5 Discussion

Using the zoological collections management software, ZIMS, this study explored UK and European captive Asian elephant herd movement, group composition and breeding history. This allowed us to explore the relationship between group composition and calf rearing success and survival between 1970 and 2018. Our results on the demographics of 93 Asian elephant females showed that most females were housed in average groups of 5 and the average age was 35 years old. Within this group only a small proportion of females were housed with adult relatives and a large proportion of females did not encounter former herd mates from other zoos. First, we tested whether the number of times female elephants were transferred between institutions predicted their calf rearing success. The results showed that there was a negative association between total number of living offspring a female had and increased management transfers. Whilst more zoo residencies were associated with having more living offspring. Some of these management transfers may have been for breeding purposes only, and therefore females may have experienced multiple short-term transfers between zoos depending on their success or failure to conceive; however, we are unable to definitively determine this with our data. It is also possible that increased management transfers mean females were not provided with the opportunity to breed at every zoo. Although birth-type was not found to be a significant effect in this analysis, it must be noted that wild-born and unknownorigin females were observed to experience more zoo transfers compared to captive-born females. This high transfer rate reflects historical management strategies that housed wild-caught elephants randomly, a practice that has changed since the formation of the EAZA Ex-situ Programme (EEP) for Asian elephants was formed (Schmidt and Kappelhof, 2019). High transfer rates in certain females may also have led to low calf rearing success as females lose the opportunity to establish strong and bonds with herd mates. Elephants cooperate in the care of offspring,

and their relationships with one another are key to successful cooperation (Kurt and Mar, 1996). Transfers between different zoo facilities may represent the breaking of bonds. If this is the case, with every transfer a female experienced an instance of breaking bonds with herd mates and then having to reform bonds with new individuals. Although wild breeding herds undergo seasonal fission and fusion of their social groups, core bond groups remain stable over a female's lifetime and complete severing of ties has been observed to be rare (Moss et al., 2011). Captive females are also capable of forming strong bonds with herd mates, however, they require time to do so (Kurt and Mar, 1996) and regular transfers may disrupt this process.

Our analysis of the effect of herd composition on calf rearing success revealed that the presence of relatives and larger average herd sizes were found to have a positive effect on the total number of calves a female gave birth to, whilst the presence of former herd mates did not have a significant effect. Data from a recent study by Lynch et al (2019) showed that the presence of sisters and mothers improved the annual reproductive rate of young breeding females. Interestingly, they note that the presence of maternal sisters aged between 0 and 5 significantly increased the annual reproduction of more inexperienced females (Lynch et al., 2019). They suggest that the presence of sisters has potential benefits such as being a social buffer to potential stressors during pregnancy and assisted rearing of calves through alloparental care (Lynch et al., 2019). Gobush et al (2008) also reported that the reproductive output of wild African elephants was greatly improved amongst females that have strong social bonds with close relatives. Schmidt and Kappelhof (2019) reported that most recent EEP studbook data shows that 76% of female elephants are now housed in maternal family groups and mean births per year have increased to 15 calves per year in most recent years. Findings such as these support the decision of many zoos to keep more stable and related breeding groups that consist of multiple generations. Conversely, larger average herd sizes

and the presence of herd mates also had a significant effect on calves surviving past 3 years old. The presence of former non-related herd mates was also positively associated strongly with a female's total number of offspring per zoo. Elephants are also capable of forming long-lasting, cooperative relationships with non-relatives and this may include cooperation of infant care (Gadgil and Nair, 1984; Kurt and Mar, 1996; Moss et al., 2011). Therefore, especially in the instance of elephant transfers for breeding purposes, it is important to further investigate the potential benefits of moving females with companions for their reproductive success in the next zoo.

In terms of assessing longevity of zoo elephants, researchers have been sceptical of elephant survivorship in zoo settings. A comparison between the survivorship between wild and captive elephants shows that the natural average lifespan in wild African elephants was 56 years old and about 41 years old in wild Asian elephants (Clubb et al., 2008). Conversely, in captivity the African elephant average lifespan was significantly reduced to 16 years old and 18 years old in captive Asian elephants (Clubb et al., 2008). Clubb et al (2008) attributed poor elephant survivorship to higher numbers of zoo transfers and elephants being removed from their mothers at younger ages. In our assessment of average residency time, older females were found to spend longer periods of time in a zoo compared to younger individuals. However, a majority of these females that had long residencies were already deceased when they were included in this study. Again, we were unable to specify cause of death in older females from ZIMS data and therefore direct correlations between transfer rates, average residency and longevity cannot be made from our data. However, further analysis of this relationship could control for cause of death in the analysis. We also measured the longevity of a female's offspring past the age of 3 years. Linear mixed models showed an association between offspring survival over 3 years of age and their mothers being housed with former herd mates. It is possible to predict that as

found by Gadgil and Nair, these offspring benefited from cooperative care from strongly bonded females despite being unrelated. Now that most female elephants in UK and European zoos are housed in family groups, further study of the factors supporting the survivorship of offspring should be conducted, taking into account the degree of relatedness between breeding females, as well as the prevalence of elephant endotheliotropic herpes virus in zoos. It would also be interesting to determine how many generations zoos are currently able to house before there is a need to transfer individuals out of these stable matrilineal herds.

6.6 Conclusion

The purpose of this study was to investigate the effects of social stability on reproductive success of female elephants in the wider UK and European zoo population. We found that the presence of family members and former herd mates improved the calf survival in our study. However, a large proportion of females in the study population had never been housed with either family or former herd mates. Increased transfer rates between zoos reduced a female's opportunity to reproduce and form strong, long-lasting bonds as found in wild herds. Many of the management practices that led to high transfer rates and the housing of unrelated females have now been stopped (Schmidt and Kappelhof, 2019), and most females are housed in family groups. With this in mind, our study may be further developed by considering the social interactions between females and breeding bulls that have higher inter-zoo transfer rates. Social network analysis may also be employed to illustrate the connectedness of all individuals in the UK and European population. Although past studies characterised captive elephant populations as unsustainable and in rapid decline, it is now important to determine whether the recent move to house family breeding groups is moving *ex situ* elephant populations towards sustainability.

Chapter 7: General discussion

The use of social networks to study elephant societies spatially and temporally has been well documented. These techniques have allowed researchers to study and describe daily, monthly and yearly networks from the dyadic level up to multi-clan level (Chiyo et al., 2011; Pinter-Wollman et al., 2009; Poole and Granli, 2011; Silva et al., 2011; Wittemyer et al., 2009, 2007). Social network analysis has the potential to provide similar information for *ex situ* elephant groups. In this thesis, I used the simple ratio index, weighted degree, weighted betweenness and eigenvector centrality to measure the social structure and individual social position of captive elephants, both from daytime observations and night-time sleeping observations. My daytime findings showed that as expected, elephant bonds were strongest between mother-calf dyads and related adults. My findings, and previous measurements of bond strength within captive elephant herds (Schmidt and Kappelhof, 2019), confirm animal managers' decisions to keep individuals in family herds where possible. Here, I also found evidence of non-relatives having strong bonds with herd mates, indicating that issues regarding social compatibility are also an important consideration. When kin are not present, female elephants are able to form bonds with non-relatives, although they require ample time to do so (Gobush et al., 2008; Kurt and Mar, 1996; Poole and Granli, 2011). However, evidence in zoos has shown that poor compatibility with herd members can lead to aggression and disruption in the herd structure (Evison et al., 2020; Schmid et al., 2001). Therefore, when deciding the compatibility of non-relatives, monitoring bond strength could help inform animal managers of whether bonds are strengthening over time, or remaining weak and causing more disruption than cohesion (Snijders et al., 2017). My study indicated that calves had the highest measures of weighted degree, betweenness and eigenvector centralities, showing that when present, they are the most central in the network herd. This again was an observation also found in wild elephant populations (Garai, 1992; Lee and Moss, 2011). The high centrality

measures found amongst calves can be attributed to the high levels of exploratory and social learning that is significant to their development. Amongst adult individuals, I observed the oldest related females in each herd to be the most central within their groups. It is possible that in the absence of calves or older herd members, associations may become weaker and less cohesive (Rose and Croft, 2015; Snijders et al., 2017). Although I was not able to test this, future investigations can do so by either studying non-breeding captive elephant herds, or simulating the removal of central individuals from the network (Lusseau and Newman, 2004; Rose and Croft, 2015).

The sleep behaviour of both zoo herds in this study has been previously studied using longitudinal night-time data sets (Evison et al., 2020; Walsh, 2017). These studies highlighted the impacts of social disruption, in the form of mating behaviour and birth events (Walsh, 2017), and individual transfers (Evison et al., 2020), on sleep quality. The information gathered from these two papers demonstrates that useful information on elephant social behaviour can be collected at night. Thus, in this thesis, I aimed to validate the use of night-time social patterns as a reliable method of monitoring herd social networks and stability over time. Overall, I found that the social bonds measured from sleeping observations were also correlated with daytime observations. Here, again, my findings showed that younger individuals were the most central within sleeping networks, and observations showed that calves either slept near age-mates or near their mothers. Average sleep times calculated in this study were found to be similar to those found by Walsh, 2017 and Evison et al. 2020. In my study, measures of centrality were positively correlated with average sleep per night, with more central members sleeping for longer. However, it is important to note that the most central individuals in the calculated sleeping networks were young calves, and longer periods of sleep are to be expected compared to adults (Evison et al., 2020; Stokes, 2017; Walsh, 2017). In their study, Walsh (2017) noted that in the presence of

calves, mothers often had less or disturbed sleeping patterns. Walsh (2017) also observed sleep being disturbed during instances of mating behaviour between a breeding bull and females in oestrus. Although there were no disturbances recorded during this study, being able to identify an elephant's position within the sleeping network will aid in determining which individuals influence the quality of sleep of others. Whilst we identified the most central individuals as having the better quality of sleep, it would be interesting to determine the sensitivity of these same individuals to night-time social disturbances – this being with the exclusion of mother-calf interactions. At night-time, degree of relatedness, age, or years as herd mates were not found to correlate with sleeping association strength in either herd, suggesting that the strength of association between sleeping partners is determined by other factors. It is possible that potential drivers in elephant sleeping associations may also include availability and preference to sleeping sites, as well as how elephants are housed at night from an early age – either as one large group or segregated into smaller groups partners (Lock and Anderson, 2013; Riss and Goodall, 1976). This study supports the decision of many zoos to use nighttime observations to study herd composition and social stability. The convenience provided of recording and storing longitudinal night-time footage means that elephant management teams are able to perform data collection and analysis during periods that fit their management schedules. Storage of long term footage also allows thorough analysis of daily sleep patterns and associations, as well as the social, management and environmental factors that may affect night-time networks (Evison et al., 2020; Tobler, 1992; Walsh, 2017; Wilson et al., 2006). The positive correlations between day and night-time associations found in this study further validates that animal managers who are not able to observe during the day, due to their daily work routines, can still make valuable observations of night-time behaviour.

My analysis of temporal changes in herd structure, both day and night, provided interesting results. In the Chester Zoo herd, I found that daytime measures of centrality were greatest during the summer months (May-August) and decreased during the late-autumn and winter periods (October – December). Nighttime sleeping associations showed that centrality measures were higher during February and April, and lower during May and December. Although these changes were not all statistically significant, these patterns in the observed data appear to have a converse relationship. When daytime associations are highest (in the summer), sleeping associations are found to be lower during similar periods. However, it is important to note that in this herd, winter periods are also associated with calf births, and so seasonality is not the main effect on association during this period. In the Dublin Zoo herd, I observed that both day and night-time associations appeared to be high from April to May and decrease in July and August. In wild elephants, temporal associations are linked to ecological factors determining food availability (Archie et al., 2006; Nandini et al., 2017; Smith et al., 2011; Wittemyer and Getz, 2007); however captive elephants do not have such ecological constraints regarding food availability, and therefore possible factors may include length of daylight hours, amount of outdoor access during warmer months versus cooler months, and zoo-specific management practices. Although monthly patterns were observed in both day and night-time associations in these study groups, it is still unclear whether ecological or management factors are driving this variation. Continuous collection of data, perhaps spanning multiple years, is required to truly understand the cyclicity of elephant sociality within captive populations.

