A Comparison of Behavioural Development of Elephant Calves in Captivity and in the Wild: Implications for Welfare

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Declaration

I declare that the work undertaken and reported within this thesis is my own and has not been submitted in consideration of any other degree or award.

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Abstract

Compromised welfare and wellbeing of elephants (*Loxodonta africana* and *Elephas maximus*) in captive facilities are significant and global problems. The period between birth and two years old is crucial for calf survival and social and environmental learning. Behaviour and developmental processes among captive elephant calves in these first years were compared with those seen in wild calves. Wild elephants calves develop within a complex, varied social context and provide one reference for normal patterns of development. Such comparisons enable insights into welfare at captive facilities.

Eleven captive elephant calves born at three UK facilities were studied from birth to 18 months (Asian$_{N=6}$; African$_{N=5}$). Older calves (Asian$_{N=2}$; African$_{N=2}$) were also sampled up to 3.5 years; making a total of 15 calves studied from 2009 to 2014. Due to the small sample size, the 11 younger calves were also discussed as individual case studies. By 2017, only two of these case study calves were both alive and not orphaned. Three additional calves (Asian$_{N=1}$; African$_{N=2}$) died on their day of birth and were not sampled. This small sample highlights the ongoing lack of self-sustaining populations of captive elephants.

This thesis collated systematic behavioural observations on captive calves across 373 days (483.5hrs). Calf maintenance activities (feeding, resting, moving), associations with mother and others, interactions and calf play were compared with behavioural observations of wild Asian$_{N=101}$ (74hrs, Uda Walawe, Sri Lanka) and wild African$_{N=130}$ (252hrs, Amboseli, Kenya) calves from ~birth to five yrs. Mothers' (captive: Asian$_{N=4}$; African$_{N=4}$; wild: Asian$_{N=90}$; African$_{N=105}$) activities were also recorded to explore synchrony with calves. Captive calves raised by their mothers had similar activity budgets to those seen in the wild. Expected age-related declines in suckling were found in captivity. However, captive calves were more independent than wild calves for their age in distance from mother and spent significantly more time in play.

A Decision Tree for whether to breed elephants in captivity was developed; benefits that a calf potentially brings to companions, e.g. multi-generational matrilineal groups, enabling social bonding and reducing abnormal behaviours, were considered against space required for families to grow and divide naturally over time, as well as ensuring that captive-bred males are socially sustained. It was recommended that facilities invest in future enclosure/housing designs which permit: free-access to other elephants; 24hr trickle feeding; juvenile males allowed to stay with their maternal group for longer, encouraging learning opportunities and further retaining age-structure/composition. Conversely, facilities unwilling to house a male or provide appropriate group size/composition are recommended to cease breeding.

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Enzo snuck in beneath his mother and allomothers in Uda Walawe National Park. Photograph taken 27th June 2011.

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Dissemination and Recognition

List of Publications

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2014: Development and Welfare of Wild and Captive Elephant Calves. *Animal Welfare and Sustainable Population Conference*, Blair Drummond Safari Park

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2012: Visual Tour of Wild Asian Elephant Behaviour. *Elephant Focus Group* (spring meeting), NEZS, Chester.

2011: Comparing Wild and Captive Elephant Calves. *Uda Walawe Primary School*, Uda Walawe, Sri Lanka.

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2014: Elephant Calves: Demography, Development & Play Behaviour. Presented at the *Scottish Conference of Animal Behaviour* (SCAB), University of Edinburgh.

2014: Elephant Demography and Development. *SPRG winter meeting*, Edzell.

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Wild Asian elephant mother and her calf in Uda Walawe. Photograph taken 16th May 2010.

"To the elephant, our scrap of consciousness
may seem as inconsequential as a space-invader blip."

—Heathcote Williams
Sacred Elephant

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> *“Freedom is the light of all sentient beings”*
>
> *—Optimus Prime*
> *Transformers*

Chapter 1: Introduction

Family herd of Asian elephants in Uda Walawe, Sri Lanka. Photograph taken 26th May 2010.

1.1 Studying Early Development

Why study elephant calves? Calf care is at the core of female elephant sociality (Moss, 1988). Yet, little is known about the behavioural development of wild or captive calves - how calves interact with mothers, the rest of the herd, with allomothers[1] or playmates. General social skills (managing aggression, learning dominance, distinguishing familiar elephants from strangers) and knowledge of the environment are learned in the highly social context of the family or larger aggregations in the wild (Lee, 1986). We do not know how well calves in captivity learn social skills from others or the effects of peer or allomother numbers on the acquisition of these skills. Thus, a greater understanding of early behaviour and the patterns and processes of development will help with predicting and managing calf survival and female reproductive performance for both wild contexts and in captivity.

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[1] I used the term allomother here and throughout the thesis to refer to typically non-reproductive female caretakers of calves (Lee, 1987).

Elephants' sheer size, large brains, capacity for long memory (Hart, Hart & Pinter-Wollman, 2008; Shoshani, Kupsky & Marchant, 2006), their structured and fluid social choices, and a lifespan of over 60 years mean that meeting their needs in captivity is an enormous challenge. Compromised elephant welfare in captivity is therefore a significant problem for zoos (Dale, 2010; Clubb & Mason, 2002; Prado-Oviedo et al., 2016; Veasey, 2006) and the wellbeing of calves – during both immaturity and their development into adulthood - is a main area of considerable concern.

To date, only a few studies have examined the social and behavioural development of elephant calves in captivity (Andrews, Mecklenborg & Bercovitch, 2005; Dale, 2010). What are the processes of development under typical or wild conditions and are these processes of development replicated in captivity? A greater understanding of the fundamentals of calf development will also increase our understanding of the needs of elephant calves in captivity and may help improve breeding in the future as well as ensuring wellbeing for the calves, both when young and later as adults.

1.2 Thesis Overview

This study explores the behavioural development of captive elephant calves during early life and compares this with that of wild elephant calves. These objectives were met by quantifying calf social development and maternal-calf interactions and comparing these against age-matched behaviour seen in wild calves. Given the similarities in life history between Asian and African elephants (Sukumar, 2003), we expect patterns of development to be similar, although this was not known at the onset of this study. Four contexts for the behavioural development of elephant calves will be explored (wild Asian, wild African, captive Asian and captive African), and I will also look more closely at the individual captive study calves, using them as case studies.

For a female elephant, the survival of all of her calves plays a major role in her lifetime reproductive success along with her rate of reproduction (Moss & Lee, 2011). Calf survival is key to understanding and modelling population viability for both captive and wild populations. Therefore, understanding the processes involved in the successful rearing of elephant calves is important for the conservation of African and Asian elephants both *in situ* and *ex situ*. Sharing best practice in the scientific understanding of calf development and identifying prerequisites for survival, wellbeing and social integration are aims of most captive facilities. My study also contributes to our theoretical understanding of proximate and ultimate mechanisms of maternal influences on calf development and fitness outcomes by comparing the two wild species.

My research thus addresses gaps in our understanding of early elephant development generally, and also provides strategies, suggestions and mechanisms to underpin welfare improvements for elephants in captive breeding facilities. Survival and subsequent reproductive success remains compromised in captive-born elephants (Brown et al., 2016; Hartley, 2016, Prado-Oviedo et al., 2016). This is the first study to examine development in wild Asian calves and to compare them with African calves in the wild or captivity.

1.3 Animal Welfare

Ethology is one of the many scientific disciplines contributing to the study of animal welfare and it can be used alongside other disciplines - such as neuroscience, physiology and veterinary studies (Fraser, 2008) - striving together for improvements in the field. Yet, among these perspectives, no single, universally accepted definition of animal welfare exists. While animal welfare encompasses a huge variety of approaches, these can be categorised into three main types: ‘biological functioning’, ‘feelings-based’ and ‘natural living’ (see Table 1.1 below; Duncan & Fraser, 1997). Regardless of theoretical approach, there is consensus that providing an animal with an environment that allows it to perform natural behaviours – which, in the case of elephants, includes complex social interactions - is necessary for good welfare to exist.

Broom's (1986) definition of welfare uses the ‘biological functioning’ approach and describes welfare as “*the state of the individual as regards its attempts to cope with its environment*” (p. 524). Animals use various strategies to try to cope and there is a variety of consequences in failing to cope (Broom & Johnson, 1993). This basic health and functioning approach has recently been augmented by the concept of Domains where we have moved from the Five Freedoms (freedom from: thirst and hunger; discomfort; pain, injury and disease; fear and distress; and the freedom to express normal behaviours; Brambell, 1965) to physical and functional domains (nutrition, environment, health and behaviour) incorporated into the 5th affective experience domain of mental state (Mellor & Beausoleil, 2015). This fifth Domain, incorporating the affective state, is, therefore, a ‘feelings-based’ approach (see Table 1.1). The Five Domains recognise and incorporate both positive (e.g. pleasurable/rewarding/playful) and negative experiences (e.g. injury/competition) in an animal’s life and explore the balance between these. The development of the Five Domains highlights that animal welfare is now recognised as being essentially linked to psychological wellbeing (Descovich et al., 2017). Dawkins (2004) also advocates the use of all three approaches for determining if an animal has good of bad welfare; and suggests asking the questions, ‘is the animal physically healthy, and does it have what it wants?’

The third approach, ‘natural living’, is the focus of this thesis and it relates to an animal’s ability to express diverse types of natural behaviours (see Table 1.1). This approach asks whether we can provide animals with environments where they have opportunities to develop and express their natural species-specific behaviours including basic social and physical opportunities necessary for adequate welfare (Kiley-Worthington, 1989). While good welfare in social species is characterised by the animals having a diverse behavioural repertoire - including affiliative behaviours and play - poor welfare is characterised by abnormal behaviours - including stereotypies - and time budgets (Buchanan-Smith, 2011; Jennings et al., 2009). These can include restlessness (e.g. pacing), lethargy, limited use of their environment, excessive eating, coprophagy (consumption of faeces) and inappropriate social behaviour including increased aggression towards conspecifics (Buchanan-Smith, 2011; Jennings et al., 2009).

Although some measures and methods of studying animal welfare may be specific to only one of the three practical approaches (e.g. measuring affective state using judgement biases lies in the ‘feeling-based’ category), in reality, many overlap two or all three categories (Table 1.1). For example, an animal’s ability to express natural behaviours is an important component of all three approaches, since an inability to perform behaviours may lead to lack of coping and negative affective states. Therefore, while the behavioural observation measures in this thesis (behavioural development, time budgets, abnormal behaviour, social interactions, and play) primarily lie under the ‘natural living’ approach, the measures actually tap into all three categories of practical approaches to studying animal welfare. Play, for example, relates to promoting positive affective states (see Section 1.3.1 below, and Chapter Six for play’s use as a welfare indicator). Reproductive success and calf survival, similarly, fall into all three approaches, assessing biological fitness, expression of natural behaviours, and even, affective state (e.g. negative emotions associated with the death of a calf or group member, or anxiety or abnormal behaviour due to incompatibilities with breeding males). The presence of youngsters also impacts on social-interactions and play, as well as the prevalence of abnormal behaviour (in non-infants; see Chapter Four, Section 4.2).

Table 1.1 Practical Approaches to Studying Animal Welfare. See also Section 1.3.

	Biological Functioning (Bodies)	**Feelings-Based (Mind)**	**Natural Living (Nature)**
Description	This approach focuses on an animal's strategies to cope with its environment, by "*assessing hindrances to achieving biological fitness, resilience & performance*"[3]. This approach investigates the animal's physical & functional/health states, as well as their physiological mechanisms.	Mental/affect states are explored in this approach, incorporating both positive[10] (e.g. happiness[21]/pleasure) & negative emotions (e.g. pain/ distress/hunger/suffering)[12]. Positive emotions[18] are inherent for good welfare. Methods are primarily experimental.	This approach is concerned with an animal's ability to express diverse types of natural behaviours[20,23,24] (for age), exhibiting a full range of 'personality' or individual variation in behavioural traits[12,31]. Collection of data is non-invasive.
Examples of Frameworks	5 Freedoms[35]		
	5 Domains[3,19]		
Examples of Indicator Tools & Direct/ Indirect Measures	• Physiological parameters - e.g. blood pressure, heart & respiration rates - reproductive & growth hormones[33,34] - corticosteroids[2,4,5,34]: activated by both unpleasant situations & presumably pleasurable activities such as mating/exercise[6] • Reproductive parameters - e.g. reproductive success[34] • Life history parameters - e.g. Longevity[34], growth • Health parameters[33] - e.g. Injury, disease-free, body weight & condition	• Valence/intensity model[9,14] • Posture & facial expression (e.g. Facial Acting Coding Systems: FACS[13]) • Qualitative behviour assesment[22,36] • Judgement bias[8,9,17] • Motivation testing[12,15] • Preference testing[7,12,16,32] • Behavioural observations[9]: - e.g. approach times; anxiety indicated by attempts to climb out of cage, autogrooming & abnormal behaviour[11,34]	• Behavioural observations[25]: - e.g. time budgets, diverse behavioural repertoire, abnormal behaviour[1,28] (e.g. stereotypies[11,26,,27,] & self-injurious behaviour[1]), appropriate social interactions (e.g. agnostic/submissive behaviour), movement rates/distances covered[29,30] • Reproductive parameters - e.g. inter-birth-interval, offspring survival
Measures discussed in this Thesis	Survival		
	Reproduction		
	Behavioural development		
	Time budgets		
	Abnormal behaviours		
	Social Interations		
	Play		
Associated Literature	[1]Broom, 1986; [2]Laws et al., 2007; [3]Mellor, 2016 (p. 14); [4]Meneragues et al., 2008; [5]Moe & Bakken, 1996; [6]Rushen & de Passillé, 1992.	[7]Bateson, 2004; [8]Bethell, 2015; [9]Bethell & Koyama, 2015; [10]Boissy et al, 2007; [11]Broom, 1983; [12]Dawkins, 1990; [13]Descovich et al., 2017; [14]Désiré et al., 2002; [15]Fraser & Duncan, 1998; [16]Fraser & Matthews, 1997; [17]Harding, Paul & Mendl, 2004; [18]Mendl & Paul, 2004; [3]Mellor, 2016; [19]Mellor & Beausoleil, 2015; Poole, [20]1992; [21]1997; [22]Wemelsfelder & Lawrence, 2001.	Broom, [11]1983, [1]1986; [12]Dawkins, 1990; [23]Duncan, 1998; [24]Kiley-Worthington, 1989; [25]Laws et al., 2007; [26]Mason, 1991; [27]Mason & Latham, 2004; [28]Mason & Mendl, 2017; [20]Poole, 1992; [29]Poole & Granli, 2009; [30]Rothwell, Bercovitch, Andrews & Anderson, 2011; [31]Tetley & O'Hara, 2012.
(applying to all approaches:)	Appleby, 1999; Broom, 2002; [32]Dawkins, 2004; [33]Duncan & Fraser 1997; [34]Fraser, 2008; Hosey et al., 2009; Hubrecht, 2014; Mason & Veasey, 2010; [35]Webster, 1994; [36]Wemelsfelder & Mullan, 2014.		

1.3.1 Welfare Indicators

Welfare indicators (Table 1.1) are ‘windows’ into an animal’s mental state and can be measures of an animal’s physiological and behavioural responses to stress. They can also be measurements of external variables “*that we might reasonably assume will affect the animal’s mental state and correlate with or indeed cause reduced welfare*” (Veasey, 2006, p. 64). There is general consensus that welfare indicators should not be used in isolation (e.g. Veasey, 2006).

Animals release hormonal compounds in complex stress responses and measuring these compounds can act as a tool for indicating their physiological welfare, as in ‘biological functioning’ approaches. The hypothalamic-pituitary-adrenal (HPA) axis responds to stress and the subsequent glucocorticoids secreted can be detected in blood (e.g. Moe & Bakken, 1996) and saliva (Menargues, Urios & Mauri, 2008), and non-invasively in urine and faeces (Ghosal, Ganswindt, Seshagiri & Sukumar, 2013; Lane, 2006; Laws et al., 2007). These methods need to be interpreted with caution as changes in glucocorticoids can be caused by presumably pleasurable, natural activities such as mating and exercise (Rushen & de Passillé, 1992). Excitement can cause elevations in glucocorticoid levels, while, in chronic stress situations, the HPA axis can be depressed (Veasey, 2006). As yet we have no baseline measures of glucocorticoids from young wild elephants.

Fitness, as in reproductive output and reduced lifespan, has commonly been used as a biological indicator of welfare (e.g. Clubb & Mason, 2002; Clubb et al., 2008). However, it is not necessarily an adequate measure of welfare on its own. For example, Cronin (1985) found temporary correlations between high rates of stereotypies in pig sows (*Sus domesticus*) and large litter size production. Sterile animals also do not necessarily have more compromised welfare than their fertile conspecifics (Veasey at al., 1996). Reduced lifespan can be an indicator of compromised welfare but this indicates the outcome rather than the cause of the compromised welfare.

Preference testing of behavioural choices allows investigators to gain insight into what individuals prefer, and the extent to which a preference can be expressed by the individual (Blom et al., 1992; Dawkins, 1976). Behavioural needs and preference tests also have limitations (e.g. in some cases, the animal may be choosing between an undesired and a slightly less undesired situation). Humans have devised the test in a captive context, and while an animal may be able to exhibit a preference between options provided, in some cases neither the original context nor the choice may actually improve welfare. It is not unexpected that animals make choices; however, that all such choices are actually improving welfare needs to be considered (e.g. rats, *Rattus norvegicus*, choosing cocaine; Manzardo, Stein & Belluzzi, 2002; Thomsen, Barrett, Negus & Caine, 2013).

We have yet to ask elephants ‘what they want’. For elephants, few choice tests have ever been carried out and preference tests have only been carried out between artificial contexts (e.g. flooring substrate choices in Asian elephants; Meller, Croney & Shepherdson, 2007). Cognitive tests show that elephants have the ability to select for size of rewards (Plotnik, Shaw, Brubaker, Tiller & Clayton, 2014) and friends (Plotnik, Lair, Suphachoksahakun & de Waal, 2011; Plotnik & de Waal, 2014) suggesting complex empathic ability (Bates et al., 2008).

Stereotypies can be used as one particular measure of welfare in captivity, alongside others such as hyper-aggression (Broom, 1983). Stereotypies are defined as characteristically repetitive unvarying behaviours, which have no clear goal or function (Mason, 1991; Odberg, 1978). This function is widely debated, however, as some suggest that performing stereotypic behaviours can psychologically and physiologically enhance sub-optimal environments (Carlstead, 1998). Animals are highly motivated and internally driven to perform ‘behavioural needs’ (Poole, 1992) and so, although there may be limited function in the expression of some specific behaviours within captive settings, the animal’s welfare may be compromised when they are unable to express them (Duncan, 1998). Stereotypies of the nature of Abnormal Repetitive Behaviours (ARBs) can form due to sustained frustration which leads to the repetition of specific behavioural patterns (e.g. object sucking in cattle calves, *Bos taurus,* Kooijman, Wierenga & Wiepkema, 1991; feather plucking in birds, e.g. chickens, *Gallus gallus*, Dixon, Duncan & Mason, 2008; bar-mouthing in pigs, Cronin, 1985; Mason & Mendl, 2017). ARBs might also develop due to distorted time budgets caused by low behavioural competition or from parental deprivation (Latham & Mason, 2008). In infant rhesus monkeys (*Macaca mulatta*), total deprivation of contact with their mother and conspecifics led to persistent ARBs (e.g. self-biting, rocking and eye-poking, Cross & Harlow, 1965, reviewed in Novak, Meyer, Lutz & Tiefenbacher, 2006; and Polanco, 2016) while studies in humans have shown similar findings (e.g. Beckett et al., 2002; Carlson & Earls, 1997; Fisher, Ames, Chisholm & Savoie, 1997; Mason & Mendl, 2017). Early weaning or separation from/loss of a mother, have also been shown to lead to higher expression of ARBs later in life (e.g. horses, *Equus ferus caballus*, Parker, Goodwin & Redhead, 2008; Waters, Nicol & French, 2002; chimpanzees, *Pan troglodytes*, Warniment & Brent, 1997; pacing and tail-biting in American mink, *Mustela vison,* Jeppesen, Heller & Dalsgaard, 2000; Mason, 1994; bar-mouthing in laboratory mice, *Mus musculus*, Würbel & Stauffacher, 1997; excessive grooming in domestic cats, *Felis catus*, Ahola, Vapalahti & Lohi, 2017; tail-chasing in dogs, *Canis familiaris,* Tiira et al., 2012). My study of immature elephants will potentially provide insight into the origins and development of abnormal behaviours in captivity.

ARBs have few false positives as welfare indicators, and their prevalence and frequency typically reflect sub-optimal husbandry on a graded level. ARBs may be best used to assess chronic stress since they are likely to reflect cumulative experience rather than just the present state (Mason & Mendl, 2017). It is important to state that poor welfare, however, may not lead to ARBs and that absence of observed ARBs (false negatives) does not equate to good welfare. For example, instead of causing ARBs, some poor welfare states can cause inactivity, while response styles can also differ between individuals (proactive versus reactive and/or predispositions to depression). For some individuals, performing stereotypies can become a coping mechanism that helps the animal to deal with challenges, perhaps by self-enriching or by repetitive self-calming (Mason, 1991; Mason & Latham, 2004). In terms of Broom's (1986) welfare definition (see above), some individuals perform stereotypies in attempts to cope with their environment, therefore, the presence of some stereotypies does not necessarily indicate that current welfare is poorer than for those not exhibiting stereotypies; rather, it may indicate that these individuals are coping better. Consequently, high or prevalent ARBs are a reliable indication of chronically poor past and present conditions but are not a good tool to identify short-lived poor welfare states (Mason & Mendl, 2017). Stereotypies are further discussed in Chapter Four.

Play is a complex and diverse behaviour, commonly seen in young animals and with a variety of current and future adaptive functions (Burghardt, 2006). Play is absent when animals are physiologically stressed (Lee, 1984) and is metabolically costly and risky (Harcourt, 1991; Kuehl, Elzner, Moebius, Boesch & Walsh 2008). Therefore, behaviours seen in captivity such as play (Held & Špinka, 2011; Sommer & Mendoza-Granados, 1995; Vicino & Marcacci, 2015), or relaxed postures and facial expressions (e.g. Facial Action Coding Systems [FACS]; Wathan, Burrows, Waller & McComb, 2015), may be indicative of positive mental states and can potentially be used as indicators of positive welfare (see Table 1.1). Their evaluation in relation to actual welfare is unknown and potentially complex (Blois-Heulin et al., 2015). The relationships between play and wellbeing are elaborated upon in Chapter Six.

1.3.1.1 Assessment of Captive Elephant Welfare

The welfare of captive elephants is historically compromised (see Section 1.7 below). Most assessments of elephant welfare have used either corticosteroids outputs or stereotypies in conjunction with poor health, obesity, and problems of gait (Harris, Sherwin & Harris, 2008; 2010). Additional traits such as vocal/postural signals of affective (emotional) state (Wemelsfelder, Hunter, Paul & Lawrence, 2012), startle/vigilance responses, or cardio-vascular disease revealed at autopsy have all been used as indicators of welfare (Mason & Veasey, 2010). Hormones and stereotypies are the best validated or cross-correlated tools for inferring elephant welfare (Elzanowski & Sergiel, 2006; Laws et al., 2007; Mason & Latham, 2004; Mason & Veasey, 2010; Rees, 2004). Rasmussen et al. (2008) have validated glucocorticoids and androgens as indices of injury stress in wild male African elephants. Other welfare indices used for elephants include female acyclicity, infant mortality rates and premature adult death (Hartley, 2016; Mason & Veasey, 2010; Prado-Oviedo et al., 2016). Movement rates and distances covered (Poole & Granli, 2009; Rothwell, Bercovitch, Andrews & Anderson, 2011) have also been considered to be indicators of welfare in elephants. Validation of measures or indices of welfare remain problematic in elephants. With careful design, choice tests or judgement bias measurements should be adaptable for all species (Bethell, 2015, Harding, Paul & Mendl, 2004). However, for elephants, this design encounters many challenges associated with a large, dangerous, long-lived species. Details of compromised welfare in captive elephants are discussed in Section 1.7.

1.3.2 Comparisons between Captive and Wild Behaviour

In this thesis, behavioural repertoire - including independent feeding, resting and moving - is assessed in calves and mothers, as well as interactions such as sucking, non-play social interactions and play, in addition to stereotypies in adults. I use wild elephants as a comparative basis for studying calves in captivity for three reasons. Firstly, wild elephants provide one reference for normal processes and patterns of development. They also represent calves in a complex and varied social context. Finally, wild elephants survive in the physical environment and respond to environmental challenges to which they are adapted. The wild - at least, potentially and historically - represents a) conditions that elephants have typically evolved to respond to and b) variance, which forms the basis of natural selection. Understanding the normal ranges of behavioural repertoires and activity budgets of wild conspecifics can help us identify characteristics that are more likely to impact upon welfare in captivity. This knowledge can allow us to create captive environments that match more closely their species-specific requirements (e.g. captive primates: Buchanan-Smith, 2011; Röder & Timmermans, 2002; and natural habitat husbandry for captive elephant footcare: Buckley, 2008). Such comparisons thus enable insight into welfare and management strategies for captive facilities.

Animals in captive environments are restricted both physically and socially; it has been argued that this results in limited behavioural repertoires (Buchanan-Smith, 2011). One goal in the overarching purpose of improving welfare of animals in captive environments is to increase the "*diversity and performance of normal (**wild, desired*** [my highlighting]*) behaviours*" (Buchanan-Smith, 2011, p. 44). Buchanan-Smith (2011) goes on to discuss the difficulty of agreeing upon what is 'normal'. Neither captive primates nor captive elephants are domesticated, nor have either been intentionally bred for specific desired traits (as is the case for species such as cattle, Diamond, 2002; working dogs, Clutton-Brock, 1995; and strains of laboratory rodents, Boice, 1977; Röder & Timmermans, 2002). In relation to primates, Buchanan-Smith (2011) highlights how behaviour such as "*locomotion, posture, foraging, nutritional requirements, food processing, hiding from threats/predators, breeding and interacting with conspecifics etc.*" (p. 44) are critical for assessing adaptations to an ecological niche. I would argue that assessing these needs is also critical for elephants since they, like primates, are a cognitively complex and long-lived taxa with enormous behavioural flexibility (Sukumar, 2003) allowing them to occupy a range of environments. Such an understanding can also be applied to captive cetaceans (e.g. bottlenose dolphins, *Tursiops aduncus,* Waples & Gales, 2002; orcas, *Orcinus orca*, e.g. www.Blackfishmovie.com, Cowperthwaite et al., 2013; beluga whales, *Delphinapterus leucas*, Castellote & Fossa, 2006).

I use wild data on calf behaviour to represent 'optimal' calves and their range of behavioural variation, in order to give captive facilities a goal to work towards. Although it is possible to simply rank zoos for welfare (for example, with the objectives of knowing how many calves survive or the rate of breeding success), collection of wild data is vital, because it can provide evidence to determine whether or not what we see in captivity is normal. By doing this, zoos will have a baseline for implementing changes to management strategies. Assessing whether wild calves are actually faring better than captive ones - or if captive calves do better given constraints in the wild, such as predation and drought - will play a key role in understanding welfare.

Behavioural observation data are relatively straightforward to collect since they are non-invasive, instantaneous and require little or no specialised technology. While comparisons between wild and captive animal behaviour can be potentially useful indicators of behavioural differences, Veasey, Waran and Young (1996) warn of their potential lack of reliability as objective assessments of animal welfare. They argue that these comparisons should be used synergistically with other techniques to demonstrate whether the absence of exhibiting wild behaviours equates to inadequate welfare (see Table 1.1). Problems with using the comparisons of wild and captive behaviour on their own arise when the absence of some wild-type behaviours does not necessarily equate to sub-optimal welfare. Similarly, wild animals free to engage in their full behavioural repertoires are not necessarily free from suffering (Veasey et al., 1996). Röder and Timmermans (2002) state that, while an animal in a captive environment is "*prevented from performing a number of species-specific activities because it is deprived of a number of opportunities that the natural world offers*", "*the animal is protected against a number of natural threats, so it no longer 'needs' to exert itself for survival*" (p. 222). While it is argued that, in order for suffering to be avoided in captive animals, they must be able to engage in the full repertoire of behaviours performed by wild conspecifics (e.g. Thorpe, 1967; Martin, 1979, both in Veasey et al., 1996), the assumption is that healthy free-living animals have 'adequate' welfare. Again, wild animals may be preyed upon, suffer from injuries and disease, experience inclement weather, and, only in extremely rarely cases do they have access to veterinary care (e.g. wildlife veterinarians vaccinating European badgers, *Meles meles,* pers. obs.). However, the fact that wild animals suffer is not a demonstration that they have continuously compromised welfare. Likewise, the absence of negative experiences in captivity does not demonstrate positive welfare: that an animal does not suffer from predation is not demonstrating positive welfare in captivity and the Domains welfare perspective (see above) suggests that both positive and negative experiences and behaviour determine mental affective states.

Challenges of assessing mental and motivational stressors - and difficulties in evaluating and interpreting physiological measures (which can be invasive) - remain (Dawkins, 1990; Veasey et al., 1996). Furthermore, Buchanan-Smith (2011) argues that "*captive animals adapt to their environment, but this behavioural change is not necessarily indicative of decreased welfare*" (p. 44) since the animal can now cope with its current environment. Whether adaptation to captivity represents positive welfare remains uncertain. Others argue that it is an unrealistic aim to expect captive animals to express wild-type activity budgets when captive and wild environments differ so greatly (Shepherdson, 1998; Veasey et al., 1996). Likewise, even for individual species, activity budgets vary across habitats and are further biased by small sample sizes and genetic population differences. Olson and Weise (2000) suggest that wild populations vary so much that it is impossible to compare them with captive populations. If social, ecological and behavioural flexibility is the result of adaptation to a range of environments, then it is exploring and understanding this capacity for variation that is of value in comparisons between wild and captive contexts. Variation enables us to understand the extent of range of the possible responses, which might never be evoked in the invariant captive context.

While comparisons between wild and captive conspecific behaviours as a tool for measuring welfare may have their drawbacks and need to be interpreted with care, their value as potentially useful indicators of behavioural differences justifies the importance of their study. How can we understand these species-specific behaviours if we only study animals in captivity? These are animals who are often deprived of a number of natural opportunities: for example, social complexity in elephants. We need to look to wild animals in their natural niches and evolved social groupings in order to build upon our understanding of the needs and behaviours of such complex animals.

For certain species in captivity, it may never be possible for us to emulate natural environments and/or to match wild behavioural repertoires and activity budgets. Although we may never reach this goal, we should nonetheless aim towards it, and at the very least, use information from wild free-living conspecifics to inform our management decisions. If, instead, we limit comparisons to those drawn between contemporary zoos and aim to achieve the standards of the ‘best’ of these zoos, we are limiting ourselves to what has come before and may overlook any opportunities for future improvements.

Finally, ecological validity remains essential; until we know the levels of variation in activities and behaviours between wild Asian and African elephants, how can we understand the variance we see in captivity? This need for understanding drives this thesis.

Asian calves at Chester, Nayan, Bala, Hari and Jamilah, engaging in play beside adult female Thi. Sadly, all four calves died of Elephant Endotheliotropic Herpes Virus (EEHV). Photograph taken 23rd April 2013.

1.4 Environmental Enrichment

Enrichment plays a crucial role in the physical and mental wellbeing of captive elephants, allowing them to express more natural behavioural patterns. Enrichment is defined by Newberry (1995, p. 230) as "*an improvement in the biological functioning of captive animals resulting from modifications to their environment*". The goal of enrichment is to enhance welfare by providing stimulating environments - both in structure and husbandry - to allow animals to exercise control and choice over their environment. Enrichment can be in many forms including social companionship, olfactory or auditory stimuli, feeding devices or toys. It encourages animals to express their natural, desired, and species-typical behaviours with the aim of increasing the diversity and performance of these wild behaviour patterns. Enrichment also aims to increase the positive utilisation of the captive environment; aims to prevent the development and reduce the frequency of abnormal behaviours; and aims to increase an individual's ability to cope with challenges more effectively (Young, 2003). These considerations are extremely important for animals that are developing. Sensory-rich environments have even been shown to induce structural and chemical changes in the brain in laboratory mice, even after minor changes in housing environments (see Mohammed et al., 2002). In captive common marmosets (*Callithrix jacchus*), providing a more complex, enriched environment enhanced the biochemical structures of their brain, even after one month in this environment (Kozorovitskiy et al., 2005). In humans, a study also experimentally enriched 3-5 year old nursery school children which resulted in long-term increases in their psychophysiological orienting and arousal, compared to children in more standard educational facilities (Raine et al., 2001).

Bloomsmith, Brent and Schapiro (1991) divided environmental enrichment into five categories: social, occupational, physical, sensory and nutritional. Social enrichment can either be through physical contact with conspecifics (or contraspecifics) or through non-contact such as visual, olfactory and auditory cues (Bloomsmith et al., 1991; Young, 2003). Occupational enrichment can encourage exercise or can be psychological, such as puzzle-solving or control of their environment (Buchanan-Smith, 2011; Buchanan-Smith & Badihi, 2012). The physical attributes of both accessories and enclosure design can provide stimulation through structures such as substrates, scratching posts and pools (Bloomsmith et al., 1991; Young, 2003). In a recent, study Meehan, Hogan, Bonaparte-Saller and Mench (2016) found the complexity of elephant enclosures, as well as social and management factors, to be more important than overall exhibit size for welfare.

The presentation of food for elephants and other captive animals is important for nutritional enrichment in terms of frequency, scheduling and its unpredictability, allowing animals to express natural behaviours while seeking and manipulating food items - especially browse in the case of elephants. This is key in captivity to allow them to express more of their natural activity budget. Wild Asian and African elephants spend 12-18hrs a day foraging, consuming hundreds of kilos of vegetation daily (see Table 4.1, Chapter Four). For example, one solitary wild Asian elephant was reportedly feeding for 93.5% of his waking time (including feeding whilst walking; McKay, 1973). In contrast, one adult male and five female captive Asian elephants at Chester Zoo spent an average 41.4% and 33.7% time feeding (between 10am-4pm) respectively (Rees, 2009). Therefore, improving feeding regimes in captivity by using creative enrichment should provide elephants in zoos with more opportunities to express natural behaviours and natural time budgets. Captive elephants need to be fed copious quantities of low energy foods to avoid both boredom[2] and obesity (Bloomsmith et al., 1991; Young, 2003) and zoos also have a responsibility to provide natural feeding regimes that do not encourage anticipatory behaviour. In one study conducted by the Elephant Welfare Group, captive elephants were shown to anticipate management events (such as cleaning and large provisions of food) and increase stereotypic behaviour rates before such events; the study concluded that waiting for these events could be stressful (Yon, 2014) (see also Badihi & Buchanan-Smith, 2005; Bassett & Buchanan-Smith, 2007 for other species). However, enrichment may never adequately compensate for the restrictions of captivity.

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[2] I used the term boredom here and throughout the thesis to the state of lack of arousal, low affect and "*thwarted motivation to experience almost anything different or more arousing than the behaviours and sensations currently possible*" (Burn, 2017, p. 3; Mason & Burn, 2011).

1.5 Characteristics of Study Species

1.5.1 Asian Elephants

There are three subspecies of Asian elephants (*Elephas maximus*); Asian mainland (*Elephas maximus indicus*); Sri Lankan (*E. maximus maximus*) and Sumatran (*E. maximus sumatranus*) (Blake & Hedges, 2004; Sukumar, 2006).

The subspecies of individual captive Asian elephants are unknown. Although records of country of birth exist for wild-caught animals, the accuracy of these original data is questionable.

Wild Asian elephant mothers and calves in Uda Walawe. Photograph taken 14th July 2011.

Sri Lanka's Elephants

For this thesis, wild Asian elephant calves were studied on the island of Sri Lanka. Sri Lankan elephants have the highest genetic diversity of Asian elephants (Fernando, Jayewardene, Prasad, Hendavitharana & Pastorini, 2011; Fernando, Pfrender, Encalada & Lande, 2000; Fleischer, Perry, Muralidharan, Stevens & Wemmer, 2001) and, although they are proposed to be a distinct subspecies from the mainland Asian elephant, genetic support for this distinction is low (Fernando et al., 2000).

Sri Lanka's wild elephant population was estimated at a minimum of 5879 in August 2011 in an island-wide survey conducted by the Department of Wildlife Conservation

(Dissanayake et al., 2012; Fernando et al., 2011). This is thought to represent over 10% of the world's population of wild Asian elephants in 2% of the global range (Leimgruber et al., 2003; Perera, 2009). Sri Lanka, therefore, has the highest proportion of remaining wild Asian elephants (Fernando et al., 2011).

Elephants are found across approximately 60% of the country, "*over almost the entire dry zone*" (Fernando et al., 2011, p. 95) with habitat preferences for regenerating forest (Fernando et al., 2008). Fernando et al. (2008) observed well-defined home ranges of 34-232 km^2 (mean 115.27 ±64.0km^2, N=10), while elephants in southern India have home range sizes between 105-320km^2 (Sukumar, 1989). Sri Lankan elephants have high fidelity to their home ranges and do not migrate long distances (Fernando et al., 2011) .

1.5.2 African Elephants

Two types of elephant inhabit Africa; the forest elephant (*Loxodonta cyclotis*) in the central and west, and the bulkier savannah or bush elephant (*Loxodonta africana*) inhabiting open habitats. Morphological distinctions and genetic evidence from dart-biopsy samples by Roca, Georgiadis, Pecon-Slattery and O'Brien (2001) support the idea that they should be recognised as separate species whilst others suggest a third species in the west (Brandt et al., 2014; Eggert, Eggert & Woodruff, 2003; Eggert, Rasner & Woodruff, 2002; Ishida et al., 2016). However, the International Union for Conservation of Nature (IUCN) African Elephant Specialist Group (AfESG) continues to refer to the African elephant as a single species. Further evidence is required on the taxonomic status of Africa's elephants to prevent hybrid populations being given unclear conservation status (AfESG, 2003). The taxonomic distinctions between forest and savannah elephants continue to be debated, along with their general conservation implications.

1.6 Current Status of Elephants

African and Asian elephants in the wild are currently assessed as being vulnerable and endangered, respectively, on the IUCN Red List of Threatened Species (IUCN, 2010). With fewer than 400,000 elephants remaining in Africa (Chase et al., 2016), and 38,000-52,000 in all of Asia (Blake & Hedges, 2004; Kemf & Santiapillai, 2000; Sukumar, 2006), *ex situ* elephants in Europe and the United States of America (US) are sometimes managed in coordinated captive breeding programmes in order to produce a sustainable population of captive elephants and to educate the public about conservation issues. Wild capture of elephants is controversial and is considered by many to be unethical (Hutchins & Keele, 2006) and trade is often illegal (CITES, 2016). Under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), transportation over international borders after capture from the wild is illegal for elephants listed under CITES Appendix I. With the exception of elephants in four African countries, all elephants, both Asian and African, are currently listed under Appendix I. Only African elephant populations in South Africa, Zimbabwe, Botswana and Namibia are listed on CITES Appendix II, and can be traded internationally for commercial purposes if the necessary permits are obtained. (However, Botswana has self-uplisted to Appendix I). To further protect elephants, outcomes from the recent CITES World Wildlife Conference (October 2016) included the agreement to close domestic ivory markets "*where they contribute to poaching or illegal trade*" and to restrict live trade to only those facilities which can demonstrate appropriate captive conditions. The 'Decision-Making Mechanism for Trade in Ivory' (DMM) was also rejected, limiting any future ivory trade in order to protect elephants from overexploitation and illegal trade (CITES, 2016).

Wild Asian calf [c329] in a large age-graded group – here with sub-adult males behind - in Uda Walawe, Sri Lanka. Photograph taken 8th June 2012.

1.7 Elephants in Captivity

In North American zoos, the last recorded importation of an Asian elephant from a range-country was in 1996 and, since then, captive breeding has been the only means of adding animals to the American captive population (Prado-Oviedo et al., 2016). In the US, 62% of the Asian elephant population is made up of imported elephants, while 78% of its African elephant population is imported and African elephant importation is still on-going (Prado-Oviedo et al., 2016). The recent (2016) and highly controversial importation of calves from Swaziland to US zoos has been justified as ‘building populations’. Internationally, neither African nor Asian *ex situ* elephant populations are self-sustaining yet (Clubb & Mason, 2002; Hutchins & Smith, 2001). The role of *ex situ* breeding programmes and their ethical implications for conservation and calves born in captivity are, therefore, particularly important.

Each calf born in captivity has the potential to spend the next 60-70 years in captive conditions; facilities have an obligation to ensure that these conditions are neither physically or mentally damaging over the very longest term for the animals under their care. New empirical and comparative knowledge about normative calf development will contribute towards the understanding of the welfare needs of captive elephants. No previous work has examined wild Asian elephant calf development; our knowledge is based upon working timber elephants or ‘rescue’ elephants (e.g. Mar, 2007). This research addresses gaps in our understanding of early elephant development and provides suggestions to underpin welfare improvements.

Broom (2002) suggests that the welfare and wellbeing of some animals is too poor to justify keeping them in captivity and that zoos should only keep animals if the positive value of the zoo offsets any negative characteristics or consequences of poor welfare. Zoos justify their existence via contributions to *in situ* and *ex situ* conservation programmes (e.g. Wildlife Conservation Society, the Zoological Society of London (ZSL) and San Diego). Across zoos, there appear to be large variations in both their capacity and commitment to support *in situ* field conservation projects (Marshall & Deere, 2011). In terms of conservation, zoos spend 4-6.7% of their income on *in situ* conservation in the wild, with the highest contribution per visitor being £4.63 (at Durrell Wildlife Conservation Trust) and a mean of 44.6p (Hambly & Marshall 2014). However, zoos also contribute to conservation education and not just financial aid (Gusset & Dick, 2010, 2011). Although zoos vary greatly in capacity and their commitment to field conservation (Marshall &

Deere, 2011), the value of zoos as sources of funding and information has been used as justification for their continued captive management of species such as elephants.

In response to a series of events and reports (including Harris et al., 2008) on the welfare, housing and husbandry of elephants in British zoos (Kingston Jones, 2015), the British and Irish Association of Zoos and Aquariums (BIAZA) is facilitating the Elephant Welfare Group; the EWG which was set up in 2010 by the Department for Environment, Food and Rural Affairs (DEFRA) and a Parliamentary Committee on Zoo Standards. Keeping elephants in captivity is challenging and has become controversial in both the United Kingdom (UK) and the US with concerns surrounding issues such as obesity, limited exercise, foot health, gait, abnormal activities, handling methods, social composition, fecundity and survivorship (Clubb et al., 2008; Cohn, 2006; Harris et al., 2010; Hutchins, Smith & Keele, 2008). Clubb et al. (2008) showed that fecundity and survivorship would need to improve in order to achieve self-sustaining zoo populations and that understanding the successes and failures of captive breeding is essential if we are to avoid managing elephants to extinction.

1.7.1 Problems with Elephants in Captivity

1.7.1.1 Problems with Elephant Reproduction and Calf Rearing in Captivity

In the wild, one of the most important contributors to calf success is the mother’s previous experience with rearing calves (Lee & Moss, 2011). The potential for gaining this experience is limited in captivity by late age at first reproduction, long interbirth intervals and early reproductive cessation. By comparison to the wild, age at first reproduction is delayed in captive African elephants (mean 21.3 years in captivity, N=26, versus 13.6 years in wild, N=509), while age at first reproduction is advanced in captive Asian elephants (minimum 6.5 years in captivity, N=28 versus ~11 years in the wild, N=21; see Table 1.2 below; Lee, Fishlock, Webber & Moss, 2016; Prado-Oviedo et al., 2016). Captive African elephants (N=26) in Prado-Oviedo and colleagues' (2016) study were around four years older when they gave birth for the first time than were the captive Asian elephants (N=28). Since the birth rates between Asian and African elephants in North American zoos do not differ, this highlights Prado-Oviedo and colleagues' (2016) suggestion “*that management decisions related to captive breeding play an important role*” here and may be limiting reproductive potential (p. 17; see also Hartley, 2016;

Hartley & Stanley, 2016). In addition, early reproductive cessation is marked in captivity, but not in the wild (Table 1.2).

As evidence of the persisting problems in captive reproduction, a questionnaire, circulated in 1996, reported that only 65% (13/20) of European and North American zoos had ever successfully bred a live calf while 55% (11/20) also reported stillbirths (N=90 females of all ages; Taylor & Poole, 1998). A subsequent survey found that only 20% of African and 15.4% of Asian female elephants gave birth between 1960-2001 in the EU population (N=786 females of all ages, Clubb & Mason, 2002). From 1990-2001 it was estimated in the EU that only one calf was produced annually per 45 Asian females (N=271) and one calf per 55 African females (N=150) of breeding age (<11 years; 1990-2001; Clubb & Mason, 2002).

In the US elephant population, the maximum number of calves that any Asian elephant female gave birth to was six (87 Asian females, total count of 64 calves, mean number of calves per female 0.74), and in African females this was three (101 African females, total count of 40 calves, mean 0.38 calves per female; Prado-Oviedo et al., 2016). Conversely, the maximum recorded number of calves a female Asian elephant in Myanmar logging camps had in her lifetime was 10 calves (Hayward, Mar, Lahdenperä & Lummaa, 2014), similar to that among wild African elephants (Moss & Lee, 2011).

As stated above, the international zoo populations of Asian and African elephants are not self-sustaining: due to skewed age structure, insufficient genetic diversity and low reproductive rates (Clubb & Mason, 2002; Hutchins & Smith, 2001). The reasons for reproductive failure are complex but relate to females being inappropriately young or old at first reproduction due to management and lack of breeding opportunities or no exposure to males (Hartley, 2016; Hartley & Stanley, 2016). In a recent study on Asian and African elephants in AZA-accredited (Association of Zoos and Aquariums) zoos in North America Prado-Oviedo et al. (2016) found 71% (141/200) of the population’s female elephants in 2012 were at least 30 years old. Furthermore, of the females who were of reproductive age (e.g. >8 years), the majority had not yet reproduced (only 32.2% of Asian and 25.7% African females had given birth by 2012) and only 73.3% of Asian and 48.5% of African elephant females were experiencing normal reproductive cycling (Prado-Oviedo et al., 2016). The captive fecundity rate in the US in 2001 of approximately 1-2% was shown to be much lower than the projected requirement of 7-8% needed for a viable stable captive population (Hutchins & Smith, 2001).

Older females in captivity are also likely to show reproductive disease, especially if nulliparous, such as acyclicity; e.g. fibroma and myoma, in common with high numbers of nulliparous females in captive breeding populations (Brown et al., 2016). Reproductive rates are further hindered by factors such as infertility and there being a limited number of facilities who keep both females and an experienced male. Additionally, a male may be overrepresented as a father in its breeding facility and many months may pass before replacements can be found and carried out (pers obsv.). Management may again play a further role as Olsen, Chen, Boules, Morri and Coville (1994) found that pregnancy rates were enhanced during a female's oestrus period when a male was left with her for 24-hours per day, compared to fewer hours of access. However, only 10% of European and North American collections surveyed by Taylor and Poole (1998) keep males and females together continuously.

Table 1.2 Reproductive Life Histories for Female Wild and Captive, Asian and African Elephants. Adapted from de Silva et al., 2013. IBI=Interbirth-interval. Fecundity=average N of female offspring per breeding female per year. Spp.= species; *E.m.*=*Elephas maximus*; *L.a.*=*Loxodonta africana*. *Age at first reproduction.

Elephant population	**Spp.**	**Captive / Wild**	**Age at 1st (yrs):**			**Mean IBI (yrs)**	**Fecundity**	**Age of senescence (yrs)**	**Period of study**	**Reference**
			Oestrus	**Conception**	**Successful livebirth**					
Myanmar timber camp	*E.m.*	Semi-captive		Min :3.5 Mean 16.5±4.7 Median 15.6 (N=391)	Min: *5.3 Mean *18.3±4.7 Median *17.8 (N=391)	Mean 5.4±2.7 Median 4.9 Range 1.8-18.1 (N=771)	-	Max 53 (N=391)	1960-1999	Mar et al., 2012; Mumby et al., 2013; Robinson et al., 2012
Tamilnadu forest camp, India	*E.m.*	Semi-captive		Min 11.4 Max 62 (N=202)	13.4 (N=202)	10.5	0.095-0.155 (N=202)	63 (N=202)	1925-1996	Sukumar et al., 1997
Biligirianganas -Nilgris, India	*E.m.*	Wild		14-15	16-17	4.5-4.7 (N=28)	0.21	-	1981-1994	Sukumar, 1989; Sukumar, 2003
Ruhuna-Yala & Southeast, Sri Lanka	*E.m.*	Wild		~10		4.0-6.5			1960-1990	Katugaha et al., 1999
Uda Walawe (this study), Sri Lanka	*E.m.*	Wild		11	13.4±2.4 (N=21)	Survived: 4.2±0.6SE (N=44) All: 3.9±0.9 (N=54)	0.157	~60	2006-2012	de Silva, Ranjeewa & Weerakoon, 2011; de Silva et al., 2013
Wasgamuwa Sri Lanka	*E.m.*	Wild		~10		4.0			1980-1982	Ishwaran, 1993
Amboseli, Kenya	*L.a.*	Wild			Min 9 Mean: 13.6± 0.4 (95%CI) (N=509)	Survived: 4.7±3.2 (95%CI) (N=2865); All: 4±2.6 (N=3237)	0.098	60+	1972-2015	Lee et al., 2016
Samburu, Kenya	*L.a.*	Wild			Range 8.5-19 (N=52)		0.1 (N=509)	54	1998-2011	Wittemyer et al., 2013
Tarangire, Tanzania	*L.a.*	Wild			Mean 11.1 (Range 1.8-1..3)	Mean 3.3±0.7 (Range 1.8*5.8)	0.090	~60	1994-2005	Foley & Faust, 2010
US zoos*	*E.m.*	Captive	~5		Mean 16.9±0.9SE Min 6.5 Max 25.8 (N=28)			40	1962-2011	Brown et al., 2016; Prado-Oviedo et al., 2016
US zoos*	*L.a.*	Captive	~≥8		Mean: 21.3±1.1SE Min 10.4 Max 32.7 (N=26)			36	1978-2011	Brown et al., 2016; Prado-Oviedo et al., 2016

In facilities where no males are housed, or where females may have health problems which prevent them from engaging in ‘natural’ mating, Artificial Insemination (A.I.) is sometimes used (Harris et al., 2010). The 2003 Elephant TAG (Taxon Advisory Group) Survey Results showed that nine of the 14 elephant collections in the UK and Ireland housed males. (In addition to these 14 collections, the UK is also home to three Asian females which belong to a circus and one additional lone Asian female in a Welsh monastery; neither of these were included in the survey however). Only five of the nine facilities were (naturally) successfully breeding, however, while a sixth facility with no males had bred through A.I. (Kingston Jones, 2015).

Despite extensive research into understanding elephant reproductive physiology for captive breeding and advanced assisted reproduction technologies including endocrine monitoring, artificial insemination and even sperm sexing to improve reproductive success (Brown et al., 2004; Hermes, Göritz, Streich & Hildebrandt, 2007), captive breeding programmes for elephants have had varying degrees of success and ensuring both ’normal’ reproductive activity and calf survival remains problematic. Stillbirths, dystocia, abortions, and poor maternal care all play a part in limiting captive reproduction rates (Hutchins & Smith, 2001; Mar, Lahdenperä & Lummaa, 2012; Taylor & Poole, 1998). Calf rejection and infanticide resulting from poor maternal care adds further to high calf mortality in captivity (Taylor & Poole, 1998). Captive Asian elephant populations in the US and Europe have almost twice the juvenile mortality rates (40-45%; Saragusty, Hermes, Göritz, Schmitt & Hildebrandt, 2009) than rates in Asian elephants in Myanmar timber camps (21-23%, Mar, 2007; see also Table 7.1 in Discussion Chapter). Most juvenile mortality in Myanmar occurs in youngsters over six months while the majority of calf deaths in zoos (68-91%) take place in the first month of life (Clubb et al., 2009; Mar, 2007; Saragusty et al., 2009).

Discrepancies also appear between captive and wild elephant in the causes of juvenile deaths. In Myanmar, these relate to “*insufficient milk intake, snake bites and accidents*” whereas the zoos deaths are due to “*stillbirths, lack of mothering, stress imposed by captivity, obesity* [of mothers], *primiparous females and infectious diseases*” (BIAZA, 2010, p. 107; Clubb et al., 2009; Saragusty et al., 2009). Clubb and Mason (2002) state the chance of a captive-bred zoo calf dying before it reaches one year as 10-30% including a 10% chance of being killed or rejected from its mother.

Another major source of captive calf mortality, mainly in Asian calves, is the rapidly lethal hemorrhagic disease caused by the Elephant Endotheliotropic Herpesvirus (EEHV)

(Richman et al., 1999; Zachariah et al., 2013). In the past two decades, up to 24% of all captive-bred Asian elephant calves in Europe and North America have been affected by EEHV, and EEHV accounted for 60% of all deaths of captive-bred Asian calves aged eight months to 15 years in North America (Zachariah et al., 2013).

No cases of EEHV have been reported either in wild or captive elephants in Sri Lanka although the strain EEHV1 has been found in southern India (Zachariah et al., 2013). A preliminary published account reports a positive case of EEHV1A in Cambodia, while anecdotal reports also suggest the occurrence of a similar disease in range countries including Myanmar, Thailand and Nepal (Reid et al., 2006). Therefore we have no information on EEHV's contribution to calf mortalities in the wild.

1.7.1.2 Problems of Excess Weight in Captive Elephants

Lee and Moss (2011) have highlighted that early growth of elephants strongly impacts on their health and survival. Clubb et al. (2009) suggested that newborn Asian calves born in zoos weigh significantly more and tend to be fatter than those born in range-countries to working dams. They also note that excess peri-natal weight in other species has been shown to have adverse long-term health consequences for offspring, such as cancer and cardiovascular disease in adulthood in humans (Rasmussen & Johansson, 1998; Samaras, Elrick & Storms, 2003; Singhal & Lucas, 2004). Obesity of captive animals, including domestic species such as horses and rabbits (*Oryctolagus cuniculus*), is a welfare concern and human care-givers have been shown to underestimate obesity in their own animals (Meredith, 2012; Wyse, McNie, Tannahil, Love & Murray, 2008). Obesity, lack of exercise and poor muscle condition are prevalent problems in captive elephants, exacerbated by poor diet which can also lead to further issues such as colic (Hatt & Clauss, 2006). Animals in captivity are restricted physically, socially and with their opportunities and external stimuli. This can lead to health problems, limited behavioural repertoires and potential boredom.

Elephants are non-ruminant herbivores and they use high rates of food intake and turnover to compensate for the lower levels of food quality available in their wild environments. As hind-gut fermenters, some fermentation of plant cell wall fibres takes place within the large caecum and colon although they have short retention time of plant matter (Lindsay, 2011).

Increased body fat in captivity could also potentially explain why captive elephants have high rates of stillbirths, large calves, low fecundity and premature adult deaths (Clubb et al., 2009; Kurt & Mar, 1996). How well these captive calves grow, and at what rate, may have implications for metabolic health. Is an increase in growth rate the result of nutrition or overweight mothers, or are other factors involved such as the amount of space available for exercise or being less active due to a lack of playmates? Play has been shown to contribute greatly to calf development, including practice of motor and social skills in young calves (Lee, 1986). Lee and Moss (2011) report that in wild African calves, play represents 3.8% of a calf's time, when not at rest. They suggest that play adds to total energy expenditure, and may be part of the maintenance of healthy physical development.

1.8 Social Structure and Calf Learning

Elephant females and calves live in units in complex multi-tiered communities and interact with other family groups (Moss & Poole, 1983). Elephants have lifetime bonds (Garaï, 1992; Kurt & Garaï, 2001; Payne, 2003) and a female calf will remain associated with her herd for life while males disperse at maturity to live alone or in male bond groups (Sukumar, 1989, 2006). The hierarchical society in the wild therefore consists of mothers, sisters and offspring in family groups (Hutchins & Smith, 2001; Rasmussen & Schulte, 1998; Schulte, 2000). Elephants require a long developmental period of up to nine years to learn both social and survival behaviour and they typically acquire skills and knowledge concerning their environment and other survival strategies from their elders (Eisenberg, McKay & Jainudeen, 1971; Gadgil & Nair, 1984; Lee & Moss, 1999; Payne, 2003; Poole et al., 1997). Elders use this learned understanding to make decisions and guide their herd to safety, food and water (Hutchins & Smith, 2001; Ishida et al., 2016; Nair, 1989; Payne, 2003). In African elephants, the larger herds with older and more experienced matriarchs (female leaders) have been found to be most successful at exploiting the best habitats and therefore safeguarding higher survival rates for calves (Foley, Pettorelli & Foley, 2008; McComb, Moss, Durant, Baker & Sayialel, 2001). Our recent research on wild African elephants suggests that females remain reproductively and socially successful until into their 60s (Lee et al., 2016). However, elephants are at risk of dying at unnaturally young ages from anthropogenic factors such as poaching, human-elephant interaction or habitat degradation, thus reducing the opportunities for young to learn from the oldest matriarchs. Essential survival knowledge for rare periods of stress, for example, drought, may then be lost with the unnaturally early death of a matriarch instead of being passed down through the generations (Foley et al., 2008; Goldenberg & Wittemyer, 2017; Sukumar, 1989).

Elephant mothers and other family members provide calves with social support and learning opportunities which contribute to normal development (Lee, 1987; Lee & Moss 1999; 2011). For example, calves learn which solid foods to eat by watching and ’testing’ the food in the mouths of experienced (and patient!) herd members (Nair, 1989; Payne, 2003). As calves age, they also learn the appropriate social behaviours. Female calves learn how to respond to attentive males during oestrus (Bates et al., 2008) or equally, male calves learn how to provide the correct signals to an available female by watching the behaviour of mature males and females during mating. Learned responses to signals as well as learning how and when to signal oestrous and musth ensure mate choice. Problems arise in captivity with learned behaviours such as oestrous behaviour, mating or calf rearing, when animals have limited opportunities to learn. Learned oestrous and mating behaviours may include, for example, the “*Demonstration by parous relatives* [which] *may encourage nulliparous females to direct oestrous behaviour towards the much larger musth males, rather than running away from them, thus helping to learn to attach themselves to males that are able to guard them*” (Bates et al., 2010, p.4). Males can also show lack of knowledge of how to ’court’ females or how to cope with them socially (pers. obsv.).

Small captive herds often have few or no playmates for calves and a restricted range of ages available for social partners. The number of herd members in wild African elephants has been noted to be an important aspect in elephant social dynamics and as such family or group size could affect some phases of development (Lee & Moss, 2011).

There are distinctive problems for males in living in captivity or in atypical groups. In the wild, male African elephants disperse from their natal groups at 10-16 years (Lee & Moss, 1999) and 10-15 years for Asian males (Sukumar, 2003). They then form strong bonds with other, often older males (Evans & Harris, 2008). In captivity, males can be separated from others (including their mothers) as young as four, for management purposes, and then they often live solitary lives in captivity. There are significant problems with male aggression towards keepers and other elephants, which may be due to their limited social experience when young (e.g. Bradshaw, Schore, Brown, Poole & Moss, 2005). Wild males deprived of older, experienced, social companions become hyper aggressive (Slotow & Dyk, 2001; Slotow, Dyk, Poole, Page & Klocke, 2000) and restricted of their learning opportunities (Evans & Harris, 2008). It is important to understand how and to what extent male calves benefit from interacting with adult males during development: this may be an important component that is often missing during male calf behavioural development in captivity. As captive breeding programmes also rely on males, their normal expression of behaviour is vital. The long-term welfare of male calves produced during captive breeding (which will produce 50% males under normal chance conditions) also requires an understanding of sex differences in early development.

A sub-adult and juvenile male Asian elephant engaged in trunk wrestling play in Uda Walawe, Sri Lanka. Photograph taken 10th June 2013.

Crucially, females growing up in their age-graded society gain knowledge of both birthing and mothering by witnessing herd births and practising calf nurturing on younger relatives. Allomothering is a central aspect of protecting and rearing calves (Gadgil & Nair, 1984; Lee, 1987) yet Prado-Oviedo and colleagues' (2016) US study suggests that one of the earliest exposures a captive female elephant has to an infant was probably the birth of her own first calf.

This leads us to ask if captive calves are receiving support from within their family in what is likely to be the consequence of an atypically small group, as found in captivity? Are captive calves behaving appropriately in developmental terms and are they able to integrate successfully into their small captive herd? And importantly, if behavioural development differs in captivity from that in the wild, what are the welfare implications for captive breeding of elephants and what improvements can be made?

Wild African elephant calves are highly dependent on their mothers in the first 24 months of life both energetically and socially (Lee & Moss, 1986). This critical window of development is sensitive to "*poor energetic conditions (e.g. droughts) and reduced growth*" and has enduring consequences for later survival and reproductive success (Lee, Bussière, Webber, Poole & Moss, 2013; Lee & Moss, 2014, p. 145). The rate of play in early infancy also predicts longevity into adulthood (Lee & Moss, 2014). Thus the study of this early development window may provide key insights into why captive elephants experience social, reproductive and welfare consequences.

1.9 Mother Experience and Calf Care

Captive elephants do not have opportunities to choose to associate with experienced individuals, who have the amassed decades of social and environmental knowledge over the length of their lifespan. It is therefore evident that captive elephants have not had sufficient opportunities for appropriate or necessary levels of maternal experience, both with their own calves and the calves of others. Kurt and Mar (1996) found 6% (n=121) of calves in European zoos and circuses were rejected by their mothers after birth and a further 10% were killed. One recent example highlights the lack of maternal experience in captive settings when a calf was euthanised at Leipzig Zoo (March 2015) less than a week after its birth (Russell, 2015). Staff believed its mother accidentally trod on the calf moments after parturition leading to the calf's fractured femur. The mother had also attacked and killed her first calf in 2012 shortly after it was born. The zoo's director, Jörg Junhold, suggested that "*it was unclear whether this was a deliberate act of aggression, or a result of pain that the new mother was experiencing*," (Russell, 2015, para. 11) and raises the question of whether her lack of experience contributed to the events. Given all the management constraints in captivity and female elephants lacking experience with calves, due to limited opportunities to learn, this may result in captive females providing poor maternal care (Taylor & Poole, 1998) with a high prevalence of mothers rejecting their own calves, abusive alloparenting, and infanticide.

Maternal infanticide has been correlated with an inexperienced mother's lack of close contact with an older female when she was young, implying that she may not have experienced or observed calf care (Taylor & Poole, 1998). By contrast, infanticide is almost unheard of in the wild: Wanghongsa, Boonkird, Rabian & Ruksat (2006) believe theirs to be the first published report and even this was committed by an aggressive Asian bull. It is, therefore, crucial to investigate when and why maternal infanticide and rejection occur in captivity. Are these atypical behaviours due to a lack of maternal experience, enclosure substrates or design limitations? Barua (1996) reports the abandonment of wild calves by Asian elephants seems to be a result of extreme stress caused by human encroachment during the birth. Abandonment and rejection of calves, therefore, seems to be an indicator of extreme stress in wild and captive mothers.

It may be possible that elephant calves that grow up under abnormal maternal care, for example, prematurely separated from mothers, or having never experienced family structures, may themselves add to the cycle by becoming poor reproducers or abusers, with high calf mortality rates, as has been seen in captive gorillas and other apes (Abello & Colell, 2006). Clubb and Mason (2002, p. 251) suggest "*What are the risk factors for poor maternal care?*" as additional possible research questions. We need to know how mothers rear their calves in captivity to stop these cycles of abuse and death in captivity.

Chester's Asian elephant calves, Jamilah and Nayan playing. Photograph taken Januay 11th 2011.

1.10 Thesis Plan

Can we make improvements to the welfare of captive elephants, in particular for calves since their production and survival are vital for sustaining captive populations? One option is to invest in costly elephant breeding technologies and improved housing, but here I suggest the importance of returning to the basics to investigate whether the calves are developing normally once we have managed to ‘produce’ one.

1.10.1 Thesis aims

The overarching aim of this thesis is to establish baseline information on developmental processes in wild elephant calves and to compare behaviour observed in captivity with that seen in the wild.

Following the two methodological Chapters (Two and Three), the first aim of the Activities Chapter (Four) was to chart normative maintenance activities (independent feeding, resting, moving) for captive and wild calves and their mothers over the calves’ first two years of life, as a measure of the energy and time costs that an individual experiences in its physical and social environment. The prediction was that Asian and African elephants would show similar changes in activity budgets with calf age and these would differ between captive and wild contexts.

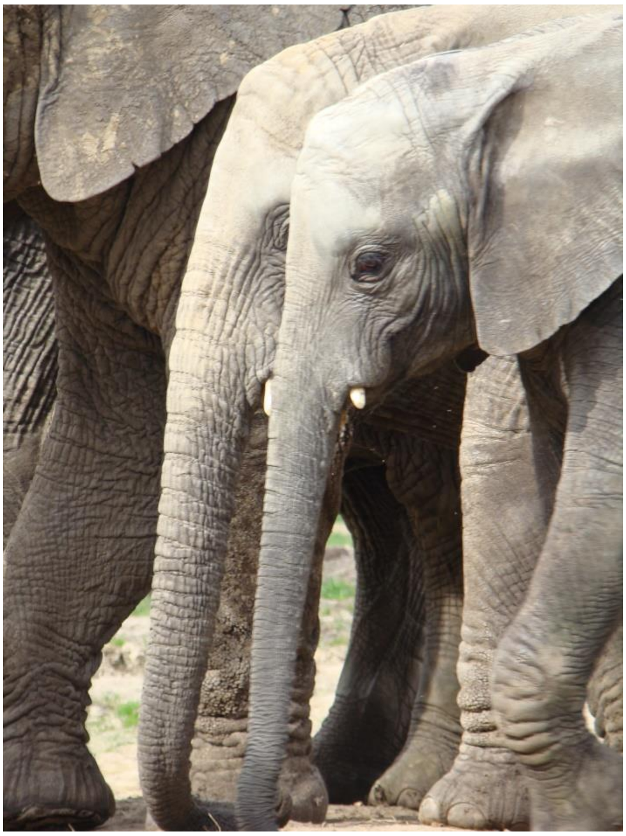
The second aim (Chapter Four) was to briefly examine stereotypies (present in non-calves) in captive elephants as these are outcome variables suggesting a history of compromised welfare and experiences. The prediction tested here was that changes in the social environment would affect rates of abnormal behaviours.

In the Interactions Chapter (Five), the aim was to assess the social experiences of elephant calves in captive and wild environments by exploring early calf interactions with mothers and others. I focused on the way mothers allocated suckling to their calves as they aged, and the potential for non-mother neighbours to be close to, and therefore, interact with calves. I also explored the synchrony between calf and mother activities. As needs and interests, in both mothers and calves, differ between captivity and wild, as well as as calves age, I predicted that any synchrony of activity may differ between these environments and between calf ages. I further predicted that both species of wild calves will show similar age changes in social proximity to others; and that, due to variation in opportunities for social learning, interactions will differ between the wild and captive contexts. Species-atypical restrictions on social group size in captivity will lead to reduced social support for both mothers and offspring. Captive females have few opportunities to develop maternal skills and offspring will receive limited allomothering and will also have limited access to appropriate play partners. I use proximity as an indicator of the potential for opportunities for learning social skills.

In the final data Chapter (Six), the aim was to explore play, a common elephant behaviour with long-term consequences for learning and survival, and to compare play types and rates for age in captive and wild environments in relation to key variables such as group size. It was predicted that if calves in captivity lacked some appropriate age-specific social skills they would engage in active behaviours, such as lone or object play, to compensate for lack of social partners.

In the Discussion Chapter (Seven) I summarise and review my general results in relation to predicted (and some unexpected) findings about early calf development in the wild and captivity. I then develop a *Decision Tree* of ethical considerations and recommendations for managers seeking to optimise the long-term welfare of elephant populations in captivity.

Chapter 2: Description of Study Sites and Subjects



African elephants at Howletts. Photograph taken 2nd April 2011.

In this Chapter, I describe the general life histories including group size, group structure and social dynamics of the four contexts which are used in all subsequent comparisons.

2.1 Wild Study Sites

2.1.1 Wild Asian Elephant Study Site: Uda Walawe National Park, Sri Lanka

Data on Asian elephant calves were collected in the Uda Walawe National Park, in southern central Sri Lanka (latitudes 6°25’-6°34’N and longitudes 80°46’-81°00’E). The park is approximately 308km^2 and is highly seasonal, covering dense riparian forest, residual tree plantations, secondary forest, dense scrub, both tall and open grassland areas.

The park has two wildlife exits, through the Dahaiyagala and Lunugamwehera corridors (Figure 2.1) (de Silva, Ranjeewa & Weerakoon, 2011), and an electric fence has been erected around more than two-thirds of the reserve’s perimeter (de Silva et al., 2013).

Uda Walawe experiences little direct human disturbance, thus making human impact on elephant behaviour unlikely (de Silva & Wittemyer, 2012). However, humans have huge indirect impacts. Fernando (2015) discusses the conservation concerns within Uda Walawe of electric fences and the (illegal) grazing of large numbers of cattle and water buffalo from nearby dairies (both exacerbating overgrazing); the decline in grassland due to the invasion of fast growing alien species, *Lantana camara* and *Eupetorium.* Few herbivores consume these herbaceous flowering plants (Fernando, 2015), resulting in their prolific spread in recent years, converting the majority of former grassland (previously the dominant vegetation cover on approximately 50% of the study area) to mixed scrubland (de Silva et al., 2013). Invasive species, along with fires (often set by cattle grazers; Fernando, 2015), have resulted in "*dynamic and persistent changes in vegetation*" (de Silva et al., 2013, para. 5).

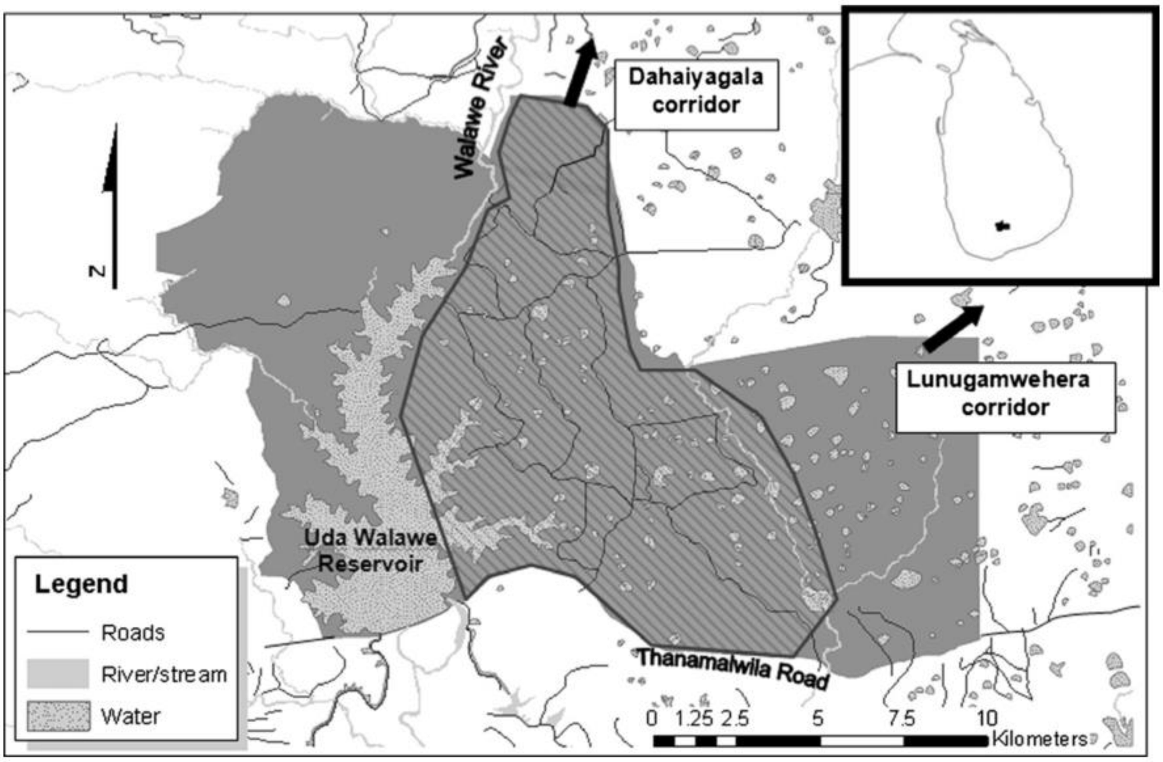


Figure 2.1 Uda Walawe National Park. Taken from (de Silva et al., 2013) Images sources: NASA Earth Observatory (http://earthobservatory.nasa.gov), the Department of Wildlife Conservation, Sri Lanka, and the Centre for Conservation Research, Sri Lanka.

The park contains one large and two smaller man-made reservoirs, where elephants congregate in the dry seasons, providing good visibility on the surrounding short grasses. These reservoirs and several seasonal natural water sources provide permanent water for both humans and wildlife (de Silva et al., 2013; de Silva, Ranjeewa & Weerakoon, 2011).

Over the study period (2011-2013), mean annual rainfall was around 1500mm with day length remaining almost constant through the year, due to the park's near equatorial position. The region experiences two annual monsoons, around March-April and October-December separated by dry seasons with low levels of occasional rain (Zubair, Siriwardhana, Chandimala & Yahiya, 2008).

Air temperature does not vary greatly in Uda Walawe throughout the year (and only varies during the year in Sri Lanka's montane regions (Burt & Weerasinghe, 2014) and so the main climatic variations are simply a function of rainfall. During data collection (May-July 2011, 2012 and 2013) temperatures in Uda Walawe ranged from 21-32°C (Ratnapura; mean 26.88°C; World Weather Online, 2016).

Lone male wild Asian elephant in Uda Walawe. Photograph taken 6th May 2011.

Conservation Threats for Sri Lankan Elephants

Sri Lanka's primary rural industry is agriculture and the country's extensive human-elephant interaction, resulting in crop damage and death of both people and elephants, is perhaps the biggest conservation threat due to the high density of both elephants and humans (Corea, 2007). Crop damage by elephants may have seasonal peaks and mitigation strategies (such as watch towers, electric wires, non-lethal explosions and chilli-grease) have been shown to be followed by reductions in crop damage (for example, in Cambodia: Webber, Sereivathana, Maltby & Lee, 2011).

Approximately US$10million pa of damage to crops and property is caused by elephants in the country and while one study reports the death of 1413 elephant and 568 people in an 11 year period (1997-2006; Corea, 2007), others cite over 200 elephant deaths annually (Fernando et al., 2011). Perera (2007) reports that the majority of human caused deaths and injuries to elephants were the result of gunshots (108 of 180 ascertained deaths in July 1999-April 2007). Death and injuries have been reported from land-mines, set during the 1982-2009 civil war, and more recently from ‘hakka-patas’; small pressure mines hidden in fruit (primarily to poach wild pigs, *Sus scrofa cristatus*), which once bitten down on can shatter the jaw (Fernando et al., 2011). Wire or cable snares can also cause deep wounds and five juvenile elephants have been observed in Uda Walawe with snare wounds since 2008 (de Silva, 2016a). Stresses to wild elephants include further human disturbance associated with habitat loss, including blocking traditional pathways and competition with cattle (Fernando et al., 2011; Perera, 2007). Tourism, while potentially generating significant revenues, can be a further source of disturbance when approaches to elephants are unregulated and too close.

In addition to these conservation threats, reports have been made regarding numerous elephant calves being illegally captured from the wild. The removal of these calves could have severe consequences for wild populations and for the welfare (and survival) of the individual calves (see Anver, 2016; de Silva, 2016b).

Uda Walawe Elephant Research Project

Wild Asian elephant data for this project was collected in generous collaboration with the Uda Walawe Elephant Research Project (UWERP). This long-term monitoring programme has collected a database of individual elephant identities (IDs) based on life histories and photographic records of adult and sub-adult males and females. However, the project had limited records on calves prior to the start of this project, subsequently allowing this project to contribute to their calf database (see de Silva et al., 2013).

UWERP Observations

The study population in Uda Walawe was estimated to be between 804 and 1160 individuals in 2011, with individual identification records for 286 adult females and 251 adult males, and a density ranging from 102 to 116 adult females per 100km^2. While the study population had seasonal movement of males and females, density remained constant throughout the year (de Silva, Ranjeewa & Weerakoon, 2011).

The study was carried out in the middle section of the park (approximately 100km^2; hashed lines, Figure 2.1), using the road network, and very occasionally driving off-road. This was kept to a bare minimum to avoid disturbing wildlife.

The Elephant Transit Home

The Elephant Transit Home (ETH) is an elephant orphanage located on the periphery of Uda Walawe, managed under a regime of "*least human interactions*" where it rehabilitates and returns calves to the wild (V. Perera, June 2011, pers. comm.). Around 15 orphaned or abandoned calves are taken in to the ETH each year where they are treated and cared for in a section of the park, "*to retain familiarity with the habitat, but to have access to both food and medical care*" (V. Perera, June 2011, pers. comm.; Daniel, 2015). Calves are allowed to graze freely in a fenced area bordering the reservoir and only have limited interactions with humans to reduce habituation; these interactions are only for bottle feeds every four hours, for any veterinary care, and when calves are brought in to the central paddock at night time (Fernando et al., 2011; Miththapala, 2009). Calves are treated and cared for around three years, with mortality rates of arrivals at around 40% (V. Perera, June 2011, pers. comm.; Daniel, 2015; de Silva & de Silva, 2007).

Asian elephant sub-adult [Athimali], was rescued, rehabilitated and released into Uda Walawe by the ETH. Photograph taken 15th July 2011.

A total of 103 elephants were released from the EHT back into the wild from 1998 to 2017 (see Table 2.1 below; ETH, 2017; Fernando et al., 2011). Up until 2010, the animals were all released into the forest bordering Uda Walawe, however, "*due to concerns of overcrowding*" release sites have since included other National Parks (Fernando et al., 2011, p. 101). Post-release studies (carried out by Born Free) observed individuals integrating into wild groups and forming their own 'juvenile groups' (e.g. in one batch of 11 elephants released together: seven formed a 'juvenile group', one male and one female integrated into wild groups, one female returned to the ETH herself and one female was injured and brought back to the ETH; Jayantha, 2006). As of 2017 and across release sites, a total of seven reintroduced juveniles have died (ETH, 2017) and there are fears that rehabilitated juveniles have also been illegally captured from the wild. These juveniles are easy targets since they: have no mother to protect them; are habituated to humans to a degree; are fitted with post-release radio-collar which would identify them; and their release details are often covered by the media (A. Silva-Fletcher, Sept 2016, pers. comm.).

It should be noted that while some of the Uda Walawe elephant population contains animals which have been rehabilitated at the ETH and released back into the wild, only one mother studied, [Indika][3], was a re-introduced animal. [Indika], however, is mother to two calves within the study. This data speaks extremely highly of the work of the ETH and it is a great success that an orphaned elephant can be reintroduced into a wild group and, when mature, become reproductively successful and raise her own calves.

Moreover, 16 births have been reported in total across release sites from reintroduced females. However, the number of reintroduced females of reproductive age in Uda Walawe during the study period was an estimated maximum 26 females (see Appendix, Table A), and these females therefore made up a small percentage of the total population of around 1000 individuals (de Silva et al., 2013). These reintroduced individuals would therefore likely play a very small role, if any, on the behaviour of study calves and mothers and herd members. The inclusion or even the presence of rehabilitated individuals in a wild group of animals may still raise the question of whether the UW elephants are still a wild population, especially when used as a reference population for comparisons with captive counterparts. However, Thorpe's (1967) commonly used definition of the behaviour of a wild animal is "*the behaviour expressed by an animal subject to environmental and evolutionary pressures with minimal human intervention*" (as cited in Veasey et al., 1996, p. 12). I hence put forward, in today's world, which wild animals are *not* effected behaviourally by human interference?

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[3] [Indika] was also known as 'Sandamali' to the ETH (Miththapala, 2009).

2.1.2. Wild African Elephant Study Site: Amboseli National Park, Kenya

Wild African savannah elephant calves were studied in the Amboseli National Park in southern Kenya (Figure 2.2). Amboseli (02°38′29″S 37°14′53″E) is a 390 km^2 protected area on the border between Kenya and Tanzania. The elephants move over a savannah ecosystem of 3000-8000 km^2. The study population of around 600-650 elephants over 3000km^2, both inside and outside the park boundaries in "*semiarid Acacia woodlands and bushlands, open alkaline grasslands and permanent swamps*" (Lee, 1986, p. 354; Lee, 1987).

At the start of the study period in Amboseli, there were 162 calves of less than six years old. Data were collected from November 1982 to November 1984, and 94 more calves were born during the study period (Lee, 1986). For all the calves investigated in this study (1982-1984), month and year of birth is known. For calves under five years old, a date of birth could also be assigned to within seven days (Lee, 1986). These calves have subsequently been tracked for the past 37 years.

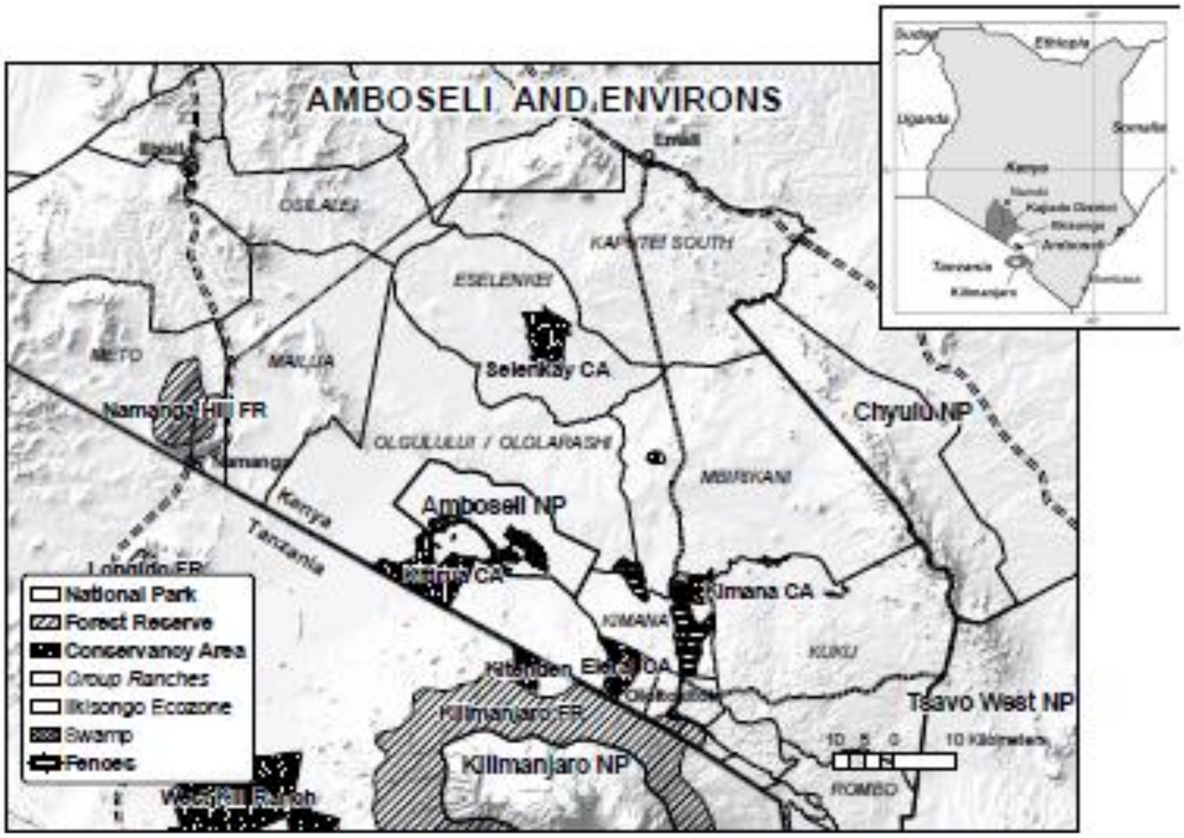


Figure 2.2 Amboseli National Park and surrounding Ecosystem**.** Figure from Croze & Lindsay, 2011. NP=National Park; FR=forest reserve; CA=conservation areas, including commercial concession wildlife areas and community conservancies.

Similar to Uda Walawe, Amboseli is highly seasonal in rainfall and plant production (Croze & Lindsay, 2011). During the study period, mean annual rainfall in Amboseli was 330mm with the majority in March-May then Nov-Dec (Lee, 1986). 1984 was a drought year (<150mm), but rainfall was normal in 1983 (Lee, 1986). Annual air temperature was cold in the dry season (as low as 5°C in Feb), and hot and humid in the wet season (reaching 35°C in July and Aug) with average annual temperatures of 23°C (Altmann, Alberts, Altmann & Roy, 2002; Croze & Lindsay, 2011). Day length was roughly constant throughout the year.

Conservation and Threats

Current threats to the population are the continent-wide poaching for ivory, although Amboseli has been very well protected in recent years. Both historically, and when these data were collected, elephants interacted with traditional Maasai pastoralists, and the main threat to elephants was spearing events during the initiation ceremonies of young male age-sets (Moran). Only some crop raiding took place during the study period, although this has since intensified as progressive land-use changes have meant that agriculture now surrounds one side of the protected area (Chiyo et al., 2014).

Amboseli Elephant Research Project (AERP)

Individual elephants in the Amboseli population have been identified using natural markings and observed continuously since 1972 (Moss, Croze & Lee, 2011). Life histories of these individual elephants have been collected by C.J. Moss and her co-workers, as part of the Amboseli Elephant Research Project. The population has approximately tripled since the beginning of the study, from around 500 individuals in 1972 to around 1500 in 2014 (Lee & Moss, 2014). The population consists of 50-63 distinct family units (female-led kinship groups; Archie et al., 2008) ranging in size from two to over 50 individuals and with more than 380 independent males. Males born into families disperse between 10-16 years of age; some remain within the Amboseli population while others disperse into adjacent populations (Archie & Chiyo, 2012; Lee & Moss, 1999). Amboseli elephants are very habituated to vehicles, and all observations were made from cars at distances of 2-10m.

2.2. Composition of Wild Elephant Groups

One of the more significant differences between Asian and savannah African elephants is that of group structure and composition. Both species live in female-kin groups (Archie et al., 2008; Fernando & Lande, 2000), but these kin units (called Family Units) are typically smaller in Asian elephants in terms of stable associates. Family units are embedded in the general population through temporary aggregations of several families and associations with males – these 'groups' form and break down over minutes to hours to days (fission-fusion sociality; Aureli et al., 2008; de Silva & Wittemyer, 2012), making elephant sociality some of the most fluid and complex for terrestrial mammal species.

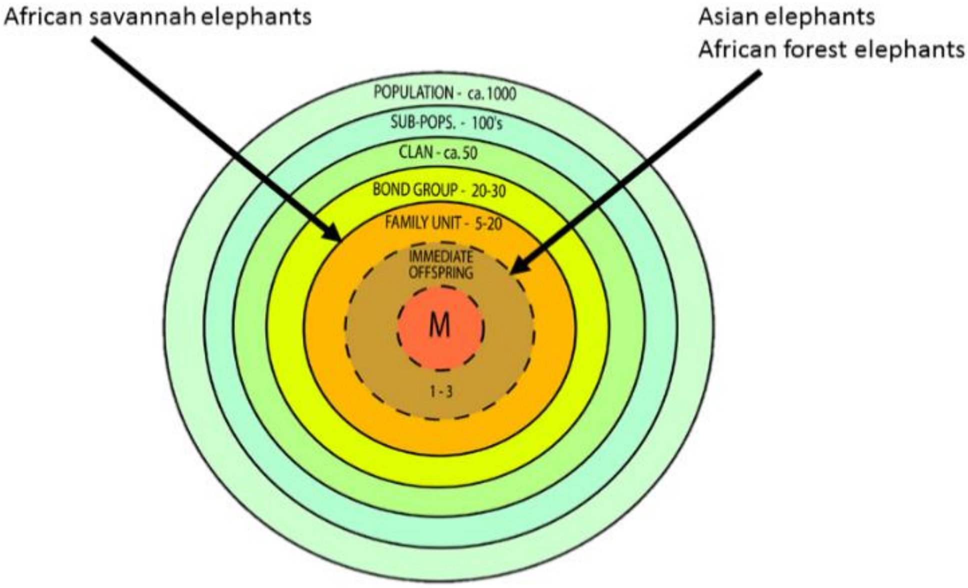


Figure 2.3 Elephant Social Groups. From Moss, 1981.

Elephant sociality can be described as social circles (Figure 2.3 above; Moss, 1981) as families do not spend all their time together but rather aggregate with others as well. The Amboseli population's sociality has been shown to be cohesive, spending 54.7% of their time in the same group as all members of their family; and gregarious, spending 72% of their time with other families. The most cohesive families were the small ones and they also spent more time in aggregations with other families (Moss & Lee, 2011).

Elephants make dynamic decisions regarding social partner choice. They choose when to associate with other families, who to associate with (on family and individual levels) and even where to associate. This ability to manage associations is lacking in captivity where individuals do not have the freedom to leave, or to join others; certainly not at the same scale as wild elephants.

Groups of elephants in this study were defined as "*a coordinated and spatially distinct body of animals*" where no individual was further away than the main diameter of the group (Lee, 1986, p390). In Amboseli, group sizes ranged from two to 400. These groups could be made of a single family, fragments of several family units, a bond group (associations of multiple family units) or any association of families (Figure 2.3). Mother-calf groups were distinguished from groups with independent adult males, called mixed groups.

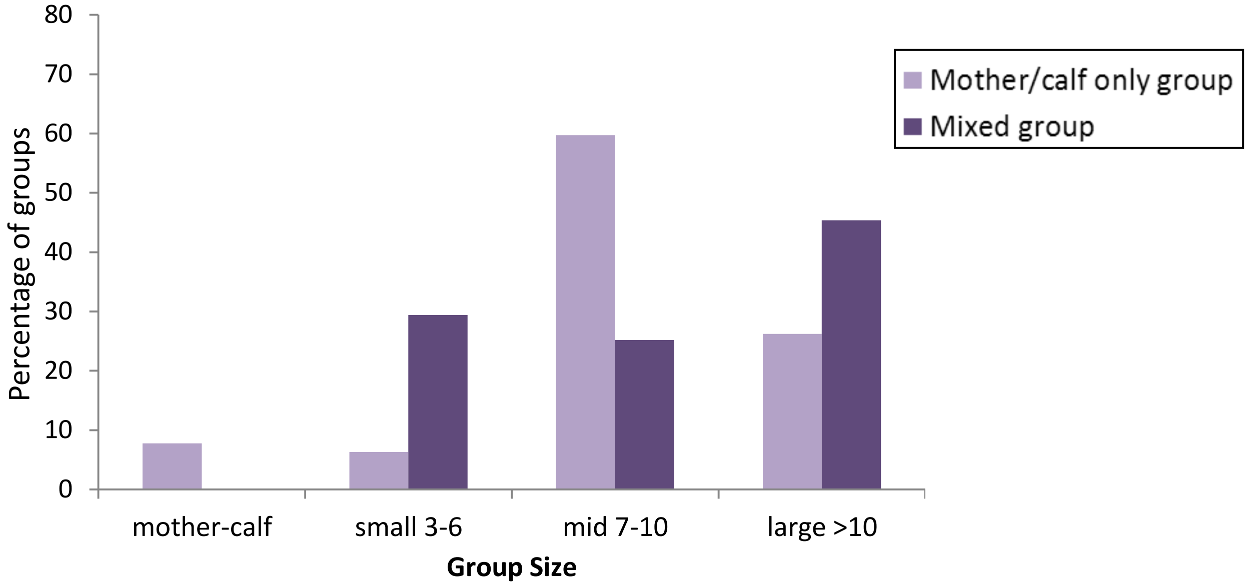


Figure 2.4 Wild Asian Elephant Group Sizes. Data from 2011-2013. Group sizes were collected at the start of calf focal studies and therefore do not include group sizes without calves.

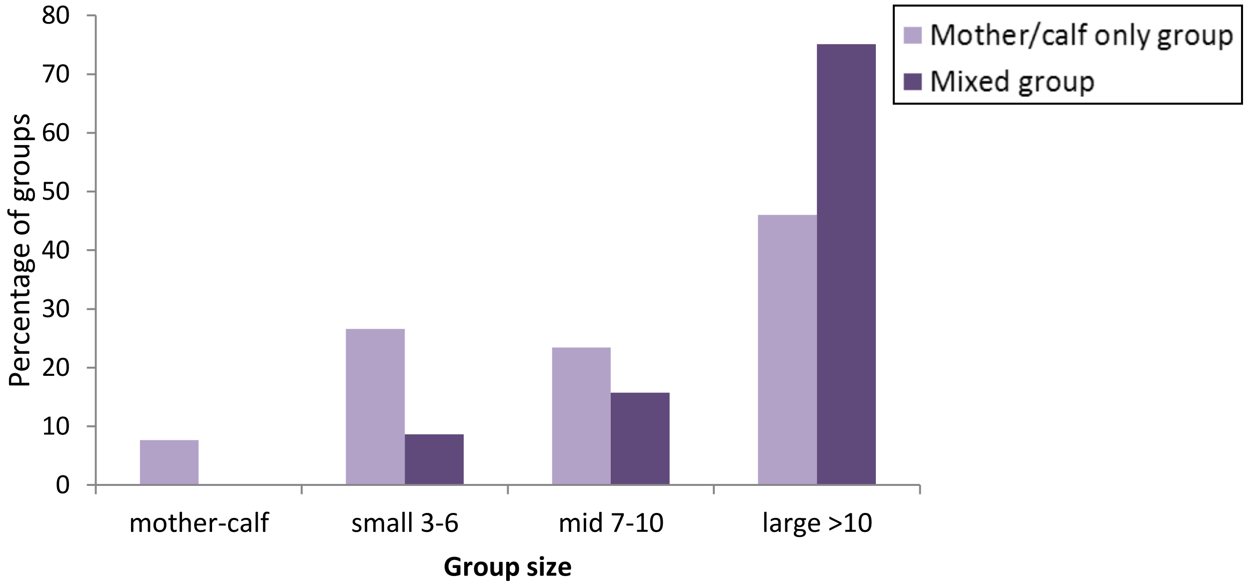


Figure 2.5 Wild African Elephant Group Sizes. Data from 1980-1985. Group sizes of one are excluded as this would have only included a lone oestrus female; and mixed groups of two as this would have only contained an oestrus female and a male. They were removed in analysis as they would not have been comparable to the wild Asian data collected, as Asian group sizes were only recorded in association with calf scans.

Group sizes in Figure 2.4 do not include those of lone males, lone females, male only groups or groups without any calves. Similarly, Figure 2.5 does not include group sizes of one and therefore also excludes those of lone males, lone females, as well as mixed groups of two comprising of an oestrus female and a male. In Uda Walawe, adult females in a family unit ranged in number from one to >10 in rare gatherings. In Amboseli, adult females in a family unit ranged in number from 1-8 (mean 3.8), and elephants less than ten years old numbered from 0-15 (mean 4.3; Figure 2.5).

In 2007/2008, the Uda Walawe population's median group size, in terms of the number of adult females encountered in a group was reported as between two and three across all seasons (de Silva, 2010; de Silva, Ranjeewa & Weerakoon, 2011). This ranged widely and was between one and 14 adult females in the dry season (of May-September) (de Silva, 2010). These median group sizes, however, also included lone oestrus females, whereas these were excluded from Figure 2.4 and Figure 2.5 (since no focal studies were carried out when no calves were present).

Data for this study were collected in the dry seasons in Uda Walawe (May-July) and it is important to note that de Silva (2010) found a greater number of larger groups in the dry season than in the wet season within the same year. Groups with more than 12 adult females only occurred in the dry season. Therefore it would be expected that calves studied here would experience an even lower proportion of time in large groups (>10 individuals) during the wet seasons and the year overall than represented in Figure 2.4.

However, smaller groups were less likely to have included calves than larger groups (simply by the laws of chance) and were consequently less likely to have been included in my group size data. The one outlier here was the case of [Grover], an emaciated UW calf found alone and constantly calling. [Grover] was presumably lost and was the only calf with a group size of one individual.

In contrast, Amboseli average group size during the study period was 26±66 (SE±0.514). African elephant group sizes are consistently bigger than Asian elephant group sizes (see Figures 2.4; 2.5).

Emaciated and presumably lost, male wild Asian calf in Uda Walawe, nicknamed [Grover]. Despite his poor body condition and distressful calling [Grover] survived and was observed in subsequent years by the UWERP team. Photograph taken 6th July 2011.

2.2.1 Constraints on Social Activity; Fission Fusion

Social interactions will be constrained or enabled by group size. Wild elephants have an active choice over their social partners including group composition and novel individuals due to their fission-fusion sociality. However, in captivity even in zoos with comparably ’big’ groups, elephants can only choose their social partners from the same individuals each day, when permitted to do so by keepers.

As group size is both an independent variable and a dependent factor possibly varying by activities, I did not analyse it. We can, however, look into frequency distributions by comparing the composition of wild populations with captive groups. Here I present the frequency distribution of male and female individuals found in the wild groups that were encountered with calves and I will present group compositions for captive sites in Section 2.4.

Wild Elephant Group Composition

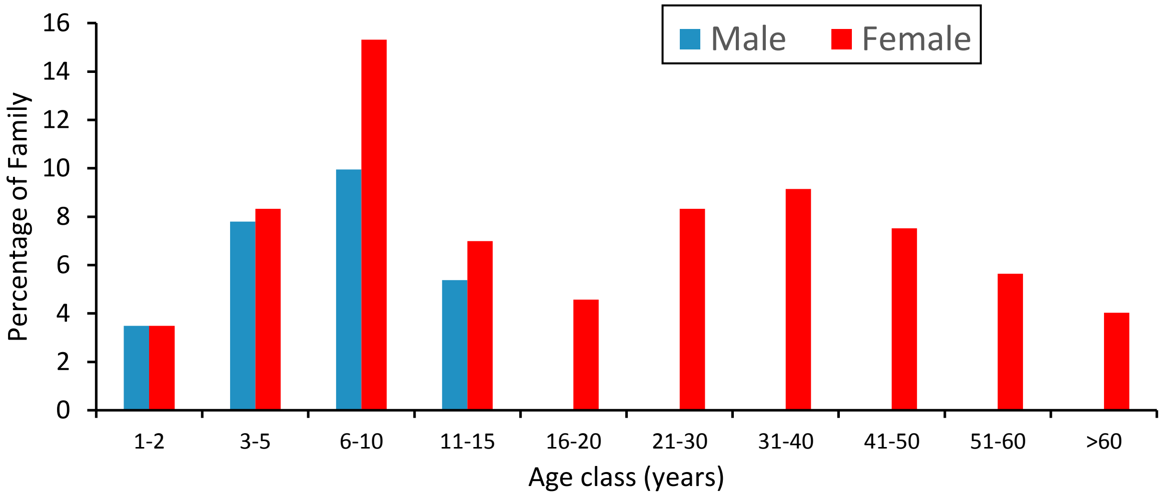


Figure 2.6 Composition of Wild Asian Mother-calf Units. Adapted from de Silva et al. (2013). Composition consisting of known individuals alive in the population at the end of 2012. After age of dispersal, males were not included in this dataset due to the low confidence in their age classification, therefore female percentages here represent higher values than reality. Total N individuals 373.

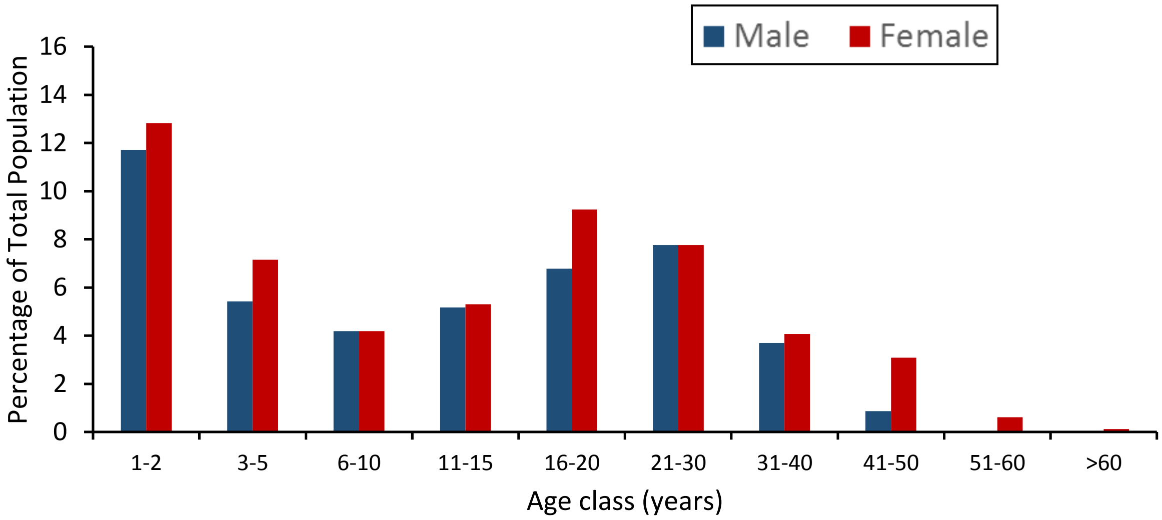


Figure 2.7 Composition of Wild African Elephant Population. Composition consisting of individuals alive in study population between 1980-1985. Males included here after age of dispersal.

It is worth noting here that this wild African population composition (Figures 2.7; 2.8) represents the period of a significant baby boom in Amboseli (1980-1985).

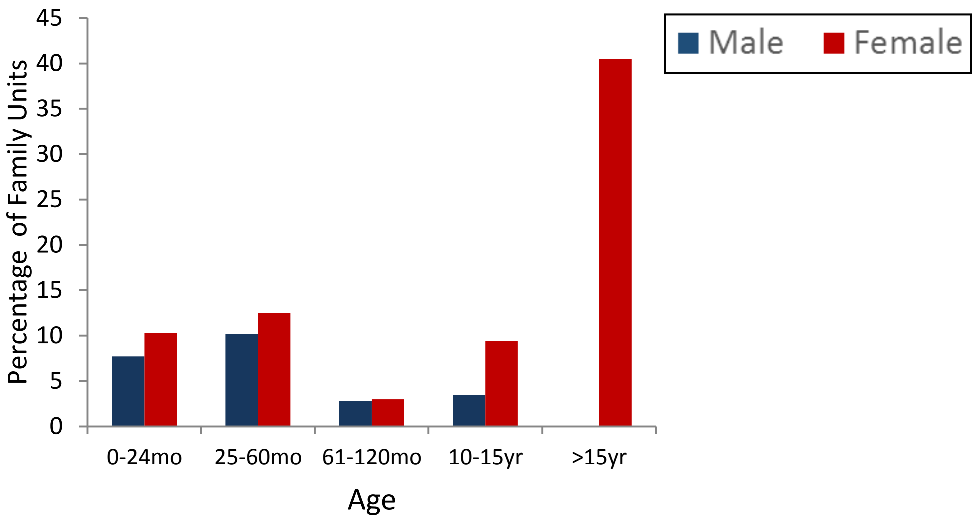


Figure 2.8 Composition of Wild African Family Units. Adapted from Lee (1987). Composition consisting of individuals alive in study population in 1980-1985.

Note the y-axis scale difference between Figures 2.8, and 2.6 and 2.7, as these charts are to illustrate unit compositions as opposed to the size of groups.

2.3 Wild Study Subjects

Both wild study populations have become habituated to vehicles on account of encounters with tourists and continuous observations.

In Amboseli, the month and year of birth were known for all study calves (those born between 1976-1984), and the majority had a birth date accurate to within seven days. UWERP’s demography files were created from estimates of the age of the calf at first sighting and approximately 75% of the study calves had a birth accuracy from a sighting within one month of birth (de Silva et al., 2013).

The term ‘immature’ is used to refer to all elephants under the age of nine years, while ‘young calves’ refers specifically to those under two years and dependent on mothers for survival nutritionally and socially. ‘Older calves and juveniles’ are those between two and five years who are socially dependent and have an increased probability of death without their mother, and ‘old juveniles/adolescents’ are those between five and nine years who are typically pre-reproductive but socially independent although still with their family.

Recognising Wild Individuals

The elephants in both Uda Walawe and Amboseli are recognised individually by natural markings on ears such as size, curves and shapes, vein patterns, notches, holes and folds (Moss, 1996); bodies, such as back shape; distinctive tails including tail lengths, kinks, hairlessness or even unusual hair colour; or tusk and tush (small tusks) size and shapes if present.

Females with a calf and obvious breast development were defined as lactating females. The lactating females were also classed as adult females; as were any female who had previously had a calf. In Uda Walawe, nulliparous females who showed no signs of having had previous calves (e.g. no breast development) were classed as sub-adults (Lee, 1987; Moss, 1983).

Photographs of the wild Asian calves were organised to create calf ID folders for the UWERP. Each folder held photographic and video records for each mother-calf dyad. These records showed unique features for identification; calf suckling its mother (and any others) to confirm mother and allomothers; body condition; and proportional growth of calves, measured against their mother’s height.

Julian Age Calculation

Calf age during each field season was calculated using their estimated birth-date and Julian dates. Julian dates in months used the year 1920 as a start year (as it was unlikely that any elephant ever studied by the UWERP or AERP was born before 1920). Ages were estimated for each calf by the observer when first seen in the UW population, or from the earliest photograph taken of the calf (when its mother had been identified). Julian ages were simply a convenience for tracking changes in ages over a long study period.

Calf Codes

All elephant calves studied in Uda Walawe with known identities are presented in Appendix B, Table B1.3. Each calf’s ID code (e.g. [c078_06]) was created using its mother’s ID (in this example [078]), the year the calf was born (here, 2006) and prefixed with ‘c’, denoting calf. This method allowed the study to distinguish between differently aged calves who shared the same mother. [c187_10] was studied in 2011 at around 15 months, while in 2013 [c187_13] was studied as a newborn calf up to one month old.

Examples of Mother-Calf Dyads and Photographic Records used for IDs. a) [218] and her newborn [c218_12], b) [Bali] and her juvenile [cBali_08], c) [Blanch] and [cBlanch_12]. Blanch also has distinctive white tail hairs, giving rise to her name. d) [838] and her first calf [c838_12].

Sampling Regime

In order to ensure comparability between the studies, similar methods were used. All data were collected by observing a single calf (focal follows – see Section 3.3). Six-month age categories were used to group calves up to 24 months old (1-6, 7-12, 13-18 and 19-24 months), and a larger age bin was used for young juveniles calves over two years and under five years into the category of 3-5 year olds. There were five age categories in total. Further details of focal samples and behavioural observations are presented in Chapter Three (Methods).

2.3.1. Wild Asian Study Calves

Approximately 74 hrs of wild Asian calf focal data were collected, across a total 65 field days (28, 21 and 16 field days in 2011, 2012 and 2013 respectively) from 101 identified calves (Table 2.1; for details of numbers of 10min focal observations see Table B1.2 in Appendix B). These totalled 50 female and 38 male calves with a further 13 calves with unconfirmed sex. Of these 101 calves, 56 were studied in 2011, 53 in 2012, and 47 in 2013. Only four calves were studied in all three field seasons ([c196_10], [c278_10], [c276_11] and [c225_10]. For details of each individual calf studied in Uda Walawe see Table B1.3; Appendix B).

Table 2.1 Number of Wild Asian Calves Sampled, by Sex and Age Category. Observations in Uda Walawe. Unknown sex and ages excluded from analyses. The total number of calves per age bin is different to the summed number of calves sampled since some calves changed age categories during the study. For individual calf IDs see Table B1.3 in Appendix.

	Age category					
Calf Sex	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	11	7	13	6	18	**38**
Female	25	11	19	7	20	**50**
Unknown	5	1	1	3	4	**13**
Overall	41	19	33	16	42	**101**

2.3.2. Wild African Study Calves

Observations on wild African calves were made by PCL (P.C. Lee) and CJM (C.J. Moss) between 1980-1984 in Amboseli National Park, Kenya. Data from 1982-1984, however, represent the core of the wild African data used in this thesis: 130 calves were studied in 1982-1984 and thirteen of these individuals had also been observed in 1980 and 1981 before being studied again in 1982-1984 at older ages (Table 2.2). Individual focal samples, totalling approximately 252 hours, were collected on 58 male and 72 female wild African calves aged from birth to five years of age (for details of number of observations and calf IDs see Appendix Tables B2.1 and B2.1, respectively).

Data from these 130 calves were used to investigate calf and mother behaviours and with proximity to mother. However, observations on the proximity of calves to their non-mother neighbour had not been collected during these individual focal samples and therefore, data on proximity to non-mother neighbours for wild African calves was instead used from unique instantaneous scans, from 1982-1984, on 237 calves from birth to six years of age. These data were collected when groups were first approached, throughout 1980-1984 (for sex and age of these calves see appropriate where they were used, Table 5.2, Interactions Chapter).

Table 2.2 Number of Wild African Calves Sampled from 1980-1984, by Sex and Age Category. Observations in Amboseli National Park. Unknown sex and ages excluded from analyses. The total number of calves per age category is different to the summed number of calves sampled since some calves changed age categories during the study. For individual calf IDs see Table B2.1 in Appendix.

	Age category					
Calf Sex	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Overall**
Male	24	24	25	12	52	**58**
Female	23	25	18	15	65	**72**
Overall	47	49	43	27	117	**130**

2.4 Captive Study Sites

Recognising Captive Individuals

Individual captive elephants were also recognised by natural marking (see ‘Recognising Wild Individuals’ in Section 2.3) and observers CEW (C.E. Webber) and RF (R. Fraser) learned individual traits of elephants until each elephant’s ID was familiar. Captive animals could be identified easily as they were always the same few individuals.

Husbandry and Management

Elephants in captivity are usually trained to participate in management practices to allow access for veterinary and routine care such as foot and skin care or for being moved from one enclosure to another. All elephant training is based on operant conditioning methods when an animal is conditioned to learn associations between their own behaviour and the consequences arising from carrying out that behaviour. This learning can be used either to increase the frequency of a requested desired behaviour or to extinguish an unwanted behaviour. The repetition of the desired behaviour can be encouraged through either ’positive reinforcement training’ (PRT) (by presenting rewards such a food or verbal praise), or by ‘negative reinforcement training’ (NRT) (by removing an aversive stimulus such as an ankus). Punishment, on the other hand, is used to reduce the frequency of undesirable behaviours, and it is important not to confuse NRT with positive punishment (PPT), where an aversive stimulus is presented. PRT, NRT and PPT are the three operant conditioning tools used in elephant training, although a fourth exists which is negative punishment (NPT; whereby a rewarding stimulus is removed, for example a favourite toy)

(Greco, Meehan, Miller, et al., 2016; Lehnhardt & Galloway, 2008; Pryor, 1984; Reynolds, 1975).