After the social bonds and herd networks were characterised for both study populations, my study focused on investigating the impacts of the observed herd dynamics on individual endocrinology using longitudinal glucocorticoid profiles. Focusing on the adult females and older calf of the Chester Zoo herd, I found clear individual variation in average daily glucocorticoid secretion. Such individual

variation in glucocorticoid secretion has been observed in other captive individuals (Brown et al., 2010; Menargues et al., 2012; Schmid et al., 2001). Analysis of longitudinal fGCM concentrations also showed both seasonal and social changes affected individual secretion. Faecal glucocorticoid levels were observed to be highest during spring, summer, and winter within this herd; patterns seemingly similar to observations in other zoo populations in the northern hemisphere (Menargues et al., 2012). It is also possible that these increases correspond with the increase in zoo visitor numbers during the summer months and more time spent indoors during the winter months; two factors that were not included in this study but should be investigated in further longitudinal studies. My findings showed clear group fGCM responses to particular social events: births and deaths. Possibly indicating that within the life of captive elephants, certain major life events elicit a common response among all herd members. Although I found no statistically significant relationship between bond strength and the magnitude of the stress response, the present body of work proving the relationship exists is cause for continued research. My findings showed that individuals varied in elevations in fGCM above their baseline ranges and in the amount of time needed to recover from such peaks. Though this is to be expected (Cockrem, 2013), further analysis of social position and glucocorticoid response would allow us to create individual profiles of sensitivity or resilience based on their social position (Grand et al., 2012). Alternatively, as observed by Gobush et al., (2008) in wild elephants, we would be able to identify individuals who would have otherwise had extreme stress responses, cope better due to the presence of close partners. Whilst elephants are capable of habituating to common stressors withing their environment (Vijayakrishnan et al., 2018); the impacts of a strong social network on reducing stress in novel situations is an important welfare issue that cannot be overlooked (Gobush et al., 2008; Hennessy et al., 2008). Furthermore, the growing literature on the relationship between glucocorticoids and reproductive endocrinology suggests the need for both hormones to be recorded longitudinally (Brown, 2000; Fanson et al., 2014; Meyer et al., 2004). As in my findings, glucocorticoids (cortisol)

and progesterone have been describes as having an inverse relationship; and during gestation glucocorticoids remain low until parturition (Fanson et al., 2014; Meyer et al., 2004). Regular monitoring of both hormones would allow for zoo institutions to more accurately predict the onset of parturition (Meyer et al., 2004), but it would also help detect uncharacteristic elevations in cortisol during or post gestation.

The final section of my study looked at the broader patterns of social stability in elephant groups in European collections and success of calf rearing. In the past, assessments of zoo elephant health and welfare have been both informative and critical, with calculations of future population viability predicting extinction (Clubb et al., 2009, 2008; Clubb and Mason, 2002; Rees, 2003; Wiese, 2000). When these studies were published, the zoo elephant population did indeed reflect the low fecundity, low population viability and inconsistent welfare practices that were highlighted. Thus, researchers were valid in their arguments to see improvement in approaches to *ex situ* elephant conservation. However, zoos and zoo governing bodies are working hard to improve on previous practices, and to care for elephants by adopting management and husbandry methods founded on species-specific scientific information (BIAZA, 2010; Carlstead et al., 2013; Hutchins, 2006; Meehan et al., 2016; Prado-Oviedo et al., 2016; Schmidt and Kappelhof, 2019). In my study of 93 females across the European captive zoo populations, I found that herd size was a significant predictor of the total number of offspring produced by a female. By contrast, high numbers of transfers between zoos (temporary residencies or permanent re-homing) were associated with fewer calves being reared. This high transfer rate, which was observed most often amongst females of wild or unknown birth origins, reflects historical management strategies that housed wild-caught elephants randomly, a practice that has changed since the formation of the EAZA Ex-situ Programme (EEP) for Asian elephants was formed (Schmidt and Kappelhof, 2019). Conversely, I found that females had better success rearing their calves over the age of 3 years old if they experienced fewer transfers

and were housed in larger herd sizes with family members or former herd mates present. A similar finding was also highlighted in the study of European elephants by Hartley and Stanley (2016). Schmidt and Kappelhof (2019) reported that most recent EEP studbook data shows that 76% of female elephants are now housed in maternal family groups and mean births per year have increased to 15 calves per year in most recent years. However, as yet it is unknown how many of these calves survive into adulthood. My findings regarding the apparent positive effect of the presence of former herd mates on calf survival past 3 years also highlights the importance of all a female's relationships, not just with relatives. And whilst keeping families together has shown success in rearing success of captive elephants (Hartley and Stanley, 2016; Schmidt and Kappelhof, 2019), it is important to remember that strong bonds with non-related individuals also have the potential to improve rearing success (Gadgil and Nair, 1984; Kurt and Mar, 1996; Moss et al., 2011). Therefore, especially in the instance of elephant transfers for breeding purposes, it is important to further investigate the potential benefits of moving females with companions for their reproductive success in the next zoo. Assessments of factors affecting the survival of a female's offspring to adulthood showed that average herd size had a positive effect. Although I was unable to determine the cause of death for all offspring in this study, it is possible to predict that as found by Lynch *et al* (2019), these offspring benefited from cooperative care from a larger support system of females. However, this point should be further investigated in the currently established breeding herds, taking into account common causes of calf deaths, including the prevalence of elephant endotheliotropic herpes virus in zoos. Recently, it has been reported that there has been a significant improvement in the reproductive output of the European and UK elephant population (Schmidt and Kappelhof, 2019). This success has been accredited to improvements in enclosure design and size, species-specific enrichment, advanced reproductive monitoring techniques, and decisions to keep breeding herds in stable family groups. It will now be interesting to investigate the

capacity of zoos to hold multigenerational herds, and what factors they would need to consider when families become too big and herds must be split.

Although this study focused on female breeding herds, my findings and methods should also be applied to study the captive population of bull elephants. Although known to roam alone in the wild, male elephants are highly social and associate with other male companions regularly (Evans and Harris, 2008). Furthermore, in the same way that young females benefit from observing and participating in mothering behaviours, young males benefit from observing mating behaviours and participating in sparring bouts with older males (Evans and Harris, 2008; Slotow et al., 2000). The current skew in the population's sex ratio means that there are more male calves and thus improvements in the housing of bulls must be equal to that of females. To address this, Schmidt and Kappelhof (2019) propose that zoos invest in developing large and more versatile enclosures that are able to house young bulls up until the age of 12 years old. In general, they propose that investment in more versatile *ex situ* habitats will hold more complex groups and facilitate in increased fission-fusion movement between group members. As zoos continue to make large advancements in *ex situ* elephant welfare and breeding, the conservation purpose of this growing population must become well defined.

The intention of this study was to spotlight the dynamics of captive elephant sociality and its impacts on factors such as calf rearing and individual endocrinology. This study aimed to use methods of monitoring animal behaviour and endocrinology already used by zoo institutions to demonstrate the power of combining these techniques to assess the welfare of captive elephant herds. It is my hope that such a study will add to the growing body of work focused on gaining a better understanding of the links between environmental, management and social factors and elephant survival *ex situ*. The challenge now is to assess whether such

multi-disciplinary approaches will be effective in reducing the predicted long-term decline of zoo elephants, especially when such results may only become evident in the future for such long-lived animals. I believe that the recent decision to ban the importing of young elephants from home range habitats to zoos (CITES, 2019) is a good opportunity for zoos to redefine their conservation relationship with *in situ* countries beyond their current involvement. It is also a good opportunity for elephant managers and zoo bodies to explicitly define the role of the now-growing ex situ population – be it as a genetic reservoir, a flagship educational exhibit, or to replenish struggling wild populations. Now that advancements in intense elephant management and research have proved to be effective in the *ex situ* context, zoos must now look to applying these methods to the safeguarding of wild populations. This will require an expansion of collaboration between zoo managers, academics and scientists, to include equal collaboration with their counterparts in elephant home range countries. It is imperative that these advancements are shared freely with the academics, conservation managers and governments to ensure that the fight to preserve this iconic and unique species is truly a global effort.

References

- Altmann, J., 1974. Observational Study of Behavior : Sampling Methods Author. Behaviour 49, 227–267.
- Anderson, J.R., 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. Sleep Med. Rev. 4, 355–373. https://doi.org/10.1053/smrv.2000.0105
- Archie, E.A., Morrison, T.A., Foley, C.A.H., Moss, C.J., Alberts, S.C., 2006a.
 Dominance rank relationships among wild female African elephants, Loxodonta africana. Anim. Behav. 71, 117–127.
 https://doi.org/10.1016/j.anbehav.2005.03.023
- Archie, E.A., Moss, C.J., Alberts, S.C., 2011. Friends and Relations: Kinship and the Nature of Female Elephant Social Relaitonships, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. The University of Chicago Press, Chicago, pp. 238–245.
- Archie, E.A., Moss, C.J., Alberts, S.C., 2006b. The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proc.
 R. Soc. B Biol. Sci. 273, 513–522. https://doi.org/10.1098/rspb.2005.3361
- AZA, 2001. Standards for Elephant Management and Care.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using Ime4. J. Stat. Softw. 67, 1–48. https://doi.org/doi:10.18637/jss.v067.i01
- Beery, A.K., Kaufer, D., 2015. Stress, social behavior, and resilience: Insights from rodents. Neurobiol. Stress 1, 116–127. https://doi.org/10.1016/j.ynstr.2014.10.004
- Bejder, L., Fletcher, D., Bräger, S., 1998. A method for testing association patterns of social animals. Anim. Behav. 56, 719–725.
- Berger, R.J., Phillips, N.H., 1995. Energy conservation and sleep. Behav. Brain Res. 69, 65–73.
- BIAZA, 2010. Managment Guidelines for the Welfare of Zoo Animals: Elephants Loxodonta africana and Elephas maximus, Third. ed. British & Irish Association of Zoos & Aquariums, London.
- Blonder, B., Wey, T.W., Dornhaus, A., James, R., Sih, A., 2012. Temporal dynamics and network analysis. Methods Ecol. Evol. 3, 958–972. https://doi.org/10.1111/j.2041-210X.2012.00236.x
- Brent, L.J.N., 2015. Friends of friends: Are indirect connections in social networks important to animal behaviour? Anim. Behav. 103, 211–222.

https://doi.org/10.1016/j.anbehav.2015.01.020

- Briga, M., Pen, I., Wright, J., 2012. Care for kin: Within-group relatedness and allomaternal care are positively correlated and conserved throughout the mammalian phylogeny. Biol. Lett. 8, 533–536. https://doi.org/10.1098/rsbl.2012.0159
- Brockett, R.C., Stoinski, T.S., Black, J., Markowitz, T., Maple, T.L., 1999. Nocturnal Behavior in a Group of Unchained Female African Elephants. Zoo Biol. 18, 101– 109.
- Broman, K.W., Broman, A.T., 2019. broman: Karl Broman's R Code.
- Broom, D.M., 1997. Welfare evaluation. Appl. Anim. Behav. Sci. 54, 21–23. https://doi.org/10.1016/S0168-1591(96)01200-2
- Brown, J.L., 2000a. Reproductive Endocrinology Monitoring of Elephants: An Essential Tool for Assisting Captvie Management. Zoo Biol. 19, 347–367. https://doi.org/10.1002/1098-2361(2000)19
- Brown, J.L., 2000b. Reproductive endocrine monitoring of elephants: An essential tool for assisting captive management. Zoo Biol. 19, 347–367. https://doi.org/10.1002/1098-2361(2000)19:5<347::AID-ZOO6>3.0.CO;2-V
- Brown, J.L., Kersey, D.C., Freeman, E.W., Wagener, T., 2010. Assessment of diurnal urinary cortisol excretion in Asian and African elephants using different endocrine methods. Zoo Biol. 29, 274–283. https://doi.org/10.1002/zoo.20268
- Brown, J.L., Paris, S., Prado-Oviedo, N.A., Meehan, C.L., Hogan, J.N., Morfeld, K.A., Carlstead, K., 2016. Reproductive health assessment of female elephants in north American zoos and association of husbandry practices with reproductive dysfunction in african elephants (loxodonta africana). PLoS One 11, 1–23. https://doi.org/10.1371/journal.pone.0145673
- Brown, J.L., Schmitt, D.L., Bellem, A., Graham, L.H., Lehnhardt, J., 1999. Hormone Secretion in the Asian Elephant (Elephas maximus): Characterizationof Ovulatory and Anovulatory Luteinizing Hormone Surges. Biol. Reprod. 61, 1294–1299. https://doi.org/10.1095/biolreprod61.5.1294
- Brown, J.L., Somerville, M., Riddle, H.S., Keele, M., Duer, C.K., Freeman, E.W., 2007.
 Comparative endocrinology of testicular, adrenal and thyroid function in captive Asian and African elephant bulls. Gen. Comp. Endocrinol. 151, 153–162. https://doi.org/10.1016/j.ygcen.2007.01.006
- Brown, J.L., Wildt, D.E., Wielebnowski, N., Goodrowe, K.L., Graham, L.H., Wells, S., Howard, J.G., 1996. Reproductive activity in captive female cheetahs (Acinonyx jubatus) assessed by faecal steroids. J. Reprod. Fertil. 106, 337–346.

Butts, C.T., 2016. sna: Toold for Social Network Analysis.

Cairns, S.J., Schwager, S.J., 1987. A comparison of association indices. Anim. Behav.

35, 1454-1469. https://doi.org/10.1016/S0003-3472(87)80018-0

- Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc. Natl. Acad. Sci. 106, 13850–13853. https://doi.org/10.1073/pnas.0900639106
- Carlstead, K., Mench, J.A., Meehan, C., Brown, J.L., 2013. An Epidemiological Approach to Welfare Research in Zoos: The Elephant Welfare Project. J. Appl. Anim. Welf. Sci. 16, 319–337. https://doi.org/10.1080/10888705.2013.827915
- Carter, C.S., Grippo, A.J., Pournajafi-Nazarloo, H., Ruscio, M.G., Porges, S.W., 2008. Oxytocin, vasopressin and sociality. Prog. Brain Res. 170, 331–336. https://doi.org/10.1016/S0079-6123(08)00427-5
- Castles, M., Heinsohn, R., Marshall, H.H., Lee, A.E.G., Cowlishaw, G., Carter, A.J., 2014. Social networks created with different techniques are not comparable. Anim. Behav. 96, 59–67. https://doi.org/10.1016/j.anbehav.2014.07.023
- Chiyo, P.I., Archie, E.A., Hollister-Smith, J.A., Lee, P.C., Poole, J.H., Moss, C.J., Alberts, S.C., 2011. Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. Anim. Behav. 81, 1093–1099. https://doi.org/10.1016/j.anbehav.2011.02.013
- Cirelli, C., Tononi, G., 2008. Is Sleep Essential ? PLoS Biol. 6, 1605–1611. https://doi.org/10.1371/journal.pbio.0060216
- Clubb, R., Mason, G.J., 2002. A Review of the Welfare of Zoo Elephants A Review of the Welfare of Zoo Elephants in Europe: A report commissioned by the RSPCA, Animal Behaviour. University of Oxford, Oxford. https://doi.org/10.1021/jp020277g
- Clubb, R., Rowcliffe, M., Lee, P., Mar, K.U., Moss, C., Mason, G.J., 2009. Fecundity and population viability in female zoo elephants: Problems and possible solutions. Anim. Welf. 18, 237–247. https://doi.org/10.1080/19325037.2001.10603479
- Clubb, R., Rowcliffe, M., Lee, P., Mar, K.U., Moss, C., Mason, G.J., 2008. Compromised survivorship in zoo elephants. Science (80-.). 322, 1649. https://doi.org/10.1126/science.1164298
- Clutton-Brock, T., 2009. Structure and function in mammalian societies. Philos. Trans. R. Soc. B Biol. Sci. 364, 3229–3242. https://doi.org/10.1098/rstb.2009.0120
- Cockrem, J.F., Silverin, B., 2002. Variation within and between birds in corticosterone responses of great tits (Parus major). Gen. Comp. Endocrinol. 125, 197–206. https://doi.org/10.1006/gcen.2001.7750
- Croft, D.P., James, R., Krause, J., 2008. Exploring Animal Social Networks, First. ed. Princeton University Press, Princeton, New Jersey.

- Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. InterJournal 1695.
- Daniel, J.C., 1998. The Asian Elephant: A Natural History, First. ed. Natraj Publishers, New Delhi.
- de Silva, S., Schmid, V., Wittemyer, G., 2017. Fission-fusion processes weaken dominance networks of female Asian elephants in a productive habitat. Behav. Ecol. 28, 243–252. https://doi.org/10.1093/beheco/arw153
- de Silva, S., Wittemyer, G., 2012. A Comparison of Social Organization in Asian Elephants and African Savannah Elephants. Int. J. Primatol. 33, 1125–1141. https://doi.org/10.1007/s10764-011-9564-1
- De Villiers, M.S., Richardson, P.R.K., Van Jaarsveld, A.S., 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (Lycaon pictus). J. Zool. 260, 377–389. https://doi.org/10.1017/S0952836903003832
- Edwards, K.L., McArthur, H.M., Liddicoat, T., Walker, S.L., 2014. A practical field extraction method for noninvasive monitoring of hormone activity in the black rhinoceros. Conserv. Physiol. 2, 1–8. https://doi.org/10.1093/conphys/cot037
- Edwards, K.L., Trotter, J., Jones, M., Brown, J.L., Steinmetz, H.W., Walker, S.L., 2016. Investigating temporary acyclicity in a captive group of Asian elephants (Elephas maximus): Relationship between management, adrenal activity and social factors. Gen. Comp. Endocrinol. 225, 104–116. https://doi.org/10.1016/j.ygcen.2015.09.011
- Evans, K.E., Harris, S., 2008. Adolescence in male African elephants, Loxodonta africana, and the importance of sociality. Anim. Behav. 76, 779–787. https://doi.org/10.1016/j.anbehav.2008.03.019
- Evison, E., McKenzie, A., Holmes, L., 2020. Social and environmental impacts on sleep in captive Asian Elephants (Elephas maximus). Zoo Biol. 1–8.
- Fairbanks, L.A., 1990. Reciprocal benefits of allomothering for female vervet monkeys. Anim. Behav. 40, 553–562. https://doi.org/10.1016/S0003-3472(05)80536-6
- Fanson, B.G., Fanson, K. V., 2014. hormLong: Longitudinal Analysis of Hormone Data.
- Fanson, K. V., Keeley, T., Fanson, B.G., 2014. Cyclic changes in cortisol across the estrous cycle in parous and nulliparous Asian elephants. Endocr. Connect. 3, 57–66. https://doi.org/10.1530/EC-14-0025
- Faraut, B., Boudjeltia, K.Z., Vanhamme, L., Kerkhofs, M., 2012. Immune, inflammatory and cardiovascular consequences of sleep restriction and recovery. Sleep Med. Rev. 16, 137–149.

https://doi.org/10.1016/j.smrv.2011.05.001

- Farine, D.R., 2018. asnipe: Animal Social Network Inference and Permutations for Ecologists.
- Farine, D.R., 2017. A guide to null models for animal social network analysis. Methods Ecol. Evol. 8, 1309–1320. https://doi.org/10.1111/2041-210X.12772
- Farine, D.R., 2013. Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol. Evol. 4, 1187–1194. https://doi.org/10.1111/2041-210X.12121
- Farine, D.R., Whitehead, H., 2015a. Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. 84, 1144–1163. https://doi.org/10.1111/1365-2656.12418
- Farine, D.R., Whitehead, H., 2015b. Appendices for: Constructing, conducting and understanding animal social network analysis. J. Anim. Ecol. 84, 1144–1163. https://doi.org/10.1111/1365-2656.12418
- Faust, L.J., Thompson, S.D., Earnhardt, J.M., 2006. Is reversing the decline of Asian elephants in North American zoos possible? An individual-based modeling approach. Zoo Biol. 25, 201–218. https://doi.org/10.1002/zoo.20054
- Fekedulgen, D.B., Andrew, M.E., Burchfiel, C.M., Violanti, J.M., Hartley, T.A., Charles, L.E., Miller, D.B., 2007. Area Under the Curve and Other Summary Indicators of Repeated Waking Cortisol Measurements. Psychosom. Med. 69, 651–659.
- Foley, C.A.H., Papageorge, S., Wasser, S.K., 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. Conserv. Biol. 15, 1134–1142. https://doi.org/10.1046/j.1523-1739.2001.0150041134.x
- Freeman, E.W., Schulte, B.A., Brown, J.L., 2010. Investigating the impact of rank and ovarian activity on the social behavior of captive female African elephants. Zoo Biol. 29, 154–167. https://doi.org/10.1002/zoo.20235
- Gadgil, M., Nair, P.V., 1984. Observations on the social behaviour of free ranging groups of tame Asiatic elephant (Elephas maximus Linn). Proc. Indian Acad. Sci. 93, 225–233.
- Ginsberg, J.R., Young, T.P., 1992. Measuring association between individuals or groups in behavioural studies. Anim. Behav. 377–379.
- Gobush, K., Kerr, B., Wasser, S., 2009. Genetic relatedness and disrupted social structure in a poached population of African elephants. Mol. Ecol. 18, 722– 734. https://doi.org/10.1111/j.1365-294X.2008.04043.x
- Gobush, K.S., Mutayoba, B.M., Wasser, S.K., 2008a. Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female

African elephants. Conserv. Biol. 22, 1590–1599. https://doi.org/10.1111/j.1523-1739.2008.01035.x

- Gobush, K.S., Mutayoba, B.M., Wasser, S.K., 2008b. Long-Term Impacts of Poaching on Relatedness, Stress Physiology, and Reproductive Output of Adult Female African Elephants - GOBUSH - 2008 - Conservation Biology - Wiley Online Library. Conserv. Biol. 22, 1590–1599. https://doi.org/10.1111/j.1523-1739.2008.01035.x
- Goldenberg, S.Z., de Silva, S., Rasmussen, H.B., Douglas-Hamilton, I., Wittemyer, G., 2014. Controlling for behavioural state reveals social dynamics among male African elephants, Loxodonta africana. Anim. Behav. 95, 111–119. https://doi.org/10.1016/j.anbehav.2014.07.002
- Grand, A.P., Kuhar, C.W., Leighty, K.A., Bettinger, T.L., Laudenslager, M.L., 2012. Using personality ratings and cortisol to characterize individual differences in African Elephants (Loxodonta africana). Appl. Anim. Behav. Sci. 142, 69–75. https://doi.org/10.1016/j.applanim.2012.09.002
- Gravett, N., Bhagwandin, A., Sutcliffe, R., Landen, K., Chase, M.J., Lyamin, O.I., Siegel, J.M., Manger, P.R., 2017. Inactivity / sleep in two wild free-roaming African elephant matriarchs – Does large body size make elephants the shortest mammalian sleepers ? PLoS One 12, 1–33. https://doi.org/10.1371/journal.pone.0171903
- Grippo, A.J., Gerena, D., Huang, J., Kumar, N., Shah, M., Ughreja, R., Sue Carter, C., 2007. Social isolation induces behavioral and neuroendocrine disturbances relevant to depression in female and male prairie voles.
 Psychoneuroendocrinology 32, 966–980. https://doi.org/10.1016/j.psyneuen.2007.07.004
- Hamilton, W.D., 1964. The Genetical Evolution of Social Behaviour II. J. Theor. Biol. 7, 17–52. https://doi.org/10.1016/0022-5193(64)90039-6
- Hamilton, W.D., 1963. The Evolution of Altruistic Behavior. Am. Soc. Nat. 97, 354– 356.
- Harris, M., Sherwin, C., Harris, S., 2008. The Welfare, Housing and Husbandry of Elephants in UK Zoos. Bristol.
- Hart, B.L., Hart, L.A., Pinter-Wollman, N., 2008. Large brains and cognition: Where do elephants fit in? Neurosci. Biobehav. Rev. 32, 86–98. https://doi.org/10.1016/j.neubiorev.2007.05.012
- Hartley, M., Stanley, C.R., 2016. Survey of reproduction and calf rearing in Asian and African elephants in European zoos 4, 1–8.

Hawkes, K., 2004. The grandmother effect. Nature 428, 128–129. https://doi.org/10.1159/000324242 Hennessy, M.B., Zate, R., Maken, D.S., 2008. Social buffering of the cortisol response of adult female guinea pigs. Physiol. Behav. 93, 883–888. https://doi.org/10.1016/j.physbeh.2007.12.005

- Hodges, J.K., Brown, J.L., Heistermann, M., 2010. Endocrine Monitoring of Reproduction and Stress, in: Kleinman, D.G., Thompson, K.V., Kirk Baer, C. (Eds.), Wild Mammals in Captivity: Principles and Techniques for Zoo Management. The University of Chicago Press, Chi, pp. 447–467.
- Holdgate, M.R., Meehan, C.L., Hogan, J.N., Miller, L.J., Rushen, J., Passillé, A.M. De, Soltis, J., Andrews, J., Shepherdson, D.J., 2016. Recumbence Behavior in Zoo Elephants: Determination of Patterns and Frequency of Recumbent Rest and Associated Environmental and Social Factors. PLoS One 11, 1–19. https://doi.org/10.1371/journal.pone.0153301
- Hutchins, M., 2006. Variation in Nature: Its Implications for Zoo Elephant Management. Zoo Biol. 25, 161–171. https://doi.org/10.1002/zoo.20087
- Hutchins, M., Smit, B., Keele, M., 2008. Zoos As Responsible Stewards of Elephants, in: Wemmer, C., Christen, C.A. (Eds.), Elephants and Ethics: Toward a Morality of Coexistence. Baltimore, pp. 285–305.
- Kent, R.G., Uchino, B.N., Cribbet, M.R., Bowen, K., Smith, T.W., 2015. Social Relationships and Sleep Quality. Ann. Behav. Med. 49, 912–917. https://doi.org/10.1007/s12160-015-9711-6
- Kohda, M., 1985. Allomothering behaviour of new and old world monkeys. Primates 26, 28–44. https://doi.org/10.1007/BF02389045
- König, B., 1997. Cooperative care of young in mammals. Naturwissenschaften 84, 95–1997.
- Koren, L., Mokady, O., Geffen, E., 2008. Social status and cortisol levels in singing rock hyraxes. Horm. Behav. 54, 212–216. https://doi.org/10.1016/j.yhbeh.2008.02.020
- Kumar, V., Palugulla Reddy, V., Kokkiligadda, A., Shivaji, S., Umapathy, G., 2014. Non-invasive assessment of reproductive status and stress in captive Asian elephants in three south Indian zoos. Gen. Comp. Endocrinol. 201, 37–44. https://doi.org/10.1016/j.ygcen.2014.03.024
- Kunz, T.H., Allgaier, A.L., Seyjagat, J., Caligiuri, R., 1994. Allomaternal care: helperassisted birth in the Rodrigues fruit bat, Pteropus rodricensis (Chiroptera: Pteropodidae). J. Zool. 232, 691–700. https://doi.org/10.1111/j.1469-7998.1994.tb04622.x
- Kurt, F., Garai, M., 2001. Stereotypies in captive Asian Elephants: a symptom of social isolation, in: H. M. Schwammer, Foose, T.J., Fouraker, M., D. Olson, A. research update on elephants and rhinos . (Eds.), Recent Research on Elephants and Rhinos : Abstracts of the International Elephant and Rhino

Research Symposium Vienna. June 7 - 11. 2001. Schüling Verlag, Münster, pp. 57–63.