Captive elephants in the UK are currently managed using these training tools under two regimes: protected contact (PC) and free contact (FC). Elephants have historically been managed in captivity under FC husbandry which allows direct interaction, husbandry or training with the keeper and animal within the same shared space, without a protective barrier, and uses both PRT and NRT as well as sometimes PPT. Traditionally, handlers use an ankus (a wooden or metal elephant hook, also known as a guide) in FC to guide or direct the elephants and, if necessary, for protection from the elephants (PPT) (Lehnhardt & Galloway, 2008; Olson, 2004).

PC differs, however, by using a physical barrier so that keepers are never in the same enclosure as the animal, thus increasing keeper safety. PC uses only PRT and asks for volunteered cooperation from the animal often by requesting the elephant to approach a target (usually a stick with a ball attached to the end) (Lehnhardt & Galloway, 2008; Olson, 2004). Although both PC and FC use PRT, Wilson, Perdue, Bloomsmith and Maple (2015) showed that elephants in PC were given PRT in the form of food and verbal praise at much higher rates than elephants in FC.

The two systems of PC and FC are surrounded in controversy in animal welfare as well as personal safety and some animal care professionals have expressed concerns over the movement of the industry from FC to PC. These have included fears that medical care cannot be provided as optimally in PC as FC (particularly in light of the EEHV epidemic in calves) and that keepers cannot physically intervene to manage aggression interactions (Priest, 1992; Wilson et al., 2015). On the other hand, research has shown that the use of aversive stimulus when training (such as NRT used in FC) is more likely to cause frustration and/or behavioural and neurological responses considered indicative of negative affective states, than by removal of rewarding stimulus (NPT) (Franklin, 1972; discussed in Greco, Meehan, Miller et al., 2016; Hiby, Rooney & Bradshaw, 2004). Wilson et al. (2015) also showed that PC allowed the elephants greater control of their environment and hence improved wellbeing than those managed in FC. Furthermore, PC husbandry still allows the use of calf-training pens which allow keepers access to the calf’s mouth and trunk or training for rectal suppositories (in the event of veterinary treatment for EEHV) and while keepers are not in the same enclosure per se, they can reach over the top of the calf-training pens.

A third regime of limited contact is also utilised in zoos and in reality, elephant training is practised along a continuum of all three regimes (Greco, Meehan, Miller, et al., 2016; Kingston Jones, 2015).

2.4.1 Captive Asian Elephant Study Site and Group Composition: Chester Zoo

Data were collected at The North of England Zoological Society's Chester Zoo in two periods, in 2006-2007 and 2010-2014. At the start of the study period in 2006, Chester held eight Asian elephants. At the start of the second study period in 2010, the Zoo held ten elephants, seven of which were the same individuals that had been present in the 2006/2007 data collection. The relatedness, sex and age for all individuals present within both study periods are shown in Figure 2.9, and group compositions by age class, sex and study year are shown in Figure 2.10.

Chester's elephant indoor housing was completed in 2006 with an Asian tropical rainforest theme. The inside area consisted of: a sand pen for cows and young covering 985m^2 which allowed them to be housed at night as a single unit and also provided keepers with the option to divide it into three enclosures; a sand-covered bull pen of 415m^2; and two training pens with rubber flooring. The outdoor 5490m^2 sand paddock (including a concrete 227m^2 corral; Papies, Sparrow, Wells & Fiby, 2007) has an additional bull sand paddock of 530m^2, which could be opened on to the main paddock (McKenzie, 2015). The main outside paddock contained a 4m deep 300m^2 concrete pool, mud wallows, timed feeders and differing terrain gradients. After data collection was completed the outdoor paddocks were also covered in fine gradient sand of at least 1m depths. There were two further sand covered outdoor off-show holding pens (270m^2 combined; Papies et al., 2007).

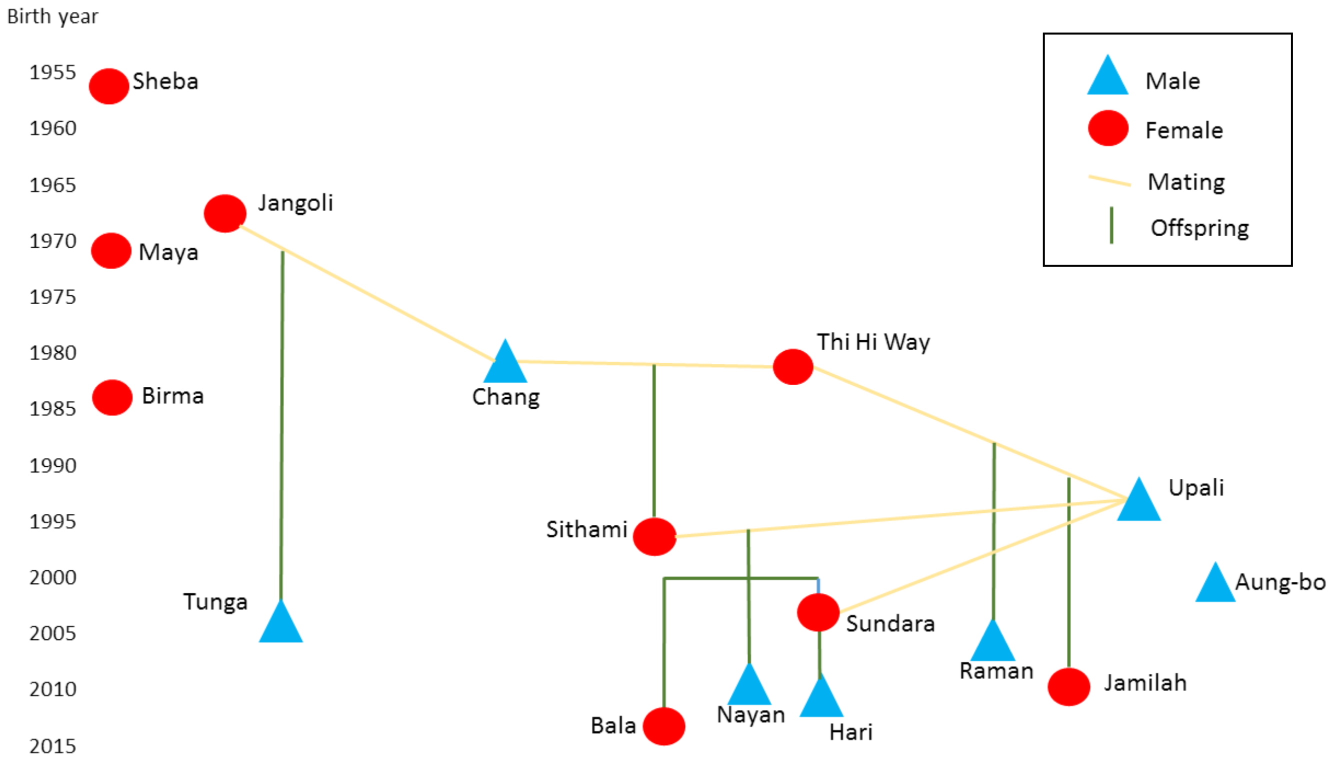


Figure 2.9 Chester Zoo Asian Elephant Family Tree (2006-2007 & 2010-2014). Chang was not present during study periods but is represented here to show relatedness. Individuals are arranged vertically in relation to their year of birth.

Of the three captive study sites, Chester has the largest indoor housing for its elephants, but the smallest outdoor areas. The schematic drawing shows all three facilities at the same scale (Figure 2.11a). Not including the outside paddocks (which were completed in 2000), Chester's elephant house cost £3,000,000 (7% of which was for design; Papies et al., 2007). The house consists of hydraulic gates; a control room with camera access (upgraded since the study period to allow 24-hour recording); weigh-bridge; race and a PC-wall (see above) for husbandry training.

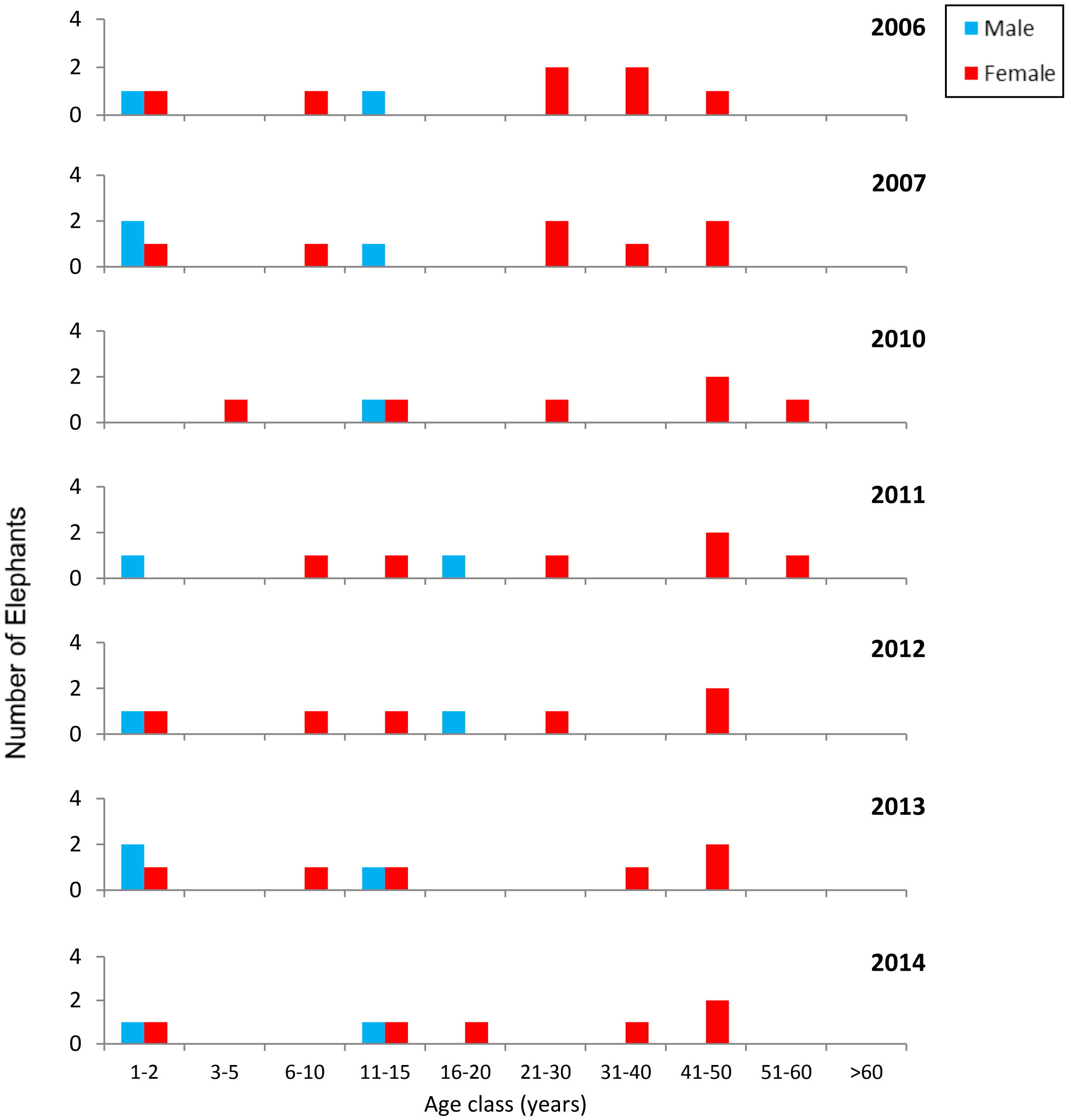


Figure 2.10 Composition of Chester Zoo's Captive Asian Elephant Group. Compositions as of January 1st for each year in study period. Males included here after age of dispersal.

Access

Elephants were kept inside at night when temperatures dropped below 8°C, when newborn calves were present; or due to social husbandry issues (e.g. to separate expectant mothers from individuals deemed by managers as unsafe around calf births). In the warmer summer months, however, the female and calf group was given access to both the main indoor and outdoor paddock except at times of training and health care or during paddock cleaning (and food restocking). In warm months, if the main group was locked inside at night, the adult male could be given full access to the outdoor paddock.

However, he was usually kept indoors due to the design of the house, as free access to choose between indoor and outdoor bull enclosures was not logistically feasible.

Protected Contact Husbandry

All elephants were trained using PC husbandry at Chester and a specialised calf training area (calf creep) has been created (and continually developed since 2010) to allow access to calves for daily health checks, particularly for herpes testing and for potential treatment.

Social Issues with Access

At times, social situations arise which cause management changes to the grouping and access to enclosures. Jangoli, for example, was an adult female unrelated to the rest of the group who has now been moved from Chester’s group to Madrid Zoo (in 2014, and then to Estepona Selwo Safari Park in 2015). After the addition of the new young male, Aung-bo (aged 11 years 2 months) to the group in 2012 he occasionally engaged in aggressive interactions with Jangoli (pers. obsv.). These conflicts escalated to the stage where Jangoli chose to stay indoors during the day instead of following the group outside, where they usually mixed with Aung-bo. This eventually led to Jangoli spending her daytime alone in the outdoor holding pens after refusing to follow the group. Although Jangoli was only solitary for less than six hours a day, this situation continued for over six months before her removal to another facility.

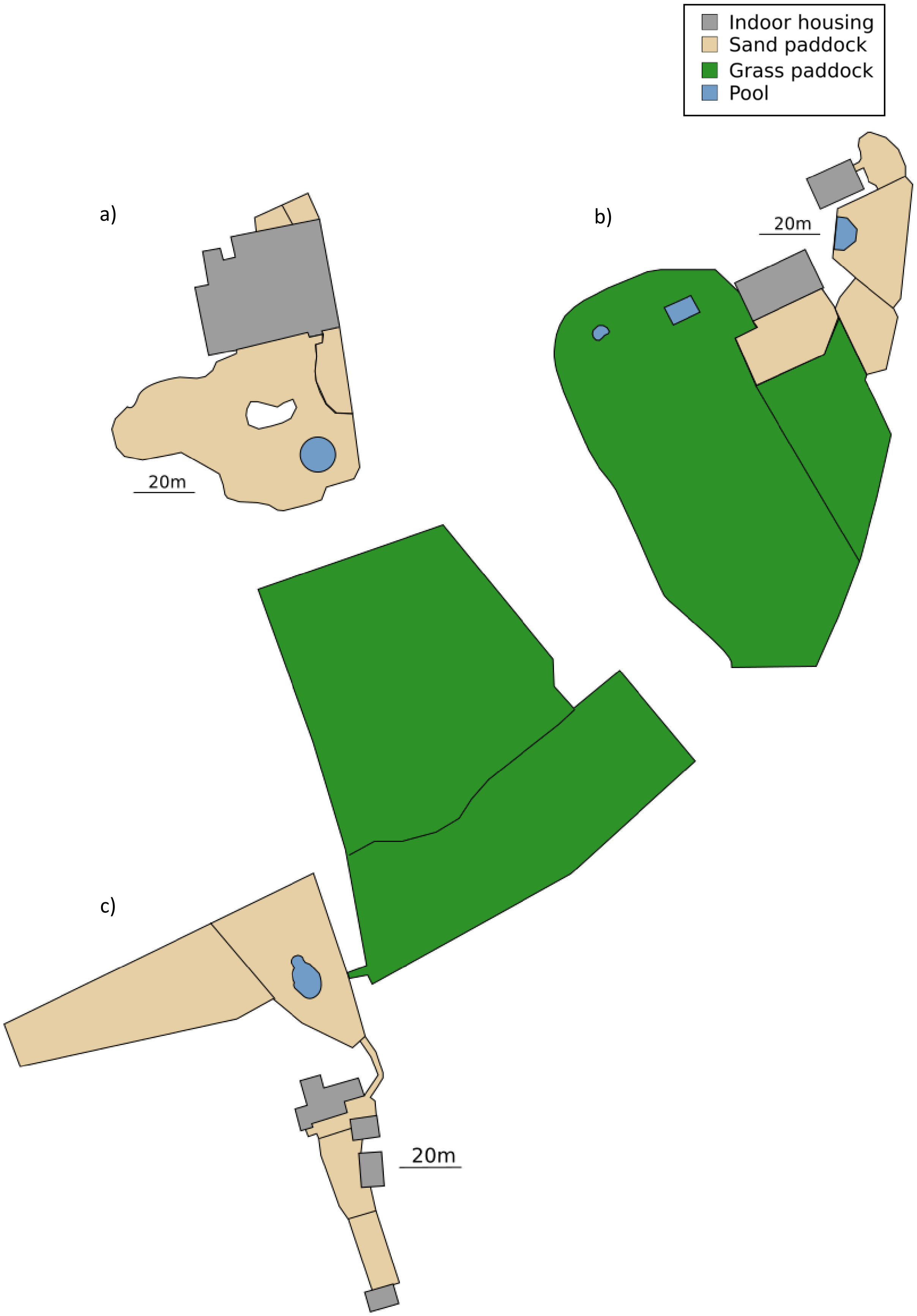


Figure 2.11 Schematic Drawings of Captive Study Sites. a) Chester Zoo, b) Whipsnade Zoo, c) Howletts Wild Animal Park. Maps are drawn to the same scale.

2.4.2. Captive Asian Elephant Study Site and Group Composition: Whipsnade Zoo

At the start of the study in 2011, ZSL's Whipsnade Zoo held nine Asian elephants (Figure 2.12). The relatedness, sex and age for each individual are shown in Figure 2.12, and group compositions by age class, sex and study year are shown in Figure 2.13.

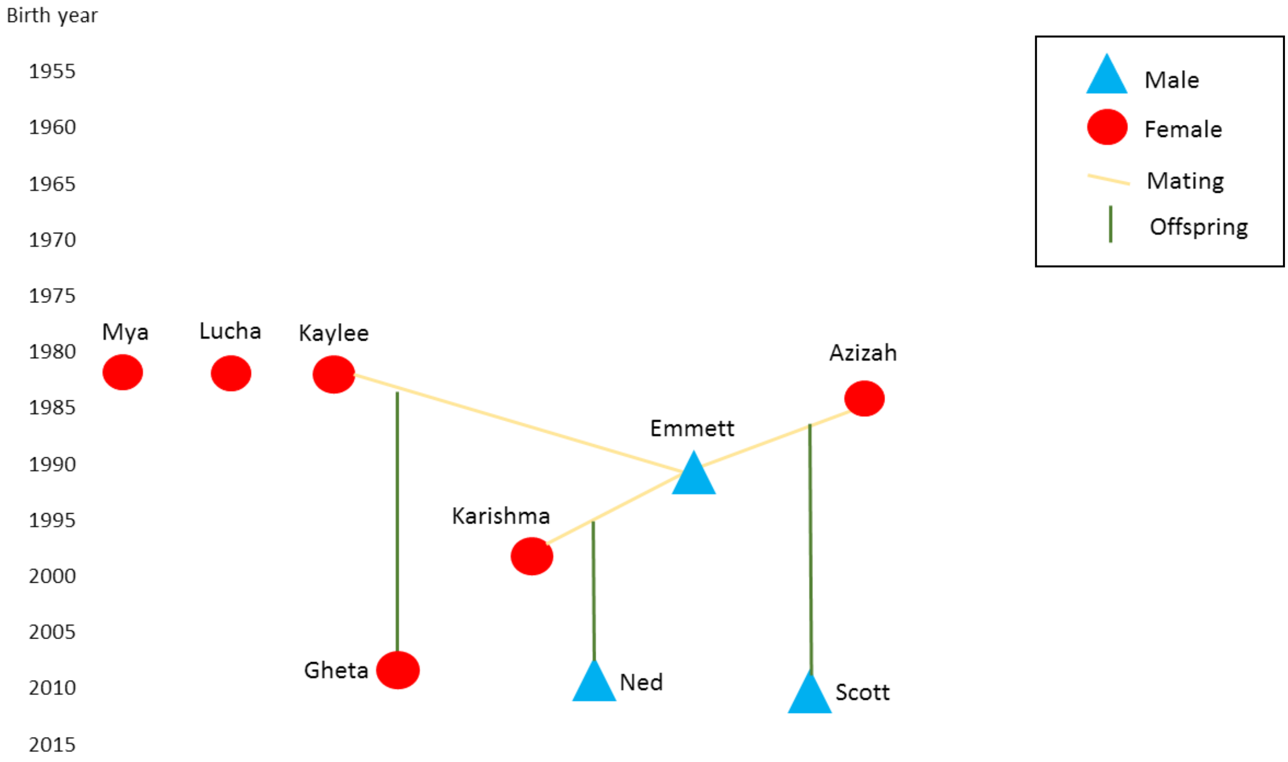


Figure 2.12 Whipsnade Zoo Asian Elephant Family Tree (2011-2014). Individuals are arranged vertically in relation to their year of birth.

Whipsnade's main indoor area for its females and calves was a concrete area covering 390m^2 (Figure 2.11b). This could be divided into five areas if required and at the time of data collection was divided into two to accommodate incompatible females (although females were never separated individually). A second indoor concrete-floored bull house (82m^2) contained a PC wall and an adjacent bull sand paddock. Of the two main paddocks, the considerably larger one was of grass and the smaller of sand, each with concrete lined pools and an additional shallow pool in the grass paddock. A secondary grass paddock was also used for the bull and an incompatible female (to separate her from another individual female). There was a further sand paddock (containing some grass) alongside the outdoor concrete training area.

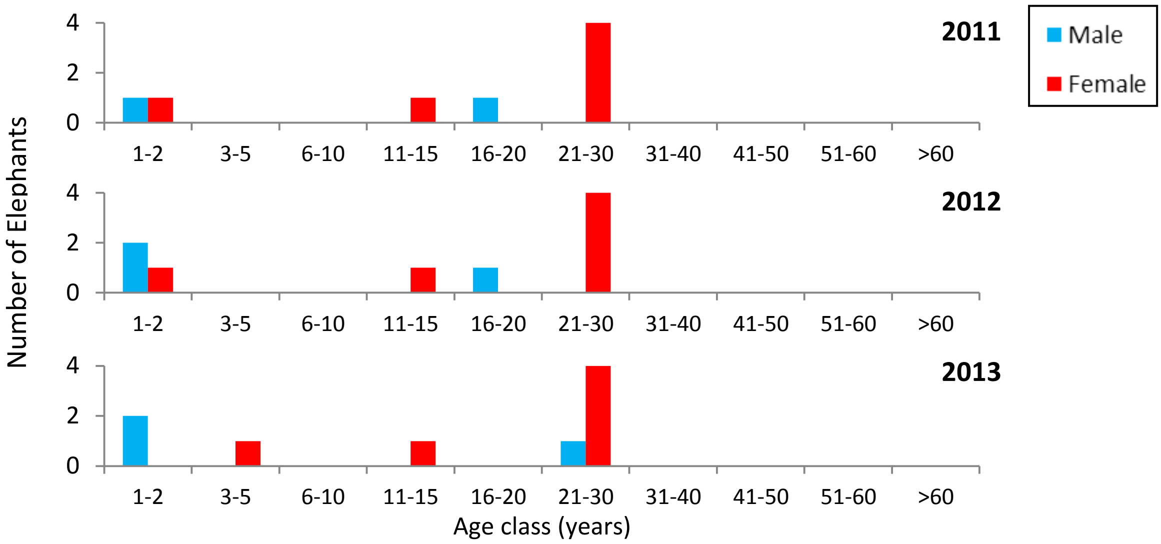


Figure 2.13 Composition of Whipsnade Zoo's Captive Asian Elephant Group. Compositions as of January 1st for each year in study period. Males included here after age of dispersal.

Access

At Whipsnade, the entire group were never mixed simultaneously due to compatibility issues between two of the adult females. However, the adult male was usually mixed with at least some other group members during the day (roughly six hours per day). A selection of the group (excluding the adult male) was taken on a daily walk outside their enclosures with keepers to grass or wooded areas around the zoo nearly every day. This selection was dictated by whether individuals got along, in addition to the number and experience of keepers available. When keeper numbers were low, or for females with a history of aggression to people (i.e. Mya), a further large grass paddock off-show from the public could be used for daily walks.

During inclement weather, the elephants spent most of their time within sand paddocks during the day. The adult male was not permitted access to the bull grass paddocks during his musth period (approximately three months in the winter) due to the stronger fencing around the sand paddocks than around the grass paddocks. Throughout the study period, elephants were kept indoors at night for over 18 hours, even on warmer nights. Subsequent to the study period, this has changed and females and calves are now locked outside 24-hours a day during the summer months. Since these changes a female was allowed to give birth amongst (part of) the group outside on the main grass paddock.

Free Contact Husbandry

Husbandry at Whipsnade for females and calves is FC (see above), although the adult male is trained in PC.

2.4.3 Captive African Elephant Study Site and Group Composition: Howletts Wild Animal Park

At the start of the study, The Aspinall Foundation's Howletts Wild Animal Park (WAP) had 16 African elephants. Relatedness, sex and ages are shown in Figure 2.14 for these 16 individuals and the two further calves in the study who were born later in 2011. Mchumba's twin who had died before the start of the study period, is also included here. Group compositions by age class, sex and study year are shown in Figure 2.15.

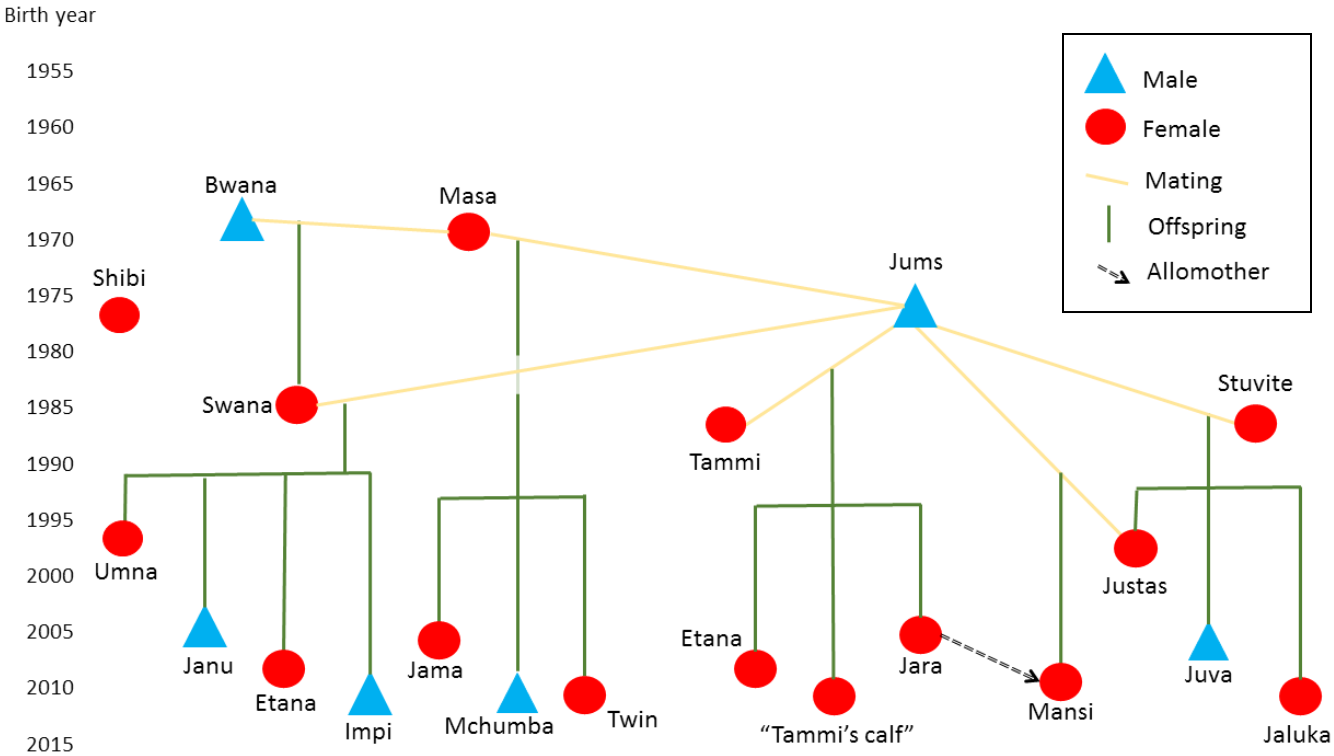


Figure 2.14 Howletts WAP African Elephant Family Tree (2011-2012). Bwana and Justas were not present during the study period but are represented here to show relatedness. Individuals are arranged vertically in relation to their year of birth.

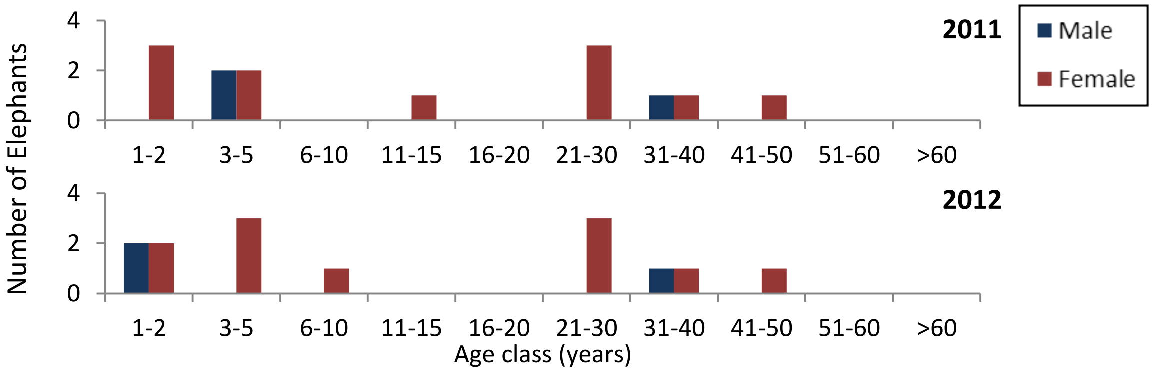


Figure 2.15 Composition of Howletts WAP's Captive Asian Elephant Group. Compositions as of January 1st for each year in study period. Males included here after age of dispersal.

The elephants had access to two large grass paddocks and two large sand paddocks, covering 30,000m^2, which could be connected or separated (Figure 2.11c). One of these sand paddocks also contains a 3.7m deep concrete pool (10m x 8m). Elephants were kept outdoors during summer months (when temperatures were above 8$^{\circ C}$ at night). At the time of the study, on colder nights (and during paddock cleaning) females with their calves were separated into four individual houses. Three of these four houses were divided further using gates, allowing trunk contact. A fifth house also held the single adult male. In winter months, elephants may have remained in these stall for 17-18 hours a day. Since data collection (2015), refrigerator flaps have been installed to the external doors on housing which now permits the keepers to give females and calves free access to houses and the adjacent sand paddocks even in colder months. This has allowed more opportunities for the females and calves to interact with each other and to choose who to sleep with by choosing which house to sleep in. For example, one orphaned calf (Jaluka) was noted to choose to spend her nights with the (unrelated) matriarch after this change in housing (N. Boyd, June 2015, pers. comm.).

Grass paddock boundary fences at Howletts are surrounded by further vegetation which provides opportunities for additional foraging (and can promote muscle use). See also Discussion. Photograph taken 17th May 2012.

Training

Howletts are mainly a limited contact facility where keepers have some level of physical contact across the barriers with elephants, particularly when hand rearing calves. Two of the elephants were also managed in PC: ongoing health treatment for one adult female and as preparation for the planned move of the adult male.

2.5 Captive Study Subjects

2.5.1 Captive Asian Study Calves

Developmental focal data were collected on six captive Asian and five captive African calves up to 18 months (calves in bold in Tables 2.3; 2.4). Data were collected from as close to birth as possible and were collected in the first month of life in all of these calves except for one, Mansi, an African calf who was nine months old when data collection commenced. Recorded births and deaths in captivity were accurate to the day. Some data were collected during the author’s internship at Chester, between November 2006 and July 2007. All other captive calves were studied between July 2010 and April 2014.

The 11 calves were analysed throughout as case studies. In addition, a further three calves died on their day of birth. All 14 of these calves are included for demographic analyses and in Tables 2.3 and 2.4.

In addition to the 14 core captive study calves, a further two Asian and two African calves were used in the analysis. Data were collected on these four calves in the 3-5 year age category (and one of the Asian calves was also studied at 13-18 and 19-24 months) since data were already being collected simultaneously on younger (core) calves at the same facilities. These four calves are also included in Tables 2.3 and 2.4.

Figures 2.16 to 2.19 show schematic timelines for the 11 case studies. All 11 calves were mother raised with the exception of African calves, ‘Tammi’s calf’ and Mansi (Figure 2.19). Mansi was the result of inbreeding between a female and her father, as was Asian calf Hari.

Table 2.3 Subject Information for all Captive Asian Elephant Calves and Juveniles at Study Sites. Case study calves in bold. Older calves sampled to 3.5yrs in italics. A.I=artificial insemination. D.o.b.=day of birth. Reported causes of calf death: [a]Elephant Endotheliotropic Herpesvirus (EEHV); [b]Stillborn/EEHV; [c]Mother killed the calf after birth. * No data. Parent origin: *w*=wild-born; *c*=captive-born; *Mn*=Myanmar; *Ml*=Malaysia; I=Indian; *I-T*=Indian and Thai descent; *T-SL*=Thai and Sri Lankan descent; *T-SL-u* =Sri Lankan, Thai descent and unknown descent; *ITu*=Indian, Thai and unknown descent; *u*=unknown.

House Name	EEP code	Sex	Birth order	Site	Sire & birth origin	Dam & birth origin	Month of birth	Age first studied (mo)	Final study month	Age last studied (mo)	Month of death
Raman	**CO6760**	**M**	**6**	**Chester Zoo**	**Upali c/T-SL**	**Thi Hi Way w/u**	**Nov 2006**	**1**	**July 2007**	**8**	**Oct 2009**[a]
Nayan	**C10343 / EEP 201000**	**M**	**2**	**Chester Zoo**	**Upali c/T-SL**	**Sithami c/*T-SL-u***	**July 2010**	**1**	**May 2012**	**22**	**July 2013**[a]
Jamilah	**C1174**	**F**	**7**	**Chester Zoo**	**Upali c/T-SL**	**Thi Hi Way w/u**	**Jan 2011**	**1**	**Jan 2013**	**25**	**July 2013**[a]
Hari	**C12763**	**M**	**1**	**Chester Zoo**	**Upali c/T-SL**	**Sundara c/*T-SL-u***	**Nov 2012**	**1**	**April 2014**	**18**	**Oct 2015**[a]
Bala	**C1310**	**F**	**3**	**Chester Zoo**	**Upali c/T-SL**	**Sithami c/*T-SL-u***	**Jan 2013**	**1**	**April 2014**	**16**	**Sept 2015**[a]
Sundara	CZ1333	F	1	Chester Zoo	Upali c/T-SL	Sithami c/*T-SL-u*	Mar 2004	32	Oct 2010	78	
Scott	**201110**	**M**	**3**	**Whipsnade Zoo**	**Emmett *c/u***	**Azizah *w/Ml***	**Oct 2011**	**1**	**April 2013**	**19**	
Gheta	200900	F	3	Whipsnade Zoo	Emmett *c/u*	Kaylee *w/Mn*	Jul 2009	28	April 2013	52	
Ned	201000	M	1	Whipsnade Zoo	Emmett *c/u*	Karishma *c/ITu*	Apr 2010	19	April 2013	36	
No name ('Woburn')	201201	F	1	Woburn Safari Park	A.I. (Raja *c/u*)	Damini *c/I*	Mar 2012	*Died on d.o.b	*	*	Mar 2012[c]
No name ('Twycross')	201202	F	1	Twycross Zoo	A.I. (Raja *c/u*)	Tara *c/ITu*	Mar 2012	*Died on d.o.b	*	*	Mar 2012[b]

2.5.1.1. Individual Life Histories: Chester (2006-2009)

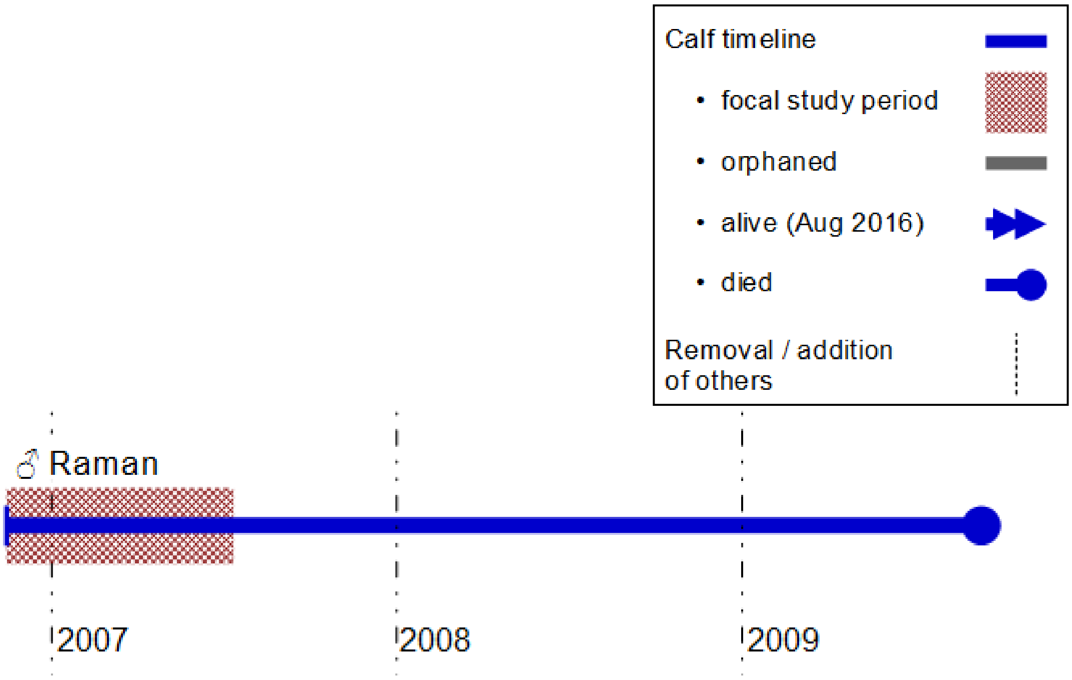


Figure 2.16 Timeline for Raman at Chester Zoo. Chart 2006–2009. No removal or additions from the group in Chester during study periods. Died EEHV.

2.5.1.2 Individual Life Histories: Chester (2010-2015)

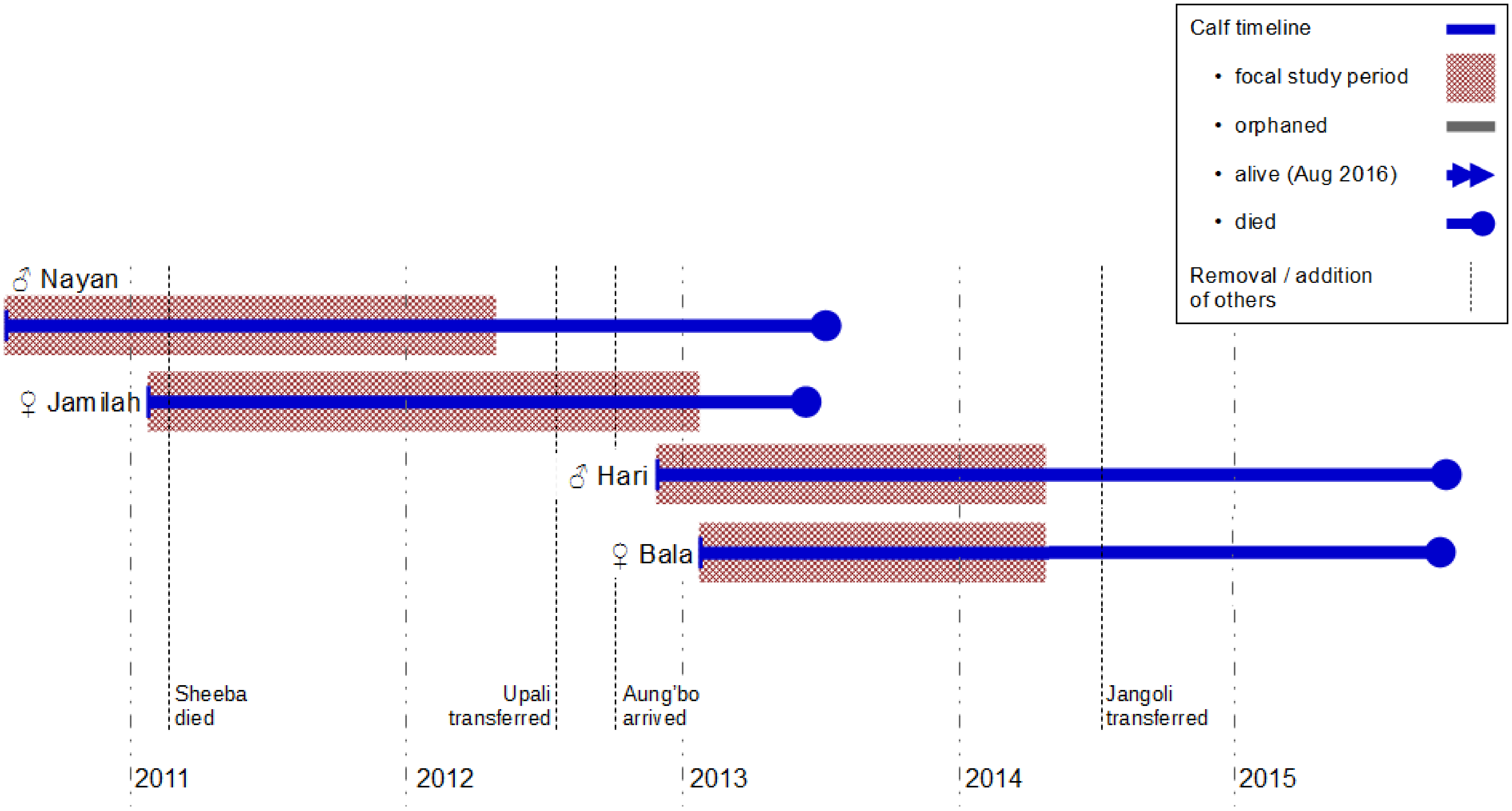


Figure 2.17 Timeline for Focal Calves at Chester Zoo. Chart 2011–2015; all four calves died EEHV. Removal and additions include transfers in and out of Chester as well as births and deaths.

2.5.1.3 Individual Life Histories: Whipsnade

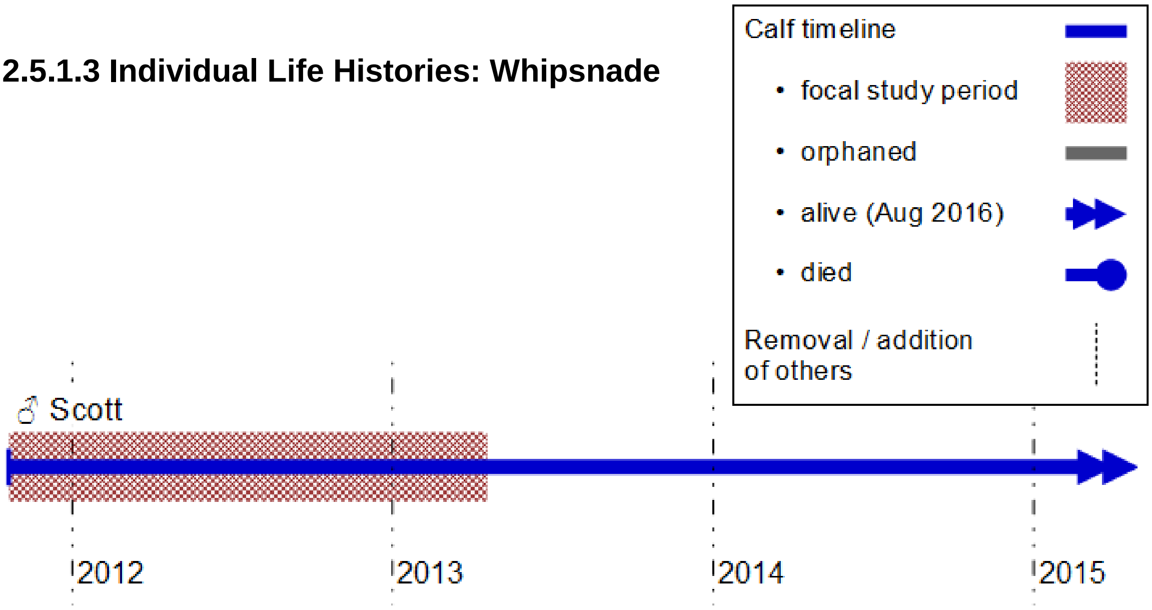


Figure 2.18 Timeline for Scott at Whipsnade Zoo. Chart 2012 – 2015; Scott still alive, July 2016. No removal or additions from the group at Whipsnade during the study period.

2.5.2 Captive African Study Calves

Table 2.4 Subject Information for all Captive African Elephant Calves and Juveniles at Howletts. Case study calves in bold. Older calves sampled to 3.5yrs in italics. [T]25min scan data days. * No data. Causes of calf death: [a]Rejected by mother; [b]Stillborn / air in lungs; [c]Colic and attacked by Janu. Parent origin: *w*=wild-born; *c*=captive-born; *Z*=Zimbabwe; *SA*=South Africa; *Sd*=South African descent; *T*=Tanzanian descent; *Z-T*=Zimbabwe & Tanzanian descent. N study days is also N days of 25min group scans.

House Name	EEP code	Sex	Birth order	Sire & birth origin	Dam & birth origin	Month of birth	Age first studied (mo)	Final study month	Age last studied (mo)	Age orphaned (months)	Month of death
Mansi	**20075**	**F**	**1**	**Jums *w/Z***	**Justa *c/Z-T***	**June 2010**	**9**	**Dec 2012**	**31**	**5**	
'Tammi's calf'	*****	**F**	**4**	**Jums *w/Z***	**Tammi *c/T***	**Jan 2011**	**1**	**Feb 2011**	**1**		**Feb 2011[a]**
Mchumba	**20078**	**M**	**5**	**Jums *w/Z***	**Masa *w/SA***	**Jan 2011**	**1**	**Oct 2012**	**21**		
Jaluka	**20081**	**F**	**3**	**Jums *w/Z***	**Stuvite *c/T***	**Feb 2011**	**1**	**Oct 2012**	**22**	**26**	
Impi	**20084**	**M**	**4**	**Jums *w/Z***	**Swana w/Sd**	**June 2011**	**2**	**Oct 2012**	**19**	**22**	
Etana	*	F	3	Jums *w/Z*	Swana w/Sd	Dec 2008	25	Oct 2012	46	68	
Uzuri	*	F	3	Jums *w/Z*	Tammi *c/T*	Feb 2008	35	Oct 2012	56		
Jama	20048	F	4	Jums *w/Z*	Masa *w/SA*	July 2006	55	Oct 2012	75		
Janu	20039	M	2	Jums *w/Z*	Swana w/Sd	July 2005	67	June 2011	70	N/A (separated at 71 mo)	
Juva	*	M	2	Jums *w/Z*	Stuvite *c/T*	Sept 2006	53	June 2011	56	N/A (separated at 57 mo)	Dec 2012[c]
Jara	20033	F	2	Jums *w/Z*	Tammi *c/T*	Apr 2005	71	Oct 2012	90		
'Mchumba's twin'	*	F	6	Jums *w/Z*	Masa *w/SA*	Jan 2011	*	*	*	N/A	Jan 2011[b]

Tammi, a multiparous female, rejected her fourth calf who then died at 31 days old. Primiparous Justas, Mansi's mother, initially rejected her calf, reaccepted her, and then died from colic when her calf was 16 weeks old (before the study period). Justa's calf was also the result of inbreeding with her father.

After the study period, Impi's mother, Swana, was euthanised (April 2nd 2013), following an attack from another adult female (Figure 2.19). Swana's injuries had left her unable to stand or get back up. Jaluka's mother, Stuvite, was also euthanised (10th April 2013) after collapsing, following treatment for a leg infection.

2.5.2.1 Individual Life Histories: Howletts

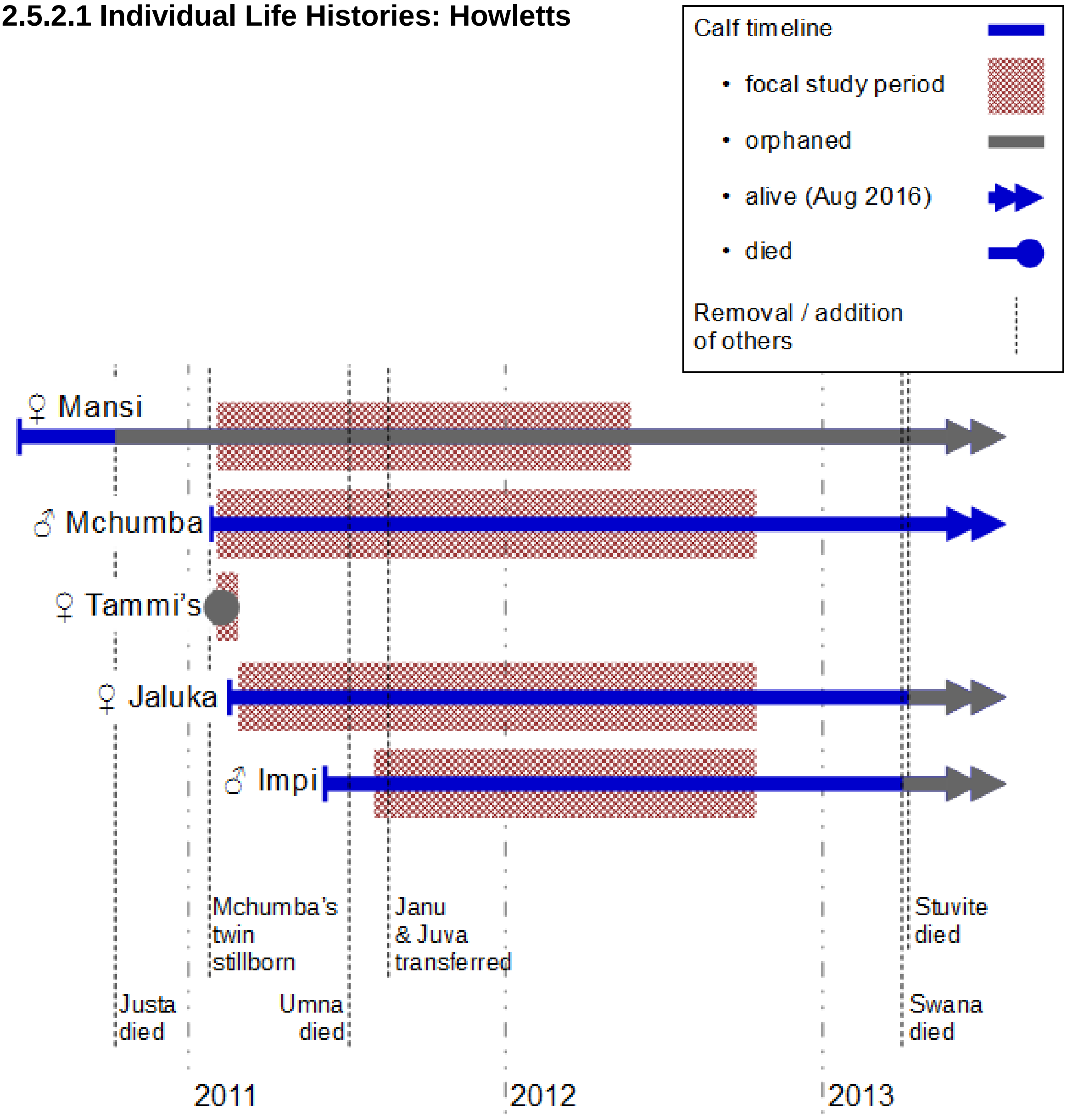


Figure 2.19 Timeline for Focal Calves at Howletts. Chart 2011–2013. To date (July 2016) four still alive, but three orphaned.

2.5.3 Summary of Group Size for Captive Study Sites

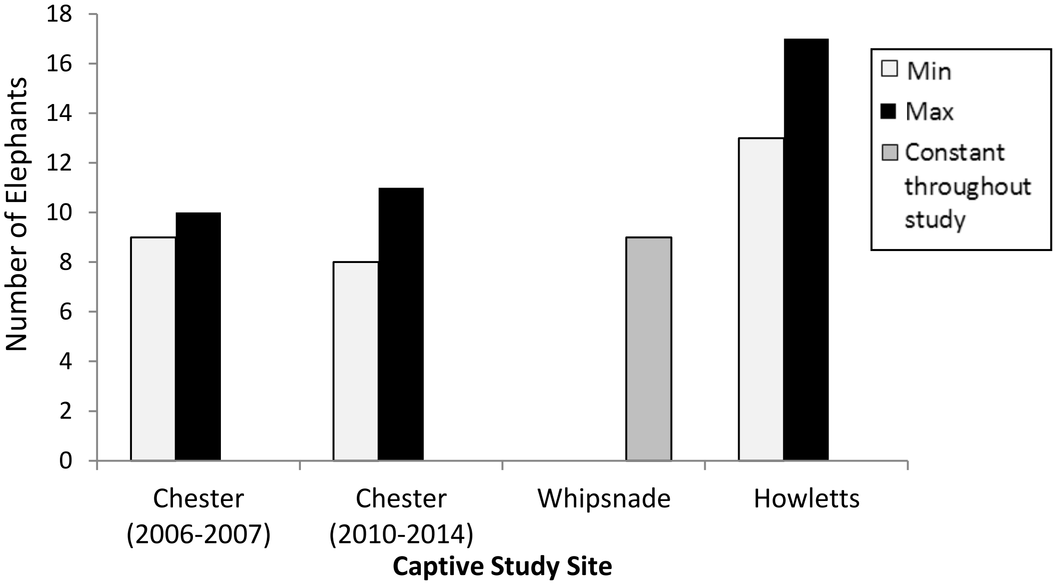


Figure 2.20 Captive Elephant Group Sizes throughout Study Period. Maximum and minimum elephant count at each facility. Fluctuations due to birth/deaths, transfers to/from other facilities. Each facility always held one adult male, except July-Sept 2013 at Chester before Aung-bo's arrival when Upali had been transferred out.

Figure 2.20 summarises the limited number of different social partners available in any period. In contrast, Amboseli elephants can recognise and interact with up to a thousand individuals (Moss, Croze & Lee, 2011). As stated earlier, group size will constrain or enable social interactions. Since captive animals cannot access novel individuals they can only make social partner choices on a daily basis from the same individuals, and then only when allowed to do so by keepers. Fission-fusion sociality, however, allows wild elephants to have active choice over their social partners.

Chapter 3: Methods

Female Asian elephant in Uda walawe, Sri Lanka. Photograph taken 1st July 2011.

This thesis covers an array of different topics addressing elephant calf development and some of their implications for welfare in captivity through comparisons of elephants in the wild and captivity. To investigate these topics, data were collected from a variety of sites namely, Uda Walawe National Park (Sri Lanka), Amboseli National Park (Kenya) and Chester Zoo, Howletts WAP and Whipsnade Zoo (all UK). Diurnal behaviour of Asian and African elephant calves aged from birth to five years (concentrating on the first two years), and that of their herd members (and any other associated elephants) was studied in both captive and wild environments.

In the wild, cross-sectional data were collected on Asian elephant calves in Uda Walawe National Park, Sri Lanka, from three years of observations by CEW. Over 100 calves (39 male, 56 female and 14 of unknown sex) were studied up to approximately five years of age using scan and focal sampling.