- Kurt, F., Mar, K.U., 1996. Neonate mortality in captive Asian elephants (Elephas maximus). Zeitschrift Fur Saugetierkunde-International J. Mamm. Biol.
- L, W., 2013. Unpublished data. Stirling University.
- Lacy, R.C., 2013. Achieving True Sustainability of Zoo Populations. Zoo Biol. 32, 19– 26. https://doi.org/10.1002/zoo.21029
- Langergraber, K., Mitani, J., Vigilant, L., 2009. Kinship and social bonds in female chimpanzees (Pan troglodytes). Am. J. Primatol. 71, 840–851. https://doi.org/10.1002/ajp.20711
- Langman, V.A., 1977. Cow-calf Relationships in Giraffe (Girraffa camelopardalis giraffa). Z. Tierpsychol. 43, 264–286.
- Lee, P.C., 1987. Allomothering among African elephants. Anim. Behav. 35, 278–291. https://doi.org/10.1016/S0003-3472(87)80234-8
- Lee, P.C., Moss, C.J., 2014. African Elephant Play, Competence and Social Complexity. Anim. Behav. Cogn. 1, 144–156. https://doi.org/10.12966/abc.05.05.2014
- Lee, P.C., Moss, C.J., 2011. Calf Development and Maternal Rearing Strategies, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. The University of Chicago Press, Chicago, pp. 224–237.
- Lees, C.M., Wilcken, J., 2009. Sustaining the Ark: The challenges faced by zoos in maintaining viable populations. Int. Zoo Yearb. 43, 6–18. https://doi.org/10.1111/j.1748-1090.2008.00066.x
- Littin, K.E., Cockrem, J.F., 2001. Individual variation in corticosterone secretion in laying hens. Br. Poult. Sci. 42, 536–546. https://doi.org/10.1080/00071660120070613
- Lock, L.C., Anderson, J.R., 2013. Kin, daytime associations, or preferred sleeping sites? factors influencing sleep site selection in captive chimpanzees (pan troglodytes). Folia Primatol. 84, 158–169. https://doi.org/10.1159/000351553
- Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. Proc. R. Soc. B Biol. Sci. 271, 477–481. https://doi.org/10.1098/rsbl.2004.0225
- Lynch, E.C., Lummaa, V., Htut, W., Lahdenperä, M., 2019. Evolutionary significance of maternal kinship in a long-lived mammal. Philos. Trans. R. Soc. B Biol. Sci. 374, 20180067. https://doi.org/10.1098/rstb.2018.0067

Maestripieri, D., 1994. Social Structure, Infant Handling, and Mothering Styles in

Group-Living Old World Monkeys. Int. J. Primatol. 15, 531–553.

- Mantel, N., 1967. The Detection of Disease Clustering and a Generalized Regression Approach. Nature 27, 209–220. https://doi.org/10.1038/214637b0
- Martin, P., Bateson, P., 1993. Measuring Behaviour: An Introductory Guide, Second. ed. Cambridge Press, Cambridge.
- Mason, G.J., Veasey, J.S., 2010. What do population-level welfare indices suggest about the well-being of zoo elephants? Zoo Biol. 29, 256–273. https://doi.org/10.1002/zoo.20303
- 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, 1– 11. https://doi.org/10.1371/journal.pone.0073044
- Maynard Smith, J., 1964. Group Selection and Kin Selection. Nature 201, 1145– 1147. https://doi.org/1475-2875-9-181 [pii]\n10.1186/1475-2875-9-181
- McComb, K., Baker, L., Moss, C., 2006. African elephants show high levels of interest in the skulls and ivory of their own species. Biol. Lett. 2, 26–28. https://doi.org/10.1098/rsbl.2005.0400
- Mccomb, K., Moss, C., Durant, S.M., Baker, L., Sayialel, S., 2001. Matriarchs As Repositories of Social Knowledge in African Elephants. Science (80-.). 292, 491–494. https://doi.org/10.1126/science.1057895
- Mehta, P.H., Josephs, R.A., 2011. Social endocrinology: Hormones and social motivation, in: Dunning, D. (Ed.), The Handbook of Social Motivation.
 Psychology Press, New York, New York, pp. 171–190.
 https://doi.org/10.4324/9780203833995
- Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance: Evidence for a dual-hormone hypothesis. Horm. Behav. 58, 898– 906. https://doi.org/10.1016/j.yhbeh.2010.08.020
- Menargues, A., Urios, V., Mauri, M., 2008. Welfare assessment of captive Asian elephants (Elephas maximus) and Indian rhinoceros (Rhinoceros unicornis) using salivary cortisol measurement. Anim. Welf. 17, 305–312. https://doi.org/10.4028/www.scientific.net/AMM.327.201
- Menargues, A.M., Urios, V., Limiñana, R., 2012. Seasonal rhythms of salivary cortisol secretion in captive Asian elephants (Elephas maximus). Gen. Comp. Endocrinol. 176, 259–264. https://doi.org/10.1016/j.ygcen.2012.02.001
- Meyer, J.M., Walker, S.L., Freeman, E.W., Steinetz, B.G., Brown, J.L., 2004. Species and fetal gender effects on the endocrinology of pregnancy in elephants. Gen. Comp. Endocrinol. 138, 263–270. https://doi.org/10.1016/j.ygcen.2004.06.010
- Mochida, K., Nishikawa, M., 2014. Sleep duration is affected by social relationships among sleeping partners in wild Japanese macaques. Behav. Processes 103,

102-104. https://doi.org/10.1016/j.beproc.2013.10.010

- Morfeld, K.A., Meehan, C.L., Hogan, J.N., Brown, J.L., 2016. Assessment of body condition in African (Loxodonta africana) and Asian (Elephas maximus) elephants in North American zoos and management practices associated with high body condition scores. PLoS One 11, 1–20. https://doi.org/10.1371/journal.pone.0155146
- Moss, C.J., Croze, H., Lee, P.C., 2011. The Amboseli Elephants: A long-term perspective on a long-lived mammal. The University of Chicago Press.
- Moss, C.J., Lee, P.C., 2011a. Female Social Dynamics: Fidelity and Flexibility, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. The University of Chicago Press, Chicago, pp. 204–223.
- Moss, C.J., Lee, P.C., 2011b. Female Reproductive Strategies: Individual Life Histories, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. The University of Chicago Press, Chicago, pp. 187–204.
- Müller, D.W.H., Gaillard, J.M., Lackey, L.B., Hatt, J.M., Clauss, M., 2010. Comparing life expectancy of three deer species between captive and wild populations. Eur. J. Wildl. Res. 56, 205–208. https://doi.org/10.1007/s10344-009-0342-8
- Mumby, H.S., Mar, K.U., Thitaram, C., Courtiol, A., Towiboon, P., Min-Oo, Z., Htut-Aung, Y., Brown, J.L., Lummaa, V., 2015. Stress and body condition are associated with climate and demography in Asian elephants. Conserv. Physiol. 3, 1–14. https://doi.org/10.1093/conphys/cov030
- Munck, A., Guyre, P.M., Holbrooke, N.J., 1984. Physiological Functions of Glucocorticoids in Stress and Their Relation to Pharmacological Actions in Stress. Endocr. Soc. 5, 25–44. https://doi.org/10.1210/edrv-5-1-25
- Nakamichi, M., Murata, C., Eto, R., Takagi, N., Yamada, K., 2015. Daytime mothercalf relationships in reticulated giraffes (Giraffa cameloparadalis reticulate) at the Kyoto City Zoo. Zoo Biol. 34, 110–117. https://doi.org/10.1002/zoo.21198
- Nandini, S., Keerthipriya, P., Vidya, T.N.C., 2017. Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. Anim. Behav. 134, 135–145. https://doi.org/10.1016/j.anbehav.2017.10.012
- Newman, M.E.J., 2004. Analysis of weighted networks. Phys. Rev. E Stat. Physics, Plasmas, Fluids, Relat. Interdiscip. Top. 70, 9. https://doi.org/10.1103/PhysRevE.70.056131
- Noser, R., Gygax, L., Tobler, I., 2003. Sleep and social status in captive gelada baboons (Theropithecus gelada). Behav. Brain Res. 147, 9–15. https://doi.org/10.1016/S0166-4328(03)00111-6

- Nunes, S., Weidenbach, J.N., Lafler, M.R., Dever, J.A., 2015. Sibling relatedness and social play in juvenile ground squirrels. Behav. Ecol. Sociobiol. 69, 357–369. https://doi.org/10.1007/s00265-014-1848-y
- O'Brien, T.G., Robinson, J.G., 1991. Allomaternal Care by Female Wedge-Capped Capuchin Monkeys: Effects of Age, Rank and Relatedness. Behaviour 119, 30– 50.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package.
- Opp, M.R., Krueger, J.M., 2015. Sleep and immunity: A growing field with clinical impact. Brain. Behav. Immun. 47, 1–3. https://doi.org/10.1016/j.bbi.2015.03.011
- Opshal, T., 2009. Structure and Evolution of Weighted Networks.
- Pepper, J.W., Mitani, J.C., Watts, D.P., 1999. General gregariousness and specific social preferences among wild chimpanzees. Int. J. Primatol. 20, 613–632. https://doi.org/10.1023/A:1020760616641
- Pinter-Wollman, N., Isbell, L.A., Hart, L.A., 2009. The relationship between social behaviour and habitat familiarity in African elephants (Loxodonta africana). Proc. R. Soc. B Biol. Sci. 276, 1009–1014. https://doi.org/10.1098/rspb.2008.1538
- Poole, J H., Granli, P., 2011. Signals, Gestures, and Behaviours of African Elephants, in: Moss, C.J., Croze, H., Lee, P. (Eds.), The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. The University of Chicago Press, pp. 109–124.
- Poole, Joyce H., Granli, P., 2011. Signals, Gestures and Behavior of African Elephants, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. The University of Chicago Press, Chicago, pp. 109–124.
- Poole, J.H., Moss, C.J., 2008. Elephant sociality and complexity: The scientific evidence, in: Wemmer, C., Christen, C. (Eds.), Elephants and Ethics: Toward a Morality of Coexistence. The Johns Hopkins University Press, Baltimore, pp. 69–94.
- Posta, B., Huber, R., Moore, D.E., 2013. The Effects of Housing on Zoo Elephant Behavior : A Quantitative Case Study of Diurnal and Seasonal Variation. Int. J. Comp. Psychol. 26, 37–52.
- Pratt, D.M., Anderson, V.H., 1979. Giraffe Cow-Calf Relationships and Social Development of the Calf in the Serengeti. Z. Tierpsychol. 51, 233–251. https://doi.org/10.1111/j.1439-0310.1979.tb00686.x
- Proctor, C.M., Freeman, E.W., Brown, J.L., 2010a. Results of a second survey to assess the reproductive status of female asian and african elephants in North America. Zoo Biol. 29, 127–139. https://doi.org/10.1002/zoo.20238
- Proctor, C.M., Freeman, E.W., Brown, J.L., 2010b. Influence of dominance status on adrenal activity and ovarian cyclicity status in captive African elephants. Zoo Biol. 29, 168–178. https://doi.org/10.1002/zoo.20292
- R Core Team, 2017. R: A Language and Environment for Statistical Computing.
- Ralls, K., Kranz, K., Lundrigan, B., 1986. Mother-young relationships in captive ungulates: variability and clustering. Anim. Behav. 34, 134–145. https://doi.org/10.1016/0003-3472(86)90015-1
- Rapaport, L., Haight, J., 1987. Some observations regarding allomaternal caretaking among captive Asian elephants (Elephas maximus). J. Mammal. 68, 438–442.
- Raulo, A., Dantzer, B., 2018. Associations between glucocorticoids and sociality across a continuum of vertebrate social behavior. Ecol. Evol. 8, 7697–7716. https://doi.org/10.1002/ece3.4059
- Rees, P.A., 2009. The sizes of elephant groups in zoos: Implications for elephant welfare. J. Appl. Anim. Welf. Sci. 12, 44–60. https://doi.org/10.1080/10888700802536699
- Rees, P.A., 2003. Asian elephants in zoos face global extinction: Should zoos accept the inevitable? Oryx 37, 20–25. https://doi.org/10.1017/S003060530300005X
- Riedman, M.L., 1982. The Evolution of Alloparental Care and Adoption in Mammals and Birds. Q. Riview Biol. 57, 405–435.
- Riss, D., Goodall, J., 1976. Sleeping behavior and associations in a group of captive chimpanzees. Folia Primatol. (Basel). 25, 1–11. https://doi.org/10.1159/000155703
- Romero, L.M., 2004. Physiological stress in ecology: Lessons from biomedical research. Trends Ecol. Evol. 19, 249–255. https://doi.org/10.1016/j.tree.2004.03.008
- Rose, P.E., Croft, D.P., 2015. The potential of social network analysis as a tool for the management of zoo animals. Anim. Welf. 24, 123–138. https://doi.org/10.7120/09627286.24.2.123
- Rosenbaum, S., Gettler, L.T., 2018. With a little help from her friends (and family) part I: the ecology and evolution of non-maternal care in mammals. Physiol. Behav. 193, 1–11. https://doi.org/10.1016/j.physbeh.2017.12.025
- Rothfels, N., 2008. Elephants, Ethics and History, in: Wemmer, C., Christen, C.A. (Eds.), Elephants and Ethics: Toward a Morality of Coexistence. The Johns Hopkins University Press, Baltimore, pp. 101–119.

- Sanderson, J.L., Nichols, H.J., Marshall, H.H., Vitikainen, E.I.K., Thompson, F.J., Walker, S.L., Cant, M.A., Young, A.J., 2015. Elevated glucocorticoid concentrations during gestation predict reduced reproductive success in subordinate female banded mongooses. Biol. Lett. 11, 4–8. https://doi.org/10.1098/rsbl.2015.0620
- Sapolsky, R.M., 2002. Endocrinology of the Stress Response, in: Becker, J.B., Breedlove, S.M., Crews, D., McCarthy, M.M. (Eds.), Behvioural Endocrinology. pp. 409–450.
- Sapolsky, R.M., 1999. Glucocorticoids, stress, and their adverse neurological effects: relevance to aging. Exp. Gerontol. 34, 721–732.
- Sapolsky, R.M., 1997. Hypercortisolism Associated With Social Subordinance or Social Isolation Among Wild Baboons. Arch. Gen. Psychiatry 54, 1137. https://doi.org/10.1001/archpsyc.1997.01830240097014
- Sapolsky, R.M., Alberts, S.C., Altmann, J., 1997. Hypercortisolism Associated With Social Subordinance or Social Isolation Among Wild Baboons. Arch. Gen. Psychiatry 54, 1137. https://doi.org/10.1001/archpsyc.1997.01830240097014
- Schmid, J., Heistermann, M., Gansloßer, U., Hodges, J.K., 2001. Introduction of foreign female Asian elephants (Elephas Maximus) into an existing group: Behavioural reactions and changes in cortisol levels. Anim. Welf. 10, 357–372. https://doi.org/10.1007/11557067_14
- Schmidt, H., Kappelhof, J., 2019. Review of the management of the Asian elephant Elephas maximus EEP: current challenges and future solutions . Int. Zoo Yearb. 1–14. https://doi.org/10.1111/izy.12233
- Schubert, M., Pillay, N., Schradin, C., 2009. Parental and Alloparental Care in a Polygynous Mammal. J. Mammal. 90, 724–731. https://doi.org/10.1644/08mamm-a-175r1.1
- Schulte, B.A., 2000. Social structure and helping behavior in captive elephants. Zoo Biol. 19, 447–459.
- Seyfarth, R.M., Silk, J.B., Cheney, D.L., 2014. Social bonds in female baboons: The interaction between personality, kinship and rank. Anim. Behav. 87, 23–29. https://doi.org/10.1016/j.anbehav.2013.10.008
- Siegel, J.M., 2008. Do all animals sleep? Cell Press. https://doi.org/10.1016/j.tins.2008.02.001
- Siegel, J.M., 2005. Clues to the functions of mammalian sleep. Nature 437.
- Silk, J., Cheney, D., Seyfarth, R., 2013. A practical guide to the study of social relationships. Evol. Anthropol. 22, 213–225. https://doi.org/10.1002/evan.21367
- Silk, J.B., Alberts, S.C., Altmann, J., 2003. Social Bonds of Female Baboons Enhance

Infant Survival. Science (80-.). 302, 1231–1234.

- Silk, J.B., Altmann, J., Alberts, S.C., 2006a. Social relationships among adult female baboons (papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. https://doi.org/10.1007/s00265-006-0249-2
- Silk, J.B., Altmann, J., Alberts, S.C., 2006b. Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. https://doi.org/10.1007/s00265-006-0249-2
- Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010a. Female chacma baboons form strong, equitable, and enduring social bonds. Behav. Ecol. Sociobiol. 64, 1733–1747. https://doi.org/10.1007/s00265-010-0986-0
- Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010b. Strong and consistent social bonds enhance the longevity of female baboons. Curr. Biol. 20, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067
- Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2009. The benefits of social capital: Close social bonds among female baboons enhance offspring survival. Proc. R. Soc. B Biol. Sci. 276, 3099–3104. https://doi.org/10.1098/rspb.2009.0681
- Silva, S. De, Rangeewa, A.D.G., Kryazhimskiy, S., 2011a. The Dynamics of Social Networks in Asian Elephants. BMC Ecol. 11, 1–15.
- Silva, S. De, Rangeewa, A.D.G., Kryazhimskiy, S., 2011b. The Dynamics of Social Networks in Asian Elephants (Supplementary Text). BCM Ecol. 11.
- Slotow, R., Van Dyk, G., Poole, J., Page, B., Klocke, A., 2000. Older bull elephants control young males. Nature 408, 425–426. https://doi.org/10.1038/35044191
- Smith, J.E., Powning, K.S., Dawes, S.E., Estrada, J.R., Hopper, A.L., Piotrowski, S.L., Holekamp, K.E., 2011. Greetings promote cooperation and reinforce social bonds among spotted hyaenas. Anim. Behav. 81, 401–415. https://doi.org/10.1016/j.anbehav.2010.11.007
- Snijders, L., Blumstein, D.T., Stanley, C.R., Franks, D.W., 2017. Animal Social Network Theory Can Help Wildlife Conservation. Trends Ecol. Evol. 32, 567– 577. https://doi.org/10.1016/j.tree.2017.05.005
- Species360, 2019. Species360 ZIMS (Zoological Information Management Software).
- Stanford, C.B., 1992. Costs and benefits of allomothering in wild capped langurs (Presbytis pileata). Behav. Ecol. Sociobiol. 30, 29–34.

https://doi.org/10.1007/BF00168591

- Stokes, H., 2017. Nocturnal behavior of orphaned Asian elephant (Elephas maximus) calves in Sri Lanka. Zoo Biol. 26, 261–272. https://doi.org/10.1002/zoo.21360
- Stone, A.I., Mathieu, D., Griffin, L., Bales, K.L., 2010. Alloparenting experience affects future parental behavior and reproductive success in prairie voles (Microtus ochrogaster). Behav. Processes 83, 8–15. https://doi.org/10.1016/j.beproc.2009.08.008
- Sukumar, R., 2006. A brief review of the status, distribution and biology of wild Asian elephants. Int. Zoo Yearb. 1–8.
- Sukumar, R., 2003. The Living Elephants: Evolutionary Ecology, Behavior, and Conservation. Oxford University Press, Inc., New York, New York.
- Sukumar, Raman, 1989. The Asian Elephant: ecology and management, First. ed. Cambridge University Press, Cambridge.
- Sukumar, R, 1989. Ecology of the Asian elephant in Southern India. I. Movement and habitat utilization patterns. J. Trop. Ecol. 5, 1–18.
- Taber, S., Thomas, P., 1982. Calf development and mother-calf spatial relationships in Southern right whales. Anim. Behav. 30, 1072–1083. https://doi.org/10.1016/S0003-3472(82)80197-8
- Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A.R., Updegraff, J.A., 2000. Biobehavioral Responses to Stress in Females : tend-befriend or flightfight. Psychol. Rev. 107, 411–429. https://doi.org/10.1037//0033-295X.107.3.411
- Thomas, P.O., Taber, S.M., 1984. Mother-Infant Interaction and Behavioral Development in Southern Right Whales , Eubalaena australis. Behaviour 88, 42–60.
- Tidière, M., Gaillard, J.-M., Berger, V., Müller, D.W.H., Bingam Lackey, L., Gimenez, O., Clauss, M., Lemaître, J.-F., 2016. Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. Sci. Rep. 6.
- Tingvold, H.G., Fyumagwa, R., Bech, C., Baardsen, L.F., Rosenlund, H., Røskaft, E., 2013. Determining adrenocortical activity as a measure of stress in African elephants (Loxodonta africana) in relation to human activities in Serengeti ecosystem. Afr. J. Ecol. 51, 580–589. https://doi.org/10.1111/aje.12069
- Tobaldini, E., Costantino, G., Solbiati, M., Cogliati, C., Kara, T., Nobili, L., Montano, N., 2017. Sleep, sleep deprivation, autonomic nervous system and cardiovascular diseases. Neurosci. Biobehav. Rev. 74, 321–329. https://doi.org/10.1016/j.neubiorev.2016.07.004

Tobler, I., 1992. Behavioral Sleep in the Asian Elephant in Captivity. Sleep 15, 1–12.

- Tobler, I., Schwierin, B., 1996. Behavioural sleep in the giraffe (Giraffa camelopardalis) in a zoological garden. J. Sleep Res. 5, 21–32.
- VanderWaal, K.L., Atwill, E.R., Isbell, L.A., McCowan, B., 2014. Quantifying microbe transmission networks for wild and domestic ungulates in Kenya. Biol. Conserv. 169, 136–146. https://doi.org/10.1016/j.biocon.2013.11.008
- Veasey, J., 2006. Concepts of care and welfare of captive elephants. Int. Zoo Yearb. 63–79.
- Vidya, T. N. C., Sukumar, R., 2005. Social and reproductive behaviour in elephants. Curr. Sci. 89, 1200–1207.
- Vidya, T. N.C., Sukumar, R., 2005. Social organization of the Asian elephant (Elephas maximus) in southern India inferred from microsatellite DNA. J. Ethol. 23, 205– 210. https://doi.org/10.1007/s10164-005-0144-8
- Vijayakrishnan, S., Kumar, M.A., Umapathy, G., Kumar, V., Sinha, A., 2018. Physiological stress responses in wild Asian elephants Elephas maximus in a human-dominated landscape in the Western Ghats, southern India. Gen. Comp. Endocrinol. 266, 150–156. https://doi.org/10.1016/j.ygcen.2018.05.009
- Walsh, B., 2017. Sleep in Asian elephants (Elephas maximus): long-term quantitative research at Dublin Zoo. J. Zoo Aquarium Res. 5, 82–85.
- Watson, R., Munro, C., Edwards, K.L., Norton, V., Brown, J.L., Walker, S.L., 2013. Development of a versatile enzyme immunoassay for non-invasive assessment of glucocorticoid metabolites in a diversity of taxonomic species. Gen. Comp. Endocrinol. 186, 16–24.
- Webber, Q.M.R., Schneider, D.C., Vander Wal, E., 2020. Is less more? A commentary on the practice of 'metric hacking' in animal social network analysis. Anim. Behav. 168, 109–120. https://doi.org/10.1016/j.anbehav.2020.08.011
- Wey, T., Blumstein, D.T., Shen, W., Jordán, F., 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. 75, 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020
- 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 Biol. 31, 442–452. https://doi.org/10.1002/zoo.20408
- Whitehead, H., 2008a. Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis, First. ed. The University of Chicago Press, Chicago.
- Whitehead, H., 2008b. Precision and power in the analysis of social structure using associations. Anim. Behav. 75, 1093–1099. https://doi.org/10.1016/j.anbehav.2007.08.022
- Whitehead, H., 1997. Analysing animal social structure. Anim. Behav. 53, 1053– 1067. https://doi.org/10.1006/anbe.1996.0358

- Whitehead, H., 1995. Investigating structure and temporal scale in social organizations using identified individuals_Whitehead_Behaviural EcologyWhitehead.pdf. Behav. Ecol. 6, 199–208.
- Whitehead, H., Arnbom, T., 1987. Social organization of sperm whales off the Galapagos Islands, February–April 1985. Can. J. Zool. 65, 913–919. https://doi.org/10.1139/z87-145
- Wich, S.A., Shumaker, R.W., Perkins, L., De vries, H., 2009. Captive and wild orangutan (Pongo sp.) survivorship: A comparison and the influence of management. Am. J. Primatol. 71, 680–686. https://doi.org/10.1002/ajp.20704
- Wiese, R.J., 2000. Asian elephants are not self-sustaining in North America. Zoo Biol. 19, 299–309. https://doi.org/10.1002/1098-2361(2000)19:5<299::AID-ZOO2>3.0.CO;2-Z
- Wiese, R.J., Willis, K., 2004. Calculation of longevity and life expectancy in captive elephants. Zoo Biol. 23, 365–373. https://doi.org/10.1002/zoo.20011
- Wilson, M.L., Bashaw, A.M.J., Fountain, K., Kieschnick, S., Maple, T.L., Zoo, L.P., Atlanta, Z., Atlanta, Z., Bashaw, M.J., Fountain, K., Kieschnick, S., Maple, T.L., Brockett, R.C., Stoinski, T.S., Black, J., Markowitz, T., Atlanta, Z., Atlanta, Z., Berger, R.J., Phillips, N.H., Capellini, I., Nunn, C.L., Preston, B.T., Barton, R.A., Gravett, N., Bhagwandin, A., Sutcliffe, R., Landen, K., Chase, M.J., Lyamin, O.I., Siegel, J.M., Manger, P.R., Cirelli, C., Tononi, G., Holdgate, M.R., Meehan, C.L., Hogan, J.N., Miller, L.J., Rushen, J., Passillé, A.M. De, Soltis, J., Andrews, J., Horne, A., Date, P., Mignot, E., Noser, R., Gygax, L., Tobler, I., Powell, D.M., Vitale, C., Santymire, R., Meyer, J., Freeman, E.W., Siegel, J.M., Stokes, H., Tobler, I., Res, S., Vorster, A.P., Born, J., Walsh, B., 2006. Nocturnal Behaviour in a Group of Female African Elephants. Zoo Biol. 25, 173–186. https://doi.org/10.1002/zoo
- Wilson, M.L., Bloomsmith, M., Maple, T., 2004a. Stereotypic swaying and serum cortisol concentrations in three captive African elephants (Loxodonta africana). Anim. Welf. 13, 39–43.
- Wilson, M.L., Bloomsmith, M.A., Maple, T.L., 2004b. Stereotypic swaying and serum cortisol concentrations in three captive African elephants (Loxodonta africana). Anim. Welf. 13, 39–43. https://doi.org/10.1108/eb051284
- Wittemyer, G., Douglas-Hamilton, I., Getz, W.M., 2007. The socioecology of elephants: analysis of the processes creating multilayered social structures. openUP.
- Wittemyer, G., Getz, W.M., 2007. Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. Anim. Behav. 73, 671– 681. https://doi.org/10.1016/j.anbehav.2006.10.008

Wittig, R.M., Crockford, C., Weltring, A., Langergraber, K.E., Deschner, T.,

Zuberbühler, K., 2016. Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. Nat. Commun. 7, 4–11. https://doi.org/10.1038/ncomms13361

- Wright, K.P., Drake, A.L., Frey, D.J., Fleshner, M., Desouza, C.A., Gronfier, C., Czeisler, C.A., 2015. Influence of sleep deprivation and circadian misalignment on cortisol, inflammatory markers, and cytokine balance. Brain. Behav. Immun. 47, 24–34. https://doi.org/10.1016/j.bbi.2015.01.004
- Young, C., Majolo, B., Heistermann, M., Schülke, O., Ostner, J., 2014. Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proc. Natl. Acad. Sci. U. S. A. 111, 18195–18200. https://doi.org/10.1073/pnas.1411450111
- Zayan, R., 1991. The specificity of social stress. Behav. Processes 25, 81–93.