Calf behaviour was also investigated in Amboseli National Park, Kenya, from over two years of focal and scan observations on African elephant calves by PCL and CJM. These consisted 58 male and 72 female calves, totalling 130 calves up to five years old for focal samples.

Research in the UK was carried out by CEW with supplemental observations on one calf by RF on captive calves at three UK zoological institutes: Chester Zoo; Whipsnade Zoo; and Howletts WAP. Chester and Whipsnade breed Asian elephants, and Howletts breed African elephants. Within each facility, some relatedness, therefore, existed between some of the individuals (Figures 2.9; 2.12; 2.14). Longitudinal data were collected on 12 Asian (seven male, five female) and eight African (two male, six female) calves up to 3.5 years. Detailed individual data were collected on 14 of these 20 calves, up to 24 months.

All but two of the captive calves had normal rearing during the study period. Those two with abnormal rearing were African calves which had been orphaned or rejected during or prior to the study period.

The general methodology outlined below is applicable to each of the variety of study sites, with the precise set up and more detailed methods and analytical procedures outlined in the relevant Chapters.

3.1 Ethics and Research Permission

All observations were non-invasive, both in the wild and captivity and were made with full local research and ethical permissions. Ethics for the study were approved by the University of Stirling’s Psychology Ethics Committee. Permission for field research in Sri Lanka was granted by the Department of Wildlife Conservation. Research clearance was granted by Kenya National Parks (now Kenya Wildlife Service) and Office of the President, Republic of Kenya. A letter of support for the research project was provided by the British and Irish Association of Zoos and Aquarium (BIAZA) Research Committee. Permission was granted to study calves at NEZS Chester Zoo, ZSL Whipsnade Zoo and Howletts WAP. Permission was also granted at Twycross Zoo (although access was not required due to calf’s death) and research permission was denied at Woburn Safari Park.

3.2 Observational Methods

Ethogram

Activities and behaviour of calves and adults were initially defined using a behavioural ethogram developed in November 2006 (CEW & RF), predominantly starting with behaviours which were universal and easy to observe, e.g. walking, resting, lying etc. This version was later combined in October 2010 with Lee's 1982 ethogram (Lee, 1986) where most adult behaviour codes have been used since 1972 and validated across more than ten observers (Moss et al., 2011). My ethogram was further revised in October 2011.

PCL and CEW worked with F. Wemelsfelder to assess activity and affect of wild and captive African elephants (in 2009 and 2010). Wemelsfelder's (ND) consensus plots of activity and affect codes between observers (for example see Wemelsfelder & Mullan, 2014) found 60% ($p<0.001$) consensus on two major dimensions of behaviour, between 12 observers (four observers were experienced with elephants, and eight were naïve to elephants).

Gross categorisation of actions is easy in a five tonne animal. Interpretation of context and outcomes are more subjective. That completely subjective interpretations of elephant affect are consistent, even for individuals who have never seen a wild elephant, suggests a reasonable/non-trivial level of concordance.

For ethogram and definitions, see Appendix C Table C1. Although being 'out of sight' was coded for, this was not included in the analyses. All analyses were done on time in sight.

Behavioural codes were mutually exclusive, and activities were also combined into general categories as defined in the ethogram. Feeding while moving was combined with feeding while standing into 'Feeding'. All other locomotion was combined into 'Moving'. 'Resting included resting standing, sleeping, and resting lying. 'Suckling interactions' were all contact with the mother's nipples, while interactions with others were coded as 'Non-play social interactions'. Unusual behaviour (e.g. tool use, keeper interaction, calf tantrum) were coded as 'Other' in these analyses and excluded from statistical testing as they were too rare to be meaningful.

Categories of behaviour (e.g. Dunbar, 1992) analysed in this thesis were (a) maintenance activities: feeding (foraging while standing or while walking), resting (lying or standing, sleeping or awake), moving (more than three steps). (b) Interactions with mother or others: sucking, touching mouth or body of another (greeting), play (separated into social and non-social play), and aggression (pokes, shoves, flee, avoid). And finally (c), proximity to mother and others; mother activity and nearest neighbour activity were recorded at the same time as calf activity. Distance to mother and others was measured in two metre units as this was the approximate length of an Asian adult female. This allowed observers to estimate distances between elephants more accurately from different vantage points. Distances were classed as: body-contact; <2m (within touching distance); 2-4m (outwith touching distance); 4-6m; … 18-20m; >20m. In Uda Walawe, measurements of >10m (the distance at which it takes mothers time to return to the calf if it is at risk) were condensed into this one category. These standardised distance measures between calves and mothers or others were condensed into three categories (close, mid and far) to allow comparison across field sites and captive sites (Table 3.1).

Table 3.1 Proximity Distance Categories. bc=body contact. Approx. length of captive adult female Asian elephant ~2m. *Lee & Moss, 2011.

Distance Categories	Unit	Close	Mid	Far
Categories used in analysis	Metres	<2 m	2-5 m	>5 m
Captivity and Uda Walawe	Elephant body length	bc, <1	1, 2	>3
Amboseli*	Metres	0m, 1-2m	2-5 m	>5 m

3.3 Behavioural Sampling Methods

General behavioural sampling methods across study sites will be outlined here first, and then further details shall be presented below when methods differ between wild and captive sampling.

Behavioural data on captive and wild, Asian and African elephant calves were obtained through focal calf and scan samples using both opportunistic encounters and searches for priority calves. Focal groups in captivity were also sampled using scans (see Altmann, 1974). Wild calf observations were made as concordant as possible between species given constraints on visibility and group sizes.

Focal infant data on individually recognised calves were collected using the ethogram (see Appendix C, Table C1) developed and used for both continuous recording and scan sampling of the activities and interactions of calves. Continuous records of all-occurrences of behaviour and interactions, including distance to the calf's mother and nearest neighbour, for an individual calf were made for periods of 10min for wild Asian and all captive calves, and 60min for wild African calves. Locations were also recorded in captivity. If focal samples were repeated on the same calf, a period of at least 10min passed between the end of one focal and the beginning of the next. When more than one focal calf was present, focals were collected on calves in rotation as much as visibility allowed with the aim of each calf having a spread of observations throughout the day. Focal collection was consistently spread throughout the day in captivity but opportunistic in the wild. All scan and focal sample observations were made during daylight hours. To ensure this spread in captivity, a tally recorded the hour of day in which focals were made for each site-visit. For wild African calves, no repeat observations of the same calf were made on the same day.

During focals, instantaneous scan records of activities and distances were taken at 5min intervals, representing three records for wild Asian and captive calves per focal, and 13 records for wild African calves per focal. If the calf was out of sight, the total N of scans was reduced.

Each 5min calf scan (from focals in all contexts) included calf activity, distance to mother, mother's activity, and the activity, distance and ID (where possible) of the nearest non-mother neighbour. All scan samples were of mutually exclusive activities. Focal samples were also used to relate concurrent activities between calves and mothers within each observation.

Due to the number of elephants in the study population in Uda Walawe and time taken to ID them, nearest neighbour records were noted as sex and age classifications (newborn, calf, infant, juvenile, sub-adult and adult). Whereas in Amboseli and captivity, the nearest neighbours could be identified as individuals.

Wild Calf Behavioural Sampling

The behaviour of elephants engaged in normal daily activities was observed from a vehicle in both wild field sites. "Day" was defined in the wild as 6am-6pm which coincided with daylight hours (and the park's opening hours in UW for safari and research vehicles). Since wild elephants are active over a 24hr period (Gravett et al., 2017), daylight sampling is likely to capture most activities and be generally representative. The elephants were habituated to research and tourist vehicles. The road network was used in Uda Walawe, and although permission was granted, the vehicle was only occasionally used off-road to prevent damage to the park's vegetation and wildlife, for example, ground-nesting birds. Due to the increased vegetation density in later field seasons, off-road driving in Uda

Walawe became a rarity as the study progressed. However, in Amboseli, the vehicle was driven directly amongst the elephants.

A video camera and note-taking were used when studying wild elephants in Uda Walawe as this allowed the observer: to be as quiet as possible around the wild elephants; to minimise disturbance; to allow other researchers to make vocal recordings of the groups for other studies; and to return to the tape to confirm the identity of nearest neighbours and mothers since large groups may interact and quickly move on. The UWERP's elephant ID files could later be referred to, to optimise the observer's ability to focus on the calf for the full 10min focal. These video records, along with photographs, also aided the calf ID files to be updated for demography databases (see de Silva et al., 2013).

The sampling schedules in both Uda Walawe and Amboseli were both necessarily flexible and highly opportunistic, taking advantage of when calves could be contacted. However, focals of the same calf were separated by at least one focal duration.

Group activity was recorded at the beginning of each calf focal in Uda Walawe and in Amboseli for initial sightings of a group (see Appendix C, Table C2).

In Uda Walawe, the project aimed to collect cross-sectional data on calves under 24 months, but older calves were also studied (Table 3.2). Data were collected by CEW across 65 field days in the dry season months of May-July, in 2011, 2012 and 2013, to take advantage of the shorter grasses, for optimal visibility. The park was entered on Mondays, Wednesdays and Fridays, avoiding any weekends or local holidays when more tourist jeeps were present. MSc student, IvB (I. van Braeckel), also recorded five videos (totalling approx. 50min) on a visit to Uda Walawe during training from CEW (and coded videos of wild Asian calf play in collaboration for his MSc project). The 101 wild Asian focal calves (see Table B1.3, Appendix B) were studied for a mean of 0.64 field-days (65/101; ST Dev ±0.26).

Table 3.2 Number of Observation Scans for Wild Asian Calves, by Sex and Age Category. Scans at 5min intervals from 10min focal observations. Unknown sex and ages excluded from analyses. For N calves, see Table 2.1.

	Age category					
Calf Sex	**1-6mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	87	72	127	63	121	**470**
Female	270	96	150	65	189	**770**
Unknown	20	6	3	6	27	**62**
Overall	377	174	280	134	337	**1302**

In the Amboseli focal samples, all calves were unweaned until the birth of their subsequent sibling and all but two five year olds were still attempting to suck. Data on 130 calves were collected by PCL and CJM across seasons, from 1980-1984 (Table 3.3)

Table 3.3 Number of Observation Scans for Wild African Calves, by Sex and Age Category. Scans at 5min intervals from 60min focal observations. For N calves, see Table 2.2.

	Age category					
Calf Sex	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	355	311	274	125	551	**1606**
Female	481	269	196	171	748	**1852**
Overall	836	580	470	296	1299	**3458**

Captive Calf Behavioural Sampling

In captivity, “day” was defined as the period when keepers (usually 8am to 6pm) and public, to a lesser extent (usually 10am to 4pm in winter, 6pm in summer), were present. Observations were made from a variety of locations to allow optimal visibility, including walking or stationed in public viewing areas. At Chester, observations were mainly made from the research huts or camera system control room (especially during adverse weather conditions or during peak tourist days) although public viewing areas were also used. Only public viewing areas were used for data collection at Whipsnade.

At Howletts, due to the large paddocks, data collection often took place from areas inaccessible to the public. The observer moved approximately every hour to different viewing points to observe focal calves previously not visible. For the observer, some viewing points were more than 10min walk away; in which time the elephants themselves had often moved!

Continuous focal studies were recorded onto a digital Dictaphone as captive animals could be identified relatively easily. This method allowed the observer to watch the calf constantly as the observer could walk around the enclosures in all-weather to gain the best visibility.

In captivity, simultaneously with calf focal data, instantaneous 25min group-scans were collected from Aug 2010 onwards of every visible group member. It was not feasible to collect these 25min group-scans for wild Asian calves due to poor visibility and the time taken to accurately ID wild individuals. These group-scans were spread evenly throughout the day.

Records of nearest neighbours in captivity included individuals who were ‘geographically’ nearest but actually separated (by bars or doors), and its separation was denoted with code [ ]. These animals could possibly see, as well as hear and smell each other, but may not have been able to be physically closer.

For captive Asian calves up to five years old, 301hrs of calf scans from 10min focals were collected (196.9hrs from four males and 104.9hrs from two females; see Table 3.4). Group scans at 25min intervals throughout the day were collected on 177 days (40 days at Whipsnade; 137 days at Chester), and an additional 204 group scans at 5min intervals across 30min periods were collected on an additional 127 days (N=8 calves; Table 3.4).

Across five captive African elephant calves, up to five years old, more than 168hrs of calf focal data (10min durations) were collected (94.3hrs from two males and 74.8hrs from three females; see Table 3.5). Group scans at 25min intervals across the day were collected on 69 days at Howletts.

Table 3.4 Number of Observation Scans for Captive Asian Calves by Age Category. Scans at 5min intervals from 10min focal observations, and 25min group scans. See Appendix B, Tables B3.2 and B3.3, for the breakdown of these scans into 5min and 25min scan per calf per age category.

	Age category					
Calf ID	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Raman ♂	318	56	0	0	0	**374**
Nayan ♂	1328	912	543	348	559	**3690**
Jamilah ♀	1110	511	351	410	284	**2666**
Hari ♂	750	274	263	0	0	**1287**
Bala ♀	603	277	262	0	0	**1142**
Scott ♂	586	264	228	0	0	**1078**
Gheta ♀	0	0	0	0	414	**414**
Ned ♂	0	0	61	164	171	**396**
Total	4695	2294	1708	922	1428	**11047**

Table 3.5 Number of Observation Scans for Captive African Calves by Age Category. Scans at 5min intervals from 10min focal observations, and 25min group scans. See Appendix B, Tables B4.2 and B4.3, for the breakdown of these scans into 5min and 25min scan per calf per age category.

	Age category					
Calf ID	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Mchumba ♂	684	410	263	224	0	**1581**
Mansi ♀	0	565	430	332	147	**1474**
Jaluka ♀	686	185	281	181	0	**1333**
Tammi’s ♀	128	0	0	0	0	**128**
Impi ♂	412	191	224	67	0	**894**
Etana ♀	0	0	0	0	756	**756**
Uzuri ♀	0	0	0	0	525	**525**
Total	1910	1351	1198	804	1428	**6691**

Data Coding: Inter-observer Reliability on Behaviour Samples

Masters students, DDM (D. D'Mello) and IvB, coded 10hrs 33min (from 71 focals) and 4hrs 44min (from 34 focals) of wild Asian elephant focals respectively, from 74hrs of video.

The ethogram used in this thesis has now been used by the EWG, while PCL's 1982 ethogram (Lee, 1986; which formed the basis for this thesis's ethogram) has been used by the AERP for the last 36yrs (and validated across more than ten observers; Moss et al., 2011).

Inter-observer reliability (IOR) was calculated for DDM, IvB, CEW and PCL using a total of 2hrs of wild Asian elephant footage. For each pair of observers, focal samples were made from two videos (each ~15min) and IOR scores were then calculated for ≤5sec accuracy using a 30sec point system. Rarely occurring behaviours may have resulted in biases between observers if the rare behaviours were not present in the 2hrs of samples and thus missed from analysis for reliability. However, all behaviours compared during IOR were those analysed in subsequent chapters. While this method did not take into account the number of agreements expected on a chance basis for each behaviour separately, the chance that pairs of observers would choose the same one of the ten behaviours (feed, rest, move, comfort, social interaction, lone play, social play, environmental exploration, abnormal and out of sight) at each 30sec interval was 0.123 (1/(9*9)). IOR scores between observers were calculated as agreements divided by agreements plus disagreements (A/(A+D); Caro et al., 1979). DDM Vs IvB: 0.719, n=56 30sec points; CEW Vs IvB: 0.845, n=45; CEW Vs DDM: 0.859, n=65; PCL Vs DDM: 0.786, n=31; CEW Vs PCL: 0.893, n=31. Cross tabulation of inconsistent codes for individual behaviours or interactions were used to detect where any 'confusions' lay; DDM and IvB often recorded calves 'out of sight' where CEW and PCL recorded a behaviour. CEW and PCL had more experience and confidence detecting behaviours in poorer visibilities. However, this might have resulted in observations by DDM and IvB being biased in that they might have missed behaviours that were harder to see or those carried out in poorer visibility, for example, eating grasses when the calf itself was amongst and obscured by long grasses. PCL was more conservative than CEW in definitions of play compared with 'exploration'.

Reliability for wild African elephants was based on focal samples where codes and behaviours were harmonised between CJM and PCL over five months.

In captivity, CEW collected behavioural data from 2010-2014. In 2006/7, both CEW and RF collected observations (during their internships) on Asian elephants at Chester. RF collected 44.5hrs of group scan observations (over 87 separate days) and acceptable inter-observer reliability was tested at the time (>0.80, 12 calf focal observations; approximately 2hrs; pers comm., Sonya P. Hill, January 2007).

Behavioural data on captive African elephants were only collected by CEW. Inter-observer reliability was therefore not analysed for this context, although CEW's reliability as an observer of behaviours analysed in subsequent chapters was calculated for both wild and captive Asian elephants.

For the core calves in captive settings, focal-sampling was spread over the day, for five days per month for the first three months of life. From three to 18 months of age, each calf was then studied for five days per quarter. If another core focal calf under the age of 18 months old was also present at the same institute, all calves under 24 months old were studied in the five day study period at that facility (or six day period at Howletts). At Howletts a sixth study day was required due to the larger paddocks when four focal-calves were present in order to reach the aim of 25 focals per calf per visit. Since the four calves were often only visible from different areas of the park, focals were taken in rotation of the visible calves. Movement and observer location was highly opportunistic, however, to limit the number of study days needed per visit to six days. Data collection occurred on any day of the week.

3.4 Analysis

Separate observations were binned together for each calf in each month of observation. The percent of time spent in different activities was calculated for each individual calf and its mother from the 5min scans that were made on calves and mothers during focal samples. Calf activity budgets were taken from both the scans at 5min (from focals) and, in captivity only, from the 25min scans from group-scans to allow the inclusion of data from four additional captive calves up to the age of five years (Table 3.6); while only 5min scan data were analysed for mother activities (Table 3.7). The results of analyses are reported as mean percentage time and 95% confidence intervals. Time out of sight was excluded from all calculations. For correlation analysis, significance was set as a function of the number of multiple tests on the same set of data.

Both of the captive African calves who were not mother-raised (Mansi and Tammi's calf) remained in the dataset for the ages at which they were sampled (see Table 2.4).

Table 3.6 Number of Calf Behaviour Observation by Context, Sex and Age Category. Data were binned together per month for analyses and calculated from scans at 5min intervals from focal observations and 25min group-scan observations (in captivity). Calves were repeatedly sampled between ages and therefore may appear in more than one age category.

		Age category (N calves)					
Calf Sex	**Context**	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	**Asian wild**	63 (11)	62 (7)	96 (14)	56 (6)	99 (19)	376 (39)
	African wild	355 (22)	311 (20)	274 (18)	125 (9)	551 (25)	1616 (52)
	Asian captive	2982 (4)	1506 (4)	1095 (4)	512 (2)	730 (2)	6825 (5)
	African captive	1096 (2)	601 (2)	487 (2)	291 (2)	0	2475 (2)
Female	**Asian wild**	212 (25)	91 (12)	119 (19)	29 (7)	190 (24)	641 (56)
	African wild	481 (19)	269 (18)	196 (13)	171 (14)	748 (38)	1865 (69)
	Asian captive	1713 (2)	788 (2)	613 (2)	410 (1)	698 (2)	4222 (3)
	African captive	814 (2)	750 (2)	711 (2)	513 (2)	1428 (3)	4216 (5)

Table 3.7 Number of Mother Behaviour Observations by Context, Calf Sex and Calf Age Category. Data were binned together per month for analyses and calculated from scans at 5min intervals from focal observations. Most captive and some wild mothers may appear with calves in more than one age category. They may also have more than one calf and appear for both sexes of calves if so.

		Age category (N mothers)					
Calf Sex	**Context**	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	**Asian wild**	58 (11)	59 (7)	86 (13)	54 (6)	90 (18)	347 (37)
	African wild	355 (22)	311 (20)	274 (18)	125 (9)	551 (23)	1616 (52)
	Asian captive	1332 (4)	646 (3)	484 (3)	133 (1)	0	2595 (4)
	African captive	449 (2)	220 (2)	272 (2)	204 (2)	0	1145 (2)
Female	**Asian wild**	211 (25)	89 (11)	110 (19)	29 (7)	179 (23)	618 (56)
	African wild	481 (19)	269 (18)	196 (13)	171 (14)	748 (38)	1865 (68)
	Asian captive	727 (2)	360 (2)	279 (2)	146 (1)	0	1512 (2)
	African captive	383 (2)	330 (2)	337 (2)	283 (2)	68 (1)	1401 (3)

Statistical Methods

Statistical analyses were conducted in IBM SPSS v.21. Data were assessed for normal distribution by histogram visualisations and tests for normality (using skew /SE skew <3; Zar, 1999). Data were non-normal, and typically could not be normalised by log or square root transformations. Generalised Linear Mixed Models (GLMM) were therefore used as they are robust to violations of normality and enable the examination of repeated data lacking a repeat measures design (Hawkins, 2015).

General Linear Mixed Model

Calf and mother activities, as well as proximities to mothers, were examined for differences by age, sex and context (Tables 3.6; 3.7; for mother proximities see Chapter Five, Table 5.1). I carried out log normal with logit link non-parametric GLMMs (SPSS v21) on these activities and proximities, expressed as the percentage of time in each activity, with calf ID as the random factor to account for repeated samples on the same calf of different ages. GLMM analysis is presented throughout on the basis of all the factors that went into the model where the dependent variable was the percentage of time in activity or percentage of time in proximity and the independent factors were age, sex, and context.

These models were designed to explore the differences between the captive and wild species, as well as between the two wild sets of data. GLMMs were run using variance components with Satterthwaite method and robust estimates of covariance. All comparisons were pairwise.

Initially, a maximal model with all potential explanatory factors, including random effects and second-order interactions, was fitted. Full models were simplified by removing terms sequentially starting from the least influential (highest P value or parameter value closest to zero). If removing this term caused a decrease in the explanatory power of the model (using the overall model fit F value), the term was reinstated. Nonsignificant interaction terms were removed first, followed by fixed effects. Each dropped term was then added back into the final minimal model to check that significant terms had not been wrongly excluded. I present the overall model fit (F value and significance), and the parameter values (coefficient β) with 95% confidence intervals for significant effects.

Probabilities were 2-tailed, and the significance level was set at 0.05 for GLMM. Pairwise comparisons for significant main effect were carried out for sex, context (captive, wild, by species, N=4) and age-categories (from birth to four years, N=5). When sample sizes were very small and skew was extreme, pairwise comparisons were limited to context.

While GLMM analysis was robust to violations of normality, results should still be treated with caution due to small N of calves in captive samples. I present GLMM analysis on the basis of all the factors that went into the model whilst all other charts are percentages of time.

Spearman's Correlation

Other tests explored associations between calf activities and examined the relationship between calf and mother activity synchrony. Spearman's correlation was used for these comparisons and significance values were corrected for multiple comparisons. Full details are in the relevant Chapters.

For case studies and proximity to nearest non-mother neighbour, descriptive statistics were used.

Constraints on Data

The data presented here are constrained by factors including visitor effects, inconsistencies in calf visibility, seasonal variations in the wild and the aforementioned small sample sizes in captivity. Further discussions of data limitations are presented in Chapters Four (Section 4.5) and Seven (Section 7.5). Due to the limitations of this research, analyses on captive calves should be treated with caution and looked at as individual patterns. Possible individual contribution to overall pattern of context, age and sex effects in the data is why captive calf data are presented first as means (95%CI) and then by individuals, as case studies. For individual data, binomial 95%CI are also shown.

Chapter 4: Activity Budgets

Wild Asian elephant groups engaged in a variety of activities, including play, by the reservoir in Uda Walawe, Sri Lanka. Photograph taken 11th July 2011.

4.1 Abstract

The aim of this Chapter was to relate the diurnal activity patterns of elephant calves and their mothers to normal processes of development in the wild and captivity. Normative maintenance activities (independent feeding, resting, moving) were determined for captive ($\text{Asian}_{N=8}$; $\text{African}_{N=7}$) and wild calves ($\text{Asian}_{N=101}$; $\text{African}_{N=130}$) and mothers (captive $\text{Asian}_{N=4}$; captive $\text{African}_{N=4}$; wild $\text{Asian}_{N=90}$; wild $\text{African}_{N=105}$) over the calves' first five years of life (concentrating on the first two years) as a measure of the energy and time costs an individual experiences in its physical and social environment.

Up to two years old, wild calves spent around 70-80% of their time feeding, resting and moving, whilst captive calves spent around 60% of their time. No sex differences were found for feeding, resting or moving.

Wild Asian calves spent significantly more time feeding than did calves in other contexts (p=0.002). Feeding increased consistently with age from 1-6 months to 3-5 years across contexts (p<0.001). For calves over 18 months, in all contexts, approx. 60% of time was spent feeding.

Resting occupied ~10% of time for captive calves and wild Asian calves, but showed strong declines with age for wild African calves (*p*<0.001). Captive Asian calves rested significantly less than all other contexts (*p*=0.002), while in pairwise comparisons wild African calves rested significantly more than other contexts (*p*<0.001). Across contexts, time spent resting decreased with age for calves from 1-6 months to 3-5 years (*p*<0.001).

Moving represented ~20% of time and varied little with context. However, time spent moving decreased with age across contexts for calves from 1-6 months to 3-5 years (*p*=0.006).

As activities are constrained by available time, correlations between different calf activities were investigated. Independent feeding was negatively correlated with resting, moving and LEGO-play (total play) in all contexts and for both sexes (except for feed and rest for captive African females; feed and move for female wild African and captive Asian calves; feed and LEGO-play for male wild African calves). Feeding was also negatively correlated with suckling interactions for both sexes and species in captive calves.

Normative diurnal maintenance activities were charted for four African and four Asian mothers in captivity and 89 wild Asian and 105 wild African elephant mother-calf pairs over the calves' first two years of life. Wild mothers of both species spent >70% of the day feeding and ~10% resting and moving, irrespective of calf age. For these activities, no overall significant differences were found for sex or age of calf although feeding and resting differed with context (*p*<0.001, *p*<0.002, respectively). In pairwise comparisons wild Asian mothers engaged in feeding significantly more than all other contexts and rested significantly less. Wild mothers fed at higher rates than did captive mothers of either species.

Stereotypies (present in non-calves) were briefly examined in captive elephants, as these are outcomes variables representing a history of compromised development. However, stereotypies showed no changes in frequency by season (warm or cold), or in relation to births, deaths or removals.

4.2 Introduction

This Chapter focuses on three main maintenance activities of independent feeding, resting, and moving as these make up most of a calf's diurnal activity budget in their first two years of life (range 57.2-84.4% across contexts) (Figure 4.1). An understanding of both the natural history and biology of elephants is crucial for managing captive populations and for breeding programmes (Osborn, 2002).

Maintenance activities represent the energy and time costs of an individual coping with its physical and social environment. These time budgets are adjusted to compensate for the cost of the various activities (Dawkins, 1990; Muller-Schwarze, Stagge & Muller-Schwarze, 1982). In observational studies, the energetic costs can only be inferred, while the trade-off between different activities over a day can be used to demonstrate which activities are prioritised and under which conditions (Dunbar, 1992). Both mother and calf activities shape their success and strategies for coping with captivity. An animal's individual biological rhythm is linked to its social status, nutritional condition and stress condition (Boyd, 1988; Kaczensky et al., 2006; Pagon et al., 2013; Scheibe, Berger, Langbein, Streich & Eichhorn, 1999). Studying activity budgets of captive and wild animals can, therefore, offer key information about the wellbeing and adaptation status of these captive individuals in comparison to their wild counterparts (Boyd & Bandi, 2002).

As discussed in detail in Chapter One, activities and their time budget help identify possible impacts of welfare. Activities – including maintenance activities, social interactions and play – were all studied in the wild as they provide us with a reference point to explore possibly restricted behavioural repertoires or abnormal time budgets for age-matched individuals in captivity. Abnormal behaviours can be described as "*those that occur in captivity but not in natural settings*" (qualitative) or "*those that occur more or less often in captivity than in nature*" (quantitative) (Erwin & Deni, 1979, in Jennings et al., 2009, p. 238). It is important to remember that "*good welfare is not about mimicking all aspects of natural life"*, and that while the performance of particular natural activities may be of significance, "*others may be relinquished harmlessly when human provisioning and protection renders them obsolete*" (Mason & Veasey, 2010, p. 238; Veasey et al., 1996). Conversely, increases in the amount of time spent in, or increases in the intensity of, certain activities may suggest fundamental problems. For example, self-directed behaviours in primates (e.g. grooming, scratching; as well as self-directed behaviours in humans; both characterised by social tension) have been validated as behavioural measures of stress as they can be alleviated by administration of anxiolytic drugs (Troisi, 2012). Difficulties therefore lie in defining these levels – of either intensity or of time spent in an activity – at which particular deviation from these 'normal' levels should be of concern (Jennings et al., 2009).

Although a subjective element remains in the classification of types of behaviour as indicative of either good or poor welfare, Jennings et al. (2009) discuss some of the behaviours which may indicate poor welfare in various primate species (including macaques (*Macaca* species), marmosets (*Callithrix* species), and tamarins (*Saguinus* species)). Several of these behaviours may also be indicators of poor welfare in captive elephants. These behaviours include: a restricted behavioural repertoire (e.g. cessation of foraging or locomotion), an abnormal time budget (e.g. decreased activity), inappropriate social behaviour (e.g. increased aggression to group members), and other abnormal behavioural patterns (e.g. stereotypies) (Jennings et al., 2009).

For some behaviours indicative of poor welfare – such as stereotypies or self-directed behaviours in non-human primates – difficulty exists in ascribing a direct cause. These behaviours also lack temporal or stimulus specificity (Descovich et al., 2017; Mason, 2006). However, behavioural measures such as activity have value as immediate, non-invasive indicators of welfare states (Bethell, 2015; Descovich et al., 2017; Mason & Latham, 2004).

Activity time budgets vary greatly between sites, seasons and time of day for wild Asian and wild African elephants and this means there is no single ‘correct’ time budget, but instead a wide range of normative time budgets in the wild. This must inform our interpretation of any results that arise from comparing captive elephant time budgets with those of baselines from the wild. Veasey et al. (1996) warn of technical criticism using wild versus captive comparisons which can “*arise when one considers the difficulty of constructing accurate and unbiased time budgets for wild animals*” (p. 13.) This study would therefore be unable to detect small deviations between activity budgets in captive and wild elephants, although gross changes would be both apparent and informative.

Feeding will be discussed here as an example of the variations in time allocated to different activities across both seasons (Lindsay, 2011; Mohapatra, Patra & Paramanik, 2013; see Table 4.1 below) and 24-hour periods (Baskaran, Balasubramanian, Swaminathan & Desai, 2010; Lindsey, 2011; Shannon, Page, Mackey, Duffy & Slowtow, 2008; see Tables 4.1 & 4.2 below). Adult wild African elephants have been shown to spend two-thirds of their daytime activity budget feeding: females spend a mean time of 66% and males in male groups spend 67% of time (Lindsay, 2011; see Table 4.1 below). However, this rate in feeding for males drops to 47% when males are with female-calf groups (Lindsay, 2011), presumably as the priority of other activities changes, e.g. mating interactions and checking the oestrous status of females.

Table 4.1 Summary of Studies - Time Spent Feeding in Elephants. *overall pattern of daytime activity was similar in drought year 1983-1984, although more time spent feeding overall. ^“*As with the other years, there was a trend for decreased feeding during the rains, with increased feeding toward the late dry season*” (Lindsay, 2011, p. 56). $^{\#}$reproductively active.

Author	Species	N observations	N / Age / Sex of individuals	Context	Time spent Feeding	Group composition	Time of day	Period of study	Location
Lindsay, 2011	*L. africana*	3384 scans	79 Adult females (>15 yr)$^{\#}$	wild	Yearly mean 66% (69% early, to 48% late wet season; increasing to 79% by late dry season)*	Female-calf groups	Daylight hrs	1982-1983 1yr (high rainfall ‘good’ yr) across seasons	Amboseli NP, Kenya
Lindsay, 2011	*L. africana*	1027 scans	70 Adult males	wild	Yearly mean 67% (70% early to 56% late wet season, increasing to 75% by late dry season)*	Adult males associating with male-only groups	Daylight hrs	1982-1983 1yr (high rainfall ‘good’ yr) across seasons	Amboseli NP, Kenya
Lindsay, 2011	*L. africana*	1198 scans	70 Adult males	wild	Yearly mean 47% (~42% from early to late wet season, increasing to 54% by late dry season)*	Adult males associating with female-calf groups	Daylight hrs	1982-1983 1yr (high rainfall ‘good’ yr) across seasons	Amboseli NP, Kenya
Lindsay, 2011	*L. africana*	24-hour focal follows	5 Adult females (>15 yr) $^{\#}$	wild	Mean 56.8%^	Female-calf groups	24hr	1983-1984 drought yr	Amboseli NP, Kenya
Guy, 1976a	*L. africana*	365hrs; mean 7hr 34m per individual (m & f)	>~10yr 27 males & 21 females	wild	12-14 hr/day		8am-5pm	73 days, May-Dec 1973. All seasons.	Sengwa Area, Rhodesia (Zimbabwe)
Guy, 1976b	*L. africana*	Each individual followed for mean 7hr 34m (m & f)	27 Adult males >~10yr	wild	Grazing 18.9%, and browsing 28.5% (totals 47.4%)		8am-5pm	73 days May-Dec 1973. All seasons.	Sengwa Area, Rhodesia (Zimbabwe)
Guy, 1976b	*L. africana*	Each individual followed for mean 7hr 34m (m & f)	21 Adult females >~10yr	wild	Grazing 12.4% and browsing 27.0% (totals 39.4%)		8am-5pm	73 days May-Dec 1973. All seasons.	Sengwa Area, Rhodesia (Zimbabwe)

Author	Species	N observations	N / Age / Sex of individuals	Context	Time spent Feeding	Group composition	Time of day	Period of study	Location
Shannon et al., 2008	*L. africana*		18 males >27yr (mean age across 3 sites 32-36yr)	wild	Mean 42%	Independent males or bachelor groups	6am-6pm.	3yrs, March 2002-June 2005	Pooled data from Pangola Game Reserve, Pilansberg NP & Phinda Private Gamer Reserve, South Africa
Shannon et al., 2008	*L. africana*		9 adult females$^{\#}$	wild	Mean 45%	Family groups	6am-6pm.	3yrs, March 2002-June 2005	Pooled data from Pangola Game Reserve, Pilansberg NP & Phinda Private Gamer Reserve, South Africa
Kalemera, 1987	*L. africana*	103hr 48m total (Mean 4hr 18m per individual; range 20m–9hr)	Adults: 57 f, 7 m. Young (with shoulder height <2.5m): 13	wild	6am-10am 37% 10am-2pm 59% 2pm-6pm 65%	Mixed: 60 family units & 18 bull groups	6am-6pm	Dry season Aug-Dec 1981 & dry season July-Aug 1982	Lake Manyara NP, Tanzania
Eisenberg & Lockhart. 1972	*E. maximus*	232 sightings	Adults: 20 m, 10 f Sub-adult: 11 m, 4 f Juvenile: 12 Calves: 4	wild	>16hr/day	Group sizes 1-17 with mixed compositions		July 1968-Oct 1969	Wilpattu National Park, Sri Lanka
McKay, 1973 (p. 58)	*E. maximus*	185 "*animal hours*"	Adults: 1 m, 18 f Sub-adults: 4m, 5f Infants: 7 Calves: 5	wild	Mean 91.1% ("*including locomotor components of feeding*")	Mixed family	8:20am-6pm	Unspecified (between full study period Feb 1967-Oct 1969)	South-East Sri Lanka
McKay, 1973	*E. maximus*	1600 "*animal hours*"	51 adult males	wild	Mean 93.%	Males only	daytime	Unspecified (between full study period Feb 1967-Oct 1969)	Lahugala tank, Sri Lanka
Mohapatra et al., 2013	*E. maximus*	12hr/day, 3 alternate days/wk		wild	Winter 8.1/12hrs Summer 7/12hrs Monsoon 6.1/12hrs		daytime	2yrs 2007-2009	Kuldiha Wildlife Sanctuary, India
Baskaran et al., 2010	*E. maximus*	>20,000 scans		wild	Mean 60% Less time in dry season than wet season	Clans and bulls	Daylight (6am-6pm)	All seasons	Nilgiri Biosphere Reserve, India

Author	Species	N observations	N / Age / Sex of individuals	Context	Time spent Feeding	Group composition	Time of day	Period of study	Location
Vancuylenberg, 1977	*E. maximus*	120.43hrs	27 elephants in 4 groups (6 adult m, 3 sub-adult m, 7 adult f, 9 juvenile, 1 infant)	wild	Mean 75%	4 mixed families	Visual obs-ervations 14:15-20:45 (max 6.5hrs/day)	Mar-Dec 1972	Gal Oya NP & the Lahugala tank, Sri Lanka
Posta et al., 2013	*L. africana*	865.5hrs	27yo adult female (mother of calf below)	captive	Mean 34% Indoors 31%, outdoors 37% Inside-day 42%, Inside night 31%, Outside-day 37%, Outside-night 13%	Mother and (A.I.) calf only at zoo	24hrs.	2 yrs June 2005-June 2007	Toledo Zoo, US
Posta et al., 2013	*L. africana*	865.5hrs	3yr (up to 5yr) A.I. calf (of mother above). Still nursing <~5% of time	captive	Mean 20% Indoors 23%, outdoors 16% Day 15%, night 31%	Mother and (A.I.) calf only at zoo	24hrs.	2 yrs June 2005-June 2007	Toledo Zoo, US
Vancuylenberg, 1977	*E. maximus*	118 continuous hrs	1 male	captive	41hrs20s of 118hrs= 34.75%	1 single housed male. Roped.	Almost 5 days continuous observatio	(pre 1977)	Hingurana Sri Lanka
Rees, 2009	*E. maximus*	140hrs	5 adult females (17-43yr), 1 adult male (17yr), a 4yo male & a 1yr female	captive	Adult male 41.4% Adult females ranged 27.4 – 36.6% Juvenile male 41.8% Infant female 24.2%	Mixed group with recordings only made on days when all members kept together.	10am-2pm (outdoors)	35 days in Jan-Dec 1999	Chester Zoo, U.K
Petraccione et al., 2017	*E. maximus*	257 instantaneous	4 adult females (18, 18, 32 & 39yrs)	captive	68-84%	Adult females and single calf (aged 2-9 wks)	10am-5pm	7 weeks May-July 2015	Rosamond Gifford Zoo, Syracuse, NY, US

Table 4.2 24-Hour Profile Activity Budget for Amboseli Elephants. Data from 1982-1984. See Lindsay, 2011. N ≥372 elephants; 6788 observations.

Time of day	Time in Basic Maintenance Activities (%)		
	Feeding	Resting	Moving
6	71.9	11.5	6.5
7	72.8	2.6	20.0
8	60.8	7.3	23.7
9	76.5	9.1	6.0
10	45.3	38.1	8.1
11	48.6	32.9	10.3
12	34.6	48.2	3.9
13	59.9	22.7	8.1
14	64.1	16.3	10.3
15	75.3	3.8	7.3
16	65.2	11.1	13.5
17	66.9	8.6	12.4
18	66.6	1.8	15.8
19	66.6	0.0	9.2
20	59.3	4.0	11.8
21	50.8	12.3	13.1
22	54.2	11.9	13.5
23	63.4	4.3	10.9
24	55.3	14.7	5.1
1	52.7	18.3	6.5
2	51.2	19.3	10.7
3	39.1	45.5	3.0
4	32.7	50.4	0.9
5	31.1	35.6	2.7

Wild adult African elephants forage for 12-14 hours a day (across seasons, N=48) and can eat 100-300Kg of vegetation daily (Guy, 1976a; Parker, Osborn, Hoare & Niskanen, 2007) and Asian elephants have been reported to spend more than 16 hours feeding (Eisenberg & Lockhart, 1972; see Table 4.1 below). Elephants eat over 400 plant species (Oliveira, West, Houck & Leblanc, 2004) and need to consume small quantities of a wide variety of plant species to minimise the effects of any one particular secondary chemical defence (Osborn, 2002). Both Asian and African elephants travel great distances to obtain the huge variety of foods they require, and their ranging patterns are affected by seasonal variations in the quality and quantity of these foods (as well as water sources) (Osborn, 2002). Among adults, these activity trade-offs may be more clearly related to energetics while among immature individuals, especially when buffered by maternal milk energy, the patterns of changes in activities with age represent developmental competencies (Miller & Byers, 1991).

Calf Activities

Elephant calves are completely dependent upon mothers until at least three months of age and remain dependent for 3-6 years (Lee, 1986, Nair, 1989). African elephant calves were unlikely to survive orphaning until they were 18-24 months of age (Lee, 1987). Similarly, Asian elephant calves from Myanmar timber camps in their first year of life were found to have a 10-fold mortality risk if their mother died (Lahdenperä, Mar & Lummaa, 2015).

Nair (1989) studied nine semi-free ranging Asian elephant calves and reported that fundamental behaviours such as suckling, walking and lying down were performed shortly after birth, whilst other activities such as independent feeding and self-maintenance (sand-bathing or comfort activities) occurred at later ages. Together feeding, travelling and resting made up over 80% of a wild African elephant calf's activity budget from birth to four years of age while their activity profiles did not appear to approach those of adults until two years of age (Lee, 1986).

Calves need to develop and practise motor skills in order to perform competent movements. These skills can be categorised as either gross motor skills, required for carrying out large movements such as play; or fine motor skills, needed for carrying out small precise movements (Moody, 2006) with trunk or mouth, such as selecting individual vines from vegetation.

Wild Asian elephant calf practising fine motor skills [c324], in Uda Walawe. Photograph taken 14th July 2011.

Nair (1989) reported that a calf began trying to pick up and hold objects using its trunk by around one week of age. The motor skills and co-ordination to control the legs, trunk and mouth are obtained around one month of age. He also found that calves began to chew on plants by around two months, as the first pair of teeth arrived. Calves then start to explore and begin attempts to feed themselves by around 3-6 months. By six months they have enough strength to acquire low grasses, herbs or other plants and are partially nutritionally independent. Asian elephant calves were reported to have well-developed feeding, drinking and dusting behaviours by about a year of age (Nair, 1989).

In this Chapter, I aim to determine the main activity budgets of calves in the wild study populations and compare these with those in captivity. Calf activity patterns will be used as indicators of developmental patterns and comparisons between contexts to investigate whether the patterns are similar between species, despite major differences in ecology and social structure (de Silva & Wittemyer, 2012; Sukumar, 2003).

While the wild African calf data have been published, no prior studies on wild Asian calves exist.

Maternal Activities

In addition to exploring calf activities, I aim to determine the maintenance activity budgets of mothers (feeding, resting, and moving) in the wild study populations and in captivity and to explore if these vary with the age or sex of their calf. How mothers (as with all individuals in social groups) allocate time to different activities can provide valuable insight in trade-off choices for different behaviours (Dunbar, Korstjens & Lehmann, 2009; Marshall, Carter, Rowcliffe & Cowlishaw, 2012). Trade-offs in maternal investment exist between current and future reproductive investment (Trivers, 1985) and individuals, therefore, need to allocate enough time to manage their social relationships, to successfully reproduce, and to gather resources (Dunbar et al., 2009). The latter is especially important in lactating females since lactation is probably the most energetically costly investment between mothers and calves, representing an estimated 75% of the costs of a reproductive event (Byers, 1997; Lee & Moss, 2011). Lactating females with offspring, therefore, spend more time foraging than non-lactating females in many species (e.g. mountain goats (*Oreamnos americanus*), Columbian ground squirrels (*Spermophilus columbianus*), red deer (*Cervus elaphus*) and bighorn sheep (*Ovis canadensis*), see Hamel & Côté, 2008).

As mothers in captivity have easier access to food, which is also more calorically dense, than do wild mothers, differences in time spent feeding would be expected between wild and captive mothers as captive mothers would need to spend less time foraging for the same energy gain.

Differences in time allocation to foraging may also be expected in mothers of calves of different sex. Mothers with sons have been shown to produce more milk and milk of higher quality than those with daughters in sexually dimorphic and polygynous mammals (e.g. Iberian red deer, *C. elaphus hispanicus*, Landete-Castillejos, Garcia, Lopez-Serrano & Gallego, 2005; mountain goats, Hamel and Côté, 2008) and male elephant calves are more energetically costly in terms of energy required to produce milk to sustain their rapid growth (Moss & Lee, 2011). Enhanced maternal care for sons result in higher costs for raising sons and it is therefore expected that mothers of sons need to forage more than mothers of daughters (Hamel & Côté, 2008). While wild mothers with sons may be expected to forage more to compensate for this greater investment than those with daughters, this difference would not be expected in captive contexts where mothers need to spend little time and effort in foraging.

Further differences in mother activities would also be expected between wild and captive contexts in the light of protecting calves from predators due to a lack of need for vigilance in captivity. In the wild, since young are exposed to higher predation risks than adults, mothers need to be more vigilant than do females without offspring (Burger & Gochfeld, 1994; Toïgo, 1999), although allomothers may also be able to provide this care in elephants. In other species, it has been suggested that increases in time spent in vigilance should result in increased predator detection and therefore juvenile survival (Hamel & Côté, 2008; Lima & Dill, 1990). Consequently, lactating females may face choices in activity trade-offs which may not be as important to mothers without offspring (Hamel & Côté, 2008), or to mothers in captivity where predation is not a risk.

Calves begin to require different care, both in terms of lactation demands and vigilance required as they grow older and become more independent. It would be expected that maternal activities would change as calves decrease their time suckling with age. A mother's time investment previously spent nursing would, therefore, be made available and she may also be able to reduce her foraging rates, due to a reduction in the energetic demands being made upon her and this freeing even more time in her activity budget. Suckling interactions between mothers and calves are further investigated in Chapter Five (Early Calf Interactions with Mothers and Others) for their relationship with calf age and independent feeding and in Chapter Six (The Importance of Play) for their relationship with calf age a play.

Abnormal Activities

Within ethology, abnormal behaviour refers to responses which are 'away from the norm' and relates to rare behaviours which differ from a specified 'normal' population (Cooper & Mason, 1998; Mason, 1991). If this 'normal' population is taken as healthy free-living conspecifics, then stereotypies can be defined as abnormal behaviours since their expression appears to be limited to captive or psychologically impaired animals (Mason, 1991). It is essential to deal with the causes of stereotypic behaviour and not just mask them by addressing their symptoms (Mason, 1991).

Abnormal behaviour, which is one indicator of compromised welfare (Mason & Latham, 2004), could potentially be related to demographic events within captive housed elephants (Greco, Meehan, Hogan et al., 2016). Stereotypies have been reported to have a range of proximate causes (Mason, 1991) including individuals who are consistently prevented from reaching a desired goal or location or unable to escape from something undesirable (Carlstead, 1998), or from maternal deprivation either from early separation or poor maternal care from inexperienced mothers (Latham & Mason, 2008). Vanitha, Thiyagesan and Baskaran (2015) argue that depriving a captive calf of associations with their maternal relatives and isolating them from conspecifics leads to the appearance of stereotypies with younger individuals being more susceptible. They suggest that this increased susceptibility in their study animals may be related to being confined by chains during "*the most active phase of their life*" (first 15 years; p. 137). Latham and Mason (2008) review the link between early separation from the mother and abnormal behaviours and state that maternal deprivation may also alter animals so that they become more prone to developing stereotypic behaviours long after separation, thus having long lasting influences on welfare. They note that "*maternal deprivation may produce changes in temperament or stress-responsiveness that influence life-long behavioural responses to stressors, or may cause neural changes that make animals more prone to 'inappropriate' repetitive behaviour*" (p. 98; see also Sanchez, Ladd & Plotsky, 2001).

For the earlier discussion of abnormal behaviours and stereotypies in relation to welfare see Chapter One (Section 1.3.1). Abnormal time budgets are tested in this Chapter by investigating adult budgets. Stereotypies, present in non-calves, are briefly examined in captive elephants as these are outcomes variables representing a history of compromised development. In order to understand the developmental potential for engaging in stereotypies I looked at when stereotypies occur and in what context (births, deaths, seasons etc.) for these captive adult elephants.

I aim to explore the effect in captivity of the addition or removal of group members, specifically in relation to births and deaths by investigating frequency patterns of abnormal behaviours in the form of stereotypies. It has been shown that the total number of transfers was a risk factor for stereotypic behaviours within the US captive elephant population which suggests that transfer experience is of importance to behavioural health (Greco, Meehan, Miller, et al., 2016).

Stereotypic behaviour has been reported to occur for much of the waking life of some circus elephants, with one individual engaging in stereotypies for 57% of time during daylight hours, and another individual for 71% (Broom, 2002). Individual variation in the stereotypies existed in the degree in which the behaviour was interrupted by social contact with conspecifics, by people in the vicinity, or when food was being given (Broom, 2002).

Greco, Meehan, Hogan et al. (2016) found that US captive elephants (42 Asian and 47 African in 39 US zoos videoed for a median of 12 hours per season during winter and summer; and a subset of 13 Asian and 19 African elephants was also observed live for a median of 10.5 hours at night) spent 15.5% of their daytime and 24.8% of their night engaged in stereotypies. Regression analysis showed that Asian elephants had a greater risk of stereotypic behaviours than did African elephants (day: $p<0.001$, Risk Ratio=4.087; night: $p<0.001$, Risk Ratio=8.015; Greco, Meehan, Hogan et al., 2016).

For both species, spending time housed separately corresponded to an increase in the risk of engaging in daytime stereotypic behaviours ($p<0.001$, Risk Ratio=1.009), whilst spending more time with juvenile elephants reduced the risk ($p<0.01$, Risk Ratio=0.985). The risk of performing high rates of stereotypies at night was also reduced when animals were kept in larger social groups ($p=0.039$, Risk Ratio=0.752; Greco, Meehan, Hogan et al., 2016).

Rees (2009) found that all five of Chester’s adult female elephants present in 1999 exhibited stereotypic behaviour. (Four of these five individuals were also present in this study - Thi (17 years), Jangoli (30 years), Sheba (43 years) and Maya (30 years) - whilst the fifth adult female was 32 year old Kumara. The other elephants present were male Chang (17 years) and calves Upali (4 years) and Sithami (1 year)). Frequencies (from

January 29th to November 4th 1999) ranged between 3.9 and 29.4% of all observations and showed individual, diurnal and seasonal variations with stereotypies negatively correlating to maximum daily temperature, with highest frequencies of stereotypies exhibited on the 10 coldest days (mean maximum daily temperature of 9.0°C) in comparison to the 10 warmest days (mean maximum daily temperature of 23.2°C) of the study (Rees, 2004, 2009). I aim to verify whether stereotypic frequencies correlate to environmental temperature in captive elephants, by investigating stereotypic frequencies in both captive adult Asian and African elephants at all three captive study sites across 12 months of the year.

In this Chapter, I will assess the basic activity patterns of calves and their mothers to examine developmental changes for wild and captive calves. Studying maintenance activity budgets of calves and their mothers helps us to understand the degree to which captive individuals may differ in their behaviour from their wild conspecifics. A better understanding of any differences between wild and captive activity budgets may highlight where improvements are needed in captive management in order to allow captive animals the opportunities to express normative activity budgets.

I predicted 1) that African and Asian calves will show similar age changes in activity, and 2) that there will be differences between captive and wild contexts in activities due to constraints on captive management.

Wild Asian elephants in Uda Walawe take shade in the heat of the day around 11am-1pm and males like this one here (on the right) have been observed in recumbent rest alongside females and calves. Photograph taken 24th July 2011.

4.3 Methods

The study sites and populations were defined earlier in Chapter Two (Description of Study Sites and Subjects). Data collection and analysis were described in Chapter Three (Methods).

Data Analyses

Activity Budgets of Calves and Mothers

Activities were defined in general terms from the ethogram (Appendix C), and several categories were combined as defined in Chapter Three. Feeding while moving was combined with feeding while standing into ’Feeding’. All other locomotion was combined into ‘Moving’. ‘Resting’ included resting standing, sleeping, and resting lying. Dusting or sand bathing, swimming etc., were included in ’Comfort’. ‘Suckling interaction’ included all contact with the mother’s nipples. Throughout the Chapters, I termed play which included Lone (L), Escalated-contact (E), Gentle-contact (G) and Object (O) play as ‘LEGO-play’ (for more details on LEGO-play, see Chapter Six, Play).

Each activity (feeding, resting, moving and proximities to mother) was tested as dependent variables using GLMM (Chapter Three). Independent factors were age (categorical), sex (M, F) and contexts (wild Asian, wild African, captive Asian, captive African). Calf age was binned together into six-month intervals from birth to 24 months, to maximise data. Later ages were then binned together (3-5 years). In all tests of calf behaviours and proximities, calf ID was entered as a random variable to take into account repeated measures. Mother ID was used only for maternal activities and not controlled for in addition to calf ID, since only two mothers contributed more than one calf to the captive dataset, and relatively few in the wild dataset.

Only significant effects in the final model are shown here. Error bars (95%CI) were provided on figures when presenting comparative data, such as means for contexts, and for figures illustrating the high variance in individual patterns.

The percent of time spent in different activities was calculated for each individual calf and its mother from each scan. For mother activities, 5 min scan data were analysed, while calf activity budgets were taken from both 5 and 25 min scan sampled data to include calves up to the age of five years. Means and 95% confidence intervals are presented throughout the text for non-log transformed values. Data were binned together per month of age per calf.

In the captive African calf dataset, both Mansi (who was rejected, re-accepted, then orphaned at 16 weeks) and Tammi's calf (who was rejected then died at 31 days) remained in the dataset.

For calf activities, a non-parametric Spearman's rank-order correlation (r_s) was run to assess any relationship between the major activities of feed, rest, move, suckling interaction and LEGO-play at each age within the wild and captive Asian and African datasets. As there were multiple correlations between these five activity categories, Bonferroni correction was applied and the significance level was set at 0.01.

Although I include suckling interactions and LEGO-play with the three main maintenance activities when investigating correlations between calf activities, I will discuss age, sex and context differences for suckling interactions in Chapter Five, and for play in Chapter Six. However, in this Chapter, the aim was to see if there were interactions between major activities and rare activities such as play or suckling interactions.

For counts of calves and calf behaviour observations included in GLMM analyses for calf activities, see Chapter Three, Table 3.6. For counts of mothers and mother behaviour observations included in GLMM analyses for mother activities, see Chapter Three, Table 3.7.

Abnormal Behaviours in Adults

Group scan data at 25 min intervals, from 8am-6pm, were used in analyses of abnormal stereotypic behaviour in captivity. Data were pooled per study visit (range 5-7 days; not necessarily consecutive days). Numbers of observations per adult elephant are represented on Figures 4.7 for Asian and 4.8 for African elephants.

Given an earlier finding that weather greatly influences captive elephant activities and especially the frequency of stereotypies (Rees, 2004), I tested for a relationship between the frequency of stereotypic behaviours and warm or cold months using a Mann-Whitney U test on pooled data across all captive contexts. Two warm and two cold months were defined from the mean maximum and minimum temperatures per month from August 2010 to April 2014 (when 25 min group data were collected) from Shawbury (355200E, 322100N, latitude 52.794, longitude -2.663, 72m AMSL) (Met Office, 2015). July and August had both the highest mean maximum and minimum temperatures and were defined as warm months, while January and December were defined as cold months since they had the lowest mean maximum and minimum temperatures.