Zepelin, H., Siegel, J.M., Tobler, I., 2005. Mammalian Sleep.

Appendix

Appendix 1 The Social Dynamics of Captive Asian Elephants (*Elephas maximus*)

Appendix 1.1 The number of days of data collected during study period. Observational data of the Chester Zoo herd were collected between February 2016 and March 2018 in 2-hour observation periods, on an average of 3 times per week. At Dublin Zoo data collected between 11 April and 26 August 2018. Scan samples were performed once an hour throughout the course of zookeepers' working day (07:00 – 18:00).

Chester Zoo			
Total Days of Data Collected	Data Collection Days - AM	Data Collections Days - PM	Total Observation hours
106	55	51	168
Dublin Zoo			
Total Days of Data Collected	Average number of scans per day	Total number of scans	
38	9	345	

Dublin Zoo Modified Methods:

Dublin Zoo data collection methods, collected by Mel Sheridan, elephant keeper. Due to the nature of daily husbandry and management of zoo elephants, we modified the data collection methods utilised by Ms Sheridan to fit within her daily schedule:

Daytime:

- 1. Data were collected between 11 April and 26 August 2018, 3 times per week
- 2. Working day started from 07:00 ended at 18:00

- 3. From the start of the working day, once per hour scan sampling of the herd was conducted to record an individual's nearest neighbours.
- 4. Nearest neighbours were recorded once an hour until the end of the working day (between 8 and 14) data points were recorded per day.
- 5. Raw data was then sent via email to the author to analyse

Night-time:

- Data of sleeping associations were collected by analysing Closed Circuit Television (CCTV) footage of the females and calves over the same period as when the day-time observations were conducted.
- 2. Data were collected for 2 3 nights per week
- 3. For each night, a 2-hour period was were randomly selected and observations commenced.
- 4. <u>All bouts of recumbent sleep were recorded within the selected 2-hour period.</u>
- 5. The start of a sleeping bout was defined as when the elephant was completely recumbent on its side, with its head and all four legs parallel to the ground.
- 6. The end of a sleeping bout was defined as when the elephant returned to a standing position on all four feet.
- 7. Sleeping associations were defined if the sleeping animals was within two body-lengths of another individual.
- 8. If any part of an elephant's body was in direct physical contact with another elephant this was noted to be a touching interaction.
- 9. When an elephant was observed sleeping, the start time of sleep and the time of wake up were recorded, as well as the individuals that were in close proximity to them as they slept.

Appendix 1.2 Chester Zoo and Dublin Zoo Asian Elephant Herds The individuals included in this study from the Chester Zoo and Dublin Zoo elephant herds. A record is kept of an individual's ID, mother (dam), and father (sire), date of birth and sex.

The Chester Zoo herd is made up of 3 related adult females and their 4 calves (CZHW family). There is also an unrelated adult female, CZM1, present in the herd. The current breeding bull mixed with the herd is CZAB1. CZM1 and CZHW1 have been housed at Chester Zoo since 1990 and 1991, respectively. Within that period CZHW1 has mothered many offspring, including CZHW2 who is included in this study. The bull elephant has been present in the herd since 2013 and has sired all represented below.

Individual ID	Sex	Date of Birth	Birth Type	Dam	Sire
Chester Zoo					
CZM1	Female (adult)	01-01-1972	Wild Born	unknown	unknown
CZHW1	Female (adult)	15-12-1982	Captive Born	unknown	unknown
CZHW2	Female (adult)	31-12-1997 – 17-09-2018	Captive Born	CZHW1	CZCH1
CZHW3	Female (adult)	07-03-2004	Captive Born	CZHW2	DZU1
CZHW4	Female (juvenile)	20-08-2015 – 26-10-2018	Captive Born	CZHW1	CZAB1
CZHW5	Female (infant)	16-12-2016	Captive Born	CZHW3	CZAB1
CZHW6	Male (infant)	17-01-2017 – 25-10-2018	Captive Born	CZHW2	CZAB1
CZHW7			Captivo		
(not included in study)	Male (infant)	17-05-2018	Born	CZHW1	CZAB1

The Dublin Zoo herd was established by the two oldest females in the herd DZB1 and DZY1, who are sisters. Both DZB1, DZY1 and DZB2 have been housed at Dublin Zoo since 2006. All calves represented below are offspring of these three females. During the time of the study, the resident bull, DZU1, had been separated from the herd as preparation for its transfer to another zoo later that year. However, under normal circumstances the bull would be mixed with the family group during the day.

Individual ID	Sex	Date of Birth	Birth Type	Dam	Sire
Dublin Zoo					
D7B1	Female	16-06-1984	Captive Born	IRM01	RAM01
	(adult)	10 00 1901	cuptive born		
D7B2	Female	07-05-2007	Cantive Born	D7B1	ΔI B01
	(adult)		cuptive born	DEDI	ALDOI
D7B3	Female	17-09-2014	Cantive Born	D7B1	D7U1
5250	(juvenile)	1, 00 2011		0201	5201
D7B4	Female	13-03-2017	Captive Born	D7B1	D7U1
	(infant)				
DZB2a	Female	19-09-2016	Captive Born	DZB2	DZU1
	(infant)				
DZY1	Female	25-11-1990	Captive Born	IRM01	RAM01
	(adult)				
DZY2	Female	26-07-2003	Captive Born	DZY1	ALB01
	(adult)				
DZY3	Male	17-07-2014	Captive Born	DZY1	DZU1
	(juvenile)				
DZY2a	Male	19-08-2014	Captive Born	DZY2	DZU1
	(juvenile)				
DZY4	Male	15-05-2017	Captive Born	DZY1	DZU1
	(infant)				
DZY2b	Male	11-02-2018	Captive Born	DZY2	DZU1
	(infant)		·		

Appendix 1.3 Ethogram of Asian elephant (Elephas maximus) behaviours categorised as broad-state, social and maternal behaviours. This ethogram was used as a reference for data collection purposes. Behaviours included in this ethogram have been defined in previous works of literature (L, 2013; J H. Poole and Granli, 2011; Posta et al., 2013).

	Broad-state behaviours
Feeding	Seeking or ingesting of food or water. Often involves gathering food with its trunk and lifting it into its mouth. Animals not engaged in any other behaviour.
Locomotion	Animal takes 2 or more steps in any direction but not in a stereotypic pattern. Does not exhibit any other overt behaviour simultaneously.
Inactive	Standing or lying while exhibiting no other behaviour including sleeping
Investigation	Exploring or manipulation any area of the environment. Includes raising trunk to smell environment, using trunk on ground or exhibit furniture to explore substrate, bars, gates, locks, spices, or other objects.
Nursing	One or more series of mouth on nipple incidents separated by less than sixty seconds.
Excretion	Excreting urine or faeces
Comfort/Body care	Picking up and throwing substrate (e.g. earth or water) onto self, rubbing against object (non-stereotypic), scratching self with trunk or foot, mud bathing, water bathing.
Vocalisation	Audible, acoustic signals ranging from low frequency rumbles, to high frequency snorts, barks, roars, cries and chirps.
Lie (asleep/rest)	Individual is in a lateral recumbence. Weight is no longer supported by legs. No other behaviours are occurring simultaneously.
Stereotypy	Any behaviour that occurs in repetitive pattern, including pacing, rocking, trunk swinging, trunk tossing head rubbing, swaying or head bobbing.

Social Behaviours	
Affiliative	

Nearest	Individuals within two body-lengths of one another are considered to be
Neighbour	associating with one another.
Touching	The use of trunk or body mass to gently brush up against another elephant for prolonged (>2sec) contact between such parts (other than tail). May use trunk to touch body, genitals, nipple, face, or mouth. May also involve the intertwining of trunks, rubbing, leaning and nudging with trunk or head.
Body Rub	Individual approaches another family member a rubs head or side against family member.
Leaning	Resting weight on and leaning on another elephant
Caress	An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too.
Greeting	Trunk tip placed in mouth, on temporal gland or between leg of a conspecific
Approach	Moving in a non-aggressive manner, within one body length of another elephant
Trunk-face	Trunk tip placed in on face/temporal gland of a conspecific
Trunk-mouth	Individual reaches trunk toward or inside another's mouth
Trunk-genitals	Touching the genital area of another elephant with trunk
Trunk-trunk	Intertwining of trunks between two elephants
Gathering	During interactions of extreme social arousal, herd members may gather together in a close cluster, pressing bodies against one another.
Greeting Ceremony	Members of family/herd may run to meet each other while emitting loud, modulated, throaty, rumbles, trumpets, roars, and screams. Raise heads and lift and spread their ears. Rub against on another they stand in parallel, back into one another, spin around, urinate and defecate. (Poole & Granli, 2011)
Trunk reach	Trunk extended towards another elephant to smell it. Trunk usually in "S" or "J" position
Heard Push	While moving together as a group, one elephant may give another a gentle push to keep individual moving with the group.

Play	Non-aggressive contact which may include rubbing against, pushing against, or backing into another elephant; interacting in water; rolling in the ground with another elephant; climbing on/with/kneeling on another elephant; sparring; wrestling; play mount; pushing; bite or "mouth" in play.
Back-Toward	When joining a resting group or in the context of high-level greetings, an elephant presents its posterior and walks backward toward another elephant, most often a high-ranking individual. (also, submissive)
Restrain	Calf attempts to move away from proximity of adult; adult prevents calf from moving away using trunk or foot.
Parallel walk	Two individuals walk side by side in a non-aggressive manner, for more than 3 steps
Follow	An elephant walks closely behind (within 2 elephant body lengths) of another elephant
Sexual monitoring	
Test genitals	An individual reaches toward the genitals of another (sniffing) for the purpose of assessment of reproductive state. Can be <i>male-male, male-female, or female-female.</i>
Test Urine	An elephant touches the tip of its trunk, over, on, or in urine/urine spot for the purpose of assessment of reproductive state. After placing tip of trunk in/on urine, the trunk may be curled and raised to the roof of the mouth where the vomeronasal organ is situated – Flehmen response.
Test Dung	Placing tip or trunk over/on dung.
Rump-present	Female elephants may back towards a male for testing or to solicit mating.

	Agonistic
Threat/Display	Aggression between elephants that does not involve contact.
Turn-Toward	Threaten another elephant by a resolute re-orienting of its body to gaze at an opponent.
Advance-toward	Purposefully taking one step toward or walking toward an opponent enough to cause a reaction.
Escalation	
Pursuit	To run after or chase an opponent

Mock-Charge	Rushing toward an adversary, with head high and ears spread that stops short of its target. May aggressively swing trunk and kick dust as it stops abruptly.
Charge	Elephant rushes toward another elephant with the apparent intention of following through. Head may be held high or lowered; ears spread and trunk curled under.
Push	One elephant makes contact with another and gradually forces or pushes against the other, often causing it to move or to be supplanted. May be body-to-body contact or the elephant may push with its forehead or base of the trunk into the back, side, head or trunk of the other.
Slap	(Common in <i>Elephas spp</i> .) An elephant hits another elephant with its trunk.
Drive	One animal follows closely behind another, the follower pushing the other animal from behind. Both animals must take more than two steps. The follower may make contact with the base of its trunk or put its trunk over the back of the first animal.
Tusking	Poking an opponent using the tip of tusks; also, an escalated form of pushing a conspecific out of the way.
Kick back	Kicks back with hind legs to push another individual (especially a calf) out of the away
Lunge	A lunging motion followed by physical contact, used to prevent another elephant standing up.
Displace	Individual moves towards another elephant and overtakes the position of that individual. Other individual immediately moves away without any intervening behaviour.
Submission	
Head-Low	Submissive elephant carries head low, below shoulder blades, in order to appear smaller. (Often observed with <i>Turn-Away</i> or <i>Retreat-From</i>)
Skirt-Around	In presence of more dominant individuals, a lower-ranking individual will make a small arc around the group to establish a better position around a food or drinking source, or place of interest.
Back-Toward	In submissive context, may be appeasement gesture/sign of respect amongst family members.