4.4 Activities Results

4.4.1 Activity Budgets: Independent Feeding, Resting and Moving

Maintenance activities of independent feeding, resting and moving are the main activities of almost all animals. For the first two years of life, wild calves spent around 70-80% of their time in feed, rest and move whilst captive calves spend around 60% of their time in these three activities (Figure 4.1). I will now go on to explore in detail differences and similarities between contexts.

Calves across all four contexts spent most of their time in maintenance activities (58.2 to 74.6% of time in first five years of life) with marked changes with age. Across all contexts, feeding increased with age while moving stayed relatively stable but still significantly decreased with age overall. Resting decreased with age in wild African calves, whereas it was more stable in the other three contexts and, again, still significantly decreased with age overall. These results are discussed in full below. For mothers, over 80% of time was spent in maintenance activities in each context (Figure 4.1).

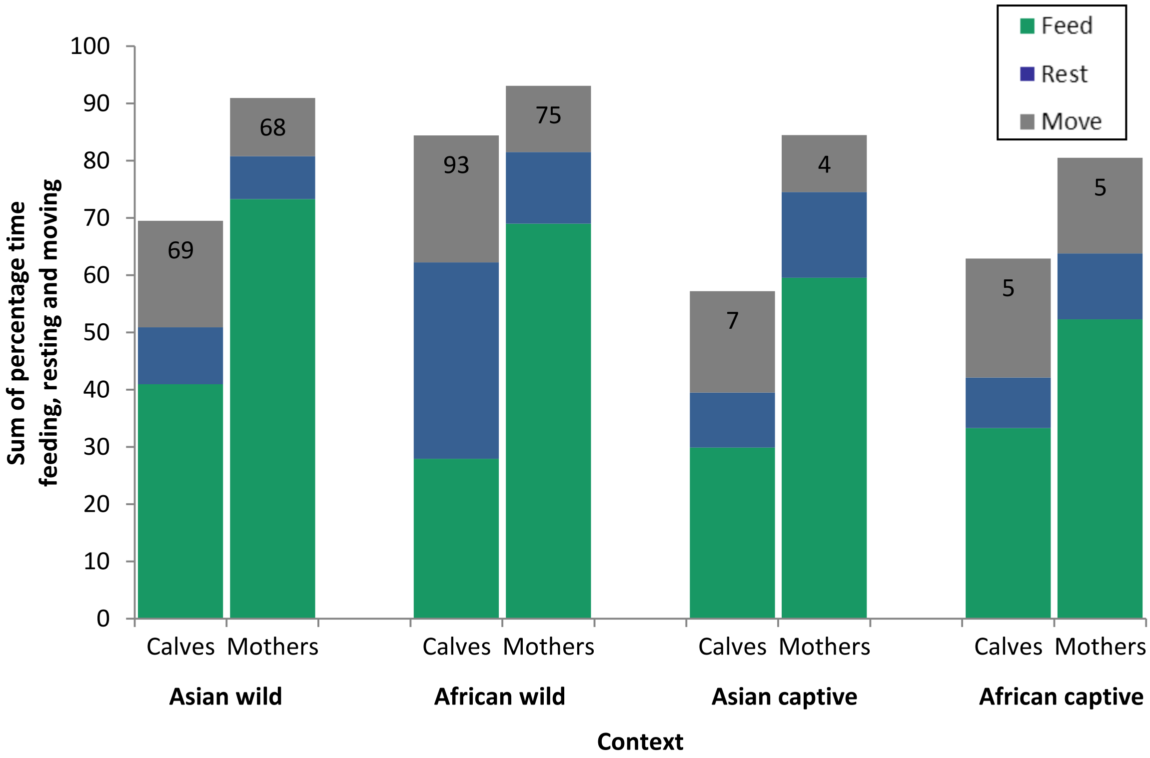


Figure 4.1 Sum of Percentage Time in Basic Maintenance Activities (Feeding Independently, Resting and Moving) for Calves in the First Two Years of Life, and Mothers of these Calves. Data labels are N animals.

4.4.2 Calf Activity Budgets

4.4.2.1 Calf Independent Feeding

The time spent feeding independently increased consistently with age (Figure 4.2 and 4.3) from 1-6 months to 3-5 years (Table 4.3). Across all contexts, the mean percentage time independent feeding in calves aged 1-6 months was significantly lower than all other ages. Pairwise comparisons showed significant differences between age-bins, except 19-24 months and 3-5 years where feeding rates plateau (Figure 4.2).

Male and female calves feed at similar rates (Figure 4.2; 4.3). No significant differences were found between the sexes (*p*=0.661), nor was there an interaction between age and sex (*p*=0.185), age and context (*p*=1.580), or sex and context (*p*=0.471; Table 4.3).

There was an overall significant effect of context on independent feeding rates (Table 4.3). In pairwise comparisons, wild Asian calves were observed feeding significantly more than wild Africa, captive Asian or captive African calves.

The interaction between sex by age within context showed that wild Asian males aged 19-24 months had significantly higher rates of feeding. There was also a significant effect of individual which while small, suggested that some calves simply spent more or less time feeding than others consistently across samples. Calf ID contributed significantly to the overall model variance (p=0.019).

Case studies of captive individuals showed that patterns in feeding were similar to those for the population as a whole (Figures 4.4; 4.5).

Table 4.3 Final General Linear Mixed Model for Calf Feed. Var (ID)=73.37, *p*=0.019. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was calf feeding; independent variables were age, sex, context, and the interactions between sex and age within context.

	Main effect *F* and *p* value	**Coefficient β (95% CI)**	***p* value**
Overall model fit	$F_{19, 350}$=14.301, *p*<0.001		
Age	$F_{4, 566}$=18.786, *p*<0.001		
1-6mo		35.700 (29.463 to 41.937)	<0.001
7-12mo		20.758 (29.463 to 41.937)	<0.001
13-18mo		8.673 (1.780 to 15.565)	<0.001
1-6mo - 7-12mo		-21.419 (-26.801 to -16.037)	*p*<0.001
1-6mo - 13-18mo		-34.237 (-39.444 to -29.030)	*p*<0.001
1-6mo - 19-24mo		-43.430 (-49.516 to -37.343)	*p*<0.001
1-6mo - 3-5yr		-42.951 (-48.580 to -37.322)	*p*<0.001
7-12mo - 13-8mo		-12.818 (-18.512 to -7.123)	*p*<0.001
7-12mo - 19-24mo		-22.011 (-28.505 to -15.516)	*p*<0.001
7-12mo - 3-5yr		-21.532 (-27.603 to -15.461)	*p*<0.001
13-18mo - 19-24mo		-9.193 (-15.509 to -2.877)	*p*=0.004
13-18mo - 3-5yr		-8.714 (-14.549 to -2.880)	*p*=0.004
Context	$F_{3, 62}$=26.768, *p*<0.001		
Asian wild		-9.169 (-15.087 to -3.251)	0.002
Asian wild – African wild		10.380 (5.167 to 15.592)	*p*<0.001
Asian wild – Asian captive		11.689 (2.996 to 20.383)	*p*=0.010
Asian wild – African captive		11.348 (1.799 to 20.897)	*p*=0.021
Sex x age (within context)	$F_{12, 568}$=6.164, *p*<0.001		
Male x 19-24mo (within Asian wild)		50.314 (13.172 to 87.456)	*p*=0.008

4.4.2.2 Calf Resting

Overall, the mean percentage time spent resting decreased significantly with age (Table 4.4). Pairwise comparisons showed significant differences between age category 1-6 months and each of the following age categories: 7-12 months, 13-18 months, 19-24 months and 3-5 years. There were also significant pairwise comparisons between 7-12 months and each of the following age categories: 13-18 months, 19-24 months, and 3-5 years. Again, calf ID showed significant variance (p<0.001).

Table 4.4 Final General Linear Mixed Model for Calf Rest. Var (ID)=89.30, *p*< 0.001. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was calf Resting; independent variables were age, context, and the interactions between them.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI)**	***p* value**
Overall model fit	$F_{19, 350}$=14.301, *p*<0.001		
Age	$F_{4, 566}$=18.786, *p*<0.001		
1-6mo		35.700 (29.463 to 41.937)	<0.001
7-12mo		20.758 (14.238 to 27.279)	<0.001
13-18mo		8.673 (1.780 to 15.565)	0.014
1-6mo – 7-12mo		7.083 (3.215 to 10.951)	<0.001
1-6mo – 13-18mo		12.319 (8.537 to 16.100)	<0.001
1-6mo – 19-24mo		15.825 (11.416 to 20.234)	<0.001
1-6mo – 3-5yr		14.812 (10.215 to 19.410)	<0.001
7-12mo – 13-18mo		5.236 (1.078 to 9.393)	0.014
7-12mo – 19-24mo		8.742 (4.050 to 13.434)	<0.001
7-12mo – 3-5yr		7.729 (2.889 to 12.570)	0.002
Context	$F_{3, 62}$=26.768 *p*<0.001		
Asian wild		-9.169 (-15.087 to -3.251)	0.002
Asian wild – African wild		-17.680 (-21.916 to -13.443)	<0.001
Asian captive – African wild		-19.252 (-27.081 to -11.424)	<0.001
African wild – African captive		-16.759 (-25.213 to -8.305)	<0.001

Age x context	$F_{12, 568}=6.164$ $p<0.001$		
1-6mo Asian wild		-31.113 (-40.193 to -22.034)	<0.001
1-6mo African wild		-23.965 (-34.928 to -13.003)	<0.001
1-6mo Asian captive		-28.472 (-43.088 to -13.856)	<0.001
7-12mo Asian wild		-14.247 (-24.974 to -3.519)	0.009
7-12mo African wild		-18.348 (-29.861 to -6.835)	0.002
7-12mo Asian captive		-19.521 (-34.097 to -4.945)	0.009
1-6mo – 7-12mo Asian captive		9.325 (2.917 to 15.735)	0.004
1-6mo – 13-18mo Asian captive		11.922 (5.018 to 18.827)	0.001
1-6mo – 19-24mo Asian captive		12.327 (3.948 to 20.706)	0.004
1-6mo – 3-5yrs Asian captive		11.735 (2.715 to 20.753)	0.011
1-6mo – 7-12mo African wild		14.942 (8.153 to 21.731)	<0.001
1-6mo – 13-18mo African wild		27.027 (19.660 to 34.395)	<0.001
1-6mo – 19-24mo African wild		41.661 (33.243 to 50.080)	<0.001
1-6mo – 3-5yrs African wild		35.700 (29.463 to 41.937)	<0.001
7-12mo – 13-18mo African wild		12.086 (4.425 to 19.746)	0.002
7-12mo – 19-24mo African wild		26.72 (18.290 to 35.149)	<0.001
7-12mo – 3-5yrs African wild		20.758 (14.238 to 27.279)	<0.001
13-18mo – 19-24mo African wild		14.634 (5.891 to 23.377)	0.001
13-18mo – 3-5yrs African wild		8.673 (1.78 to 15.565)	0.014

There was an overall significant effect of context on resting and captive Asian calves rested significantly less than other contexts (Table 4.4). Wild African calves were also observed resting significantly more than wild Asian, captive Asian or captive African calves in pairwise comparisons. The interaction between age and context suggested that there was a significantly higher percentage of time spent resting in wild African calves aged 1-6 and 7-12 months.

Male and female calves rested at similar rates (Figure 4.2; 4.3). No significant differences were found between the sexes, nor was there an interaction between age and sex, sex and context or sex and age within context (Table 4.4).

For individual captive calves, percentage time resting decreased with age overall similar to the patterns across contexts with the exception of male captive African calves, Impi and Mchumba, who showed slight increases in rest between 13-18 and 19-24 months (Figures 4.4; 4.5).

4.4.2.3 Calf Moving

Overall, the mean percentage of time that calves spent moving decreased with age, and pairwise comparisons showed significant differences between 1-6 months and 19-24 months; 1-6 months and 3-5 years; 7-12 months and 13-18 months; and between 7-12 months and 3-5 years (Table 4.5).

Table 4.5 Final General Linear Mixed Model for Calf Move. Var (ID)=100.51, $p<0.001$. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was calf Moving; independent variables were age, sex, and the interactions between them.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI) and *p* value**	***p* value**
Overall model fit	$F_{9,\,557}=2.793$, $p=0.003$		
Age	$F_{4,\,615}=3.686$, $p=0.006$		
1-6mo		7.039 (1.208 to 12.870)	0.018
1-6mo – 19-24mo		6.287 (1.769 to 10.806)	0.006
1-6mo – 3-5yr		4.983 1.104 to 8.862)	0.012
7-12mo – 13-18mo		4.299 (0.166 to 8.432)	0.042
7-12mo – 19-24mo		7.260 (2.521 to 11.998)	0.003
7-12mo – 3-5yr		5.955 (1.759 to 10.152)	0.005
Age x Sex	$F_{5,\,463}=2.329$, $p=0.042$		
13-18mo male		7.078 (0.385 to 13.772)	0.038
1-6mo – 19-24mo male		9.682 (3.182 to 16.181)	0.004
1-6mo – 3-5yrs male		6.604 (0.950 to 12.259)	0.022
7-12mo – 19-24mo male		7.949 (1.134 to 14.763)	0.022
13-18mo – 19-24mo male		9.546 (2.771 to 16.322)	0.006
13-18mo – 3-5yrs male		6.469 (0.634 to 12.304)	0.030
1-6mo – 13-18mo female		6.518 (1.076 to 11.959)	0.019
7-12mo – 13-18mo female		10.195 (4.259 to 16.131)	0.001
7-12mo – 3-5yrs female		7.039 (1.208 to 12.870)	0.018

Male and female calves rested at similar rates (Figure 4.2; 4.3). No significant differences were found between the sexes, nor was there an interaction between sex and context, age and context, or sex and age within context (Table 4.5).

For captive individual calves, moving showed less of a clear trend than independent feeding or resting did. However, moving decreased slightly or remained roughly constant with age for all captive individual calves regardless of context or sex (Figures 4.4; 4.5). The major effect overall in the GLMM was individual.

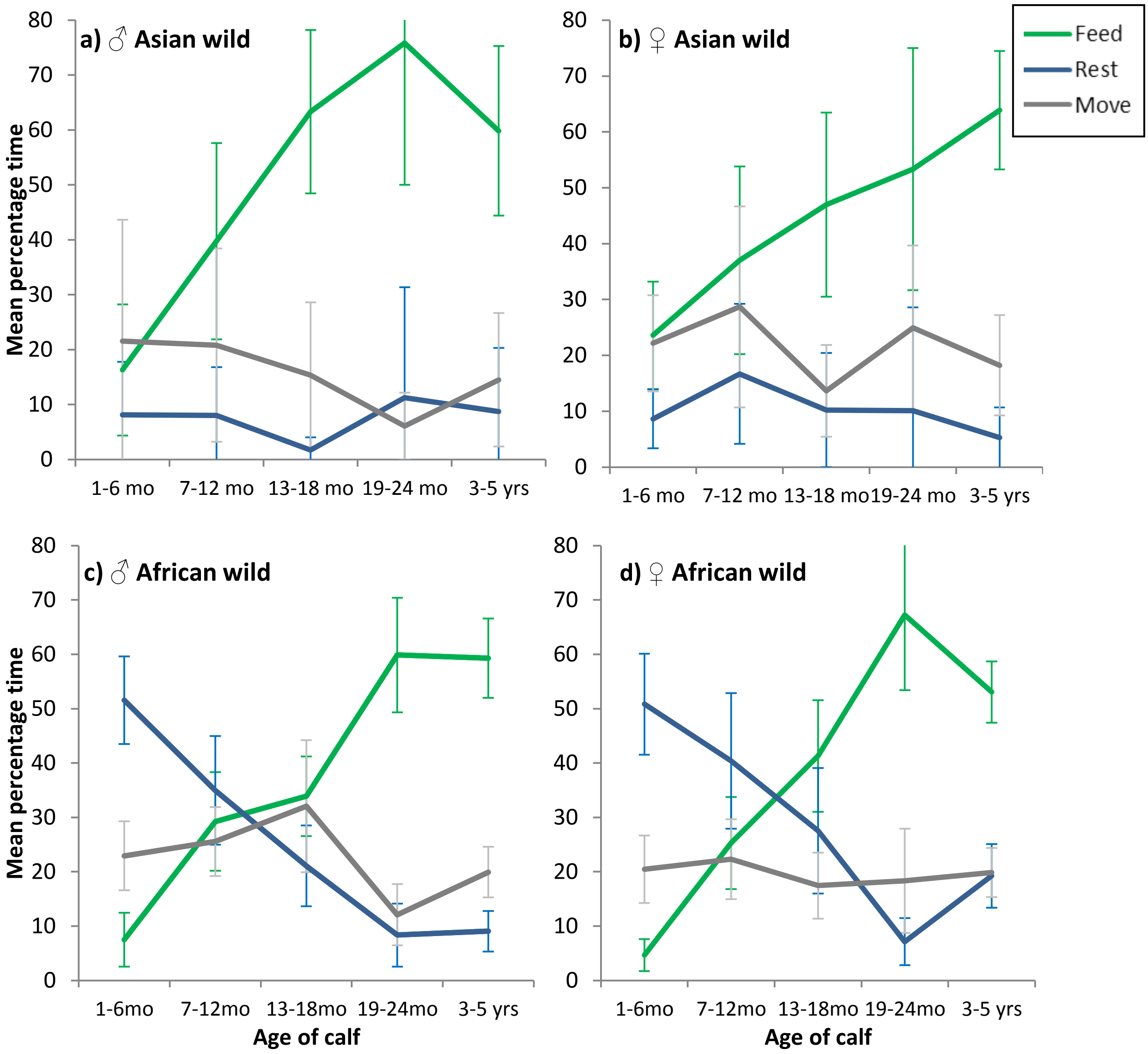


Figure 4.2 Mean Percentage of Time Spent in Feeding, Resting and Moving for Wild Asian and African Calves by Age and Sex. 95%BCI. See Table 3.6, Chapter Three, for N.

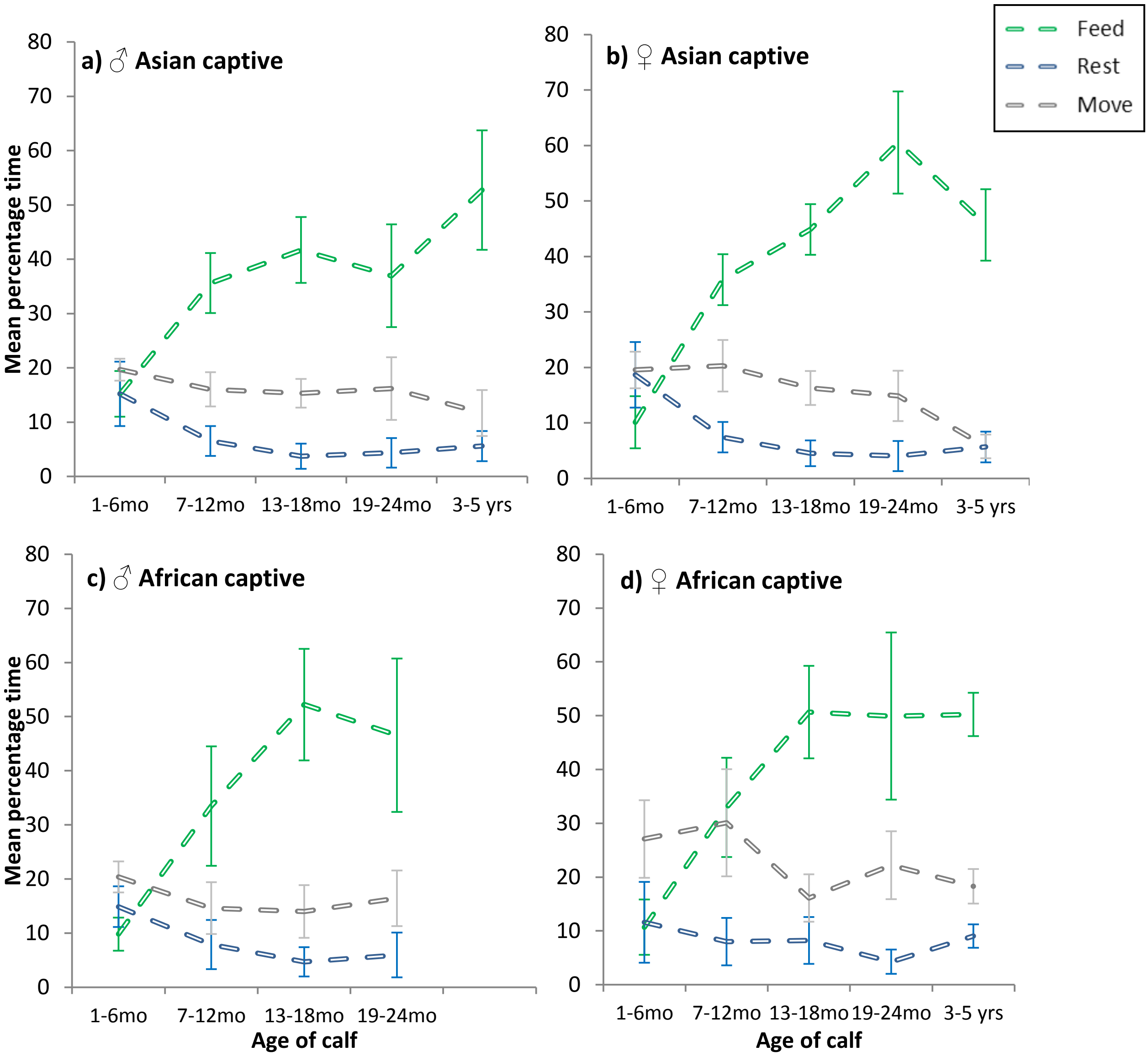


Figure 4.3 Mean Percentage of Time Spent in Feeding, Resting and Moving for Captive Asian and African Calves by Age and Sex. 95%BCI. See Table 3.6, Chapter Three, for N.

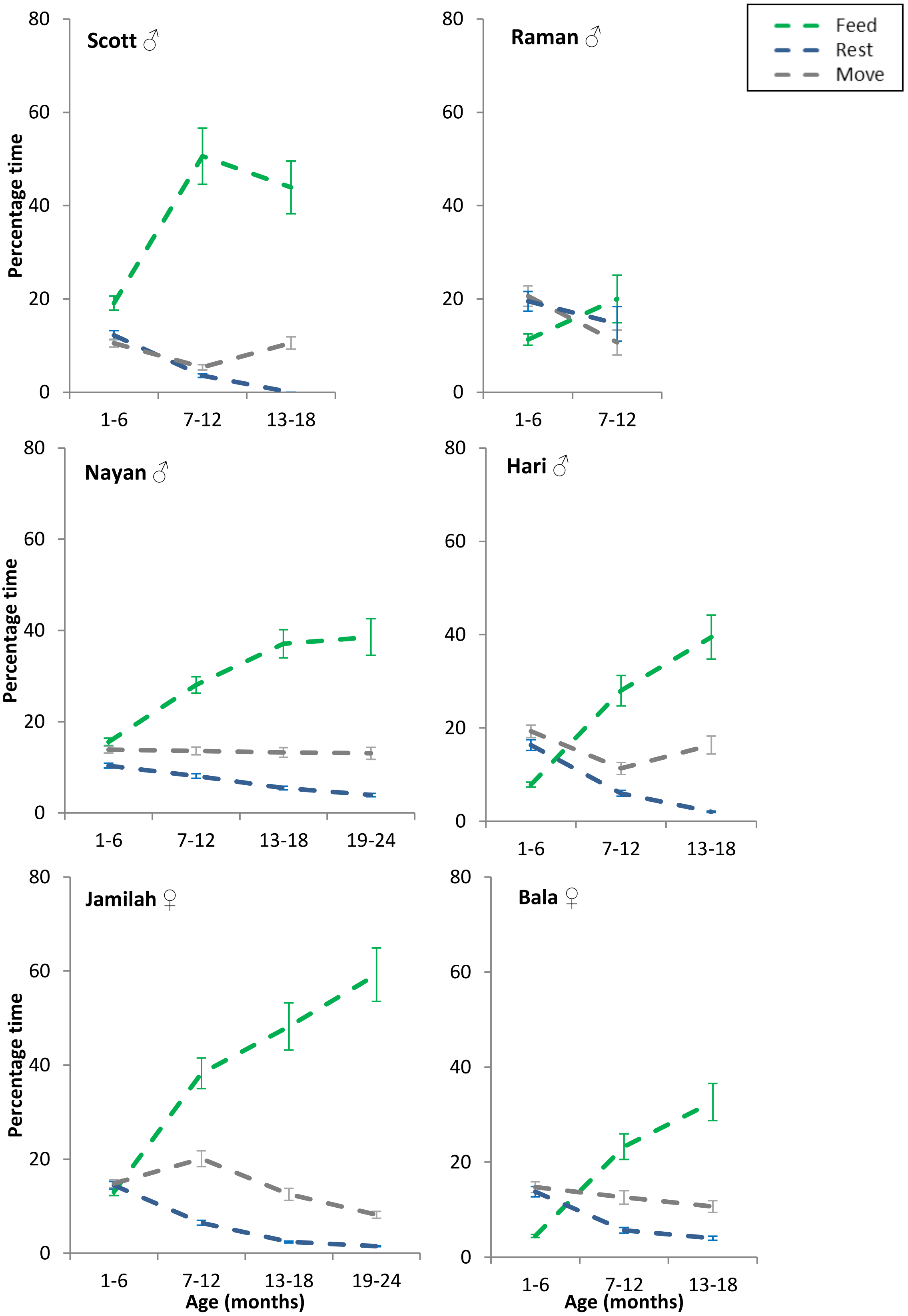


Figure 4.4 Percentage Time Spent Independent Feeding, Resting and Moving in Individual Captive Asian Calves from Birth to Three Years of Age. Data from scans at 5min intervals from 10min focal observations. For N of observations per individual, see Table 3.4, Chapter Three. Binomial 95% CI.

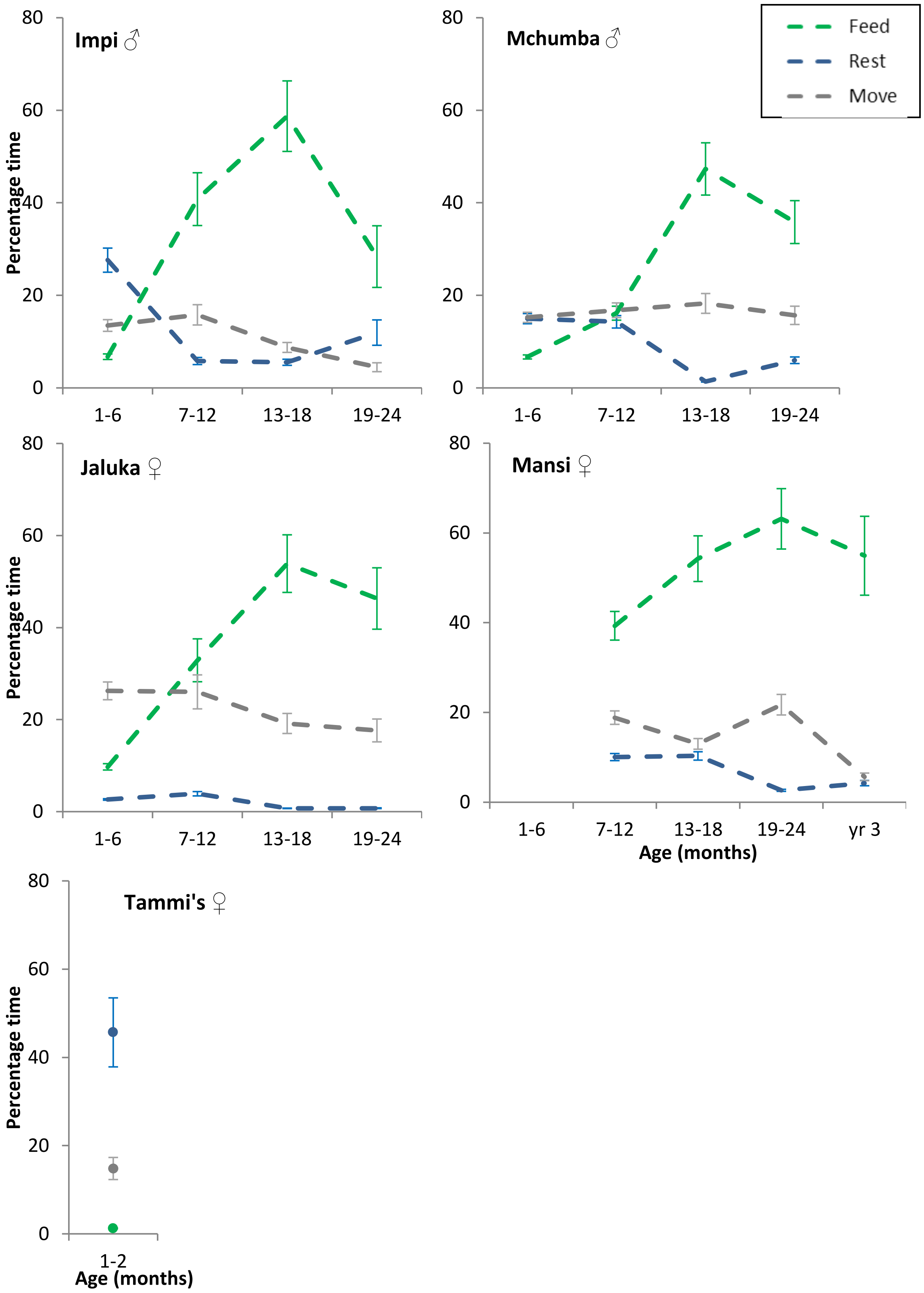


Figure 4.5 Percentage Time Spent Independent Feeding, Resting and Moving in Individual Captive African Calves from Birth to Three Years of Age. Data from scans at 5min intervals from 10min focal observations. Impi: 7-12 mo rest at 0% from 5min scans, replaced with 5.81% from 25min group scans (10 of 172 visble 25min group scans). Jaluka 7-12 mo rest at 0% from 5min scans, replaced with 3.88% from 25min group scans (4 of 103 visible 25min group scans). For N of observations per individual, see Table 3.5, Chapter Three. Binomial 95% CI.

4.4.3 Correlations Between Calf Activities

As the major activity, we might expect time feeding to determine how much time was available for other activities. Independent feeding was negatively correlated with rest, move and LEGO-play in all contexts and for both sexes, with the exception of female captive African calves, where feeding and resting were unrelated (Table 4.6). Among female wild African and captive Asian calves moving was unrelated to feeding while for male wild African calves time spent feeding was unrelated to LEGO-play.

Independent feeding was negatively correlated with suckling interactions for both sexes and species in captive calves. Suckling interactions were positively correlated with rest in captive Asian female and African male calves and positively correlated with LEGO-play in captive female African calves (Table 4.6).

Table 4.6 Spearman Correlation Coefficients of Calf Behaviour, by Sex and Context. *p* significant at ≤0.01 and noted in bold. Significant results in bold. Suckling=suckling interaction. N here is N of samples; for N of individuals see Table 3.6.

			Correlation coefficient r_s				
Sex	**Context**	**Behaviour**	**Rest**	**Move**	**Suckling**	**LEGO**	**N**
Male	Asian wild	**Feed**	**-0.328 (*p*=0.005)**	**-0.471 (*p*<0.001)**	-0.206 (*p*=0.081)	**-0.417 (*p*<0.001)**	73
	Asian wild	**Rest**		0.150 (*p*=0.204)	-0.167 (*p*=0.158)	-0.003 (*p*=0.983)	73
	Asian wild	**Move**			-0.052 (*p*=0.664)	-0.112 (*p*=0.347)	73
	Asian wild	**Suckling**				0.047 (*p*=0.695)	73
	African wild	**Feed**	**-0.808 (*p*<0.001)**	**-0.376 (*p*<0.001)**	-0.016 (*p*=0.253)	-0.159 (*p*=0.085)	118
	African wild	**Rest**		-0.021 (*p*=0.820)	0.028 (*p*=0.764)	0.058 (*p*=0.529)	118
	African wild	**Move**			-0.120 (*p*=0.196)	-0.091 (*p*=0.325)	118
	African wild	**Suckling**				-0.033 (*p*=0.725)	118
	Asian captive	**Feed**	**-0.541 (*p*<0.001)**	**-0.403 (*p*<0.001)**	**-0.286 (*p*=0.003)**	**-0.387 (*p*<0.001)**	106
	Asian captive	**Rest**		-0.209 (*p*=0.032)	0.237 (*p*=0.014)	-0.078 (*p*=0.428)	106
	Asian captive	**Move**			-0.037 (*p*=0.708)	-0.107 (*p*=0.277)	106
	Asian captive	**Suckling**				-0.056 (*p*=0.568)	106
	African captive	**Feed**	**-0.665 (*p*<0.001)**	**-0.511 (*p*=0.001)**	**-0.758 (*p*<0.001)**	**-0.460 (*p*=0.002)**	42
	African captive	**Rest**		0.129 (*p*=0.416)	**0.426 (*p*=0.002)**	0.032 (*p*=0.840)	42
	African captive	**Move**			0.225 (*p*=0.151)	0.228 (*p*=0.146)	42
	African captive	**Suckling**				0.387 (*p*=0.011)	42

			Correlation coefficient r_s				
Sex	**Context**	**Behaviour**	**Rest**	**Move**	**Suckling**	**LEGO**	**N**
Female	Asian wild	**Feed**	**-0.278 (*p*=0.003)**	**-0.424 (*p*<0.001)**	-0.052 (*p*=0.583)	**-0.392 (*p*<0.001)**	110
	Asian wild	**Rest**		-0.069 (*p*=0.472)	0.056 (*p*=0.556)	0.167 (*p*=0.078)	110
	Asian wild	**Move**			-0.137 (*p*=0.151)	-0.081 (*p*=0.399)	110
	Asian wild	**Suckling**				0.024 (*p*=0.801)	110
	African wild	**Feed**	**-0.787 (*p*<0.001)**	-0.204 (*p*=0.019)	-0.115 (*p*=0.187)	**-0.249 (*p*=0.004)**	130
	African wild	**Rest**		-0.192 (*p*=0.027)	0.006 (*p*=0.944)	0.139 (*p*=0.114)	130
	African wild	**Move**			0.010 (*p*=0.910)	-0.133 (*p*=0.130)	130
	African wild	**Suckling**				-0.086 (*p*=0.327)	130
	Asian captive	**Feed**	**-0.570 (*p*<0.001)**	-0.295 (*p*=0.016)	**-0.434 (*p*<0.001)**	**-0.552 (*p*<0.001)**	66
	Asian captive	**Rest**		0.068 (*p*=0.589)	**0.318 (*p*=0.009)**	-0.105 (*p*=0.404)	66
	Asian captive	**Move**			-0.007 (*p*=0.956)	-0.114 (*p*=0.362)	66
	Asian captive	**Suckling**				0.023 (*p*=0.852)	66
	African captive	**Feed**	-0.095 (*p*=0.423)	**-0.485 (*p*<0.001)**	**-0.297 (*p*=0.010)**	**-0.354 (*p*=0.002)**	74
	African captive	**Rest**		-0.141 (*p*=0.231)	-0.083 (*p*=0.481)	-0.130 (*p*=0.268)	74
	African captive	**Move**			0.170 (*p*=0.149)	0.020 (*p*=0.865)	74
	African captive	**Suckling**				**0.399 (*p*<0.001)**	74

4.4.4 Maternal Activity Budgets: Feeding, Resting and Moving

4.4.4.1 Mother Feeding

Overall, there was a significant difference between contexts in the mean percentage time that mothers engaged in feeding (Table 4.7). Both wild Asian and African mothers fed at significantly higher rates than did the captive mothers of either species. Despite predictions that males would be more expensive and therefore mothers might need to feed for longer to sustain sons, no sex differences were found (*p*=0.772). Note that mother ID did not significantly contribute to variance in mother feeding.

Table 4.7 Final General Linear Mixed Model for Mother Feed. Var (ID)=73.756, *p*=0.054. See Table 3.7, Chapter Three, for N of calves and N of observations. Dependent variable was mother Feeding; independent variable was context.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI)**	***p* value**
Overall model fit	$F_{3, 46}$=10.836, *p*<0.001		
Context	$F_{3, 46}$=10.836, *p*<0.001		
Asian wild		6.035 (0.558 to 11.512)	0.031
African wild		-17.469 (-27.739 to -7.199)	0.001
Asian captive		-18.095 (-30.177 to -6.013)	0.005
Asian wild – African wild		6.035 (0.558 to 1.512)	0.031
Asian wild – Asian captive		23.504 (13.076 to 33.931)	<0.001
Asian wild – African captive		24.130 (11.914 to 36.345)	<0.001
African wild – African captive		18.095 (6.013 to 30.177)	0.005
Asian captive – African wild		-17.469 (-27.739 to -7.199)	0.001

4.4.4.2 Mother Resting

Overall, there was a significant difference between contexts for the mean percentage time mothers rested (Table 4.8). Pairwise comparisons showed wild Asian mothers rested significantly less than did wild African mothers and captive Asian mothers, but not captive African mothers. Again, there was no significant variance due to mother ID.

Wild Asian mother and group resting after a rain shower whilst calf rests whilst lying down by her feet. Photograph taken 6th July 2011.

Table 4.8 Final General Linear Mixed Model for Mother Rest. Var (ID)=31.451, p=0.117. See Table 3.7, Chapter Three, for N of calves and N of observations. Dependent variable was mother Resting; independent variables were calf age, context, calf sex and the interactions between them.

	Main effect *F* and *p* value	**Coefficient β (95% CI)**	***p* value**
Overall model fit	$F_{36, 179}$=1.293, p=0.0136		
Context	$F_{3, 44}$=5.697 p=0.002		
Asian wild – African wild		-8.387 (-12.566 to -4.208)	<0.001
Asian wild – Asian captive		-8.953 (-16.812 to -1.093)	0.027
Age x Sex	$F_{4, 438}$=0.309 p=0.872		
19-24 mo x male		19.315 (3.314 -35.316)	0.018
Sex x Age (within Context)	$F_{10, 440}$=0.850 p=0.580		
Male x 1-6 mo (within Asian wild)		-13.391 (-72.538 to -0.245)	0.048

4.4.4.3 Mother Moving

No significant differences were found in the mean percentage time that mothers (of calves) spent moving, in sex or age of calf (*p*=0.789), context (*p*=0.394), or interactions between them (age by sex, *p*=0.382; age by context, *p*=0.478), sex by context (*p*=0.083), or sex by age within context (*p*=0.195; overall model fit $F_{36, 507}$=1.437, *p*=0.051). There was, however, a highly significant contribution of mother ID (Var (ID)=679.463, *p*<0.001). (See Table 3.7, Chapter Three, for N of calves and N of observations; dependent variable was mother Moving; independent variables were calf age, context, calf sex and the interactions between them).

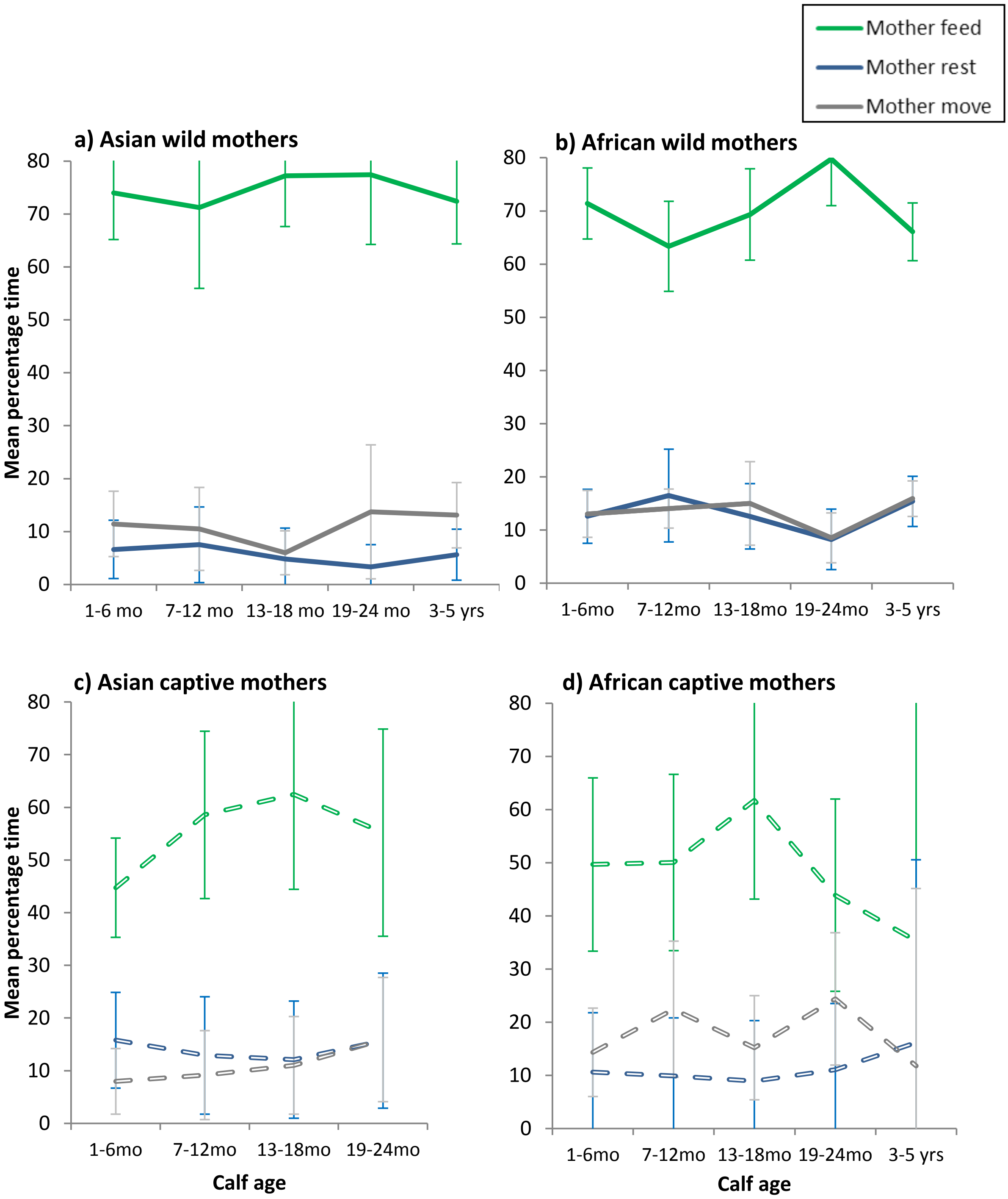


Figure 4.6 Mother Activity Budgets by Context and Calf Age. Mean percentage time mothers feeding, resting. Calf sex here not separated here as not significant differences between calf sexes. See Table 3.7, Chapter Three, for N. 95% CI.

4.4.5 Abnormal Behaviours

No relationship was found in captivity between the addition or removal of group members (including births and deaths) and frequency patterns of abnormal behaviour in adults in the form of stereotypies (Figure 4.7; 4.8). Neither Asian elephants at Chester (Figure 4.7) nor African elephants at Howletts (Figure 4.8) showed any relationships when mean stereotypic frequency per adult was calculated per study visit (5-7 days).

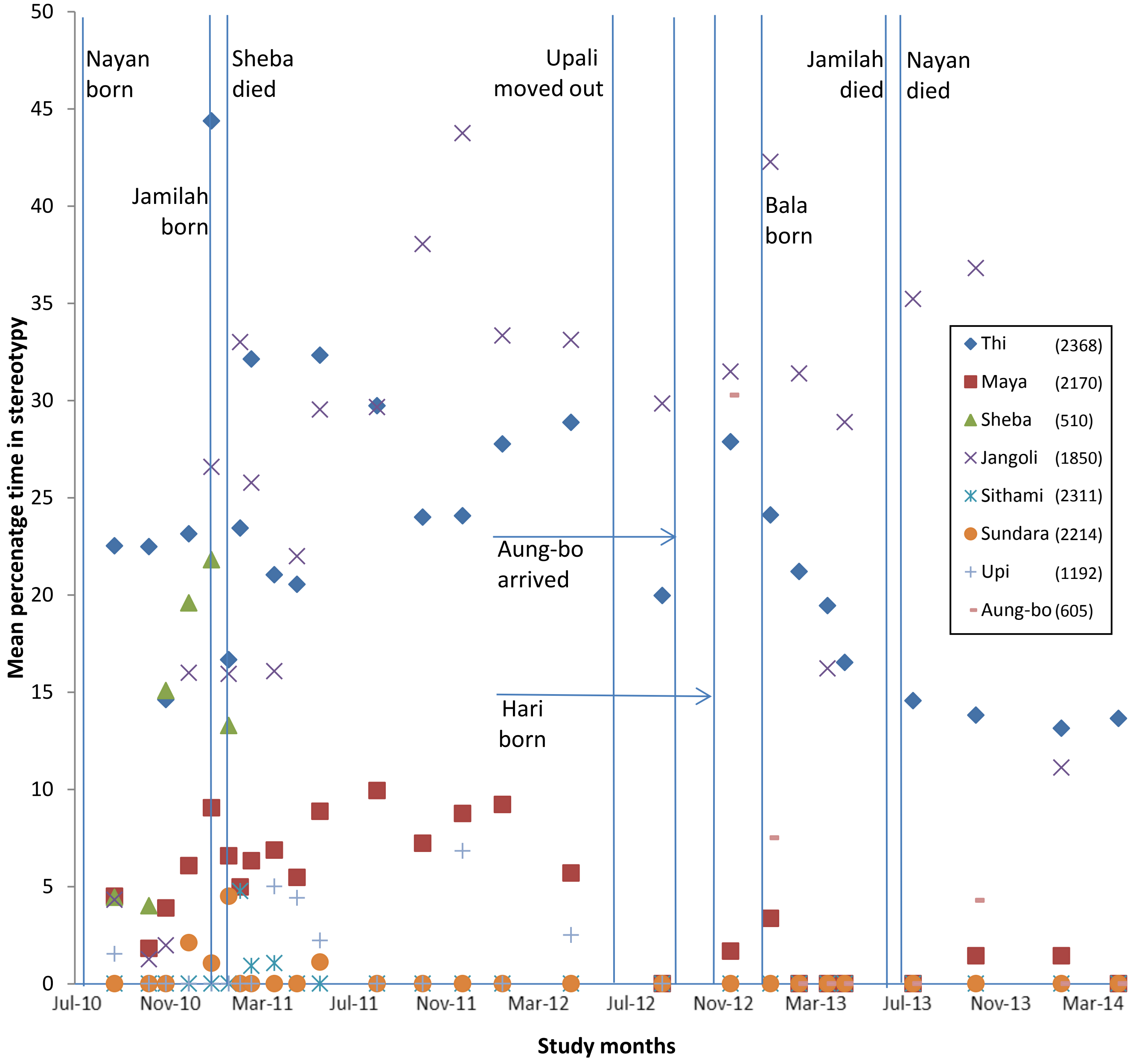


Figure 4.7 Mean Percentage Time Exhibiting Stereotypic and Abnormal Behaviours at Chester Zoo for Adult Asian Elephants. Key includes N scans per elephant. Data from 25min group scans from 8am-6pm, July 2011 to April 2014. Means across visits of 7 study days in Jan/Feb 2011, Feb 2011, and Feb/Mar 2013; and 5 day visits for all other points.

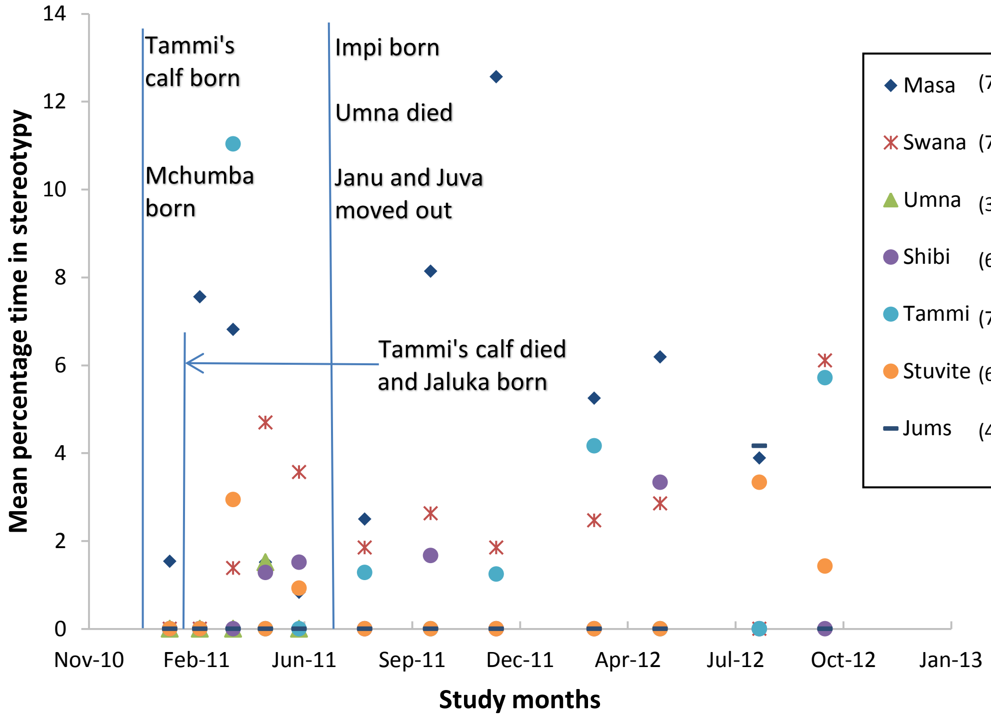


Figure 4.8 Mean Percentage Time Exhibiting Stereotypic and Abnormal Behaviours at Howletts WAP for Adult African Elephants. Key includes N scans per elephant. Data from 25min group scans from 8am-6pm. Means across visits of 5 study days in May 2012, August 2012, and October 2012; 6 day visits for all other points.

The captive elephants carried out abnormal behaviours, including stereotypies, in various ways. Table 4.9 shows which abnormal behaviours each elephant performed (age range: 1-55 years) at Chester. Keepers at Whipsnade actively command Azizah to stop swaying.

Maya's stereotypy seems to have changed since 1999 as she no longer appears to exhibit the particular stereotypic pacing Rees (2004) documented "*which involved repeatedly walking towards the door of the elephant house, walking in an arc around a wall to a steel fence, and then back again*" (p38).

Rare-occurrence stereotypies with short durations were not captured within scan recording for non-adult individuals. However, captive African female, Etana (two years old), was observed performing a similar leg-shake stereotypy as her older brother, Janu (five years old). In addition all captive African females above the age of ten years (plus Mansi, Juva and Jara - aged one, five and six years, respectively in January 2011) were recorded 'dusting themselves' using faecal matter during 25 min instantaneous scans, indicating that this abnormal behaviour was not a particularly rare occurrence. However, the activity of using faecal matters as dusting material was never seen in the wild in Asian or African elephants (pers. obsv. for wild Asian elephants; P.C. Lee, June 2015, pers. comm. for wild African elephants).

Table 4.9 Stereotypic and Abnormal Behaviour Exhibited by Individual Captive Elephants. **Rees (2004) reported stereotypies in 1999 of Chester Zoo's elephants. #Mansi (1yr), Juva (5yrs), Jara (6yrs) and all captive African females above the age of 10yrs were recorded 'dusting themselves'.

ID	Age in Jan 2011 (yrs)	Zoo	Species	Sex	Stereotypies and Abnormal Behaviour
Sundara Hi-Way	~7	Chester	Asian	F	Very rarely seen: small head and body bobs, usually around time of high arousal (i.e. birth of a new calf in the group); fast head bobbing; head shaking; weaving head whilst eating hay.
Aung-bo	~10	Chester	Asian	M	Subtle pacing of same large pattern.
Upali	~15	Chester	Asian	M	Subtle repetitive slow pace walking with trunk movement, turn and slight kick at same points. (**No stereotypy in 1999).
Sithami Hi-Way	~18	Chester	Asian	F	Rare: kicking or digging sand (Frustrated? Absent minded?). (**No stereotypy present in 1999).
Thi Hi-Way	~29	Chester	Asian	F	Side-weave and sway; head side to side weave. (**Weaving from side-to-side).
Maya	~42	Chester	Asian	F	Side sway; slow walking back and forth; sucking own trunk; touching & pulling on own nipples; resting trunk between legs. (**Head-bobbing, linear pacing, and pacing-arc around an obstruction).
Jangoli	~42	Chester	Asian	F	Assortment of walk back & forth; side & diagonal weave (weight shift all 4 feet); figure-of-eight on front legs; rocking; sucking trunk. (**Head-bobbing and linear pacing; walking forward then backwards).
Sheba	~55	Chester	Asian	F	Assortment of weaves and head-bobbing (**Head-bobbing up and down).
Azizah	~27	Whipsnade	Asian	F	Head & trunk sway, weaving No clear function to her occasional yawns or raising of her front foot.
Kaylee	~27	Whipsnade	Asian	F	Extremely rare: Walking back and forth slowly.
Lucha	~29	Whipsnade	Asian	F	Extremely rare: Slow pace back and back & forth by gate with repeated pattern.
Tammi's calf	1mo	Howletts	Asian	F	Sucking enclosure doors and bars.
Mansi	~1	Howletts	African	F	#Wind-sucking on trunk; almost-handstand.
Juva	~5	Howletts	African	M	# 'Moonwalking'.
Janu	~6	Howletts	African	M	#Leg-shake.
Jara	~6	Howletts	African	F	Perhaps following her mother's pacing, rather than her own stereotypy.
Tammi	~24	Howletts	African	F	# Indoor pacing before being let out in morning. Coprophagy.
Swana	~26	Howletts	African	F	# Rare: sway; head-bob; crossing-legs; and trunk behaviours.
Shibi	~34	Howletts	African	F	# Rare: sway with head & neck.
Masa	~42	Howletts	African	F	# Sway. Coprophagy.

Eating faeces was observed, rarely, in wild calves in Amboseli NP among the age class that was starting to be more reliant on independent feeding. While eating faeces was, therefore, a normal but rare behaviour observed in wild Asian and wild African calves (and captive calves); coprophagy was only observed in non-infants within the context of captive African elephants, and was so observed rarely in wild non-infants as to be a distinctive and surprising behaviour (Table 4.9; pers. obsv. for wild Asian; P.C. Lee, June 2015, pers. comm. for wild African elephants).

Wild African calf of around 18 months in Amboseli eating faeces. Photograph credit: P.C. Lee

Orphaned and bottle-fed captive African calf Mansi had abnormal standing postures, presumably as a result of gastrointestinal discomfort. On occasion, she would almost be doing a handstand with one or more of her (crossed legs) lifted slightly off the ground. This abnormal posture was not observed in any other elephant regardless of age or context. Tammi's rejected and bottle-fed calf displayed different abnormal behaviours such as trying to suckle at enclosure doors or bars.

Captive female African orphan Mansi's abnormal standing posture. Photographs taken (left) 17th May 2012; (right) 6th March 2012.

For all captive elephants, the percentage of scans spent stereotyping did not differ by season (warm or cold: Mann Whiney U, $Z=-.056$, $p=0.95$, $N_1=67$, $N_2=90$), despite previous observations in Asian elephants at Chester by Rees (2004).

4.5 Discussion

Individual calf ID was a significant factor in analysis of calf feeding, resting and moving as well as mother moving, which means there was, unsurprisingly, a large individual contribution to the overall pattern of the data. Despite this considerable (and significant) contribution of individual to the variance patterns in the tests presented, calf age and context still significantly influenced the calf behaviours over and above the effect of the individual. I would note again, however, that due to small samples, high individual variance and non-normal distributions of data, results are interpreted with caution.

For all contexts, maintenance activities of independent feeding, resting and moving occupied the majority of activity budgets for both calves and mothers. There were some notable changes in calf activity with age as feeding increased consistently in the first five years of life (with plateaus after 18 months), resting and moving decreased with age overall. No differences were found across contexts for mother activity of moving, while context differences were found in mother feeding and mother resting behaviours. Wild mothers engaged in more time feeding than captive mothers, while both wild African and captive Asian mothers rested more than wild Asian mothers.

A variety of stereotypic behaviours were performed by the captive study animals. However, no relationships were found between the percentage time captive elephants spent performing stereotypies and the transfers, births and deaths of other group members, or between seasons.

Animals are forced to choose between activities when they cannot be carried out simultaneously. This can incur costs to the individual in that their opportunities to engage in one biologically important activity may need to be traded off against another (Dunbar, 1992; McFarland, 1974). Animals need to make decisions on how to best use their day, which is a fixed period of time, and these decisions can affect energy resource acquisition, reproductive success and may even have social consequences. Decisions made reflect biological priorities and it has been suggested that time allocated to feeding is an "*absolute priority*", essential to survival, whereas time allocated to behaviours such as resting seem to make use of a pool of "*uncommitted free time that can be converted into another activity when required*" (Dunbar, 1992, p.37).

However, not all behaviours need to be traded off completely as a few can be carried out at the same time, although there still may still be trade-offs in the efficiency of the combined behaviours when compared to being exclusively engaged in only one or the other. Captive and wild mothers and calves spent comparable time moving. Although it may be expected that wild elephants need to move more in order to forage for resources than captive animals do, perhaps wild elephants are moving whilst foraging and these behaviours of 'feed walk' would have been included in feeding for analysis.

The transition from suckling to independent feeding in infants is marked by the occurrence of 'weaning conflicts' where mothers begin to try to prevent their young from suckling by actively denying them access to the nipple (Barrett, Dunbar & Dunbar, 1995). In elephants, females do this by moving their forelegs back to cause a physical barrier or by walking away from the calf. Parent-offspring conflict theory (Trivers, 1974) predicts that such weaning behaviour will arise when the interests of mothers and infants differ in terms of the amount of investment the infant should receive from the parent (in the form of milk). This conflict is typically described as a "*genetic conflict of interest*" (Barrett et al., 1995, p. 805). While mothers are related to each of their offspring to the same degree and therefore are selected to provide equal investment to each of them, individual offspring are more closely related to themselves than they are to their siblings and they consequently demand more maternal care for themselves than their mother is selected to invest (Trivers, 1974).

However, Altmann (1980) and Dunbar and Dunbar (1988) propose that weaning behaviour may not solely be the result of the parent-offspring conflict about the amount of investment provided to offspring, but may result from disagreements about the scheduling of this investment. Conflicts therefore arise when mothers try to teach their offspring to suckle at times when this infant activity does not interfere with her own activities (Barrett et al., 1995). This is especially important for nursing females, who have the added energy demands of lactating, and therefore need to forage more to fuel this demand (Lee, 1987). However, this scheduling hypothesis may relate more to primates rather than elephants since as primate infants grow, their presence on a mother's nipple further inhibits her ability to carry out activities such as foraging and mothers are further constrained by carrying infants. The growth of an elephant calf would be unlikely to have the same effect of encumbering mother activity since an elephant mother can engage in foraging at the same time as nursing, regardless of calf size. However, the slow movements of young calves inhibit wild mothers' rates of travel and feeding (Lee, 1987). Thus allomothers take on some of the mother's protective functions when they are available.

While elephants have to choose trade-offs in their time budgets, biases in sampling methods may report different proportions of activity budgets observed than the true proportions actually being expressed. One example is that the behaviour of small calves within long dense vegetation (resulting in poor visibility of them) is more likely to be recorded as out of sight than are taller elephants whose same behaviour (perhaps foraging for vines as an example) would be visible above the vegetation and therefore recorded. If recordings are not made of certain behaviours and are repeatedly missed, then not only will this behaviour be underrepresented as a proportion but all other behaviours expressed will increase as a calculated proportion. This is particularly important in this study when comparisons are being made between contexts where sampling methods differ in habitat and distances between the animals and observer, thus affecting visibility differently between the contexts.

Although temperatures may have had effects on the behaviour of elephants being observed, samples in Amboseli were balanced by month, season, and time of day (day length does not vary), as were those for captive calves. In Sri Lanka, where data were only collected in May-July in the dry season, the temperature remained relatively constant across the year and therefore should not have biased my results.

Some biases may have arisen as a function of day length in captivity. Both captive Asian elephant facilities, Chester and Whipsnade, had natural and artificial lighting. However, only artificial lighting was used in the housing at Howletts for captive African elephants. Season may have had an impact on behaviour over and above affecting temperature and day length because (prior to 2015) the groups at Howletts were either locked inside in the houses in cold conditions (<8°C at night) or locked outdoors in the paddock in warmer months. It might be expected that the complexity of social grouping, grazing opportunities and space allowed in the warmer months when locked outside (versus the small barren concrete indoor houses, with 0-3 other elephants) would have as strong if not stronger impacts on elephant behaviour than time of day, temperature and day length.

It is probable, however, that resting behaviour recorded in wild Asian elephants was affected by a major sampling bias in observational methods and must therefore be interpreted with care. While observations in Amboseli and the UK were spread out across the day, in Uda Walawe researchers generally left the park during the peak heat of the day, from around 11.30am-1.30pm, and therefore few observations were made in these hours. This was due to the combination of elephants seeking shade during this period of the day and of researchers needing to seek shade themselves. In the peak heat of the day, wild Asian elephants were resting in shade under trees (pers. obsv.) and a decision was made not to collect data on individuals since there seemed to be little if any variance in their activity from rest. When groups rested together under trees, visibility of calf behaviour was further hindered at times by the physical presence of many larger elephants in close proximity, i.e. calves are often hidden in a ‘forest of legs’. The significantly lower percentages of time wild Asian calves and mothers were shown to be resting compared to wild African and captive Asian calves and mothers is probably a function of this sampling bias showing less resting than is truly occurring.

Wild Asian group containing adult females (including [Bali], [Bashi] and [278]), sub-adults, juveniles and calves all taking shade together in the midday heat in Uda Walawe. Photograph taken 22nd June 2011.

These biases may also explain why percentage time in independent feeding was higher in wild Asian calves than all other contexts since it follows that if less resting was recorded in wild Asian elephants due to sampling bias, then the proportion of time calculated for other activities will be altered to show higher proportions in the daily activity budgets.

Comparison of daily activity between contexts may also be skewed since behavioural observations were only collected during the day (see Chapter 3, section 3.3 for definitions of day). Calves and mothers may therefore be engaging in different behaviours in 24hr periods across contexts than is reflected in the diurnal data collected in this study. For example, captive Asian elephants in the UK were found to rest at different times than wild African elephants did (see, Williams, Bremner-Harrison, Harvey, Evison & Yon, 2015).

On the other hand, Table 4.2 (Section 4.2) illustrates that the Amboseli day time sample was representative of 24hr activities (Lindsay, 2011). From 6am-5:59pm, the Amboseli elephants (n≥372) were shown to feed for 55.5% of their time, rest for 16.7% and move for 10.3%. Similarly, from 6pm-5:59am, they fed for 46.4% of their time, rested for 18.0% and moved for 7.3% (Table 4.2). For Sri Lanka, time of day within a 24hr period would be expected to affect elephant behaviour by varying in: ambient temperature and the need for the elephants to keep warm/cool; daylight; in predator activity and subsequent avoidance of them; and in human activity (i.e. local villagers, traffic and tourists). In captivity the effects of time of day are expected to be marked due to public and keeper presence (e.g. Yon, 2014). Other more intense confounding factors affecting behaviour in captivity may include: no feeding at night; being housed in different social groupings at night; different housing/enclosures (sometimes without outdoor access) at night depending on temperature, season, weather and the presence of new calves or expectant mothers; and no interruption from humans at night. Indeed, in addition to showing that time of night was a factor affecting rest bout duration in captive Asian elephants, Williams et al. (2015) showed that they also had substrate preferences when choosing where to rest and rested more when conspecifics were nearby.

At time of data collection, observation of nocturnal behavioural data was not feasible as only Chester had cameras and these were not detailed enough for behavioural observations in the dark. However, newer night-vision cameras have now been installed at all three facilities, permitting studies to be carried out from 2012 on resting behaviour and social patterns at night (Williams et al., 2015; R. Wazara PhD project, ongoing).

As expected, wild mothers of both contexts engaged in feeding for more time than captive mothers. This highlights a need for husbandry changes in captivity to allow captive mothers to engage in more foraging opportunities.

Abnormal Activities

Although in the three UK captive facilities of this study, stereotypies in calves were rare, Vanitha et al. (2015) found that stereotypies were more prevalent in young captive elephants in southern India than in those older than 15 years. Their study of 144 captive Asian elephants (45 in temple, 44 in private and 55 forest department management systems) showed that both the number of elephants performing stereotypic behaviours and the duration of the stereotypies decreased significantly with age. They also found a strong negative correlation between the prevalence of stereotypies and free access to conspecific association until the juvenile stage (age not specified) and suggest that younger elephants were more susceptible to developing stereotypies in private and temple systems due to isolation from conspecifics and the disruption of association with maternal relatives (Vanitha et al., 2015). In order to mitigate stereotypies developing in younger age classes they therefore recommend that juvenile and sub-adult females are given free access to conspecifics to help them overcome the initial loss of their mother. They highlight the potential importance of attachment processes and social relationships between females and others who are not their mother, stating that "*sharing of mutual interests, sharing experiences, doing things together, sharing the responsibilities and thus reducing stress, are all part of social life of the species*" (Kurt and Garaï, 2007; Vanitha et al., 2015, p. 144). Within my study none of the captive calves were studied during or shortly after the loss of their mother (although Mansi had lost her mother four months prior to the start of data collection, and Jaluka and Impi both lost their mother after data collection was completed) and all calves were given free access to at least one other conspecific (with the exception of Tammi's calf).

No abnormal or stereotypic behaviour was observed in the wild although captive and wild calves (<24 months) of both species were observed eating faeces and this behaviour can be considered normal in infants. However, it is atypical in older ages, yet was observed regularly and repeatedly in older ages of captive African elephants. Classification of 'abnormal' behaviours includes behaviours which are both species atypical, only being observed in captivity, or those that are performed at higher rates in captivity than they are in the wild (Birkett & Newton-Fisher, 2011; Hopper, Freeman & Ross, 2016). Coprophagy has only been reported at very low levels in wild elephants, particularly in adults. Leggett (2004) stated that coprophagy has only been reported once in wild African elephants before his own report of a three month old female calf (in 2002) and two adult males (approximately 20 and 40 years old, in 2003). This earlier account was in 1977 when Guy observed two sub-adult females, one sub-adult male and two juveniles (of unkown sex; ages not specified) eating faeces of the dominant female. In my study no coprophagy was observed in non-infants in the wild. Coprophagy in non-infant elephants would therefore traditionally fall into the latter category where it ‘differs from the norm’, resulting in it being grouped with other abnormal behaviours which are used in captive environments as indicators of poor welfare (Birkett & Newton-Fisher, 2011; Hopper et al., 2016). This is also the case for captive chimpanzees, although Hopper and colleagues (2016) caution that classifying coprophagy with other abnormal behaviours “*has arisen from a top–down approach based on a prior assumptions*” and that “*categorising all abnormal behaviours together ignores variation in their etiologies, which limits our ability to understand them and provide useful interventions*” (p. 112).

Hopper et al. (2016) went on to carry out Principle Components Analysis on observed behaviours of 60 captive chimpanzees, showing that coprophagy loaded onto the ‘social’ factor (positive social behaviours such as giving and receiving grooming) and not onto the ‘abnormal’ factor (abnormal behaviours such as abnormal body manipulations). Coprophagy in chimpanzees was also performed at higher rates in captivity when chimpanzees were mother-raised than in those which were human-raised (Hopper et al., 2016). It has been suggested (Freeman & Ross, 2014; Hopper et al., 2016) that coprophagy in chimpanzees is a socially learnt ‘cultural’ behaviour. However, while coprophagy may be a ‘disagreeable normal behaviour’ in captive chimpanzees, it should be reiterated here that in elephants, coprophagy is extremely rarely observed in adults in the wild; with no cases observed in the wild in this study, and within captive settings only non-infants were observed engaging in coprophagy. Copraphagy should thus remain at present, classed as an abnormal behaviour in non-infant elephants.

In young animals (e.g. foals) coprophagy is an important biological trait and it is thought that the ingestion of fresh faecal matter enables individuals to populate their guts with relevant bacteria (Francis-Smith & Wood-Gush, 1977; Mullen, Yasuda, Divers & Weese, 2016). However, in foals this activity was not reported before the age of two weeks or after the age of five weeks (Francis-Smith & Wood-Gush, 1977). The low digestive efficiency of elephants may also explain why some older individuals are sometimes observed engaging in coprophagy. Intact items, especially in captive elephants fed on diets including fruit and vegetables (pers. obsv.) sometimes appear in the faeces even after being passed through the digestive system and these items may be of interest for other elephants to re-ingest (Hatt & Clauss, 2006).

Other records of captive elephants ‘dusting themselves’ by throwing faeces onto themselves or around the enclosure in repeated unvarying manners (Clubb & Mason, 2002; Stoinski, Daniel & Maple, 2000; Wilson, Bloomsmith, Crane & Maple, 2001) were also only found in African elephants.

Abnormal behaviour observed in the captive female African calves (Tammi's calf and Mansi) may be associated with their separation from their mothers. The separation of offspring from their mothers, through either translocation or the death of their mother, has been shown to be associated with both long and short-term effects such as increased anxiety, increased stress, poorer social skills and the development of abnormal behaviours (Latham & Mason, 2008; Ljungberg & Westlund, 2000; Prado-Oviedo et al., 2016).

Stereotypic behaviour is a major welfare concern in captive elephants and has been reported to be performed by 54% of UK and Irish zoo elephants during the day ($total_N$=77, $Asian_N$=41, aged 0.6-50yrs; $African_N$=36, aged 0.5-40yrs), and by 48% at night (N=41) (Harris et al., 2008). In another report, 40.9% of 22 female captive elephants ($Asian_N$=13, $African_N$=9) were shown to perform stereotypies with mean frequencies higher in Asian (6.8%, range 0-29.0%) than African elephants (0.9%, range 0-4.0%) (Clubb & Mason, 2002). Rees (2009) suggests captive elephants express anticipatory behaviour when waiting to be given access to outdoor or indoor areas (which are usually stocked with food to encourage movement into the new area), and stereotypies have been reported to increase just before feeding times or before being given access to outdoor or indoor areas (Harris et al., 2008).

In contrast to Rees (2004), this study's data did not find any relationship between frequency of stereotypies and season (warm or cold). Data collection, however, differed in that data from this thesis was collected across all seasons (in all 12 months of the year and even across different years totalling more than five times as many study days), covered a greater range of the day, included indoor as well as outdoor behaviour, included three facilities and observed both Asian and African elephants. Rees's (2004) study compared the warmest and coldest months but did not collect data for, arguably the coldest, 12 weeks of the year. He states the maximum and minimum daily temperatures as 28°C and 4.3°C, whereas observations from this study involved daytime temperatures of -5°C (when both researcher and elephants were outside during indoor cleaning of enclosures).

I chose not to investigate the relationship between stereotypies and season any further for two reasons. Firstly, my analyses did not indicate any degree of relationship. Secondly, season and temperature are confounded by many other variables such as: colder months are also when the group are generally kept indoors for more hours; in poor weather groups were also kept indoors when newborn calves were present; day-length is reduced; visitor numbers are lower; and even that diet changes with a reduction in fresh browse availability.

A further explanation for the contrasting findings between this thesis and Rees's (2004) study in 1999 may possibly be an improvement in zoo husbandry in the last 10-15 years and this could perhaps have reduced the percentage time elephants engage in stereotypic behaviours. Negative correlations have been reported between the frequencies of stereotypic and feeding behaviour (Rees, 2009) and an increase in food enrichment and browse in captive diets in recent years is therefore likely to have increased the time captive elephants engage in foraging compared to activity budgets a decade or more ago. In addition, the intensity of anticipatory behaviours could possibly have been lessened by forage being provided across more of the day rather than in bulk times. For example, at Chester in 2006, there were three main feeding times, in addition to daytime scatter feeds and hay boxes being opened: once during morning FC training – pellet feed with vitamins, plus training food such as apples around 8am; a second time when given access to the outdoor paddock – mainly hay and vegetable, with some browse around 10am; and a third when they were allowed back inside for the evening – mainly hay, some browse and enrichment such as hidden apples (pers. obsv.). During data collection at Chester (2010-2014) however, food provision was spread out more evenly across the day (and night, using haynets on hoist and timer systems; the development of enrichment is discussed further in Chapter Seven, Discussion). Therefore it is logical that stereotypies may have reduced due to the opportunity to forage more and thus also increased time spent in feeding activities. Management improvements may also cause reductions in the elephants' motivation to access and move into enclosures set up with food, thus reducing anticipatory behaviour. 'Hunger' is a management tool used in captivity for many species to entice animals to move between enclosures (e.g. feeding meat to tigers in their indoor enclosure to 'bring them in' from outdoors areas for the night). However, use of this tool in animals such as horses and elephants, who spend most of their day feeding in the wild, is a welfare concern in captivity if they are denied the opportunities to express natural time budgets. This is discussed in more detail in Chapter Seven, Discussion.

In further support for the suggestion that management improvements may have helped reduce the occurrence of stereotypies in the past decade, research in the US captive Asian and African populations showed that the risk of stereotypic behaviour is mitigated in both captive adult males and females by the presence of calves in the group (Greco, Meehan, Miller, et al., 2016). In the case of Chester again, only one individual was present under the age of 24 months during Rees's (2004) study whereas up to four calves under the age of 24 months were present during data collection for this study. Prado-Oviedo et al. (2016) highlight that successful breeding may therefore provide captive elephants with a protective effect from the development of future stereotypic behaviours by increasing the numbers of young animals present in groups.

Chapter 5:
Early Calf Interactions with Mothers and Others

Captive Asian newborn Scott beside his mother, Azizah, as young female Gheta investigates. Photograph taken 23rd October 2011.

5.1 Abstract

This Chapter aimed to assess the social experiences of elephant calves in captive environments (Asian$_{N=8}$; African$_{N=7}$) by exploring early calf interactions with mothers (Asian$_{N=4}$; African$_{N=4}$) and other elephants. I then compare these interactions to those for both wild Asian (calves$_{N=101}$; mothers$_{N=90}$) and African elephants (calves$_{N=237}$ for proximity to non-mothers and calves$_{N=130}$ for all other behaviours; mothersn$_{N=105}$). I focus on lactation as the primary energetic contribution of maternal care and how this changes with calf age. I explore the relationship between calf and mother activity synchrony since the needs and interests, of both the mothers and calves, differ between captive and wild environments as well as with calf age. I also investigate time spent in close proximity to – and therefore the potential to interact with - mothers and non-mother neighbours and non-play social interactions with these neighbours.

Mother activities correlated with calf activities but without any consistent patterns by age or context. Wild African elephant mothers and calves, however, showed greatest

synchrony of activity, such as moving, which was correlated between mothers and calves across all calf ages up to 24 months (1-6, 7-12, 13-18 months: $p<0.001$; 19-24mo: $p=0.002$).

As calves aged, they all spent less time close to mothers ($p<0.001$). Wild Asian calves spent more time in close proximity compared to other contexts ($p<0.001$) and tended to engage in suckling interactions more frequently for age than did wild African calves ($p=0.020$). Across contexts, time spent in suckling interactions decreased significantly between 1-6 and 19-24 months ($p=0.015$).

Proximity to non-mothers was qualitatively similar across contexts except captive African females were less likely to have close neighbours. Non-play social interactions were diverse and least frequent in wild African calves of all ages (pairwise with: wild Asian $p<0.001$; captive Asian, $p=0.012$; captive African: $p=0.018$).

Case studies for individual captive calves are presented to illustrate the variance between calves in captivity.

5.2 Introduction

Mothers invest both time and energy resources in parental care of their offspring, at the expense of maintenance, survival or future reproduction (Altmann & Samuels, 1992). Investment of lactation has been studied for decades and will be investigated here in terms of the time calves spend in suckling interactions.

Elephants are also well known for providing allomaternal care (Lee, 1987; Vidya, Fernando, Melnick & Sukumar, 2005) and allomothering by young females and siblings contributes positively to the wellbeing and survival of calves in the wild (Lee, 1987). In this Chapter, I therefore examine mother and non-mother neighbour (NN) proximities to calves as representatives of the potential for interactions, such as allocare. Finally, non-play social interactions with these neighbours and the issues of availability of these social partners will be investigated.

Lee (1986) found sex differences in interaction and relationships and suggested these were "*related to later mating tactics and association patterns of adults*" (p. 388). Males, who intensively compete for access to females for mating, grow at faster rates than females and, in due course, may weigh twice as much as females when fully grown (Poole, 1994). While males are more likely to interact with ‘strangers’ than females are, females show more interest in interacting with and allomothering young calves (Lee, 1987).

Animals that live in groups have a need to synchronise their activities, such as feeding resting and moving, in order to maintain group cohesion (Aivaz & Ruckstuhl, 2011; Conradt & Roper, 2000). If individuals are unable to coordinate their activity with the rest of their companions then they may need to separate (Ruckstuhl, 1998). Individuals differ in their interests and physiological needs, and these demands influence behavioural synchrony within pairs or groups (Altmann, 1980; Fichtel, Zucchini & Hilgartner, 2011; Stevens, Bertelsen, Sijmons, Van Ranst & Maes, 2013). The demands themselves differ across age, sex and reproductive state and result in potential trade-offs. For a mother-calf dyad who has diverse needs for food, water and security, it would seem that both individuals would benefit from coordinating their activities. Coordinating mother and infant activities may have further benefits to mothers such as maximising their time budgets for energy intake. In primates, as an infant grows and still attempts to nurse, infants begin to interfere with their mother’s energetic efficiency (Barrett et al., 1995). However, Barrett et al. (1995) found that infant gelada baboons (*Theropithecus gelada*) over the age of four months, were more likely to suck when their mother was at rest or socialising; when nursing did not hinder her other foraging activity. This maternal activity influence on infant activity resulted from rejection of infants during activities where the presence of an infant hindered the mother; it was suggested that the mothers were training their infants to make contact at appropriate times, rather than limiting access to the nipple (Barrett et al., 1995). In this Chapter I will therefore look at co-ordination between mother and calf activities. As needs and interests, in both mothers and calves, differ between captivity and wild, as well as with calf age, it would be expected that any synchrony of activity may differ between these contexts.

Calves need to be in close proximity to their mothers during suckling interactions, but also for comfort and protection, from predators and the environment (Nair, 1989). Proximity to mother is used in this Chapter as an indicator of the potential for care-giving since when individuals are physically close (<2m), they can interact and provide care. I investigate the nature of time spent in close, mid and far proximity (see Table 3.2) between mothers and calves and, as in the previous Chapter, I ask whether proximity differs with calf age, sex, species or captive or wild contexts.

Captive African newborn Mchumba, suckling from his mother, Masa, Photograph taken 3rd March 2011.

In addition to learning how to schedule her activity budget with her calf's, a first-time elephant mother needs to learn to respond to their calf's requests to suckle in order to optimise the costly allocation of lactation (Lee & Moss, 2011). In mammals, the central component of maternal care is producing milk to aid the growth of offspring (Jonas & Woodside, 2015) and lactation is thought to be the most costly phase of the mammalian reproduction cycle; requiring an estimated 75% of the energetic cost of a reproductive event (Andrews et al., 2005; Byers, 1997; Moreno, Ibáñez & Barbosa, 2011). The costs of lactation are so great that during poor seasons mothers of calves under two years of age face higher mortality risks (Lee et al., 2011). The costs of lactation have been estimated for many species (e.g. gazelle, *Gazella cuvieri* and *G. dama mhorr*) through maternal weight loss, infant growth and infant mortality, in addition to investigations on suckling frequency and milk intake (Moreno et al., 2011).

While suckling may not directly equal intake (Cameron, 1998; Hinde, Power & Oftedal, 2009), suckling and suckling interactions stand as proxies in this study for allocation of care and time. Time is an important constraint on the reproductive potential of a multi-year lactating species like elephants. Previous studies have found that post-natal maternal care in mammals decreases with the age of the offspring (savannah baboons, *Papio cynocephalus,* Altmann & Samuels, 1992; humans, Butte, Wills, Jean, O'Brian Smith & Garza, 1985).

In this study, in addition to successful suckling, maternal social interactions include behaviours such as Solicit Suckling, where a calf will try to gain access to a teat by walking in parallel to its mother while pushing against her front legs or using its trunk to touch the breast (Poole & Granli, 2011). Begging calls may accompany this behaviour (Lee, 1987; Lee & Moss, 1986), although we did not record them here, due to variations in the capacity to accurately detect these across wild and captive sites. Mothers can allow the calf to suck, generally remaining very still, or can block its access by moving her leg back or simply walking off. A mother can also reject a calf who is already suckling and this may even be done aggressively either by bumping the calf away with her elbow or slapping or pushing (Lee, 1987; Lee & Moss, 1986). Again, frustration calls, cries and roars are often made by the calf upon a rejection from suckling but were not recorded here (Poole & Granli, 2011). For definitions of all other suckling-related behaviours see the Ethogram (Appendix C, Table C1).

This Chapter provides a detailed exploration of suckling interactions and I will compare wild mothers (energy limited) with captive mothers (energy unlimited) in relation to whether this affects how they interact with calves and allocate time to their own maintenance activities (see Chapter Four). Lee & Moss (1986) have shown that in wild African elephants male calves attempt to suckle more often than females. These males were also more successful than the females in their attempts and consequently were estimated to have higher milk intakes than females as well as higher growth rates (Lee & Moss, 1986). Hourly rates of suckling also decline with age in wild African calves, while independent feeding increases (Lee & Moss, 1986). In captive calves of both species and sex, independent feeding was found to negatively correlate with suckling interactions (see Chapter Five, Section 5.4.3). Hence, in this study it is expected that calves across all contexts will suck less with age, that male calves will suckle more often and that there will be no differences in suckling interaction rates with species or between captive or wild contexts.

Early growth of elephants strongly impacts their health and survival (Lee & Moss, 2011) and calves are highly dependent on their mothers for their first two years of life, while nutritional intake in the first three months of a calf's life is exclusively from their mothers (Lee & Moss, 1986). The initial secretion of colostrum, provided to newborn mammals, is essential to support a healthy immune system and helps develop normal gastrointestinal function by supplying immunoglobulins, growth factors, and prebiotics, such as oligosaccharides (Abbondanza, Power, Dickson, Brown & Oftedal, 2013). In elephant milk, lactose is the dominant carbohydrate, and, after at least a month of lactation time, lactose is supplemented by oligosaccharides (Kunz, Rudloff, Schad & Braun, 1999; Osthoff et al., 2008; Osthoff, de Wit, Hugo & Kamara, 2007). While lactose remains an energy source for calves, milk oligosaccharides may also provide anti-infection protection and milk oligosaccharides in human milk are reported to "*promote the growth of the bifidus flora"* in a newborn baby's intestine (Kunz et al., 1999; Uemura et al., 2006, p. 477). Uemura et al. (2006) suggest that sialylated oligosaccharides in Asian elephant milk may also have a significant function in the development of a calf's brain which is both large and grows rapidly (Kunz et al., 1999).

Andrews et al. (2005) found patterns of suckling in an individual captive born male African calf were similar to patterns seen in the wild in Amboseli. Their study also found the growth rate of this naturally sucking calf was reduced compared to that of hand-reared Asian calves.

Along with prolonged and intense maternal care, elephants are known for allomothering (Gadgil & Nair, 1984; Lee, 1987). Females, including nulliparous females and grandmothers, allomother by acting as guardians who provide comfort to related calves, through touch, and occasionally through allosuckling (Gadgil & Nair, 1984; Lee, 1987; Lee & Moss, 2011; Nair, 1989). Allonursing itself is likely to have a pacifying effect on calves rather than to supply nutrients, and one wild sub-adult Asian female in India has been recorded allowing a calf to suck on the tip of her trunk (Vidya, 2013).

Caretaking and allomothering of calves plays a vital role in the social structure of elephants and is thought to be a strong selective factor in the evolution of these social structures (Gadgil & Nair, 1984; Lee, 1987; Schulte, 2000). Allomothering may strengthen social bonds, by increasing affiliative and cooperative behaviours within a group as well as limiting aggression. Schulte (2000) therefore predicts that there may be higher levels of aggression in captive groups who lack a history of allomothering, compared to captive or wild groups with this experience. He states that the degree of relatedness and length of time together should be reflected within a captive group and that it is crucial to provide nulliparous females with allomothering experiences if allomothering enhances the rearing success of her own calf in the future (Schulte, 2000). In Asian elephants in European zoos, lack of allomothering or maternal experience was shown to significantly influence reproductive failure (Hartley, 2016; Hartley & Stanley, 2016). Although the difference between experienced and first-time mothers in calf survival is high in the wild a complete lack of allomothering experience in captive or orphaned females could result in even greater losses.

[Bare-tail] and juvenile allomothering [nBlanch_12] while grazing in Uda Walawe, Sri Lanka. Photograph taken 20th June 2012.

Elephant calves in Amboseli born into families with multiple allomothers (young pre-reproductive females) have enhanced survival rates (Lee, 1987; Moss & Lee, 2011). One suggestion for this is that if calves, possibly from inexperienced mothers, ever get lost, this would result in death in the wild. However, allomothers ensure calf safety and that they remain close to others in the group. Due to the importance of allomother in calf survival, in this Chapter I qualitatively examine calf and non-mother neighbour proximities (NN) as representation of potential to allocare. Proximity to individual others cannot be formally tested as the environments and social partner availability are too variable between species and context to justify any statistical comparisons. Additionally, while social partners are invariant in captivity on a day to day basis, wild baselines in Uda Walawe could not be collected to investigate the function of age, sex and relationships of the ‘others’, and partners in Amboseli were hypervariable (FF sociality, large groups). Therefore, I will paint a qualitative portrait of patterns by age, sex and individual case studies.

I will then go on to explore whether non-play social interactions with neighbours change with calf age, calf sex or wild or captive contexts. Here I compare the percentage of time spent in non-play social interactions. Such interactions tend to be rare events (e.g. Lee, 1987, found a baseline of 0.2 to 0.7 interactions per hour) and thus unlikely to be detected in focal samples, and comparisons will be biased by differences in recording techniques and visibility. Despite their rarity, analysis of these events will enable a qualitative picture to emerge. This evaluation assumes that time is equally available for social, non-play interactions across all contexts and thus we must be careful during its interpretation. I do not examine partner preferences for interactions with non-mother others as these are again limited by constant availability in captivity and by the unpredictable nature of small fission-fusion groupings in wild Asian elephants.

I predicted that 1) both species of wild calves will show similar age changes in social proximity and 2) interactions will differ between all contexts due to both time availability and partner constraints.

5.3 Methods

The study sites and populations were defined earlier in Chapter Two (Description of Study Sites and Subjects). Data collection and analysis were described in Chapter Three (Methods).

Data analyses

For assessing whether mother activity influenced calf activities, a non-parametric Spearman's rank-order correlation (r_s) was run in SPSS (v21) to assess any relationship between the mother activities of feed, rest, move, with calf activities of feed, rest, move, LEGO-play, suckling interactions, comfort and explore. These relationships were investigated for the first two years of life for calves in six month age bins until 3-5 years, considered as a single age category. Captive Asian and African data were pooled to investigate the relationship in captivity due to small samples, whereas wild Asian and wild African datasets were separately correlated. Again, as there were multiple correlations between these three activity categories, Bonferroni correction was applied and the significance level was set at 0.006.

Non-parametric Generalised Linear Mixed Models (GLMM – SPSS v21) were carried out on calf suckling interactions, non-play social interactions and proximities to mothers, expressed as percentage of time (scans). These models were designed to explore the differences between the captive and wild species, as well as between the two wild sets of data. GLMMs were run using variance components with Satterthwaite method and robust estimates of covariance. All comparisons were pairwise. GLMM is robust to violations of normality and enables the examination of repeated data lacking a repeat measures design (Hawkins, 2015). Analysis on proximity to the nearest non-mother neighbour was not carried out due to the lack of appropriate baseline comparisons and the percent of scans are presented for qualitative comparisons. As in Chapter Four, factors were context, age category, sex, and any interaction between factors.

Again, as in Chapter Four (Activities), the models presented here are the final models with a table presenting significant factors only. In all tests, calf ID was entered as a random factor to account for repeated measures. As only two mothers contributed more than one calf to the captive dataset, and relatively few in the wild dataset, mother ID was not controlled for in addition to calf ID. Therefore, for analysis of mother activities ID acts as a proxy for maternal identity.

For counts of calves and calf behavioural observations included in GLMM analyses see Chapter Three, Table 3.6. For counts of mothers and mother behaviour observations included in GLMM analyses, see Chapter Three, Table 3.7.

For counts of calves and observations of proximity to mother included in GLMM analyses, see Table 5.1. For counts of calves and observations of proximity to non-mother nearest neighbour included in the dataset, see Table 5.2 (see Methods Section 3.2). Data were not presented here for non-mother nearest neighbour for wild African calves as these data have already been published (Lee & Moss, 2011) and proximity data for African calves was derived from population scans rather than focal samples.

Table 5.1 Number of Mother Proximity Observations by Context, Calf Sex and Calf Age Category. Scans at 5min intervals from 10min (wild Asian, captive Asian, captive African) and 60min (wild African) focal observations; and 25min group scans in captivity.

		Age category (N calves)					
Calf Sex	**Context**	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	**Asian wild**	71 (11)	63 (7)	88 (13)	57 (6)	95 (18)	374 (37)
	African wild	369 (23)	311 (20)	216 (17)	125 (9)	547 (25)	1568 (54)
	Asian captive	1796 (4)	763 (4)	595 (3)	319 (2)	168 (1)	3641 (5)
	African captive	522 (2)	237 (2)	282 (2)	206 (2)	0	1247 (2)
Female	**Asian wild**	215 (25)	89 (11)	115 (19)	32 (7)	189 (24)	640 (54)
	African wild	484 (24)	246 (24)	195 (16)	171 (15)	734 (40)	1830 (72)
	Asian captive	781 (2)	380 (2)	295 (2)	146 (1)	399 (1)	2001 (3)
	African captive	442 (2)	379 (2)	358 (2)	292 (2)	379 (3)	1850 (5)

Table 5.2 Number of Non-Mother Proximity Observations by Context, Sex and Age Category. Scans at 5min intervals from 10min focal observations (wild Asian, captive Asian, captive African), and from unique scans (for wild African).

		Age category (N calves)					
Calf Sex	**Context**	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	**Asian wild**	66 (11)	63 (7)	90 (13)	56 (6)	98 (19)	373 (37)
	African wild	361 (36)	145 (30)	82 (15)	69 (13)	842 (33)	1499 (58)
	Asian captive	1380 (4)	784 (4)	529 (3)	157 (2)	0	2850 (4)
	African captive	507 (2)	234 (2)	281 (2)	207 (2)	0	1229 (2)
Female	**Asian wild**	213 (25)	74 (10)	122 (21)	53 (7)	16 (24)	625 (54)
	African wild	408 (44)	130 (40)	122 (16)	135 (14)	842 ()	1637 (72)
	Asian captive	781 (2)	387 (2)	296 (2)	126 (1)	24 (1)	1614 (2)
	African captive	428 (2)	368 (2)	354 (2)	291 (2)	68 (1)	1509 (5)

One of the constraints on interactions between calves and others is the composition of the group. Group composition and partner availability were presented in detail in Chapter Three, Methods.

5.4 Interaction Results

Part 1: Early Mother-Calf Interactions

5.4.1 Maternal Scheduling

Some maternal activities were positively associated with and therefore coordinated with calf activities of feed, rest, move and LEGO-play but the associations between mother and calf activities were highly variable between contexts and differed between the age categories of calves (Table 5.3). Maternal activity was found to have no association with calf activities of either comfort or explore.

Table 5.3 Correlations of Mother and Calf Activities for First Two Years. Mother activities of feed, rest and move, correlated against calf activities of feed, rest, move, and LEGO-play. Spearman's rho. 2-tailed. Corrected for multiple tests, p<0.006. Only significant r_s shown. N is N of samples (binned data per month per calf); for N of individuals see Table 3.6 for calves and 3.7 for mothers.

			Coefficient r_s and *p* value (N)		
Calf age	**Mother activity**	**Calf activity**	**Wild Asian**	**Wild African**	**Captive**
1-6 mo	**Feed**	**Rest**			-0.420, *p*=0.005 (44)
	Feed	**Move**		-0.417, *p*=0.003 (49)	
	Rest	**Rest**	0.650, *p*<0.001 (51)		
	Rest	**Move**			-0.456, *p*=0.002 (44)
	Move	**Move**	0.571, *p*<0.001 (51)	0.720, *p*<0.001 (49)	
	Move	**Play**		-0.409, *p*=0.004 (48)	
7-12 mo	**Feed**	**Feed**		0.589, *p*<0.001 (41)	
	Feed	**Rest**		-0.517, *p*=0.001 (41)	
	Rest	**Rest**		0.547, *p*<0.001 (41)	
	Rest	**Play**			0.553, *p*=0.002 (28)
	Move	**Move**		0.731, *p*<0.001 (41)	
13-18 mo	**Feed**	**Move**		-0.526, *p*=0.002 (32)	
	Rest	**Rest**	0.663, *p*<0.001 (39)		
	Move	**Move**		0.679, *p*<0.001 (32)	
19-24 mo	**Feed**	**Feed**		0.671, *p*<0.001 (24)	0.695, *p*=0.001 (18)
	Rest	**Feed**	-0.623, *p*=0.004 (19)		
	Rest	**Rest**	0.648, *p*=0.003 (19)		
	Move	**Move**	0.635, *p*=0.003 (19)	0.598, *p*=0.002 (24)	0.626, *p*=0.005 (18)
	Move	**Feed**		-0.667, *p*<0.001 (24)	

Feeding was correlated between mothers and calves after six months of age in wild African and captive contexts. When wild African mothers were moving, their calves were also moving; while the association was positive for wild Asian mothers and calves only at 1-6 and 18-24 months (Table 5.3). This effect was not seen for the captive contexts until 19-24 months (Table 5.3). When wild Asian mothers were resting, their calves were also likely to be resting. Other significant correlations tended to be negative: maternal-feed was negatively correlated with calf-move and with calf-rest, but again with different patterns for each age and context. Maternal-rest was negatively correlated with calf-move for young captive calves and with calf-feed for older wild Asian calves. Maternal-move negatively correlated with calf-feed for older wild African calves (Table 5.3).

5.4.2 Proximity to Mother

Overall, as calves aged they spent less time in close proximity (Table 5.4), and more time in mid or far proximity from their mothers (Table 5.5; 5.6; Figure 5.1). In their first year of life, calves spent significantly more time in close proximity to their mothers, than they did at later ages; and significantly less time in far proximity (Table 5.4; 5.6; Figure 5.1). Mean percentage time in mid proximity was also significantly lower in the first 18 months (Table 5.5, Figure 5.1b). An interaction between age and context was found for both close and far proximity (Table 5.4). There was a significant contribution of individual to overall variance for proximity <2m (*p*=0.01) and >5m from mother (*p*=0.002) but not for 2-5m (*p*=0.072).

Table 5.4 Final General Linear Mixed Model of Close-Proximity to Mothers <2M. Var (ID)=127.46 *p*=0.010. See Table 5.1, Chapter Three, for N of calves and N of observations. Dependent variable was close-proximity; independent variables were age, context, and the interactions between them.

	Main effect *F*, and *p* value	**Coefficient *β* (95% CI)**	***P* value**
Overall model fit	$F_{19, 282}$=13.090, *p*<0.001		
Age	$F_{4, 296}$=17.714, *p*<0.001		
1-6mo		28.674 (20.124-37.225)	<0.001
7-12mo		22.630 (13.601-31.660)	<0.001
1-6mo – 7-12mo		11.373 (4.673-18.073)	0.001
1-6mo – 13-18mo		22.514 (15.804-29.223)	<0.001
1-6mo – 19-24mo		23.075 (15.669-30.481)	<0.001
1-6mo – 3-5yr		28.131 (19.392-36.870)	<0.001

7-12mo – 13-18mo		11.141 (3.900-18.381)	0.003
7-12mo – 19-24mo		11.702 (3.802-19.601),	0.004
7-12mo – 3-5yr		16.758 (7.618-25.898)	<0.001
Context	$F_{3, 52}$=33.155, *p*<0.001		
Asian wild		29.483 (21.324-37.642)	<0.001
Asian wild – African wild		27.740 (22.037-33.444)	<0.001
Asian wild – Asian captive		27.746 (17.342-38.149)	<0.001
Asian wild – African captive		22.245 (10.088-34.149)	0.001
Age x context	$F_{12, 337}$=1.917, *p*=0.031		
1-6mo – 19-24mo Asian wild		13.662 (0.894-26.431)	0.036
1-6mo – 3-5yrs Asian wild		20.266 (11.087-29.445)	<0.001
13-18mo – 3-5yrs Asian wild		13.065 (3.502-22.627)	0.007
1-6mo – 7-12mo Asian captive		25.768 (13.075-38.460)	<0.001
1-6mo – 13-18mo Asian captive		36.388 (22.605-50.171)	<0.001
1-6mo – 19-24mo Asian captive		37.233 (21.505-52.960)	<0.001
1-6mo – 3-5yrs Asian captive		41.928 (22.183-61.717)	<0.001
1-6mo – 13-18mo African captive		20.214 (2.203-38.225)	0.028
7-12mo – 13-18mo African captive		18.432 (0.144 to 36.721)	0.048
1-6mo – 13-18mo African wild		26.251 (15.878-36.624)	<0.001
1-6mo – 19-24mo African wild		25.386 (13.648-37.124)	<0.001
1-6mo – 3-5yrs African wild		28.674 (20.124-37.225)	<0.001
7-12mo – 13-18mo African wild		20.207 (9.388-31.026)	<0.001
7-12mo – 19-24mo African wild		19.342 (7.479-31.205)	0.001
7-12mo – 3-5yrs African wild		22.63 (13.601-31.660)	<0.001

Table 5.5 Final General Linear Mixed Model of Mid-Proximity to Mother 2-5M. Var (ID)=62.00, *p*=0.008. See Table 5.1, Chapter Three, for N of calves and N of observations. Dependent variable was mid-proximity; independent variables were age and context.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI)**	***p* value**
Overall model fit	$F_{7, 57}$=19.339, *p*<0.001		
Age	$F_{4, 476}$=6.210, *p*<0.001		
1-6mo		-10.809 (-15.442 to -6.176)	<0.001
7-12mo		-9.666 (-14.859 to -4.474)	<0.001
13-18mo		-6.671 (-11.705 to -1.637)	0.009
1-6mo – 19-24mo		-7.270 (-13.070 to -1.469)	0.014
1-6mo – 3.5yr		-10.809 (-15.442 to -6.176)	<0.001
7-12mo – 3-5yrs		-9.666 (-14.859 to -4.474)	<0.001
13-18mo – 3-5yrs		-6.671 (-11.705 to -1.637)	0.009
Context	$F_{3, 27}$=33.137, *p*<0.001		
African wild		20.527 (11.339 to 29.716)	<0.001
Asian wild – African wild		-19.939 (-24.142 to -15.735)	<0.001
African wild – Asian captive		17.195 (9.487 to 24.903)	<0.001
African wild – African captive		20.527 (11.339 to 29.716)	<0.001

Table 5.6 Final General Linear Mixed Model of Far-Proximity to Mother >5M. Var (ID)=87.42, *p*=0.002. See Table 5.1, Chapter Three, for N of calves and N of observations. Dependent variable was far-proximity; independent variables were age, context, and the interactions between them.

	Main effect *F* and *p* value	**Coefficient β (95% CI)**	***p* value**
Overall model fit	$F_{19, 321}=7.711$, $p<0.001$		
Age	$F_{4, 332}=15.912$, $p<0.001$		
1-6mo		-19.077 (-26.199 to -11.956)	<0.001
7-12mo		-10.364 (-17.885 to -2.842)	0.007
1-6mo – 7-12mo		-9.992 (-15.579 to -4.406)	<0.001
1-6mo –13-18mo		-19.038 (-24.633 to -13.443)	<0.001
1-6mo – 19-24mo		-17.719 (-23.893 to -11.5446)	<0.001
1-6mo – 3-5yr		-20.950 (-28.215 to -13.684)	<0.001
7-12mo – 13-18mo		-9.046 (-15.0846 to -3.008)	0.003
7-12mo –19-24mo		-7.726 (-14.313 to -1.139)	0.022
7-12mo – 3-5yr		-10.957 (-18.560 to -3.354)	0.005
Context	$F_{3, 65}=16.387$, $p<0.001$		
Asian wild		-11.450 (-18.242 to -4.659)	0.001
Asian captive		27.335 (12.232-42.438)	<0.001
Asian wild – African wild		-7.490 (-12.233 to -2.747)	0.002
Asian wild – Asian captive		-25.300 (-33.878 to -16.723)	0.001
Asian wild – African captive		-22.821 (-32.856 to -12.787)	0.001
African wild – Asian captive		-17.810 (-26.256 to -9.365)	0.003
African wild – African captive		-15.331 (-25.253 to -5.410)	0.003
Age x context	$F_{12, 373}=3.138$, $p<0.001$		
1-6mo Asian wild		13.219 (2.770 to 23.668)	0.013
1-6mo Asian captive		-20.804 (-38.714 to -2.893)	0.023
7-12mo Asian wild		15.161 (2.725 to 27.597)	0.017
1-6mo – 7-12mo Asian wild		-10.656 (-20.685 to -0.626)	0.037

1-6mo – 7-12mo Asian captive	-17.238 (-27.822 to -6.653)	0.001
1-6mo – 13-18mo Asian captive	-31.235 (-42.729 to -19.741)	<0.001
1-6mo – 19-24mo Asian captive	-36.033 (-49.145 to -22.922)	<0.001
1-6mo – 3-5yrs Asian captive	-39.881 (-56.321 to -23.441)	<0.001
7-12mo – 13-18mo Asian captive	-13.998 (-26.598 to -1.398)	0.030
7-12mo – 19-24mo Asian captive	-18.796 (-32.921 to -4.671)	0.009
7-12mo – 3-5yrs Asian captive	-22.643 (-39.928 to -5.358)	0.010
1-6mo – 13-18mo African captive	-19.251 (-34.270 to -4.231)	0.012
7-12mo – 13-18mo African captive	-15.887 (-31.139 to -0.635)	0.041
1-6mo – 7-12mo African wild	-8.713 (-16.691 to -0.736)	0.032
1-6mo – 13-18mo African wild	-23.840 (-32.488 to -15.192)	<0.001
1-6mo – 19-24mo African wild	-19.362 (-26.145 to -6.579)	0.001
1-6mo – 3-5yrs African wild	-19.077 (-26.199 to -11.956)	<0.001
7-12mo – 13-18mo African wild	-15.126 (-24.146 to -6.107)	0.001
7-12mo – 3-5yrs African wild	-10.364 (-17.885 to -2.842)	0.007

No sex differences were found in any of the proximities to mother (close p=0.585; mid p=0.665; far p=0.331). Time spent close, mid and far from mother all differed between contexts (Table 5.4; 5.5; 5.6; Figure 5.1). Wild Asian calves were in close proximity to their mothers significantly more often than were calves from the other contexts (Table 5.4, Figure 5.1a); wild African calves were in mid proximity significantly more than were calves in the other contexts (Table 5.5; Figure 5.1b); and captive Asian calves were found at far proximity significantly more than were calves in the other contexts (Table 5.6; Figure 5.1c). For far proximity, significant pairwise comparisons were only found between captive Asian and each of the wild contexts (Table 5.6). Interestingly, wild Asian calves were found at far proximity significantly less than other contexts, both overall and pairwise (Table 5.6; Figure 5.1c).

In captivity, patterns in proximity to mother across age were similar between individual Asian calves (Figure 5.2); but varied much more between individual African calves (Figure 5.3).

The reduction in time in close proximity to mother with age is seen clearly in each of the individual captive Asian calves (Figure 5.2), but only in Mchumba for captive African calves (Figure 5.3). Similarly, as they aged, each individual captive Asian calf also showed increases in time spent in far proximity from their mother (Figure 5.2). Again, these patterns were not strong in individual captive African calves (Figure 5.3).

For the orphaned captive African calf, Mansi, proximity remained constant from six to 18 months of life and at 19-24 months she showed the reverse to the pattern found overall in close and far proximities to ‘mother’ (Figure 5.3). However, it must be noted that these proximities were for Mansi’s allomother in place of her birth mother, who died. Mansi was, therefore, spending more time near her allomother (both close and mid proximities) at 19-24 months.

Jaluka’s already high levels of being in close proximity to her mother at 1-6 months increased further at 7-12 months; before decreasing at later ages (Figure 5.3). Both Mansi and Jaluka will be discussed further in Section 5.4.6 (Case studies).

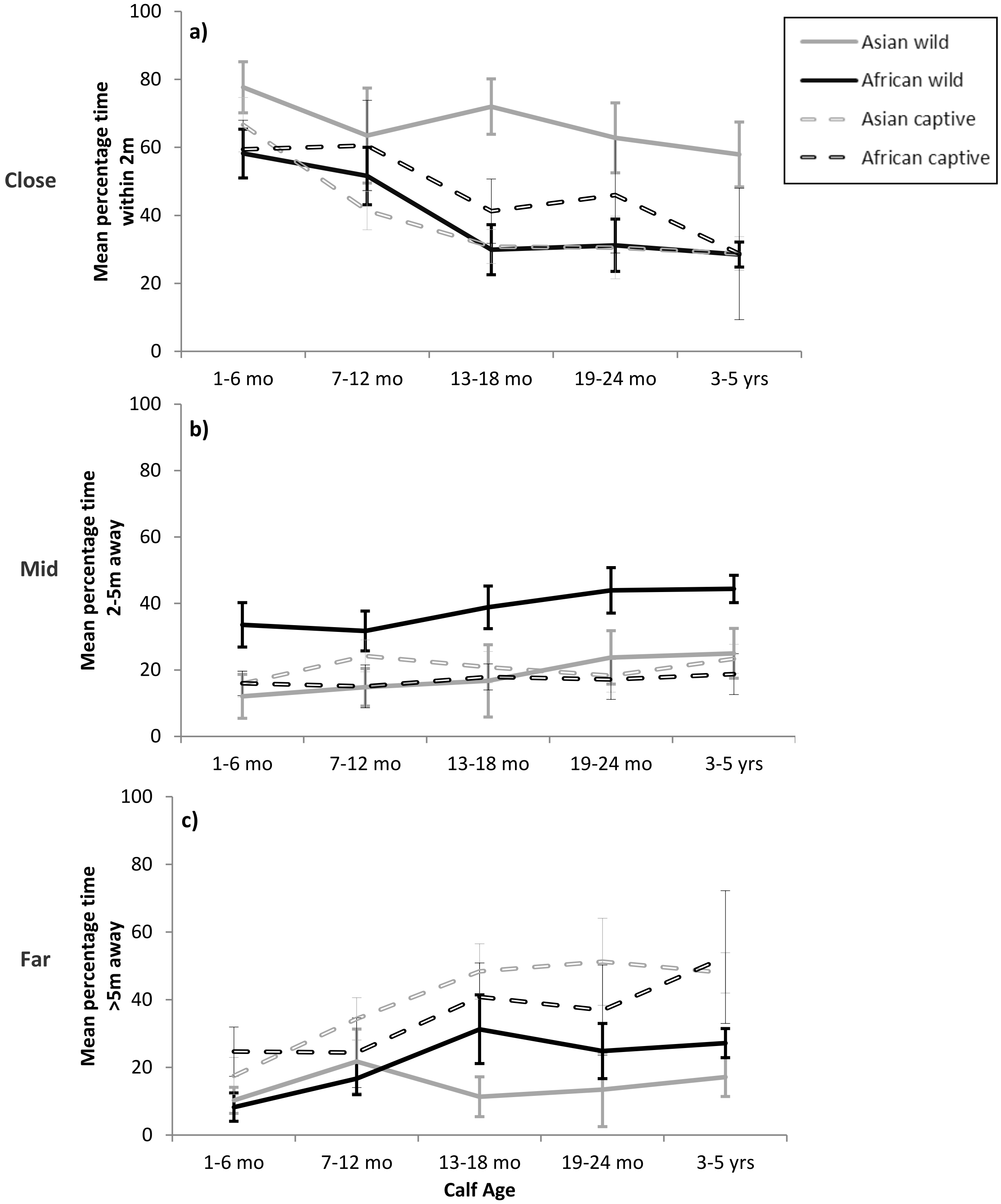


Figure 5.1 Proximity to Mother as Mean Percentage Time for Calves' First Five Years. Proximities from mothers: a) close, within 2m; b) mid, 2-5m; c) far, >5m. Sexes combined as no significant differences found in GLMM analysis. 95%BCI. For N, see Table 5.1.

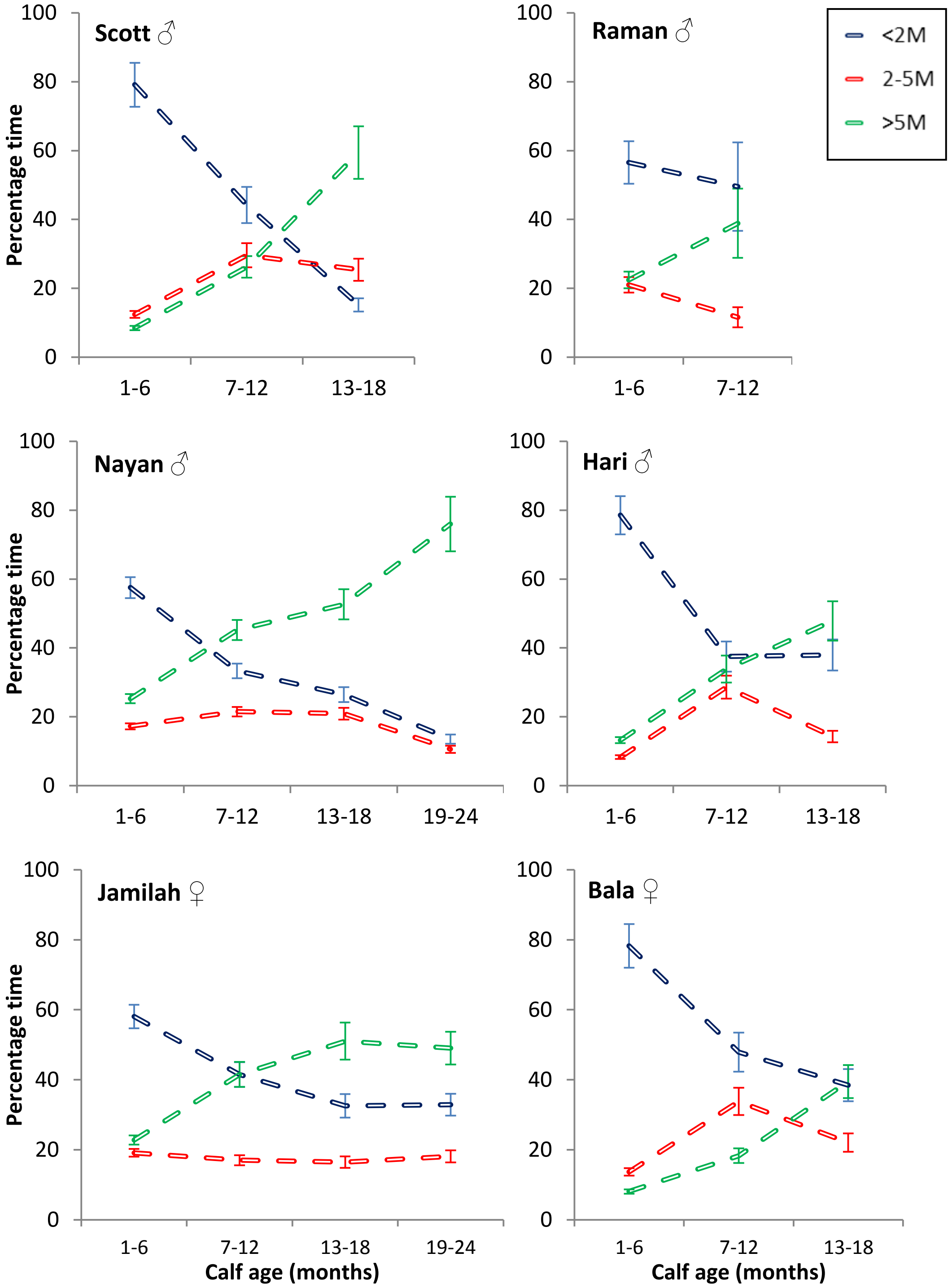


Figure 5.2 Individual Patterns of Proximity to Mother as Time for Individual Captive Asian Calves. Proximities from mothers: a) close, within 2m; b) mid, 2-5m; c) far, >5m. For N of observations per individual, see Table 3.4, Chapter Three. Binomial 95%CI.