	Used to avoid triggering an aggressive response in a larger social context.
Retreat	
Turn-Away	An elephant will avoid conflict with a threatening individual by orienting away from aggressor while looking back.
Retreat	An elephant will avoid conflict with a threatening individual by walking, retreating from aggressor while looking back.
Run-Away	An elephant may run away from aggressor during times of escalated aggression; common response to a <i>Pursuit</i>
Apprehension	
Tail raising	When elephants are highly excited and are in increased state of fearfulness, the individual raises its tail;
	Individual stands or walks with jaw tilted upward and tail raised, causing it to have exaggerated sway-back.
Panic Running	An elephant retreats, running quickly, quietly and smoothly; with its ears flattened and tail raised.
Freezing	Head oriented towards another elephant or change in the environment, no movements occurring, elephant looks 'alert'
Group Defence	
Full-Retreat	Following a threat to an adversary, an individual or group of elephants may do an about-face and make a rapid retreat from the danger
Bunching	When an elephant is under threat, adult females will cluster together with the calves in the middle, and the diameter of the circle is tight. The adult females face outwards with heads up and ears spread.
Group Charge	An entire family charges toward an adversary <i>en</i> masse in a highly coordinated manner
Intervening	An individua places its body between the aggressor and the target, 'protecting' target elephant from the attack.

Standing over	Standing in one particular place with little movement or interest in any
calf	other activity (but with slight body movements, ear flaps, trunk swinging,
	etc.) but with some part of calf's body/head/legs underneath while calf
	rests/sleeps.
SUCKIING	Occurring in calves and young infants only, milk is suckied from the
	mother's teat. Trunk is lifted back over the infant's head to allow the
	mouth access to the teat.
Solicit-suckling	An infant/calf walks parallel to its mother, pushing against her legs or
	touching around or onto her breast or nipple with its trunk, or places trunk
	around mother's leg. Often accompanied by rumbling or begging calls.
Poinct Suckling	Adult famale blocks access to her breast with her log or by walking away
Reject-Sucking	Addit Terriale blocks access to her breast with her leg of by waiking away.
Suckle-Stance	A female suckling a calf is in an attentive posture, with forelimb position
(Nursing)	forward to give calf access to her breast.
Hiding	Occurring only in young calves, standing next to or underneath an older
	elephant
Bunching	When an elephant is under threat, adult females will cluster together with
	the calves in the middle, and the diameter of the circle is tight. The adult
	females face outwards with heads up and ears spread.
Protecting	An adult elephant pushes or pulls a calf under their belly, usually to protect
Protecting	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf.
Protecting Reassurance &	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf.
Protecting Reassurance & Protection	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf.
Protecting Reassurance & Protection	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf.
Protecting Reassurance & Protection Caress	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf,
Protecting Reassurance & Protection Caress	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth;
Protecting Reassurance & Protection Caress	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or
Protecting Reassurance & Protection Caress	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles
Protecting Reassurance & Protection Caress	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too.
Protecting Reassurance & Protection Caress Shepherding	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd,
Protecting Reassurance & Protection Caress Shepherding	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety.
Protecting Reassurance & Protection Caress Shepherding Social Play	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety.
Protecting Reassurance & Protection Caress Shepherding Social Play	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety.
Protecting Reassurance & Protection Caress Shepherding Social Play Solicit play	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety. An elephant stretches its head down and out and looks out over its tusks at
Protecting Reassurance & Protection Caress Shepherding Social Play Solicit play	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety. An elephant stretches its head down and out and looks out over its tusks at a potential playmate. In an invitation to play, an elephant gently waggles
Protecting Reassurance & Protection Caress Shepherding Social Play Solicit play	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety. An elephant stretches its head down and out and looks out over its tusks at a potential playmate. In an invitation to play, an elephant gently waggles its head side to side; older calves lay down or get on their knees to
Protecting Reassurance & Protection Caress Shepherding Social Play Solicit play	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety. An elephant stretches its head down and out and looks out over its tusks at a potential playmate. In an invitation to play, an elephant gently waggles its head side to side; older calves lay down or get on their knees to encourage younger calves to play.
Protecting Reassurance & Protection Caress Shepherding Social Play Solicit play Play pursuit	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety. An elephant stretches its head down and out and looks out over its tusks at a potential playmate. In an invitation to play, an elephant gently waggles its head side to side; older calves lay down or get on their knees to encourage younger calves to play. Individuals switch between chasing and being chased. The chasing
Protecting Reassurance & Protection Caress Shepherding Solicit play Play pursuit	An adult elephant pushes or pulls a calf under their belly, usually to protect the calf. An elephant may wrap a trunk over the back and around the belly of a calf, or over calf's shoulder and under its neck, often touching its mouth; reaching out to touch the genitals, temporal glands, face, legs, mouth, or trunk of another individual. Most often exhibited by adults and juveniles toward calves but may caress one another too. Adult or juvenile female uses her body, feet, trunk, or tail to shepherd, check for the presence of, gently guide or assist an infant or calf to safety. An elephant stretches its head down and out and looks out over its tusks at a potential playmate. In an invitation to play, an elephant gently waggles its head side to side; older calves lay down or get on their knees to encourage younger calves to play. Individuals switch between chasing and being chased. The chasing individual will have the head, ears and tail raised.

Grasp-Tail	An individual may hold onto and pull on the tail of another in a playful manner
Play mount	During periods of play, young calves and juveniles will mount each other playfully irrespective of each other's sex.
Play-Social-rub	A gentle form of play, elephants push at the body, head, or legs of another, who may be laying down or playing with another elephant.
Climb on	A game that calves play that leads to a big pile of wiggling, kicking out, and squirming elephants.
Trunk twining	A gentle contact form of play where two elephants twist their trunks together in a spiral.

Appendix 1.4 Association matrices of two captive elephant groups Dublin Zoo (n = 11) and Chester Zoo (n = 5) calculated using the simple ratio index.

Dub	lin	Zoo
Dub		200

	DZB1	DZY1	DZY3	DZB4	DZB2	DZY2	DZY2A	DZY2B	DZB3	DZY4	DZB1
DZB1	0.000	0.272	0.172	0.077	0.132	0.059	0.037	0.058	0.402	0.131	0.073
DZY1	0.272	0.000	0.401	0.104	0.075	0.087	0.055	0.077	0.133	0.393	0.049
DZY3	0.172	0.401	0.000	0.071	0.071	0.119	0.119	0.075	0.164	0.239	0.053
DZB4	0.077	0.104	0.071	0.000	0.132	0.111	0.104	0.280	0.116	0.194	0.232
DZB2	0.132	0.075	0.071	0.132	0.000	0.093	0.103	0.087	0.100	0.070	0.334
DZY2	0.059	0.087	0.119	0.111	0.093	0.000	0.369	0.298	0.061	0.079	0.091
DZY2A	0.037	0.055	0.119	0.104	0.103	0.369	0.000	0.160	0.067	0.081	0.093
DZY2B	0.058	0.077	0.075	0.280	0.087	0.298	0.160	0.000	0.111	0.208	0.262
DZB3	0.402	0.133	0.164	0.116	0.100	0.061	0.067	0.111	0.000	0.147	0.123
DZY4	0.131	0.393	0.239	0.194	0.070	0.079	0.081	0.208	0.147	0.000	0.140
DZB1	0.073	0.049	0.053	0.232	0.334	0.091	0.093	0.262	0.123	0.140	0.000

Chester Zoo

	CZHW1	CZHW2	CZHW4	CZHW3	CZM1
CZHW1	0.000	0.439	0.732	0.264	0.406
CZHW2	0.439	0.000	0.467	0.342	0.352
CZHW4	0.732	0.467	0.000	0.296	0.390
CZHW3	0.264	0.342	0.296	0.000	0.286
CZM1	0.406	0.352	0.390	0.286	0.000

Appendix 1.5 Parameters of network permutations calculated to determine whether the observed network parameters are significantly different from random networks. The mean and standard (SD) of the observed network, and the mean standard deviation of the permuted networks. Significance of the observed networks is calculated by comparing the observed network coefficients to the distribution of permuted network coefficients. If Pr is < 0.025 the observed parameters are significantly greater than the permuted networks, indicating a stable observed network. Conversely, a Pr value of > 0.975 indicates that the permuted network values are significantly greater than the observed network parameters. Significant values are highlighted in bold font.

		Obse	rved	Perm	uted
Network	Node Metric	Mean	SD	Mean SD	Pr
CZ herd	Weighted Degree (Si)	1.589	0.289	0.107	0.000
DZ herd	Weighted Degree	1.432	0.162	0.101	0.014
	Eigenvector Centrality	0.299	0.037	0.0002	0.000
	Weighted Betweenness	3.273	3.57	0.271	0.00

Individual	Institution	Sex	Age	Mean SRI	Weighted Degree	Eigenvector Centrality	Weighted Betweenness
CZM1	Chester	F	44	0.287	1.43		
CZHW1	Chester	F	35	0.368	1.841		
CZHW2	Chester	F	19	0.320	1.60		
CZHW4	Chester	F	3	0.377	1.88		
CZHW3	Chester	F	15	0.238	1.18		
DZB1	Dublin	F	34	0.150	1.412	0.299	3
DZY1	Dublin	F	28	0.135	1.646	0.351	4
DZY3	Dublin	М	4	0.129	1.482	0.317	2
DZB4	Dublin	F	1	0.109	1.420	0.296	0
DZB2	Dublin	F	11	0.124	1.197	0.244	0
DZY2	Dublin	F	15	0.108	1.366	0.276	4
DZY2A	Dublin	М	4	0.147	1.188	0.239	0
DZY2B	Dublin	М	2 months	0.129	1.616	0.326	9
DZB3	Dublin	F	4	0.153	1.423	0.298	1
DZY4	Dublin	М	1	0.132	1.682	0.354	10
DZB2A	Dublin	F	2	0.150	1.450	0.288	3

Appendix 1.6 Measures of association and centrality of two captive elephant social networks. The table below is a list of individual simple ratio (SRI), weighted degree, eigenvector and weighted betweenness measures. These values characterise an individual's position and role within the herd structure.

Appendix 1.7 Analysis of Captive Elephant Social Bonds Overtime: Chester Zoo. To determine the stability of elephant bonds over time, monthly networks calculated using the simple ratio index were correlated with one another using the Mantel test. Significant correlations between monthly networks (in bold) indicate similarity in bond strengths between two months. The Mantel test statistic r and p-value are provided, and each correlation was specified at 1000 permutations.

	r	p
February x April	0.320	0.217
February x May	0.166	0.317
February x July	0.584	0.033
February x August	0.538	0.050
February x September	0.227	0.242
February x October	0.333	0.225
February x November	0.452	0.108
April x May	0.495	0.067
April x July	0.438	0.050
April x August	0.347	0.167
April x September	0.167	0.308
April x October	0.097	0.392
April x November	0.294	0.083
May x July	0.316	0.300
May x August	0.712	0.100
May x September	0.438	0.117
May x October	0.035	0.383
May x November	0.129	0.400
July x August	0.620	0.100
July x September	0.225	0.183
July x October	0.620	0.083
July x November	0.214	0.400

August x September	0.803	0.017
August x October	0.623	0.117
August x November	0.170	0.433
September x October	0.575	0.042
September x November	-0.059	0.550
October x November	0.050	0.417

Appendix 1.8 The comparison of weighted degree over time. Full results of LMM of individual weighted degree over months. No statistically significant relationship was found between weighted degree and month of year. The model estimates, standard error, degrees of freedom (df), t and p values are presented. The permuted P value (Prand) was calculated by comparing the observed estimates of each comparison with estimates from 1000 permuted estimates. Significance was determined if the observed estimate was greater than the permuted estimates.

Chester Zoo

		Estimate	s.e	df	t	р	P _{rand}
February							
	Intercept	1.658	0.148	6.741	11.180	0.000	0.000
	April	0.178	0.109	28.000	1.636	0.113	0.533
	Мау	0.277	0.109	28.000	2.545	0.017	0.351
	July	-0.257	0.109	28.000	-2.369	0.025	0.175
	August	0.210	0.109	28.000	1.929	0.064	0.360
	September	0.162	0.109	28.000	1.496	0.146	0.423
	October	-0.039	0.109	28.000	-0.362	0.720	0.531
	November	-0.258	0.109	28.000	-2.380	0.024	0.716
April							
	May	0.099	0.109	28.000	0.910	0.371	0.360
	July	-0.435	0.109	28.000	-4.005	0.000	0.659
	August	0.032	0.109	28.000	0.294	0.771	0.371
	September	-0.015	0.109	28.000	-0.140	0.890	0.088
	October	-0.217	0.109	28.000	-1.998	0.056	0.482
	November	-0.436	0.109	28.000	-4.015	0.000	0.686
May							
	July	-0.534	0.109	28.000	-4.915	0.000	0.758

	August	-0.067	0.109	28.000	-0.616	0.543	0.451
	September	-0.114	0.109	28.000	-1.050	0.303	0.126
	October	-0.316	0.109	28.000	-2.908	0.007	0.698
	November	-0.535	0.109	28.000	-4.925	0.000	0.798
July							
	August	0.467	0.109	28.000	4.298	0.000	0.217
	September	0.420	0.109	28.000	3.865	0.001	0.216
	October	0.218	0.109	28.000	2.007	0.055	0.086
	November	-0.001	0.109	28.000	-0.010	0.992	0.533
August							
	September	-0.047	0.109	28.000	-0.434	0.668	0.549
	October	-0.249	0.109	28.000	-2.292	0.030	0.676
	November	-0.468	0.109	28.000	-4.309	0.000	0.793
September							
	October	-0.202	0.109	28.000	-1.858	0.074	0.667
	November	-0.421	0.109	28.000	-3.875	0.001	0.993
October							
	November	-0.21913	0.10863	28.00001	-2.017	0.05336	0.667

<u>Dublin Zoo</u>

		Estimate	s.e.	df	t	p	P _{rand}
April	(Intercept)	1.489	0.060	22.268	24.621	< 2e-16	0.000
	May	-0.008	0.057	40.000	-0.144	0.886	0.645

	June	-0.121	0.057	40.000	-2.122	0.040	0.376
	July	-0.207	0.057	40.000	-3.644	0.001	0.649
	August	-0.171	0.057	40.000	-3.009	0.005	1.000
May							
	June	-0.112	0.057	40.000	-1.978	0.055	0.287
	July	-0.199	0.057	40.000	-3.501	0.001	0.532
	August	-0.163	0.057	40.000	-2.865	0.007	0.361
June							
	July	-0.087	0.057	40.000	-1.522	0.136	0.764
	August	-0.050	0.057	40.000	-0.887	0.380	0.635
July	August	0.036	0.057	40.000	0.636	0.529	0.369

Appendix 2 Maternal care and allomothering in captive Asian elephants (*Elephas maximus*)

Appendix 2.1 Relatedness between individuals in each dyad is specified to compare the rate of maternal and allomothering behaviour based on relatedness to calf. After the birth of two more calves, the number of dyads in the group increased (n = 21).