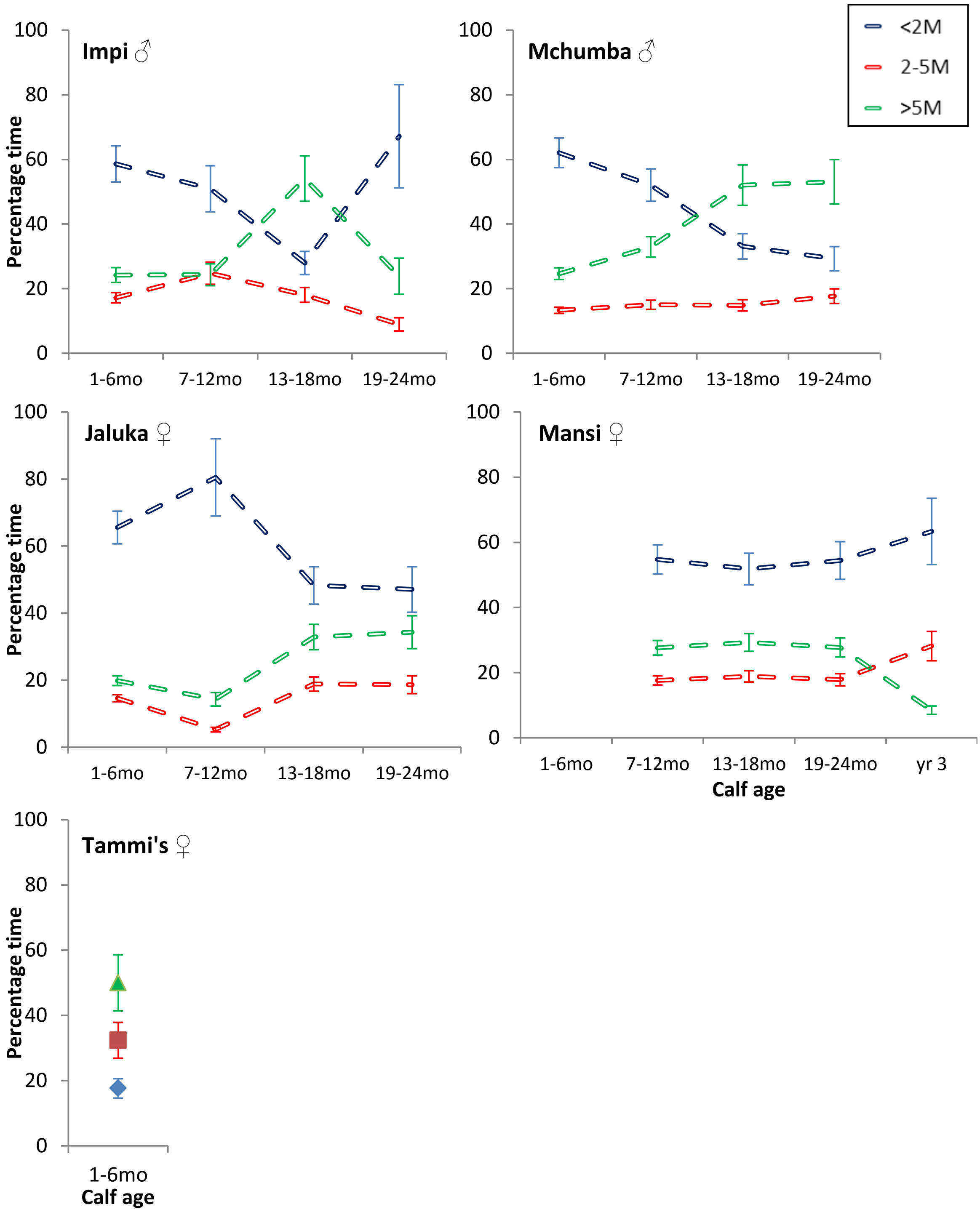


Figure 5.3 Individual Patterns of Proximity to Mother (or Allomother) as Time for Individual Captive African Calves. Proximity to mother for Impi, Mchumba, Jaluka and Tammi's; allomother from Mansi. Proximities from mother/allomother: a) close, within 2m; b) mid, 2-5m; c) far, >5m. For N of observations per individual, see Table 3.5, Chapter Three. Binomial 95%CI.

5.4.3 Suckling Interactions

While time spent in suckling interactions appeared to decrease with age (Figure 5.4) this change was gradual and significantly variable between individuals and therefore was not significant overall; pairwise comparisons between 1-6 and 19-24 months did differ significantly (Table 5.7).

In comparisons between the different contexts, wild Asian calves were observed in suckling interactions significantly more frequently than were wild African calves for the same age (Table 5.7). No sex differences were found (*p*=0.385).

Table 5.7 Final General Linear Mixed Model for Calf Suckling Interactions. Var (ID)=27.36, *p*=0.001. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was Suckling Interactions; independent variables were age and context.

	Main effect *F* and *p* value	Coefficient *β* (95% CI)	*P* value
Overall model fit	$F_{7, 103}$=1.697, *p*=0.118		
Age	$F_{4, 593}$=1.387, *p*=0.237		
1-6mo - 19-24mo		2.762 (0.293 to 5.232)	0.015
Context	$F_{3, 45}$=1.936, *p*=0.137		
Asian wild – African wild		2.616 (0.424 to 4.808)	0.020

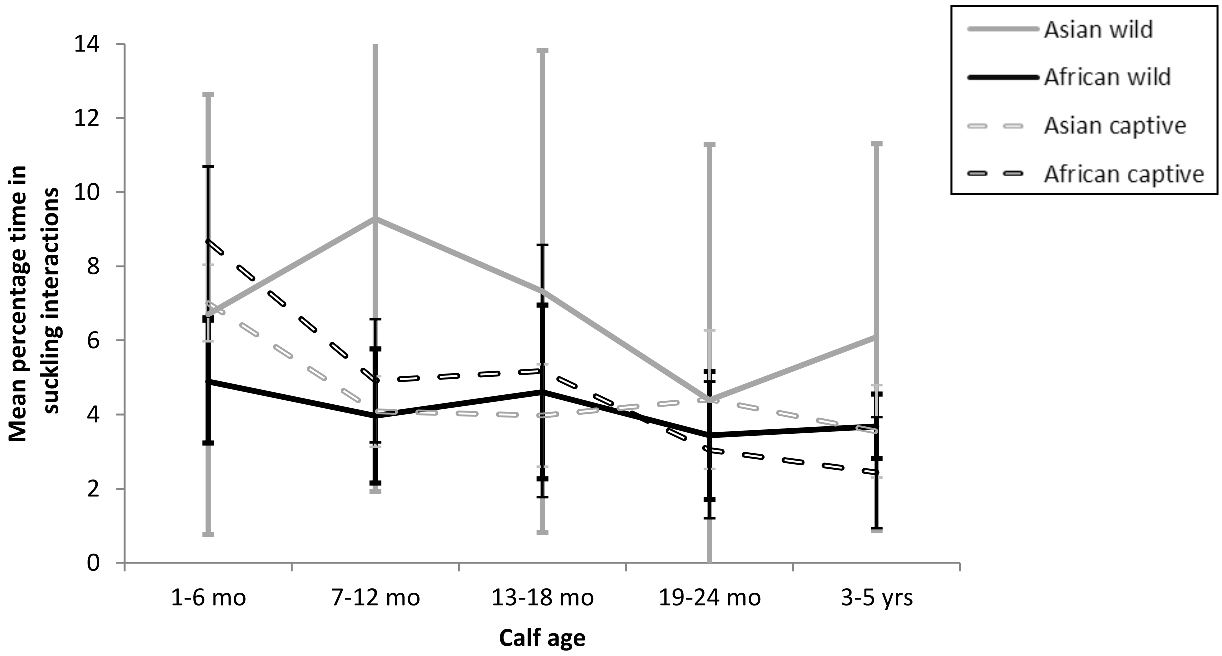


Figure 5.4 Mean Percentage Time in Suckling Interactions for Calves' First Five Years. Sexes combined as no significant differences found in GLMM analysis. ±95%CI. See Table 3.6, Chapter Three, for N.

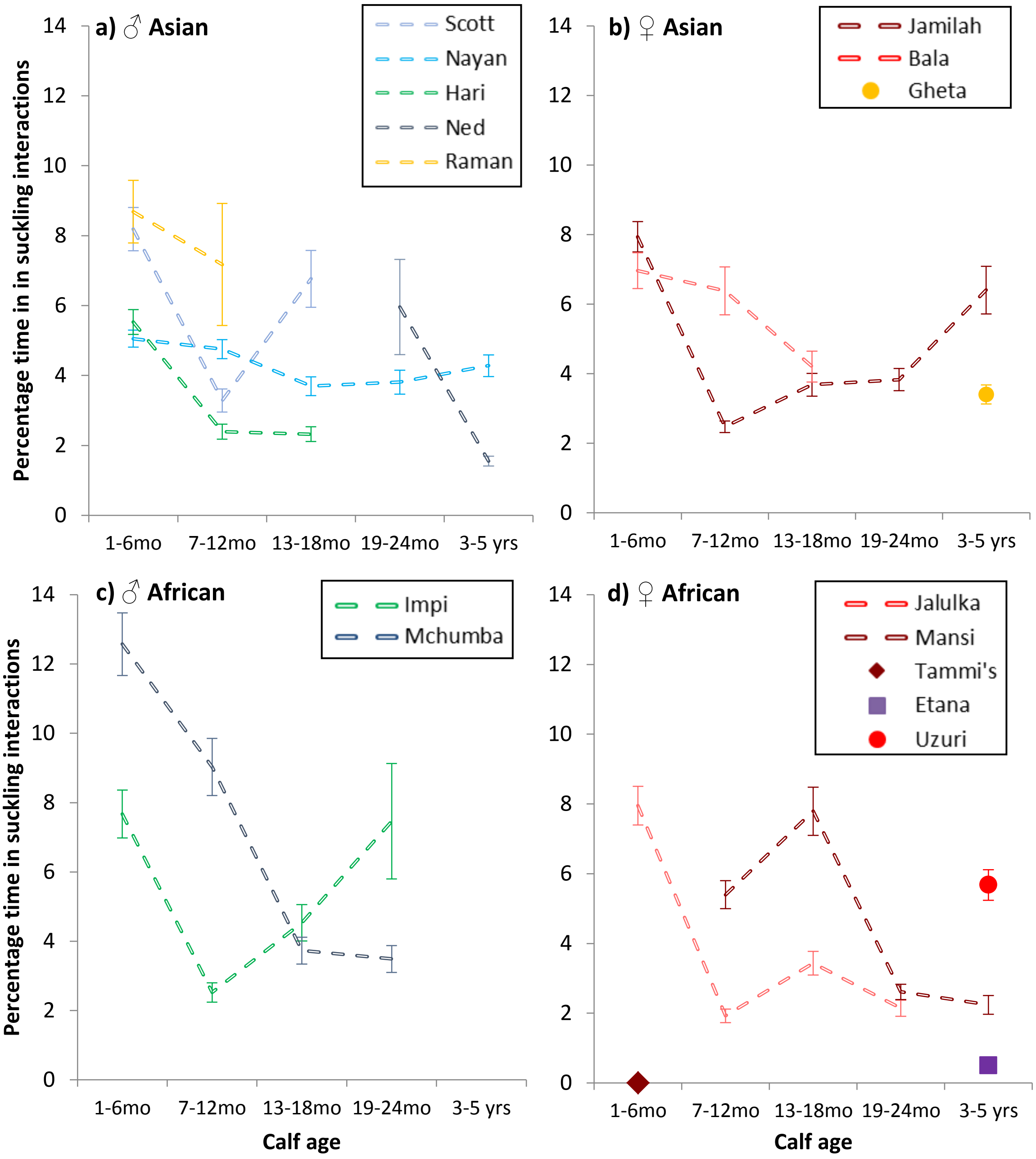


Figure 5.5 Individual Patterns of Time in Suckling Interactions in the First Five Years for Captive Calves. For N of observations per individual, see Tables 3.4 and 3.5, Chapter Three. Binomial 95%CI.

Patterns in suckling interactions varied greatly between the individual captive calves (Figure 5.5). For example, Jamilah and Impi increased their rates of suckling interactions from 7-12 months to, respectively, 3-5 years and 19-24 months. In contrast, Bala and Mchumba's rates both continued to drop from 1-6 months to, respectively, 13-18 and 19-24 months.

Part 2: Interactions with Others

5.4.4 Proximity to Nearest Non-Mother Neighbour

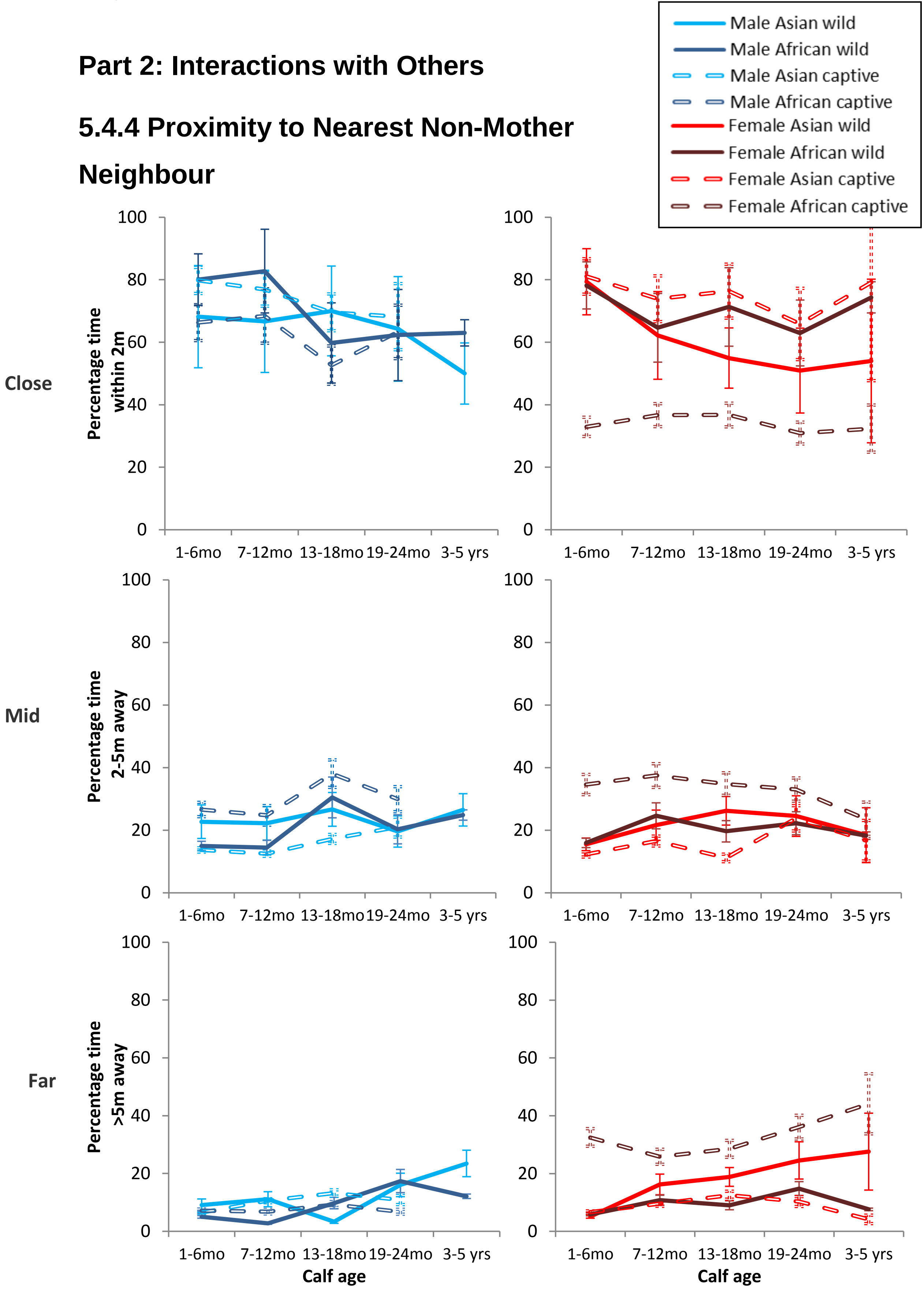


Figure 5.6 Proximity to Nearest Non-Mother Neighbour by Sex, as Mean Percentage Time for Calves' First Five Years. Proximities from non-mother others. Binomial 95% CI. See Table 5.2, for N. Scans at 5min intervals from 10min focal observations (wild Asian, captive Asian, captive African), and from unique scans (for wild African).

As mentioned earlier, statistical analysis on proximity to the nearest non-mother neighbour was not carried out due to differences in the collection of proximity data in wild African elephants.

The means for captive female African calves were highly skewed by two of the three study animals here being ‘abnormal’ (rejected, and orphaned) (Figure 5.6). For all other sexes and contexts, the data suggest fewer differences between contexts in proximity to others than were found for proximity to mothers (Figures 5.1; 5.6). Close proximity to others remained above 50% in the first two years of life in all contexts of both sexes (excluding female captive African means) and far proximity did not increase greatly in the first 18 months.

Proximity to nearest non-mother neighbours is discussed as case studies in Section 5.4.6 below.

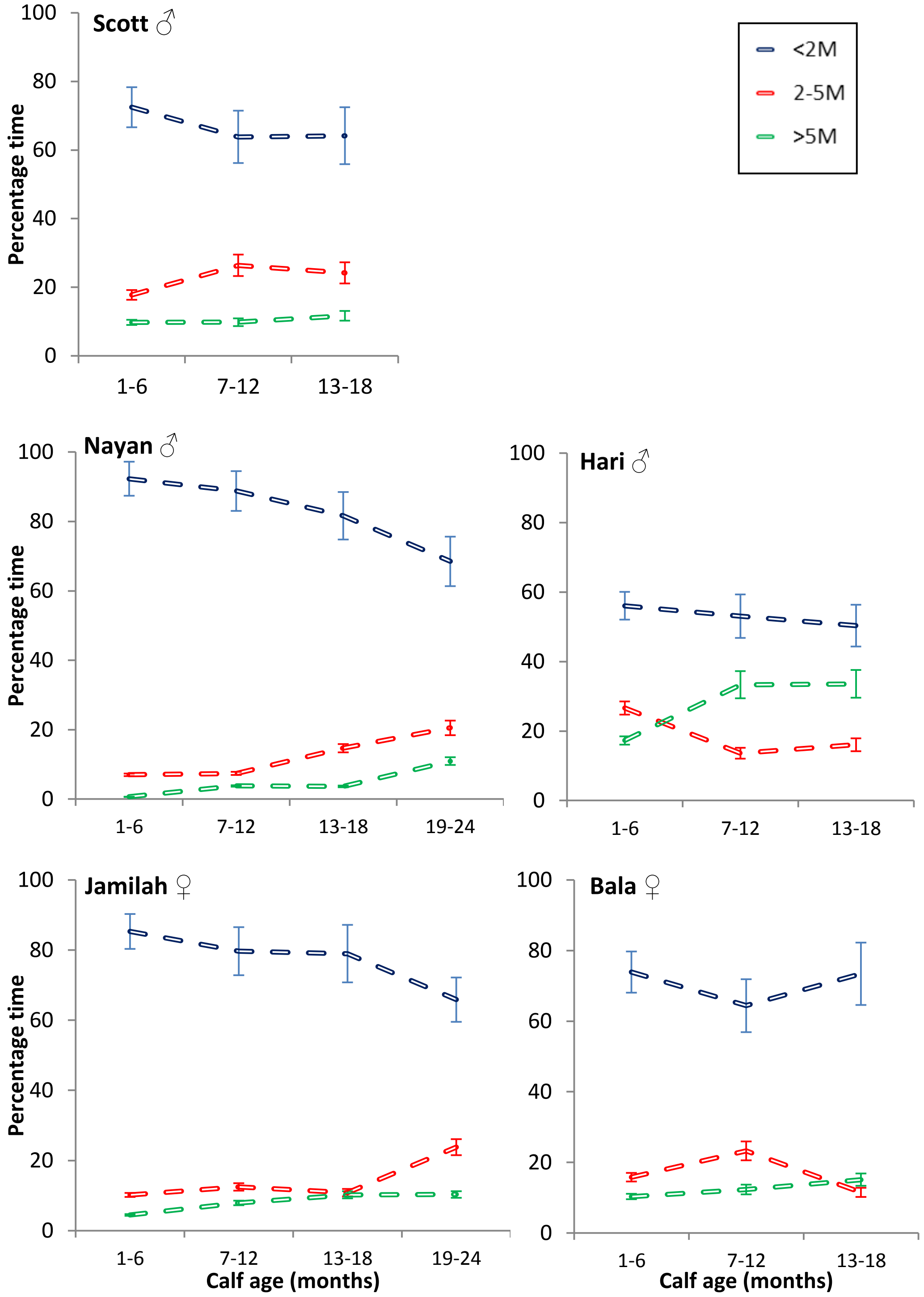


Figure 5.7 Individual Patterns of Proximity to Nearest Non-Mother Neighbour as Time for Individual Captive Asian Calves. Proximities from non-mother others: close, within 2m; mid, 2-5m; and far, >5m. Raman not included here as nearest non-mother neighbour data were not recorded before 2010. For N of observations see Table 3.4. Binomial 95% CI.

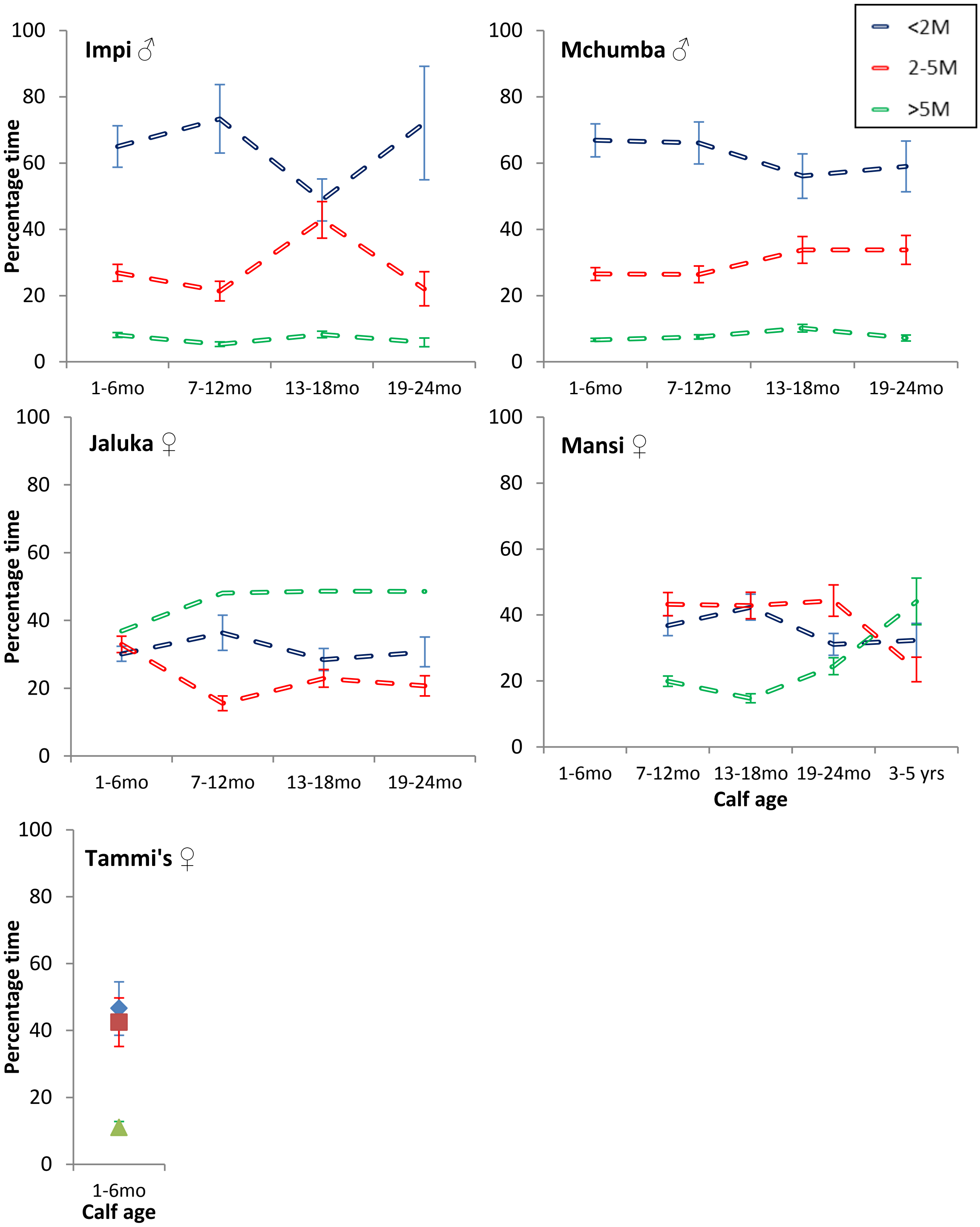


Figure 5.8 Individual Patterns of Proximity to Nearest Non-Mother Neighbour as Time for Individual Captive African Calves. Proximities from non-mother others: close, within 2m; mid, 2-5m; and far, >5m. For Jaluka, this is proximity to non-allomother others. For N of observations see Table 3.5. Binomial 95% CI.

5.4.5 Non-play Social Interactions

Table 5.8 Who does What With Whom?: Matrix of Different Types of Interactions**.** Adapted from (Lee, 1987)

	Calves with…	**Adults with…**
…Calves	• Greetings (touch other with trunk) • Initiate play (touch, rub followed by play) • Relaxed & friendly investigations of others (touching trunks, rubbing parts of the body against another • ‘Investigate food’ (touch mouth or food of other) – social learning	• Greetings (touch other with trunk) • Relaxed, friendly greetings investigations of others (touching trunks, rubbing parts of the body against another) • Allomothering (comforting, assisting and protecting calves) • Responding to extreme distress through reassurance when calves are lost or threatened by predators • Pulling from holes or when stuck in mud etc. • Aggressive (pokes, trunk-slaps, shoves and threats resulting in avoidance) rarely directed at young calves by elephants other than the mother • Rescuing from aggression received from others
…Adults	• Greetings (touch other with trunk) • Relaxed & friendly investigations of others (touching trunks, rubbing parts of the body against another) • ‘Investigate food’ (touch mouth or food of other) – social learning • Seeking comfort (calves less likely to initiate interactions with older males) • Expressing extreme distress when lost or threatened by predators • Suckling interactions with mother (and sometimes allosuckling, but very rare in wild African)	• Greetings (touch other with trunk) • Relaxed & friendly investigations of others (touching trunks, rubbing parts of the body against another) • Comfort • Aggressive (pokes, trunk-slaps, shoves and threats resulting in avoidance) rarely seen in wild.[#]

Footnote: [#]Field notes (21/4/14): 11:30am aggression from Bala directed at Hari over strip of bark Hari has; 12:30pm Hari knocked over by either Sithami or Aung-bo (at feeder wall. Aung-bo displaced Sithami then one of the two of them knocked over Hari).

Most calf-other interactions are friendly contacts, opportunities for learning about others, or helpful. Direct aggression is very rare and mostly seen towards stroppy young males or occasionally females from other families. Dominance-subordinance interactions between females are rare in wild Asian elephants (de Silva, Schmid & Wittemyer, 2016) and in the Amboseli wild African context (Archie, Moss & Alberts, 2006; Lee, 1987), but aggression is common in captivity, particularly between adult females, but less often directed towards calves or juveniles.

Table 5.9 Final General Linear Mixed Model of Non-Play Calf Social Interactions. Var (ID)=2.29, *p*=0.679. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was non-play social interactions; independent variables were age and context.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI)**	***P* value**
Overall model fit	$F_{7, 5}$=12.639, *p*=0.007		
Age	$F_{4, 283}$=11.400 *p*<0.001	8.908 (2.380 to 15.437)	0.008
1-6mo		4.322 (2.680 to 5.964)	<0.001
1-6mo - 7-12mo		4.452 (2.629 to 6.275)	<0.001
1-6mo – 13-18mo		5.074 (3.263 to 6.886)	<0.001
1-6mo – 19-24mo		4.669 (2.588 to 6.751)	<0.001
1-6mo – 3-5yrs		4.322 (2.680 to 5.964)	<0.001
Context	$F_{3, 2}$=11.759, *p*=0.055		
Asian wild		4.322 (1.353 to 4.456)	<0.001
Asian captive		4.919 (1.951 to 7.887)	0.012
African captive		4.502 (1.321 to 7.682)	0.018
Asian wild – African wild		2.905 (1.353 to 4.456)	<0.001
Asian captive – African wild		4.919 (1.951 to 7.887)	0.012
African captive – African wild		4.502 (1.321 to 7.682)	0.018

The mean percentage of time spent in social interactions irrespective of its context (rare aggressive or common friendly interactions) by calves was a function of calf age and context (Table 5.9). Calves in their first six months of life socially interacted significantly more than older ages. In pairwise comparisons, wild African calves socially interacted significantly less than the other contexts, while each of these three contexts differed significantly overall.

The nature of interactions could not be compared between contexts or across ages due to the relative rarity of these events (96.3% zeros) and small N of individuals. As with proximity, the variance in potential partner availability meant that any comparison of who did what with whom would simply reflect the constraints of the captive context or the hyper-variability of fission-fusion groups for wild elephants. Even a comparison of age-sex engagement would suffer from the same limitations.

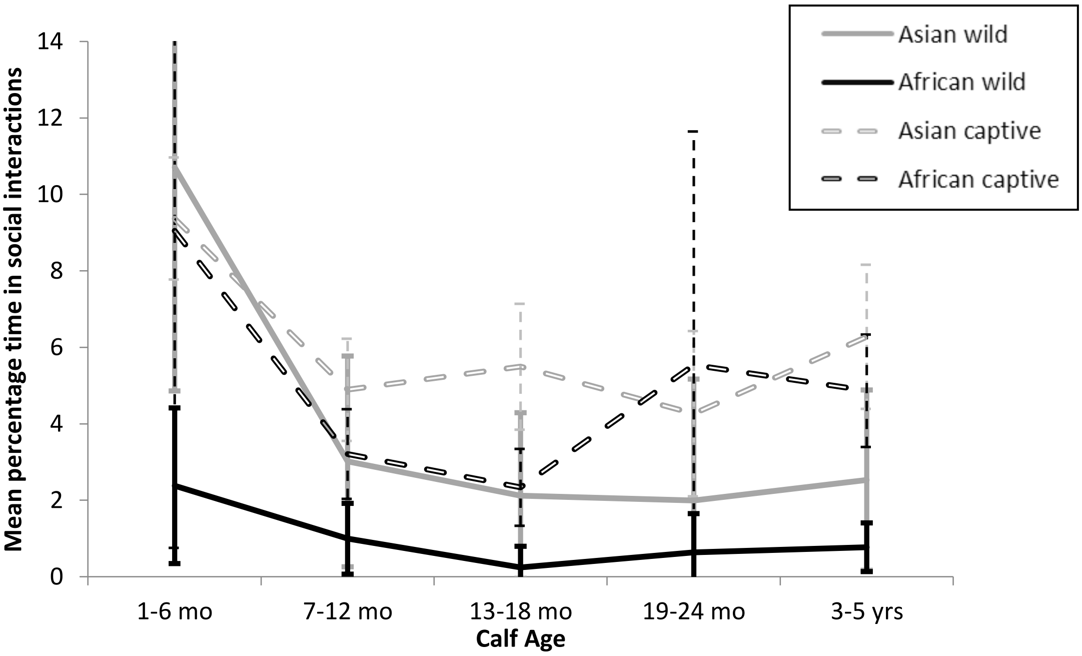


Figure 5.9 Mean Percentage Time in Non-play Social Interactions for Calves' First Five Years. Sexes combined as no significant differences found in GLMM analysis. See 3.6, Chapter Three, for N. ±95%CI.

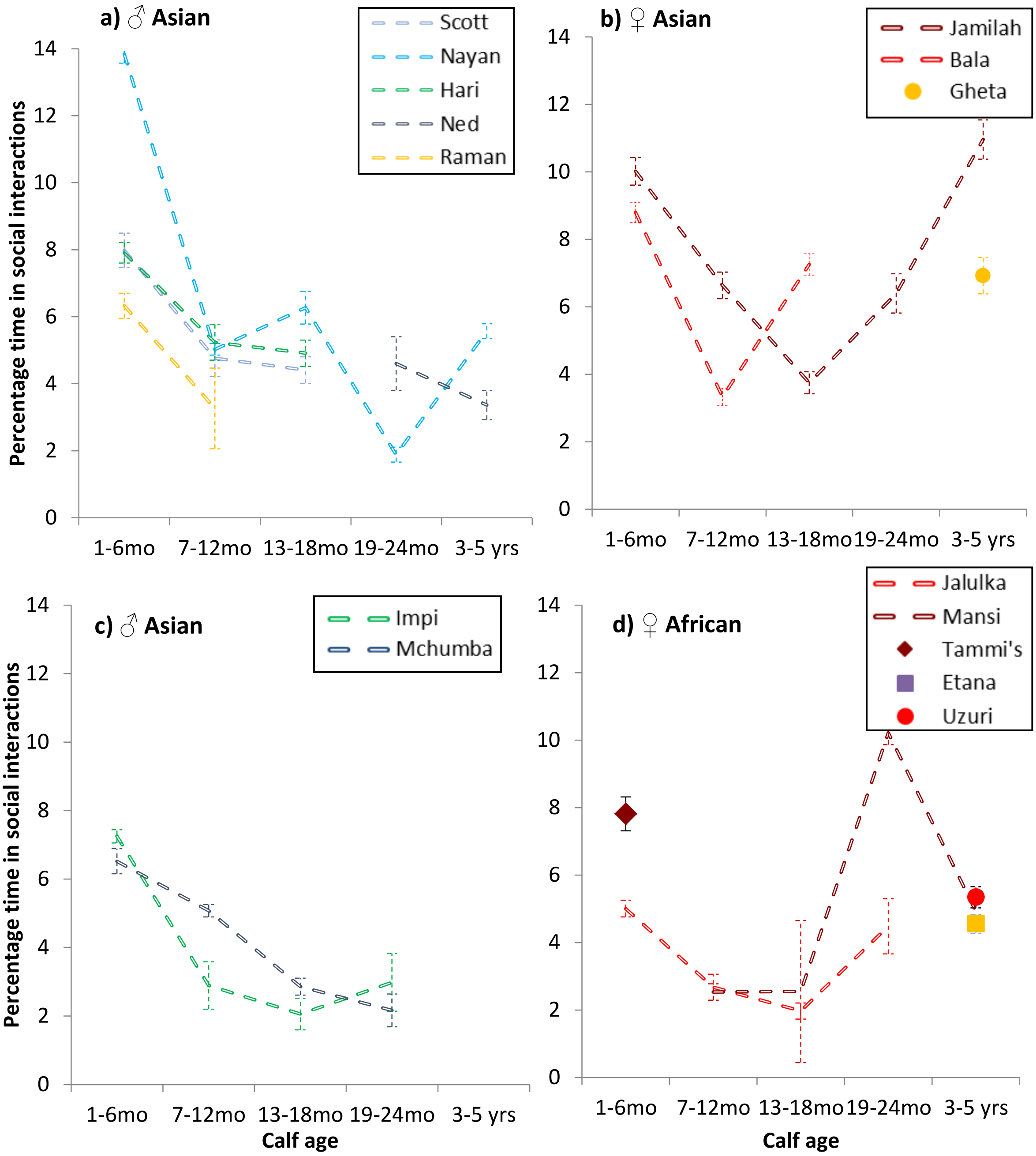


Figure 5.10 Individual Patterns for Time in Non-play Social Interactions for Individual Captive Calves. For N of observations per individual see Tables 3.4 and 3.5. ±95%CI.

5.4.6 Case Studies

Patterns from case studies on captive calves may shed light on variability in interactions with others. For individual captive calves, the pattern for proximity to nearest non-mother neighbour was similar across all Asian calves, with the exception of Hari. The male African calves also followed similar patterns. Hari and two of the female African calves will be discussed in detail here. As data were only available for the third female, Tammi's rejected calf, in her first month of life, I comment on her in the Discussion Section (5.5) of this Chapter.

Hari

At ages 1-6 months Hari already spent a greater percentage of his time >5 m from non-mother neighbours than did the other captive Asian calves (Figure 5.2). This is particularly interesting when we see that this rate almost doubles after six months, but remains roughly constant across ages for all other captive Asian, and the male African calves (Figures 5.2; 5.3). It is also worth noting that Hari spent the least time in close proximity to non-mother neighbours across all ages for captive Asian calves. I discuss here how these rates may be related to both mother social choices and captive management.

Hari's subordinate mother, Sundara, had a strong social tie with Jangoli, an adult female outwith Sundara's family unit. Jangoli and Sundara (and therefore Hari) were often found on the outskirts of the main group. Sundara was 'disliked' (e.g. displaced, ignored, rejected) by her own grandmother (and mother to an extent) while Jangoli had no family of her own at Chester having only given birth to male calves (which had been moved on to further facilities).

During the first six months of Hari's life (and prior to his birth), both Sundara and Jangoli joined the main group during the day (approx. 10am-3pm; 25/25 study days) when they were outside in the main paddock. However, in later months Jangoli was not mixed with the rest of the group during the day (mixed for 1/10 and 0/10 study days, when Hari 7-12 and 13-18 months, respectively). Initially mixing did not take place due to management of foot-care where Jangoli initially was kept in the PC and holding-pens for routine husbandry, and later primarily because of the new adult male, Aung-bo. Aung-bo expressed aggression towards Jangoli, possibly from frustration and lack of experience around adult females (in addition to being much shorter than Jangoli). At first, keepers managed this by separating Jangoli on occasions while the rest of the group were mixed with Aung-bo (i.e. when Jangoli was in oestrus). However, Jangoli continued to be attacked by Aung-bo and she eventually began to elect not to follow the female group outside, where they would associate with the male.

The management decision to bring in a new and inexperienced male (to replace Chester's experienced but overrepresented male), resulted in Jangoli choosing isolation as an alternative to the company of the other females when associated with the male. The consequence of this management decision and isolation also had an effect on her 'friend', Sundara, and importantly, on her calf, Hari. Sundara's principal companion was no longer in the group during the day and Sundara continued to position herself on the outskirts of the main group. Therefore if Hari chose to be near to his mother he would be locating himself far from non-mother neighbours. Although this pattern would not be seen when all the females and calves were mixed (in the late afternoon, over night and early morning), the majority of data collection took place in the hours when the group were either in PC-training or outside in the main paddock. This effect is reflected in the percentage of time Hari spent in proximity to his mother and others: at 7-18 months, Hari spent ~33.5% of time >5 m from non-mother neighbours (Figure 5.7), and ~37.5% of time <2 m from his mother (Figure 5.2). At 1-6 months, when Jangoli was available as a non-mother neighbour for Hari, he was more likely to be closer rather than far from his non-mother neighbour; and this pattern switched at later ages.

The facility's management decision, to bring in a new unexperienced male seems to have played a role in isolating Hari at least in terms of proximity to others while he was still so young as to need to be close to his mother.

In addition to changes in social dynamics, this case study highlights the effect that management decisions have on the welfare of an individual. Aungo-bo's arrival at Chester clearly led to Jangoli gradually, then wholly, spending hours each day isolated from her companions; until she was transferred to a non-breeding facility (Madrid Zoo, June 2014).

It could be suggested that Hari's rates of close proximity to non-mother neighbours were already low prior to Jangoli's daytime absence from the group. Perhaps his mother's atypical sociality was exacerbated by her isolation.

For further insights, I look at patterns in proximities in individual African calves, Jaluka, and Mansi.

Jaluka

Jaluka and Mansi, like Hari, showed low time spent in close proximity to non-mother neighbours at all ages (Figure 5.8). Jaluka's proximity patterns may be explained by similar mechanisms as Hari's patterns, both being offspring of subordinate mothers who were often isolated from the main group, partially by daily management and partially by choice (their own or that of their group members).

Stuvite, Jaluka's mother, and her offspring (occasionally along with 'old' Shibi) were often divided from the main group during the day to provide company for the adult male. On these days Jaluka's access to others was reduced and her neighbour choices were limited. This was especially true after Jaluka's first five months when her maternal brother, Juva, was moved to Port Lympne (with Janu) since siblings frequently interacted. Juva was present for 26/30 study days when Jaluka 1-6 months.

Stuvite and her calf Jaluka separated by barrier from other group members. Some social interactions and play can still occur across the fence. Photograph taken 28th May 2012.

However, even on the days when Stuvite and her offspring were mixed with the main group, Stuvite was usually found far from the other adult females, particularly from Tammi who would aggressively give chase. It can be debated as to whether these chases were started by assertive Tammi, or by Stuvite's flight which encouraged an aggressive chase to develop. If Jaluka chose to be in close proximity to her mother whilst Stuvite avoided other adults, Jaluka would thus be distancing herself from her neighbours (with the exception of her brother before his removal).

Unlike the other captive calves, Jaluka's high levels of close proximity to her mother increased in her first year (Figures 5.2; 5.3). Suckling interactions alone fail to explain this increase in close proximity since Jaluka's suckling interactions drop dramatically from 1-6 to 7-12 months (similar to all other captive calves; Figure 5.5). The absence of Juva after five months may have had some effect here as his earlier presence may have encouraged her to venture further from their mother (to greet and investigate others or what they were doing); whereas with his absence, her already considerably limited neighbour choice was reduced further.

Mansi

In the case study for African calf, Mansi, it is first important to note that her proximity data were for her allomother as her mother had died, and then included her non-allomother neighbour. Nutrition gained from suckling interactions would, therefore, have played no part in Mansi's choice of proximity to her allomother unlike other calves and their mothers.

When proximity data were collected, in addition to distance, it was also noted if a barrier physically divided the two elephants (even if they could touch through it, and only if they could not walk around it, i.e. their access had been limited by management (see Section 3.3). Only orphan Mansi is worth noting here as her barrier-proximities were <2.5% in her first 24 months, but rose for close, mid, and far proximities at year three for non-mother neighbours (Figure 5.11). As Mansi and her allomother's family were not separated during the day (except occasionally for the month when Tammi's calf was alive), Mansi always had the choice at least two neighbours, in addition to her allomother. However, at year three Mansi chose to spend 41.7% of her time both far from others, and closer to elephants in separate paddocks/pens than the one she was in. If we look at distance only (ignoring barriers), Mansi spent 44.1% of her time far from others.

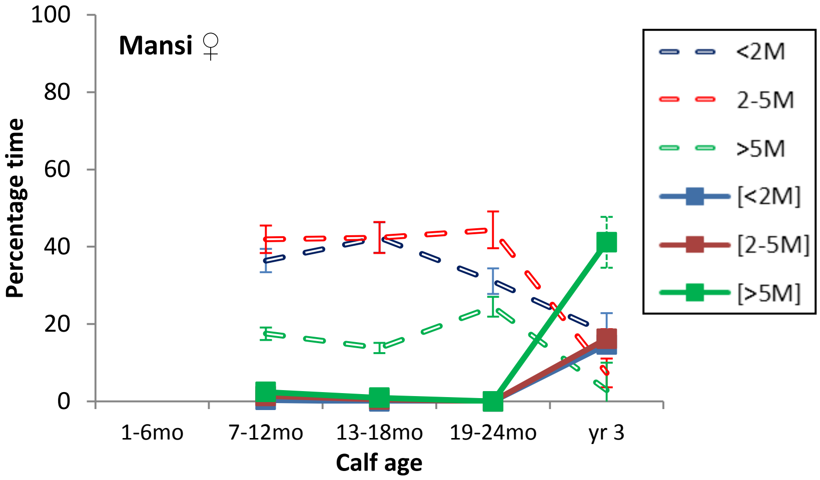


Figure 5.11 Proximity to Nearest Non-Allomother Neighbour as Percentage Time for Mansi. [With] and without barriers. For N of observations see Table 3.5. Binomial 95%CI.

It may be possible that when Mansi was choosing to avoid others in her paddock, her nearest non-allomother neighbour just happened to be in another paddock. However, from personal observation, it seems more realistic to suggest that Mansi had a very limited interest being around other elephants. Rather than actively avoiding the other elephants, it appeared that she failed to actively seek them out.

5.4.7 The Issue of Availability of Others

In captivity, calves have limited diversity in their available social partners compared to the wild (particularly in African elephants). However, captive calves also have fewer choices over proximity to others due to enclosure constraints (i.e. they cannot leave their enclosure area) and therefore appear to interact with others more than wild African calves do.

It is also worth remarking that the captive elephants here were observed to have more events of aggression than wild study animals as mentioned earlier. This is most likely to be a function of smaller living areas and an inability to leave the group, whereas wild animals have the space to avoid one another, and confrontations, at will. For example, during a focal study in Uda Walawe a two year old calf, [cRighthole_10], was observed avoiding an adult male and later even fleeing (even though adult male has shown no signs of aggression at the time).

Another example, recorded during focal studies in Uda Walawe, was of an aggressive interaction initiated by a juvenile who shoved an adult female, seemingly unprovoked. What followed was an intense but short-lived aggressive interaction where a second adult female charged and rammed the first. This second adult was possibly ‘protecting’ her juvenile, although he did not appear to need her assistance. The female who was shoved, leaves proximity, choosing distance as a mechanism to manage her relationships.

Heightened aggression interactions in captivity not only led to relocations and interruption/termination of ‘friendships’ but also to injury or deaths within the captive study groups, as described below.

When Sundara was around three years old (2006-2007), Jangoli, who became her ‘closest friend’ in later years, would intermittently attack her, especially when the two were confined together. One such incident saw Jangoli pin Sundara to the rubber flooring with enough force to break Sundara’s tush (pers. obsv.).

Focal sample videos also captured the aforementioned aggression from Tammi directed towards Stuvite. After data collected terminated, Swana was euthanised following an attack from another adult female (and Stuvite’s eventual euthanasia a week later when she collapsed after being treated for an infection to one of her back legs).

5.5 Discussion

As with Chapter Four (Activities), individual calf ID was a significant factor in some of the analysis in this Chapter: close and far proximities from mothers as well as suckling interaction. This again means that there was a large individual contribution to the overall pattern of these data. Despite this considerable (and significant) contribution of individual (calf ID) to the variance patterns in the tests presented in this Chapter, calf age and context still significantly influenced these behaviours over and above the effect of the individual. Furthermore to results again requiring cautious interpretation due to high individual variance, non-normal distributions of data and small sample sizes; the interpretation of non-play social interactions with others also requires caution in this Chapter due to its infrequency. However, I do have a robust sample from the wild and therefore, this again provides our baseline for interpretation.

Most activity synchronisation between mothers and calves occurred amongst the youngest calves and wild African calves. Synchrony during foraging over large areas was necessary to avoid mothers and calves becoming separated and leaving calves vulnerable to predators. Captive calves may have more opportunities to do what they want irrespective of their mother's activity and this may also be reflected in the finding that captive Asian calves spent more time further from their mothers than calves did in the other contexts, indicating that they were more independent. Wild Asian calves were also observed in close proximity to their mothers more than others calves were.

Across all contexts, proximity to mother revealed changing patterns as calves became more independent with age and ventured further from their mothers. As expected, suckling interactions occurred most frequently in the first year of life, showing age-related declines although this was not constant, nor significant due to high inter-individual variation. Similarly, most non-play social interactions occurred in early life for calves.

Suckling and Allosuckling

Wild African mothers have been shown to be equally tolerant to suckling demands of sons and daughters when calves are younger. Although they become less tolerant of their older sons' demands, sons still have higher frequencies of successful suckling than daughters do in the first three years of life (Lee & Moss, 1986). Lactating females other than grandmothers were generally intolerant to allosuckling in Amboseli and rejected calves aggressively (Lee, 1987). Nulliparous females, however, were tolerant of allosuckling (Lee, 1987).

In some cases (14.6%, N=48), older calves continued to suckle from their mother along with their younger sibling, sucking simultaneously from opposite nipples (Lee & Moss, 1986). In two of these cases, the younger calf died (one in the first month and one in the twelfth month of life). Pairs where the younger calf died were both male-female sibling pairs, and the third recorded male-female pair only ‘double suckled’ for two months (Lee & Moss, 1986).

Following the birth of captive Asian calf Jamilah to the group at Chester, the Zoo was concerned for her health and development since older calf Nayan was also suckling from Jamilah’s mother, Thi, who was also his grandmother. Studies have found that total solids and fat levels in elephant milk varied widely (Mainka et al., 1994; Oftedal, 1984) and Mainka et al. (1994) suggested that these fat level variations may be a result of differences in sampling times from the onset of nursing. They suggest that fat levels were highest at the onset of nursing and dropped to their lowest levels as nursing is complete. When concerned with the welfare of a new calf whose milk supply is being shared by an older calf, it is, therefore, important to ask at which point in the onset of nursing is the older calf taking milk, in addition to durations in months or minutes.

Within the study period, Nayan was usually only observed successfully suckling when Jamilah was on the contralateral teat. If he alone was attempting to suckle, he was often roaring as Thi would push him away, using her trunk, kicking him, or moving her front legs to block access to her teat. Jamilah also attempted to double suckle from Hari’s mother when Hari was a few days old, although this behaviour only lasted a few days in Jamilah. (She also had to bend or kneel down in order to suckle Sundara). In Mainka and colleagues' (1994) study, they noted that when they collected milk samples opportunistically, it was ‘almost impossible’ to express milk unless the calf was sucking at the same time from the contralateral teat. It, therefore, appears that lactating females can choose whether to allow calves to suck. In terms of calves which are not their own, this highlights the element of choice in allocare.

Jamilah attempting to double suck from Sundara whilst newborn Hari suckles from his mother's other nipple. This behaviour was only seen in Sundara for a few days. Photograph taken 27th November 2012.

Conversely, other social pressures may be playing a role here and affecting this allocare choice, such as dominance. In Sri Lanka, for examples, a sub-adult male was seen nursing from an adult female and then moved on to nurse from a second. This male was almost the same height as the first female and it is thought that he was perhaps the son of the second, taller female [Tanya]. This assumption was made on the basis that [Tanya] was the most dominant female in the group (and her group were also relatively dominant within Uda Walawe; de Silva, June 2012, pers. comm.) and I suggest that this male may have developed this habit as a result of his mother deterring other females from pushing him away in his early years, by aiding him with her presence if he cried out in frustration. Non-mother females may therefore have been discouraged from disciplining this male against suckling from them and it would appear that his mother chose not to push him away either, despite his unusual age to be observed suckling. However, this is conjecture and we currently have no evidence that he is related to either of the females involved. A juvenile, approximately five years old, was also observed gently displacing a newborn calf who was nursing, in order to take milk from the same nipple (2013, pers. obsv.). In this case, it appeared that the mother of the newborn may not have been aware until the newborn gave up and walked under its mothers head, and at this point she appeared to become aware of the older calf and pulled her nipple away by moving forwards.

Wild Asian sub-adult male suckling from two different adult females in Uda Walawe. Still images taken from footage filmed on 11th June 2012

Lactation, Calf Growth and Maternal Diet

Mammals show considerable diversity in their reproductive strategies and this is highlighted by differences in maternal effort between species, for example, hooded seal pups suckle for four days whereas chimpanzees and elephants can suckle for to eight years (Lee, 1996). The energy content of milk scales with maternal mass (Oftedal, 1984) and experimental studies in rodents have shown that milk composition can be influenced by variation in maternal diets. Rat mothers produced more saturated fats in their milk when fed a high saturated fat diet and effects of maternal diets on milk composition has been shown to have long lasting effects on offspring phenotype (see Jonas & Woodside, 2015; Priego, Sánchez, García, Palou & Picó, 2013; Trottier et al., 1998).

However, diet may also play a role in offspring development even before birth and subsequent lactation, with major implications for birthing success. Hartley (2016) found that birth weight of Asian elephant calves in European zoos was a significant risk factor associated with dystocia. He suggested that increased calf weight may be linked to the position of the calf in the uterus since large calves would be less able to change their position than a smaller calf would (Hartley, 2016). High incidence of stillbirths in European zoo elephants, compared to Asian elephants in logging elephants in Myanmar or wild African elephants in Amboseli, may be related to captive females being overweight (Taylor & Poole, 1998).

It is important to ask whether captive calves are born bigger than wild calves and do they grow faster? How well these captive calves grow, and at what rate, may have implications for metabolic health. Is an increase in growth a result of nutrition and/or overweight mothers alone, or are other factors involved such as the amount of space available for exercise or being less active due to a lack of playmates? Play has been shown to contribute greatly to calf development including motor and social skills in young calves

(Lee, 1986) and is discussed in detail in the next Chapter. Lee and Moss (2014) report than in wild African calves, play represents 3.8% of a calf's time, when not at rest. They suggest that play adds to total energy expenditure, and may be part of the maintenance of healthy physical development and was associated with greater longevity.

Developing Maternal Skills

The importance of allomothering was discussed earlier and it has been shown in wild African elephants that longevity also has reproductive advantages brought about by the presence of grandmothers, suggesting that an extended lifespan and consequently prolonged fertility has been positively selected for (Lee et al., 2016). In addition to this, Hartley (2016) has shown that maternal or allomothering experience was an important factor in elephants in European zoos in reducing poor maternal behaviour and thus improving calf survival.