Dyad	Dyad Relationship
CZHW1 – CZHW4	Mother – Calf
CZHW2 – CZHW6	Mother – Calf
CZHW3 – CZHW5	Mother – Calf
CZHW2 – CZHW4	Sister – Calf
CZHW3 – CZHW6	Sister – Calf
CZHW1 – CZHW6	Grandmother – Calf
CZHW2 – CZHW5	Grandmother – Calf
CZHW4 – CZHW5	Calf – Calf
CZHW4 – CZHW6	Calf – Calf
CZHW5 – CZHW6	Calf – Calf
CZHW1 – CZHW5	Related Adult - Calf
CZHW3 – CZHW4	Related Adult - Calf
CZM1 – CZHW4	Unrelated Adult - Calf
CZM1 – CZHW5	Unrelated Adult - Calf
CZM1 – CZHW6	Unrelated Adult - Calf
CZHW1-CZHW2	Related Adults
CZHW1-CZHW3	Related Adults
CZHW2-CZHW3	Related Adults
CZHW1-CZM1	Unrelated Adults
CZHW2-CZM1	Unrelated Adults
CZHW3-CZM1	Unrelated Adults

Appendix 3 The Social Dynamics of Captive Asian Elephants (*Elephas maximus*)

Appendix 3.1 Night-time measures of association and centrality of two captive elephant social networks. The table below is a list of individual simple ratio (SRI), weighted degree, eigenvector and weighted betweenness measures. These values characterise an individual's position and role within the sleeping social networks.

Individual	Institution	Sex	Age	Node Metric						
				Mean SRI	Eigenvector Centrality	Weighted Degree	Weighted Betweenness			
CZM1	Chester	F	44	0.554		2.217				
CZHW1	Chester	F	35	0.686		2.746				
CZHW2	Chester	F	19	0.613		2.453				
CZHW3	Chester	F	3	0.5		2.002				
CZHW4	Chester	F	15	0.698		2.795				
DZB1	Dublin	35	F	0.29	0.201	2.968	3			
DZY1	Dublin	28	F	0.439	0.299	4.399	4			
DZY3	Dublin	5	Μ	0.451	0.306	4.512	2			
DZB4	Dublin	2	F	0.58	0.362	5.406	0			
DZB2	Dublin	12	F	0.398	0.272	3.989	0			
DZY2	Dublin	16	F	0.35	0.238	3.521	4			
DZY2A	Dublin	5	М	0.351	0.235	3.511	0			
DZY2B	Dublin	1	М	0.517	0.349	5.176	9			
DZB3	Dublin	5	F	0.47	0.317	4.7110	1			
DZY4	Dublin	2	М	0.512	0.343	5.086	10			
DZB2A	Dublin	3	F	0.540	0.346	5.128	3			

Appendix 3.2 Comparisons of strengths over time. To investigate the stability of elephant bonds over time, monthly SRI values were compared across months using the Mantel test. The Pearson correlation coefficient (r) and p value are provided based on 1000 permutations.

	Monthly Comparison	r	p
Chester Zoo			
	February - April	0.889	0.008
	February - May	0.682	0.041
	February – December	0.649	0.1
	April - May	0.676	0.075
	April – December	0.471	0.208
	May – December	0.747	0.008
Dublin Zoo			
	April - May	0.6283	<0.001
	April - June	0.7636	<0.001
	April - July	0.7425	0.002
	April - August	0.7857	<0.001
	May - June	0.7516	<0.001
	May - July	0.7307	<0.001
	May - August	0.5386	0.004
	June - July	0.8632	<0.001
	June - August	0.7387	<0.001
	July - August	0.7774	<0.001

Appendix 3.3 Full results of linear mixed effects models (LMM) comparing weighted degree over non-consecutive months in 2016. Due to the non-independent nature of observed network metrics, significance of network metrics, significance of the LMM was calculated by 1) calculating the model using the observed networks, 2) comparing the coefficients from the model to coefficients calculated using 4000 permutations of the network, 3) calculating one tailed significance (Prand) by comparing the where the observed estimate fell relative to the permuted estimates (Farine, 2013). The tables below summarise the results below, significant models are highlighted in bold.

			Estimate	s.e.	t	P _{rand}
Chester Zoo						
Degree	February	April	0.31	0.045	6.817	0.113
		May	-0.116	0.1022	-1.41	0.576
		December	-0.615	0.238	-2.577	0.931
	April	Мау	-0.4270	0.146	-2.915	0.897
		December	-0.926	0.28	-3.3017	0.978
	May	December	-0.498	0.171	-2.910	0.921

Dublin Zoo						
Degree	April	May	-0.1673	0.2487	-0.673	0.5696
		June	-0.6338	0.2487	-2.549	0.8788
		July	-0.7856	0.2487	-3.159	0.7876
		August	1.4669	0.2487	5.899	0.0334
	Мау	June	-0.4665	0.2487	-1.876	0.8154
		July	-0.6183	0.2487	-2.486	0.7434
		August	1.6342	0.2487	6.571	0.0376
	June	July	-0.1518	0.2487	-0.610	0.4498
		August	2.1007	0.2487	8.447	0.00
	July	August	2.2525	0.2487	9.058	0.0588
Eigenvector Centrality	April	May	0.0037047	0.0162862	0.227	1
-		June	-	0.0162862	-0.045	1
			0.0007408			
		July	0.0048916	0.0162862	0.300	1
		August	0.0088196	0.0162862	0.542	0.591
	Мау	June	-0.004446	0.016286	-0.273	0.4292
		July	0.001187	0.016286	0.073	0.3668
		August	0.005115	0.016286	0.314	0.814
	June	July	-0.1518	0.2487	-0.610	0.541
		August	2.1007	0.2487	8.447	<0.001
	July	August	0.003928	0.016286	0.241	0.8786

Appendix 4 Investigating the relationship between sociality and endocrinology in Asian elephants (*Elephas maximus*)

Appendix 4.1 Faecal sample extraction and analysis for corticosterone EIA analysis

All faecal samples used for analysis for each study elephant from 1 February 2016 to 30 December 2018 (with the exception of CZHW4 and CZM1, who had less samples stored):

Elephant	# of samples
CZHW1	451
CZHW2	379
(01 Feb. 2016 – 5 Sept. 2018)*	
CZHW3	464
CZM1	163
(7 Mar. 2017 – 01 June 2018)	
CZHW4	179
(7 Mar. 2017 – 02 Oct. 2018)*	
Total	1636 samples

* Individuals died before the end of data collection period.

Sample Running schedule for Corticosterone EIA analysis

The full list of days during which faecal extraction and EIA analysis occurred. All lab work was conducted in the Chester Zoo Science centre and all samples were those collected and stored from the Chester Zoo elephant herd. Most sample analysis was conducted by the author, however when this was not possible, analysis was conducted by Chester Zoo Laboratory coordinator, Rebeca Mogey (identified in bold). Apart from my extraction training, all extractions were performed by Chester Zoo Science team staff as part of routine reproductive endocrinology monitoring.

Month	Day
June 2017	Aug 20 – June 2 (faecal extraction training week) 05 – 09 (faecal extraction training week) 13, 20, 21, 27, 28, 30 (EIA assay training)
July 2017	12, 20
October 2017	23 - 27
November 2017	6 - 10
January 2018	10, 11, 18
February 2018	6,7
April 2018	5,12,17,26
May 2018	3, 10
September 2018	24-28
October 2018	24 – 26, 29, 30
February 2019	2

Appendix 4.2 The social and faecal Corticosterone profiles of the female elephants of Chester Zoo. The age and reproductive status of each female is detailed below. Bond strength values of each female is expressed as both a Simple Ratio Index (SRI) and Composite Sociality Index (CSI) values. For each elephant an SRI value is calculated using an elephant's frequency of association with each of its herd mates, and the sum of its top 3 relationships is used. The CSI is calculated using an elephant's rate of affiliative interactions with each of its herd mates, and the sum of its top 3 relationships is used in this study. Faecal corticosterone levels are expressed as logged values for this study. The cut-off is the threshold value for peaks above the calculated baseline (mean + (n*SD)); points below the cut-off are considered to be baseline, and those above are considered to be peaks. Base mean is the average of all points determined to be baseline; and peak mean is the average of all points classified as peaks. Finally, peak base is the ratio of peak-to-baseline, calculated as peak mean/base mean.

Elephant ID	Age (years)	Parous/Nulliparous	SRI value (from top 3 associations)	CSI Values (from top 3 associates)	Weighted Degree			Faecal Cor	ticostero	one (ng/g)		
						min	mean	max	sd	cut-off	base	peak
											mean	mean
CZHW1	36	Parous	1.246	5.928	2.433	2.752	17.727	62.052	7.485	28.056	16.44	34.581
CZHW2	21	Parous	0.949	5.01	2.212	2.645	15.408	48.806	6.598	21.558	13.39	27.556
CZHW3	14	Parous	0.911	4.133	2.0244	3.862	14.591	148.636	10.43	19.995	12.012	28.4

215

CZHW4	3	Nulliparous	1.323	7.554	2.568	4.437	19.714	99.168	9.956	30.324	17.785	40.799
CZM1	46	Nulliparous	0.667	4.142	1.695	8.247	18.157	43.165	7.213	23.802	15.93	33.218
Appendix 4.3 Summary statistics of corticosterone and progesterone faecal concentrations of 3 Asian elephant females. Faecal corticosterone and progesterone levels are expressed as logged values for this study. The cut-off is the threshold value for peaks above the calculated baseline (mean + (n*SD)); points below the cut-off are considered to be baseline, and those above are considered to be peaks. Base mean is the average of all points determined to be baseline; and peak mean is the average of all points classified as peaks. Finally, peak base is the ratio of peak-to-baseline, calculated as peak mean.

Elephant.ID	Hormone	n	mean	median	sd	s.e.m	% CV	min	max	cut-off	base mean	peak mean	peak base
CZHW2	Corticosterone (Fc)	379	15.408	14.118	6.598	0.339	42.824	2.645	48.806	14.994	10.995	21.011	1.911
CZHW2	Progesterone (Fc)	391	39.57	35.39	22.299	1.128	56.353	7.16	117.42	20.798	16.253	48.468	2.982
CZHW3	Corticosterone (Fc)	464	14.591	12.851	10.43	0.484	71.482	3.862	148.636	10.673	8.132	18.022	2.216
CZHW3	Progesterone (Fc)	514	33.867	28.7	20.288	0.895	59.905	6.7	146	15.867	12.179	40.048	3.288
CZHW1	Corticosterone (Fc)	451	17.727	17.14	7.485	0.352	42.224	2.752	62.052	11.563	8.97	20.552	2.291
CZHW1	Progesterone (Fc)	580	43.492	38	24.575	1.02	56.505	6.5	214.8	22.345	16.768	52.4	3.125

Appendix 5 The social history and reproductive success of female Asian elephants in UK and European zoos

Appendix 5.1 The females selected for this study were all females currently above the age of 5 years old, born between 1970 and 2013. Data collected using ZIMS include the factors below. Data on all factors were collected for all individuals were available.

Current age	At death or still alive					
Status	Alive or Dead (as of dd/mm/yyyy)					
	Captive-born					
Birth origin	Wild born					
	Unknown origin					
Number of inter-zoo transfers	The number of unique zoos a female has been house in. This excludes any short-term transfers for breeding purposes, but includes transfer from the wild if wild born					
Number of management transfers	The number of transfers a female has experienced. This includes both long- term and short-term (for breeding purposes), and includes transfer from the wild if wild born					
Age when arrive to institution & Age when moved from institution	Age in years					
Number of relatives present	Relatives include all related females > 5 years old					
Number of offspring given birth at said institution	Number of calves a female gives birth to at a zoo, regardless of calf survival					
Total years at institution	In years					
Number of former herd mates present	Former herd mates are those with which a female has been previously housed with at other institutions over her lifetime. This is a count of how many individuals are transferred as					

with companions, or cross paths at
different zoos over their lifetime.