During my study, Tammi rejected her newborn calf. This was surprising as Tammi has successfully raised three calves before and it is unusual, even in captivity, for a mother who has successfully reared a calf before to reject further calves. Usually it is the inexperienced, for example, Thi killed her first calf and keepers removed her second calf due to her being "*extremely aggressive towards her calf*" (Lyons, 1995, para. 2) although she went on to successfully raise five following live-born calves (although two of these subsequently died around two years of age due to EEHV; they did not die as a result of her aggression towards them). While Tammi's calf appeared healthy at birth, the calf's rejection was possibly as a result of a disability which her mother identified, but which we as humans have failed to detect. This raises the question of how many elephant calves have been rejected by their mothers for such disabilities and opens up an ethical debate as to whether we should be investing resources for endangered and vulnerable species into hand raising calves in captivity who have been rejected in this way since they are unlikely to develop into functioning group members. Although these rejected calves will most likely be few in comparison to those killed in captivity by aggression, one such rejected calf in the wild, as cared for at The David Sheldrick Wildlife Trust (DSWT) Elephant Nursery in Nairobi, Kenya. The calf was autopsied after its death and was found to have poor brain development; presumably, the mother rejected her for this reason (P.C. Lee, September 2016, pers. comm.). Although it is important to rehabilitate calves which have been orphaned or injured through human-made activities, it may be valuable to further develop our understanding and ability to identify developmental disabilities as well as further details in the complex interactions between mother and calf in order to concentrate our efforts on raising calves with a stronger chance of survival.

Experience of Births of Herd Mates

In Prado-Oviedo and colleagues' (2016) study investigating offspring births in captive Asian and African elephants in US zoos, they found 58% (115/200) of females had been exposed to at least one recorded herd mate birth with higher rates among Asian than African females. A total of 188 of these 200 females were of reproductive age and 29% (54/188) were recorded as giving birth at least once. They also found that captive-born females had a 96% higher rate of giving birth than did imported females (from range countries). In African elephants, captive-born females had higher rates of being exposed to a herd mate birth within her facility than imported females; but this effect was not found in Asian elephants (Prado-Oviedo et al., 2016). The result seems logical as a captive-born animal will likely already be in a breeding facility whereas a wild-born captive animal may be in either a breeding or a non-breeding facility (or even in a successful versus non-successful breeding facility.) This is also in line with their demographic findings that captive-born females were more likely to be exposed to births within their facility than were imported females; and that captive females first experienced this at younger ages than imported females (Prado-Oviedo et al., 2016).

Importantly, Prado-Oviedo et al. (2016) report the mean age at first offspring birth to be 15 years younger than the mean age that these females are first exposed to the birth of another herd mate. We, therefore, have serious problems in elephant captive breeding where young females are being denied the experiences of calves to allomother or of births that they would normally gain exposure to within their herd before they ever give birth themselves for the first time.

These captive case studies and the comparisons with the wild calves further illustrate the considerable individual variation we see in both captive and wild elephant calves, suggesting that there is no easy way to replicate a ‘standard’ environment for development in captivity.

Chapter 6: The Importance of Play

Captive African calves, Mchumba, Jaluka and Impi engaging in escalated contact play during a group dusting session at Howletts. Photograph taken 2nd October 2011.

6.1 Abstract

In this Chapter, I examine play behaviour in detail a) as it has been suggested as a potential welfare indicator and b) play has been associated with long-term survival in elephants. I break down play into play types and both social and non-social play are investigated. Play partner availability is explored in captive (Asian$_{N=8}$; African$_{N=7}$) and wild calves (Asian$_{N=101}$; African$_{N=130}$). Social (gentle and escalated-contact) play was the most frequent social interaction among immature elephants, accounting for 3-9% of time. Non-social (object and lone) play account for an additional 1-11% of time.

Most LEGO (total) play was seen in captive Asian calves (*p*<0.001), particularly at 1-6 months, while wild African calves spent the least time in play (pairwise with: wild Asian *p*=0.001; captive Asian, *p*<0.001; captive African: *p*<0.0011) although they had the greatest number and most diverse play partners.

Time spent playing was unrelated to time spent suckling (except for captive Asian female calves, $p<0.001$) and was negatively correlated with time spent independent feeding. These results suggest that maternal energy via lactation does not limit play early in life but energy acquired independently does affect play.

Play, while a potential indicator of compromised welfare for many species when absent, may act as a displacement activity for bored captive elephants.

6.2 Introduction

Play is a complex behaviour with a variety of costs and benefits for playing organisms. It is widely distributed across taxa, from invertebrates to fish, birds and mammals (Burghardt, 2006). The quest for a single ‘function’ of play has been fruitless – rather, recent approaches have concentrated on two key areas: (1) what does play accomplish for a playful organism in its current context (Gomendio, 1988) and (2) what does play effect over the lifecourse of the organism. These distinctions, between juvenile adaptations and ‘scaffolding’ (Bateson, 1981), might be especially important when examining play behaviour in a captive context, as these differ markedly from the animal’s wild social and ecological environments.

Similarly, defining play – and uncertainty around which behaviours qualify as play – has also remained problematic (see Burghardt, 2006). To recognise play in all species – including humans – Burghardt (2006) updated the working definition of play using five criteria. For the label of play to be applied, all five criteria must be satisfied, simultaneously. These five criteria state that play is:

1) “*incompletely functional in the context in which it appears*”
2) “*spontaneous, pleasurable, rewarding, or voluntary*”
3) “*differs from other more serious behaviours in form (e.g., exaggerated) or timing…*”
4) “*is repeated, but not in abnormal and unvarying stereotypic form…”*
5) “*is initiated in the absence of severe stress*” (Burghardt, 2006; Graham, Burghardt & Wiens, 2010, p 394).

Play behaviour was investigated in detail in this study, as there have been several studies that consider play as a potential indicator of welfare and wellbeing (Fagen & Fagen, 2004; Held & Špinka, 2011; Mintline et al., 2013; Yamanashi, Nogami, Teramoto, Morimura & Hirata, in press). This will be discussed further in the Welfare and Play subsection below.

Elephants are a taxon where play may be especially revealing of state or affect since play occurs throughout the lifetime of elephants, and both sexes play in many different ways (Lee & Moss, 2014). Although play is generally seen most frequently in young animals, elephants have been observed in play well into their 40s and 50s (Lee & Moss, 2014). Additionally, play in early development in elephants has been shown to have long-term effects on survival. Play rates for age in early life appears to indicate high individual quality whereas elephants with reduced rates of play may be associated with reduced growth rates and, consequently, increased mortality (Lee et al., 2013; Lee & Moss, 2014).

Most species of mammals (for example: ground squirrels, *S. beldingi*, Nunes, Muecke, Sanchez, Hoffmeier & Lancaster, 2004; lowland gorillas, *Gorilla gorilla gorilla*, Maestripieri & Ross, 2004; horses, McDonnell & Poulin, 2002; brown bears, *Ursus arctos,* Fagen & Fagen, 2004; grey wolves, *Canis lupus,* Cordoni, 2009; bottlenose dolphins, *Tursiops truncates,* Paulos, Trone & Kuczaj, 2010) and many birds (for example, psittacines; Eurasian babblers, *Turdoides spp.;* and corvids, Diamond & Bond, 2003) and even insects and molluscs (Burghardt, 2006) play in both captivity and the wild, while rates and types differ both between the species and within them; seasonally, by sex, or due to individual differences.

Escalated-contact social play in the form of vigorous pushing, between captive African calves Jaluka and Impi at Howletts. Photograph taken 17th May 2012.

Bekoff (1976) states that play normally occurs only once more pressing physiological needs have been satisfied. Play is fuelled by energy, even if the metabolic costs are small (Martin, 1982, 1984) and therefore play tends to diminish from the repertoire when individuals are under energy stress (e.g. vervet monkeys, *Cercopithecus aethiops*, Lee, 1984; wolves, Cordoni, 2009). Early in development, most energy derives from the mother through suckling, and therefore I examined play behaviour in relation to suckling interactions. Weaning is a further stressor for some species, and play declines in frequency when individuals experience both a loss of energy and attention from the mother (e.g. domestic pigs, Donaldson, Newberry, Špinka & Cloutier, 2002; cattle, Krachun, Rushen & de Passillé, 2010). As elephant calves age, independent feeding replaces milk energy, which then has to sustain both growth and play (Bekoff & Byers, 1992; Miller & Byers, 1991). It can thus be predicted that play will have to be balanced between the other activities also requiring energy, such as travel. As was shown in Chapter Four, these activities change with age and differ to some extent between male and female calves. The relationships between suckling interaction and play, and between independent feeding and play are examined here.

In investigating play, there are a number of ways of classifying the types of play. Since the costs and potential benefits of the main play types (social and non-social) may vary, I have examined these separately and used definitions of elephant play that have been provided in the literature (from Lee & Moss, 2011, 2014; Poole & Granli, 2004; Table 6.1 below). It should be noted that no previous study of wild Asian elephant calves has yet described play in detail, so the definitions used here will need further validation in other populations.

Escalated-contact social play between captive African calves Jaluka and Impi at Howletts during a game of ‘king of the castle’. Photograph taken 17th May 2012.

Play types include social play, which involves interactions with others, and non-social play, where play is neither with nor directed towards conspecifics (Lee & Moss, 2011; Mendoza-Granados & Sommer, 1995). Play can also be further divided into a third category as parallel play, which is play “*socially facilitated without interaction*” but this was not considered in this study due to the difficulties detecting interactions without physical contact (Muller-Schwarze et al., 1982, p. 85).

Social play can include both escalated and gentle-contact play with conspecifics. Sparring is the most commonly known form of social play in elephants, particularly between males (Poole & Granli, 2011). Chasing is also frequent with roles changing between flight and pursuit at varying speeds (Mendoza-Granados & Sommer, 1995).

Table 6.1 Play Types in Elephants. Definitions from Lee & Moss, 2011, 2014; Poole & Granli, 2004.

	Play type	Description of play	Age-sex classes (in African elephants)
Non-social	Lone (L)	Floppy-running, swinging head or head low in mock-charge. Spinning, rocking, kicking, kneeling down on front legs and/or allowing the trunk to flop their own head from a raised position while opening their mouth (Flop-Trunk-on-Head). Often accompanied by ‘play’ (low, pulsating) trumpets. - This can also include tactile lone play in the form of swimming without contact (e.g. ducking, splashing).	All ages; swimming especially seen in adolescent & adult males
	Object (O)	Playfully exploring objects with trunk, mouth, tusks or feet in a vigorous or gentle manner; throwing objects, rolling objects, general intense manipulation of objects. Repeated acts, associated with playful head and ear movements (signals) - This can also include tactile object play in the form of play with mud or water, dust, vegetation or other tactile stimuli.	All ages
Social	Gentle-contact (G)	Climb upon, wiggling, lean on, rub against, roll onto, shove gently, trunk twining and gentle trunk wrestle. Can also include kneeling down on front legs or Flop-Trunk-on-Head. - This can also include tactile play in the form of swimming with gentle-contact (e.g. trunk-twining in water).	Infant & juveniles, often older juvenile females play with young calves
	Escalated-contact (E)	Mount, reaching over the back of another, tail grasping, chase, push vigorously, vigorous sparring head to head. Trunk in relaxed position. - This can also include tactile play in the form of swimming with escalated-contact (e.g. wrestling in water).	Juvenile & adolescent males and females, adult; swimming especially seen in adolescent & adult males

Gentle-contact social play in the form of vigorous pushing, between captive African calves Jaluka and Impi at Howletts. Photograph taken 17th May 2012.

Burghardt (2006) puts forward the case that environmental exploration is distinct from play - although it can lead to play. He suggests that individuals gather information about their environment through exploration and that they use object play to discover what can be ‘done’ with the object (including repeating actions which have similar outcomes “*long after an animal knows what can be ‘done’ with the object*”) (p.58). The distinction is difficult to make, however, as these behaviours lie among a continuum, particularly for species like elephants. Adding to this difficulty, Burghardt (2006) states that the two processes are linked developmentally (Welker, 1971, in Burghardt, 2006) and “*thus may not be distinguishable early in ontogeny, including in human infancy*” (p. 58). While features of exploratory behaviour have been characterised as deliberate and of neutral or negative affect (Burghardt, 2006; Johnson, Christie & Yawkey, 1999; Pellegrini & Boyd, 1993; Panskepp, 1998), exploratory behaviour in young elephants is often not deliberate and can also be of positive affect. Although Burghardt (2006) suggests that “*describing all play, especially extended and repetitive play, as nothing but exploration is not useful*” he concedes that “*exploration and curiosity may be components of play*” (p. 60).

In elephants, environmental exploration may include kicking-dust or approaching, chasing or vocalising at objects (birds, monkeys, other species) in the environment typically with exaggerated movements of the head, trunk and body and often with trumpeting vocalisations. These behaviours can occasionally appear or become aggressive (Poole & Granli, 2011).

Likewise, active solicitation behaviours (alone or in combinations) are often found leading to social play and are signals of intentions to play. These signals may include tusking the ground, kneeling invitations, waggling their head, raising their trunk (spar invitation) and curling their trunk over their own tusk with their head back (Poole & Granli, 2011).

In order for older and larger elephants to elicit play in younger, smaller individuals they may self-handicap for example, lie down or get down on their knees. This not only allows the younger animal to have more physical contact and to even climb on them but also makes them appear less intimidating (Poole & Granli, 2011). Older males have even been observed to solicit play in this kneeling fashion to spar with a younger male who may have "*shown signs of being afraid to participate*" (Moss, 1988; Poole & Granli, 2011, p. 212).

Example of self-handicapping in play by Etana in order to elicit play in younger calves Jaluka and Impi. Photograph taken 17th May 2012.

Non-social play included both object and lone locomotor play. Locomotor play is usually solitary and can involve intense or sustained locomotor movements, again without any apparent purpose (Burghardt, 2006). Elephants engage in many forms of lone and object play, primarily seen in young animals, presumably for amusement (Poole & Granli, 2011). Some behaviours which are particularly fun (at least for the observer involved!) include face-planting, trunk-squelching and swinging their trunk and simultaneously spraying water (Poole & Granli, 2011).

The first objective of this Chapter is to investigate whether captive and wild elephant calves engage in the same types of play. I also examine differences between Asian and African calves as well as any effect of calf age, and sex. I hypothesise that wild calves play more than captive calves due to the availability of partners and that play types will decrease with age in each context as is common in many species. I further hypothesise that captive calves use engaged active behaviours such as lone play or object play to compensate for the lack of social partners and social interactions in captivity.

It was possible to investigate play partners for captive calves and for wild African but not wild Asian calves because determining an individual ID for play partners in Uda Walawe was extremely difficult. Furthermore, in captivity, calves had so few play partners that partners were not comparable between the four contexts. This Chapter goes on, however, to assess whether groups size and composition affect elephant calf play behaviours.

The third section explores whether relationships between play and suckling interactions in relation to weaning dynamics change with calf age, sex, species or differ between the wild and captivity. Finally, the fourth section assesses whether relationships between play and independent feeding change with calf age, sex, species or differ between the wild and captivity as a function of energetics.

Welfare and Play

Play is important for socialisation including self-assessment of physical and social abilities (Thompson, 1998), and Pellis, Pellis and Bell (2010) showed that juvenile rats that play were more socially competent as adults. It is therefore important to ask if play is limited in captivity, due to lack of novel stimulus or play partners, compared to the wild.

Play has been identified as a potential positive indicator of an individual’s welfare and has been even been described as an “*opioid-mediated pleasurable emotional experience*” (Boissy et al., 2007; Descovich et al., 2017; Held & Špinka, 2011, p.891). In young animals, play only occurs when individuals are free from stress in the absence of threats and when their basic short-term needs have been met (Bateson & Martin, 2013, Lee, 1984). Individuals may reduce their expression of play or may drop it from their behavioural repertoire entirely when: conditions become challenging, energy availability is low, maternal care is reduced or when they are deprived social contact with conspecifics; or due to ill health (Descovich et al., 2017; Fraser & Duncan, 1998; Held & Špinka, 2011; Špinka, Newberry & Bekoff, 2001).

The challenge of providing good welfare for an individual is predominantly in providing the presence of positive experiences – including pleasure e.g. excited playfulness or affectionate sociability – rather than merely in ensuring the absence of negative experiences (Boissy et al., 2007). Play behaviour in mammals is often labelled as fun, is linked to positive emotions and is frequently accompanied by pleasure (Cooke & Shukla, 2011; Fraser & Duncan, 1998; Held & Špinka, 2011; Panksepp & Burgdorf, 2003; Špinka et al., 2001). Centuries ago Darwin (1871) recognised it as being universally rewarding, writing, "*Happiness is never better exhibited than by young animals, such as puppies, kittens, lambs, etc., when playing together, like our own children*" (p. 39).

However, play's validity as a positive indicator of welfare is under debate (e.g. Hausberger, Fureix, Bourjade, Wessel-Robert & Richard-Yris, 2012; Yamanashi et al., in press) and we need to be cautious when interpreting play as a welfare indicator. Yamanashi et al. (in press) investigated social play in captive adult chimpanzees and suggested that chimpanzees were using social play to reduce tensions since social play increased before feeding; was higher in male-male groups (compared to mixed-sex groups); was negatively correlated to mutual social grooming; and had no relationship with aggressive interactions (although mutual social grooming negatively correlated with aggressive interactions). Similarly, in adult riding school horses, the most playful individuals were shown to be those suffering most chronic stress, suggesting that adult play in horses is linked to poor welfare (Hausberger et al., 2012). Chronic stress was calculated from measures including vertebral disorders, altered time budgets, stereotypic behaviours and physiological parameters e.g. cortisol levels. Play might be seen as a coping strategy for individuals with compromised welfare.

Predictions regarding play were that a) play will decline similarly with age for both species, b) captive calves will exhibit more lone play than social play due to constraints of partner availability, and c) social play could be an indicator of positive affect and welfare.

6.3 Methods

The study sites and populations were defined earlier in Chapter Two (Description of Study Sites and Subjects). Data collection and analysis were described in Chapter Three (Methods).

Activities were defined in general terms from the ethogram (Appendix C), and several categories were combined. I looked at the four main categories of play which can be divided into either social or non-social play for analysis (Table 6.1). Social play included both gentle-contact and escalated-contact play (G & E), while non-social play included lone and object play (L & O). When all four play types (L, E, G & O) are discussed together, I termed this 'all-play' as LEGO-play.

The percent of time spent in play categories, suckling interactions, or independent feeding were calculated for each individual calf from 5 min scans (taken from 10 min focal samples for Asian and captive, and from 60 min focal samples for wild African). For captive elephants, activity budgets were also calculated using 25 min scan data to include calves up to the age of five years. Means and 95% confidence intervals are presented throughout the text for non-log transformed values. Data were binned together per month per calf.

In the captive African calf dataset, both Mansi (who was rejected, re-accepted, then at 16 weeks, orphaned) and Tammi's calf (who was rejected, then died at 31 days) remained in the dataset.

Data analyses

The effect of age (binned together in six month intervals from birth to 24 months and then 3-5 years), sex and context and their interactions on the time spent in play (social, non-social and LEGO-play) were examined using GLMM (see Methods, Chapter Three). For sample sizes of calves and calf behavioural observations in GLMM analyses per age category, sex and context, see Chapter Three (Methods, Table 3.6). Only final models are presented and full models are in the Appendix. Individual calf ID was used as a random variable to control for repeated measures.

6.4 Play Results

6.4.1 Play Types

Calves across all contexts engaged in both social and non-social play (Figures 6.1; 6.2). Context had an overall significant effect on time spent in the combined LEGO-play (Table 6.2; 6.3) as well as social-play (Table 6.4) and non-social play (Table 6.5) separately. Below I present the findings of total LEGO-play across context, age and sex, and then decompose this into social and non-social play categories. For graphical convenience, as with previous Chapters, I will start with the analysis of calf means for all contexts. This will be followed by play charts of wild calves by species; then captive calves by species; before breaking play down for individual captive Asian; and finally individual captive African calves. This presentation optimally allows for the large numbers of charts to be visually compared across contexts.

Table 6.2 Mean Percentages of Total Activity Budget in Social, Non-Social and LEGO-Play for Calves <24 mo, by Context. See Table 3.6, Chapter Three, for N.

	Social Play				Non-social Play				LEGO-play			
Context	Mean %	Median %	IQR %	95% CI	Mean %	Median %	IQR %	95% CI	Mean %	Median %	IQR %	95% CI
Wild Asian	4.89	0.00	0.00	2.69-7.09	6.19	0.00	0.00	3.72-8.66	11.08	0.00	16.67	7.52-14.63
Wild African	2.82	0.00	7.14	1.83-3.85	0.70	0.00	0.00	0.21-1.20	3.54	0.00	7.69	2.36-4.73
Captive Asian	9.17	8.66	13.16	7.97-10.39	11.29	9.76	11.85	9.87-12.70	20.46	18.75	14.77	18.55-22.37
Captive African	5.71	3.92	7.84	4.56-6.85	10.34	10.14	9.49	8.81-11.85	16.04	14.71	15.79	13.94-18.14

6.4.1.1 LEGO-play

Context had an overall effect on LEGO-play, as did age, and the interaction between age and context (Table 6.3). Calf sex, however, had no overall effect in LEGO-play (*p*=0.089).

Mean percent time spent in LEGO-play in either species in captivity was significantly greater than that for either species in the wild (Figures 6.1; 6.2). Captive Asian calves engaged in significantly higher levels of LEGO-play than all other contexts (Table 6.2; 6.3). This was also the case for pairwise comparisons between captive Asian and wild

Asian; wild African; and captive African calves. Further pairwise contrasts showed significantly higher play for captive African than wild African and wild Asian. Wild Asian calves had significantly higher rates of LEGO-play than did wild African calves (Table 6.3)

The mean percentage time calves engaged in LEGO-play was highest in 1-6 months compared to all other ages in pairwise comparisons (Table 6.3).

Significant interactions were also found for LEGO-play between age and context in 1-6 months with wild Asian spending higher percentages of time in play than other contexts while all other age groups were lower in total play by comparison to 13-18 months captive Asian calves (Table 6.3). Note that there was considerable significant individual variance in time spent in LEGO-play.

Table 6.3 Final General Linear Mixed Model for LEGO-play. Var (ID)=24.98, *p*=0.003. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was LEGO-Play; independent variables were age, context, and the interactions between them.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI)**	***p* value**
Overall model fit	$F_{19, 385}$=10.135, p<0.001		
Age	$F_{4, 492}$=11.614, p<0.001		
1-6mo - 7-12mo		6.532 (3.735 to 9.330)	<0.001
1-6mo - 13-18mo		7.878 (5.140 to 10.616)	<0.001
1-6mo - 19-24mo		7.957 (4.103 to 10.338)	<0.001
1-6mo - 3.5yr		7.221 (4.103 to 10.338)	<0.001
Context	$F_{3, 58}$=26.0337, p<0.001		
Asian captive		24.770 (18.192 to 31.348)	<0.001
Asian wild – African wild		4.659 (1.869 to 7.448)	0.001
Asian wild – Asian captive		-14.020 (-18.622 to -9.419)	<0.001
Asian wild – African captive		-5.695 (-10.721 to -0.668)	0.027
African wild – Asian captive		-18.679 (-23.195 to -14.162)	<0.001
African wild – African captive		-10.353 (-15.302 to -5.405)	<0.001
Asian captive – African captive		8.326 (2.150 to 14.501)	0.010
Age x context	$F_{12, 540}$=3.696, p<0.001		

1-6mo Asian wild	12.308 (6.039 to 18.577)	<0.001
13-18mo Asian captive	-11.243 (-19.563 to -2.923)	0.008
1-6mo – 7-12mo Asian wild	16.494 (10.432 to 22.556)	<0.001
1-6mo – 13-18mo Asian wild	16.233 (11.254 to 21.213)	<0.001
1-6mo – 19-24mo Asian wild	17.440 (11.013 to 23.867)	<0.001
1-6mo – 3-5yrs Asian wild	16.309 (11.747 to 20.871)	<0.001
1-6mo – 13-18mo Asian captive	5.299 (0.209 to 10.389)	0.041
13-18mo – 3-5yrs Asian captive	-7.955 (-14.766 to -1.144)	0.022
1-6mo – 13-18mo African captive	9.267 (2.806 to 15.727)	0.005
1-6mo – 19-24mo African captive	9.318 (2.492 to 16.144)	0.008
1-6mo – 3-5yrs African captive	11.229 (2.501 to 19.956)	0.012
7-12mo – 13-18mo African captive	7.588 (0.950 to 14.226)	0.025
7-12mo – 19-24mo African captive	7.639 (0.619 to 14.660)	0.033
7-12mo – 3-5yrs African captive	9.550 (0.824 to 18.276)	0.032

6.4.1.2 Social Play

For social play, there were overall significant effects between contexts and in the interaction between age and context. Neither age nor sex affected rates of social play overall (Table 6.4).

Similar to LEGO-play, captive Asian calves engaged in significantly higher percentages of social play than did calves from all other contexts (Table 6.4). This was again also the case for pairwise comparisons between captive Asian and wild Asian; wild African; and captive African calves. Likewise, further pairwise contrasts found significantly higher percentages of social play for captive African than wild African; and than wild Asian.

Additionally, significant interactions were found between age and sex (male 1-6 months; male 7-12 months; male 13-18 months; male 19-24 months) as well as between age and context (wild Asian calves 1-6 months) (Table 6.4).

An overall interaction was found between calf sex and context for male wild Asian calves (Table 6.4).

Finally, there was an interaction between calf sex and age within contexts. Significant interactions were found in wild Asian male calves at 1-6, 7-12, 13-18 and 19-24 months; in wild African male calves at 1-6, 7-12, 13-18 and 19-24 months; and in male captive Asian calves at 1-6 months (Table 6.4). These interactions suggest a consistent pattern for males spending more time in social play. There were no significant contributions of individual to these patterns.

Table 6.4 Final General Linear Mixed Model for Social Play. Var (ID)=2.86, *p*=0.132. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was social play; independent variables were age, context, sex and the interactions between them.

	Main effect *F* and *p* value	Coefficient *β* (95% CI)	*p* value
Overall model fit	$F_{38, 194}$=3.554, *p*<0.001		
Context	$F_{3, 37}$=20.282 *p*<0.001		
Asian captive		11.304 (5.080 to 16.988)	<0.001
Asian wild – Asian captive		-7.459 (-9.776 to -5.141)	<0.001
Asian wild – African captive		-2.722 (-5.267 to -0.177)	0.037
African wild – Asian captive		-8.002 (-10.209 to -5.796)	<0.001
African wild – African captive		-3.266 (-5.711 to -0.821)	0.010
Asian captive – African captive		4.737 (1.819 to 7.655)	0.003
Age x sex	$F_{4, 513}$=1.015 *p*=0.399		
1-6mo x male		15.432 (2.340 to 28.523)	0.021
7-12mo x male		17.668 (4.251 to 31.085)	0.010
13-18mo x male		16.534 (3.106 to 29.962)	0.016
19-24mo x male		15.363 (6.125 to 24.601)	0.001
Age x context	$F_{12, 384}$=2.191 *p*=0.012		
1-6mo x Asian wild		8.128 (1.134 to 15.123)	0.023
Sex x context	$F_{3, 39}$=1.515 *p*=0.226		
Male x Asian wild		14.583 (1.715 to 27.450)	0.026
Sex x age (within context)	$F_{11, 607}$=1.360 *p*=0.187		
Male x 1-6mo (within Asian wild)		-22.313 (-36.892 to -7.733)	0.003
Male x 7-12mo (within Asian wild)		-24.955 (-40.546 to -9.364)	0.002
Male x 13-18mo (within Asian wild)		-19.655 (-34.484 to -4.824)	0.009
Male x 19-24mo (within Asian wild)		-18.429 (-31.036 to -5.821)	0.004
Male x 1-6mo (within African wild)		-15.970 (-30.125 to -1.816)	0.027
Male x 7-12mo (within African wild)		-17.117 (-31.694 to -2.541)	0.021
Male x 13-18mo (within African wild)		-14.826 (-29.598 to -0.054)	0.049
Male x 19-24mo (within African wild)		-15.882 (-27.459 to -4.304)	0.007
Male x 1-6mo (within Asian captive)		-12.666 (-25.046 to -0.287)	0.045

6.4.1.3 Non-social Play

Context had an overall effect on percentages of time spent in non-social play. Non-social play in wild African calves was significantly lower than in all other contexts while wild Asian calves played non-socially significantly less than both Asian and captive African calves (Table 6.5). Across the ages, captive calves engaged in more non-social play than did wild calves, and although not significantly different, time spent in play was always higher in wild Asian than wild African calves.

There was an overall effect of age on percentages of time in non-social play, and an interaction between age and context (Table 6.5). Calves engaged in non-social play significantly more when aged 1-6 months; and also pairwise, significantly more other ages.

No significant differences were found between the sexes (*p*=0.122) in time spent in non-social play. However, as with LEGO-play, there was a marked contribution of individual to these patterns.

Table 6.5 Final General Linear Mixed Model for Non-social Play. Var (ID)=12.35, *p*>0.001. See Table 3.6, Chapter Three, for N of calves and N of observations. Dependent variable was non-social play; independent variables were age, context, and the interactions between them.

	Main effect *F* and *p* value	**Coefficient *β* (95% CI)**	***p* value**
Overall model fit	$F_{19, 445}$=9.918, *p*<0.001		
Age	$F_{4, 528}$=18.537, *p*<0.001		
1-6mo - 7-12mo		6.007 (4.166 to 7.847)	<0.001
1-6mo - 13-18mo		6.697 (4.896 to 8.498)	<0.001
1-6mo - 19-24mo		5.872 (3.786 to 7.958)	<0.001
1-6mo - 3-5yr		5.752 (3.672 to 7.831)	<0.001
Context	$F_{3, 66}$=18.146, *p*<0.001		
African wild		13.852 (9.420 to 18.284)	<0.001
Asian wild – African wild		3.504 (1.639 to 5.369)	<0.001
Asian wild – Asian captive		-6.356 (-9.508 to -3.205)	<0.001
Asian wild – African captive		-3.897 (-7.334 to -0.461)	0.027
African wild – Asian captive		-9.860 (-12.957 to -6.764)	<0.001

African wild – African captive		-7.401 (-10.787 to -4.015)	<0.001
Age x context	$F_{12, 555}=3.302$, $p<0.001$		
1-6mo Asian wild		8.626 (4.466 to 12.789)	<0.001
1-6mo African captive		9.311 (2.799 to 15.824)	0.005
7-12mo Asian captive		-6.723 (-12.080 to -1.366)	0.014
13-18mo Asian captive		-7.735 (-13.233 to -2.236)	0.006
1-6mo – 7-12mo Asian wild		10.448 (6.440 to 14.456)	<0.001
1-6mo – 13-18mo Asian wild		9.007 (5.719 to 12.296)	<0.001
1-6mo – 19-24mo Asian wild		8.501 (4.251 to 12.752)	<0.001
1-6mo – 3-5yrs Asian wild		10.172 (7.147 to 13.198)	<0.001
1-6mo – 7-12mo Asian captive		7.269 (4.166 to 10.371)	<0.001
1-6mo – 13-18mo Asian captive		7.519 (4.182 to 10.856)	<0.001
1-6mo – 19-24mo Asian captive		4.975 (0.972 to 8.979)	0.015
7-12mo – 3-5yrs Asian captive		-6.839 (-11.287 to -2.391)	0.003
13-18mo – 3-5yrs Asian captive		-7.090 (-11.590 to -2.590)	0.002
19-24mo – 3-5yrs Asian captive		-4.546 (-9.080 to -0.012)	0.049
1-6mo – 7-12mo African captive		4.648 (0.393 to 8.903)	0.032
1-6mo – 13-18mo African captive		9.359 (5.119 to 13.598)	<0.001
1-6mo – 19-24mo African captive		8.303 (3.824 to 12.782)	<0.001
1-6mo – 3-5yrs African captive		10.858 (5.003 to 16.713)	<0.001
7-12mo – 13-18mo African captive		4.711 (0.362 to 9.060)	0.034
7-12mo – 3-5yrs African captive		6.210 (0.373 to 12.047)	0.037

6.4.1.4 Play Categories for Wild Calves

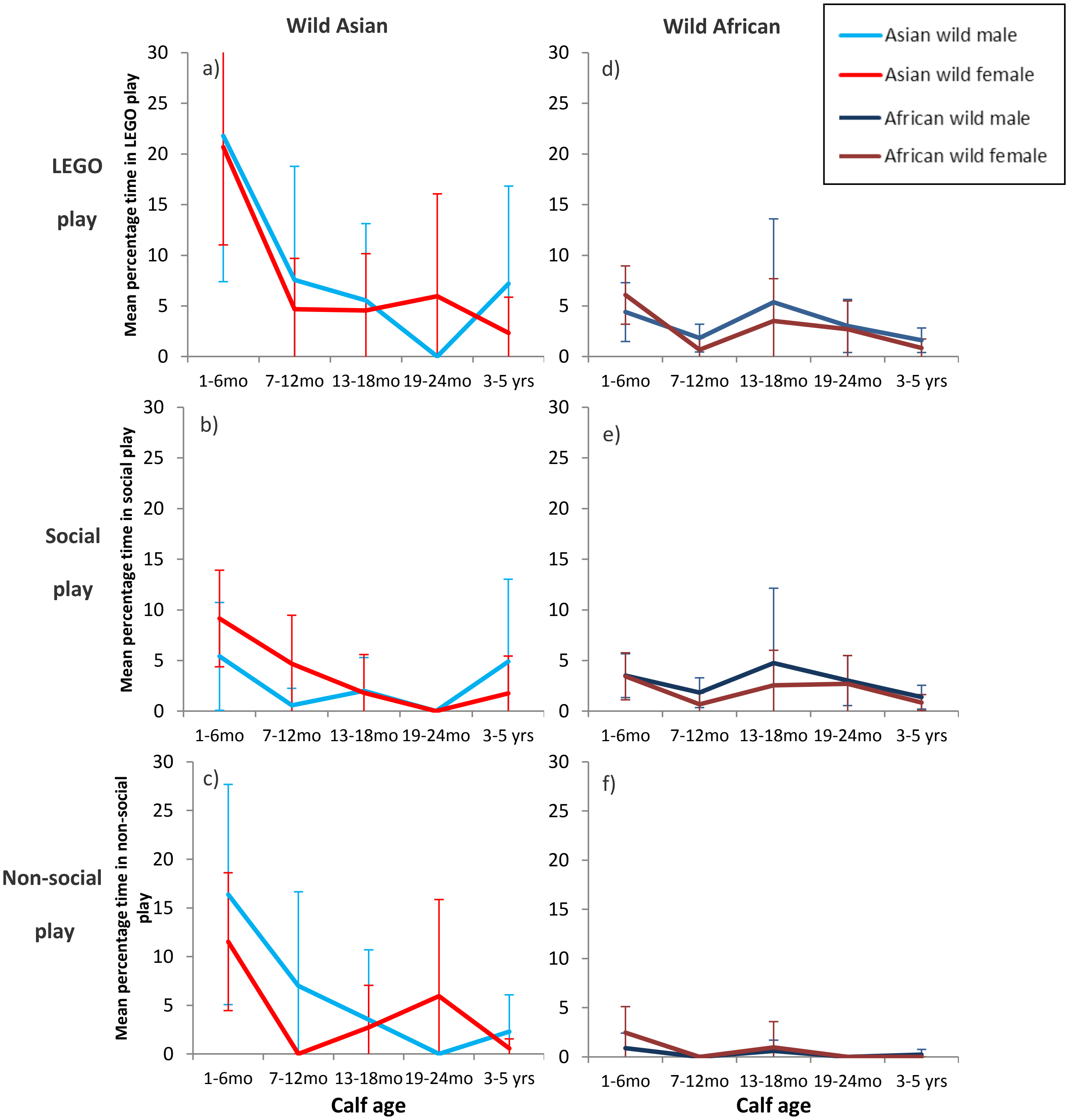


Figure 6.1 Mean Time in Play Categories for Wild Calves across Ages. Mean percentage time ±95%CI. a) LEGO-play wild Asian calves, b) social play wild Asian calves, c) non-social play wild Asian calves, d) LEGO-play wild African calves, e) social play wild African calves, f) non-social play wild African calves. See Table 3.6, Chapter Three, for N.

6.4.1.5 Play Categories for Captive Calves

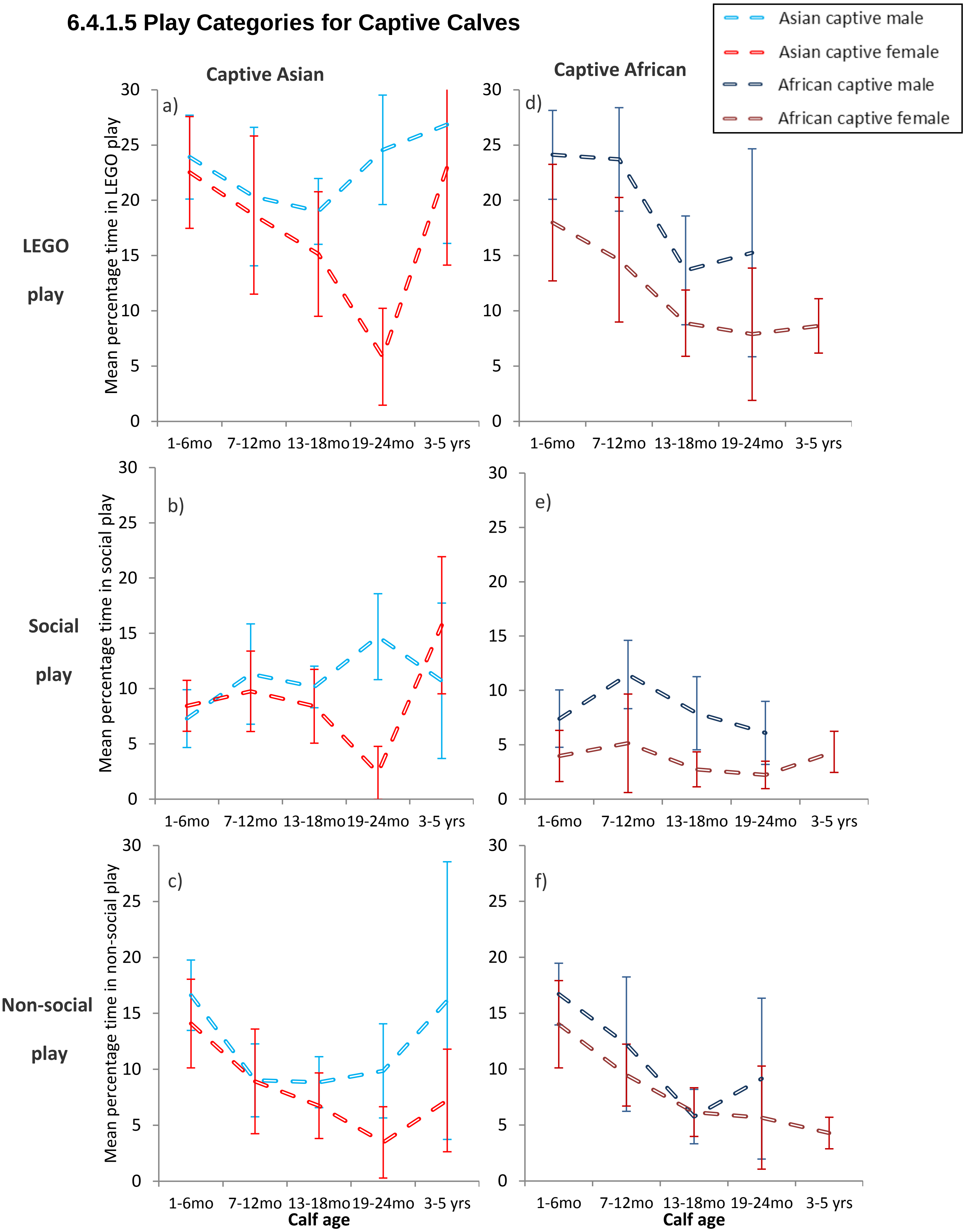


Figure 6.2 Mean Time in Play Categories for Captive Calves across Ages. Mean percentage time ±95%CI. a) LEGO-play captive Asian calves, b) social play captive Asian calves, c) non-social play captive Asian calves, d) LEGO-play captive African calves, e) social play captive African calves, e) non-social play captive African calves. See Table 3.6, Chapter Three, for N.

Each individual captive Asian and African calf engaged in both non-social and social play. There appeared to be no overall trends in age and proportion of play types (Figure 6.3; 6.4) as play fluctuated considerably from calf to calf although some patterns worth noting are described here.

Captive Asian calves at Chester play bouts including climbing. Top, and bottom left images are Bala, taken 25th April 2013 and 8th February 2014, respectively. Bottom right image of Hari climbing beside Maya, taken 22nd April 2014.

Individual Captive Asian Case Studies

There are some specific points of interest, for example, from birth to 18 months for Hari, time spent in non-social play decreased, while social play increased, similarly to wild male calves. Hari's LEGO-play, therefore, remained roughly constant (Figures 6.3; 6.1).

Female Asian calf, Bala, was born two months later than Hari at the same facility. Bala had remarkably higher levels of non-social (and correspondingly, of LEGO-play) for a female calf in captivity or the wild (Figures 6.1; 6.2; 6.3).

It is worth noting that in the first and second months of Hari's life, before Bala was born, Hari's social play was 1.35 and 0% of time. This rose to 13.33% in month three when Bala was first present as an available play partner. On average Hari's social play from birth to 18 months was 10.11%, and when months were excluded from the analysis where Bala was not yet present Hari's time spent in social play dropped to 7.75%. Hari was quite a lethargic and small newborn calf; whereas Bala was highly playful even from several days of age and in her first month she spent 23.94% time in LEGO-play (Figure 6.3).

Another noteworthy calf is Asian male Raman. At 1-6 months Raman engaged in low levels of non-social play, increasing across his first year of life (Figure 6.3); whereas wild Asian means, captive Asian means and all other individual captive Asian calves decreased time spent in non-social play over the same period (Figures 6.1; 6.2; 6.3). During this period he also showed increases in social (and consequently LEGO-play), whilst female Jamilah showed both the opposite pattern and lower time spent in all three play categories. Raman's time spent in social play was the highest of any of the captive Asian calves and roughly twice that of male wild Asian calves at 1-6 months, and 13.7% higher at 7-12 months.

Individual Captive African Case Studies

Tammi's rejected calf was only observed very infrequently in non-social play in her single month of life, and exhibited no social play. The two incidences of lone play were trunk-behaviours and it could be debated whether these were playful or fidgety-boredom (Figure 6.4).

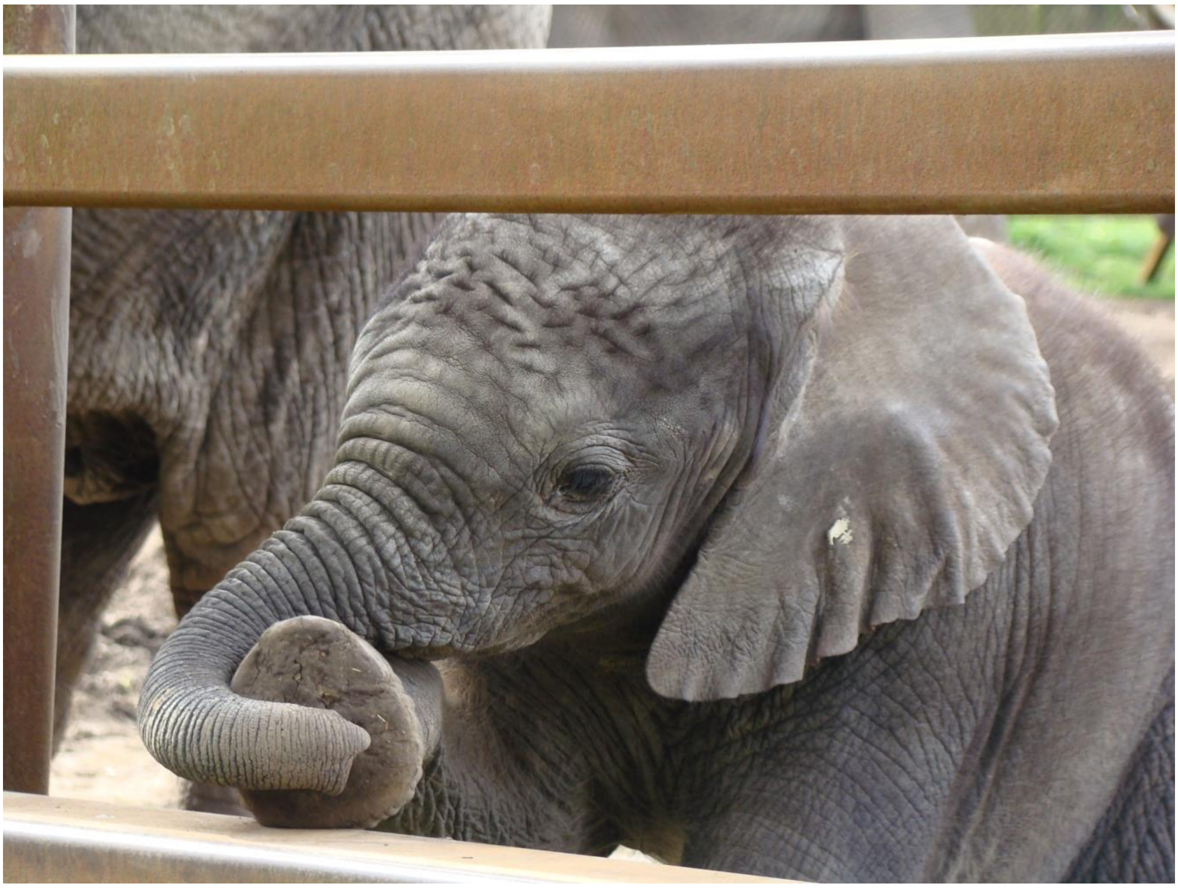
Orphaned African female calf, Mansi, is also worth remarking as having low time spent in non-social play (Figure 6.4). However, even at 7-24 months this was higher than in wild African calves (Figures 6.2; 6.4).

As Tammi's calf and Mansi are two of the three captive female African calves studied, the mean time spent in play (Figure 6.2) must be approached with great caution. Data from (mother-raised) Jaluka (Figure 6.4) alone may, therefore, be a better representation of play in 'normal' captive female African calves than are the pooled means. Clearly, however, these results still represent play for one personality type, one subordinate family and of course, one facility.

As with Asian Bala, African Jaluka was a particularly playful female character during data collection. Jaluka was often away from her subordinate mother (who was avoiding the ‘crowds’/bullies; see also Chapter Five) and seeking out her playmates from different families instead (pers obsv.). However, unlike Bala, Jaluka did not have 24-hour access to her playmates: she was not housed at night with them as Bala was (other than when outdoors on warmer nights); access was provided during the day on various days of the week; on the other days she only had access through large paddock fences. (For the latter, she was placed in paddocks with her mother, the adult male and a non-breeding female, Shibi, to provide company for the male).

Captive African calves Mchumba and Jaluka engaged in escalated-contact play sparring at Howletts. Note Mchumba’s posture is pushing forwards, using his back legs to drive his weight towards Jaluka, as opposed to simply trunk-twining or gentle trunk-wrestling which are both gentle-contact play types. Photograph taken 2nd April 2011.

Although Jaluka’s LEGO-play percentages remained comparable to the other two mother-raised captive African calves, males Impi and Mchumba (who were never separated outdoors due to Mchumba’s mother being Impi’s grandmother), when this is broken down into social and non-social forms, her percentages look quite different (Figure 6.4). Interestingly, her limited access to play partners (which were already limited in choice compared to wild conspecifics), may explain Jaluka’s low time spent in social play and comparably high time spent in non-social play (the opposite to orphan Mansi who rarely played unless instigated by others).



Captive African calf Jaluka engaged in a non-social play bout involving climbing on the fence and playing with her own foot. Photograph taken 1st April 2011.

It would be interesting to know if differences in play types and rates were affected by proximities between potential play partners. However, even access to potential partners were under the control of keepers and management activities, so this could not be tested.

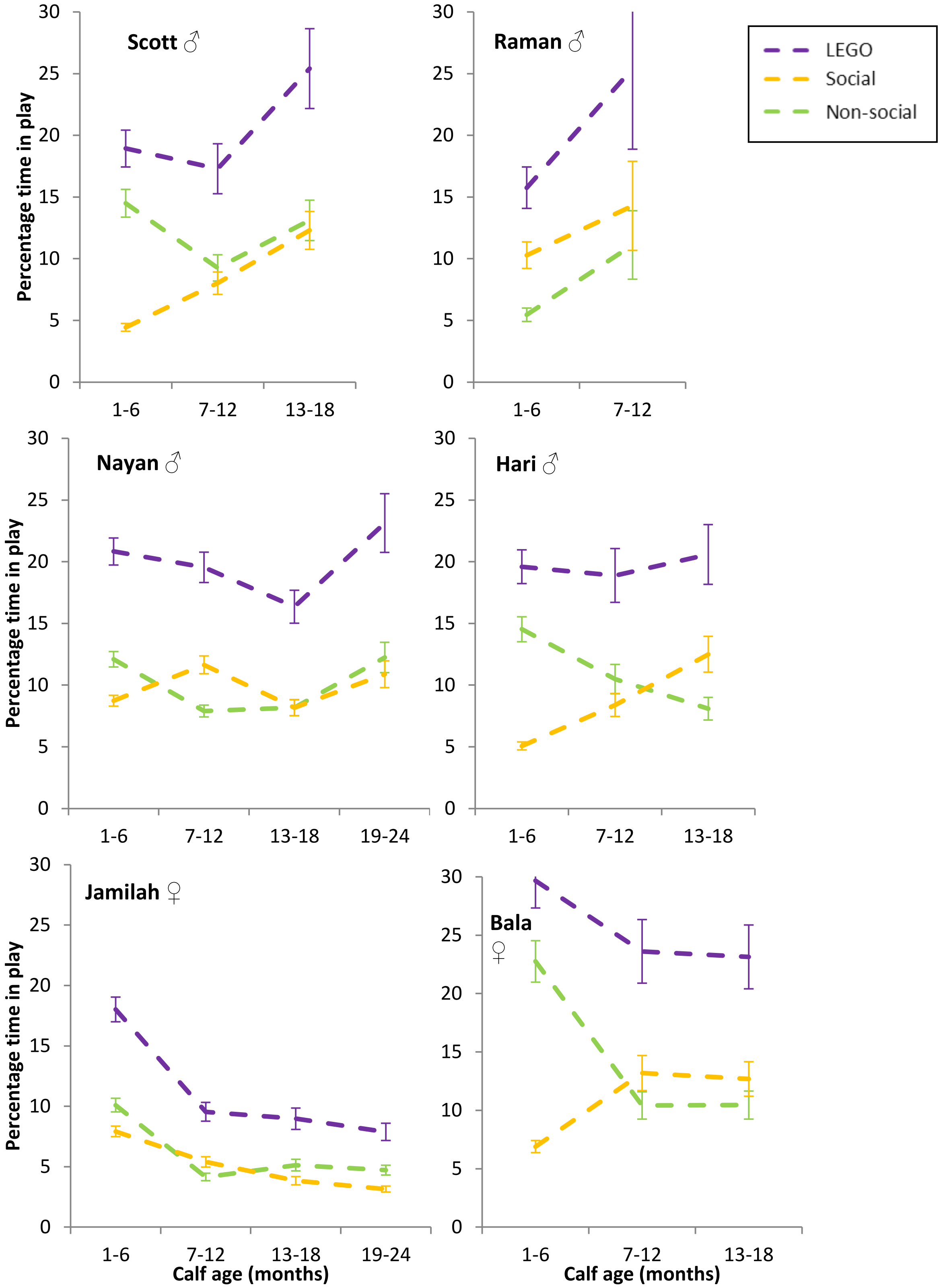


Figure 6.3 Play Categories for Individual Captive Asian Calves. Social, non-social and LEGO play types. Data from scans at 5min intervals from 10min focal observations. For N of observations per individual, see Table 3.4, Chapter Three. Binomial 95%CI.

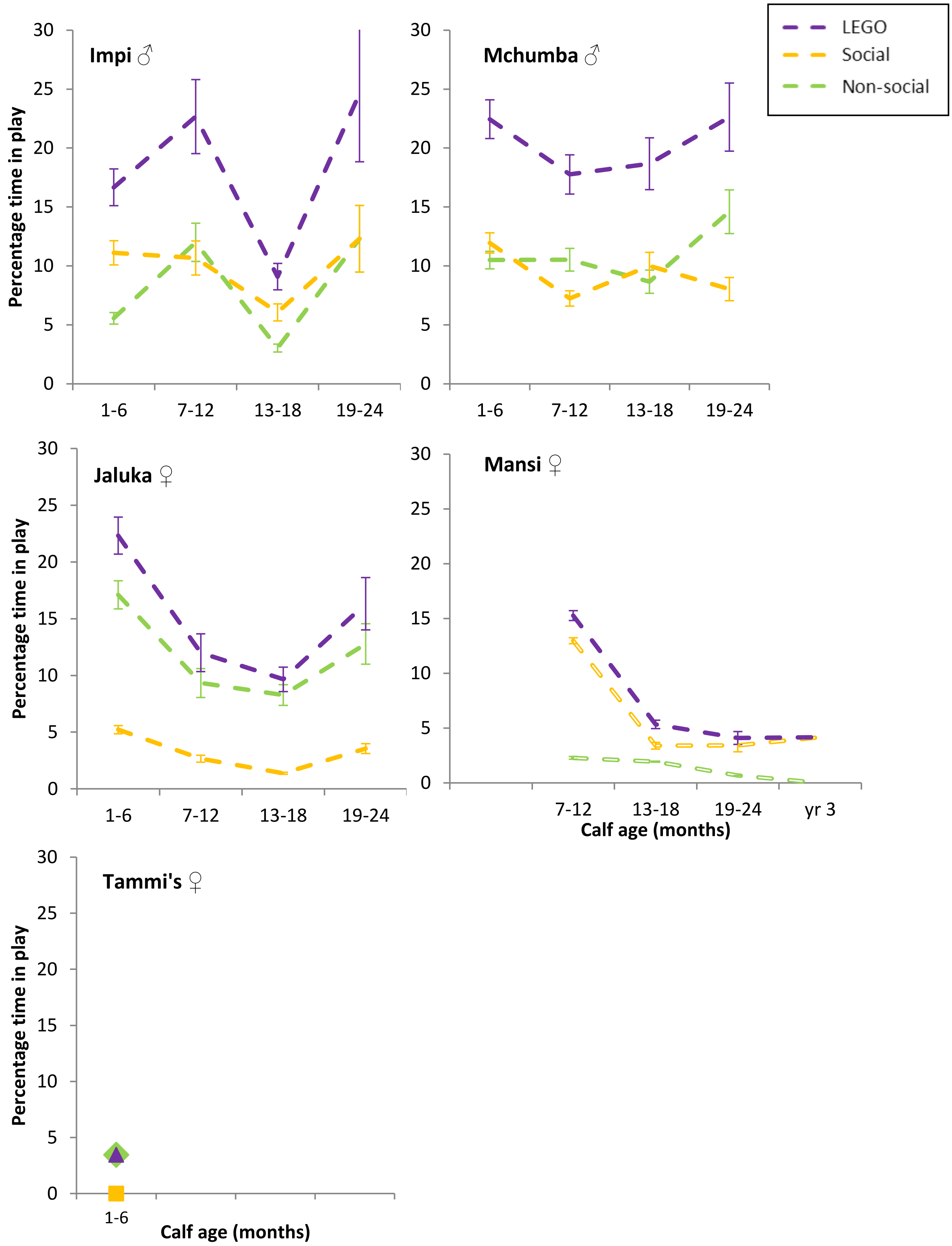


Figure 6.4 Play Categories for Individual Captive African Calves. Social, non-social and LEGO play types. Data from scans at 5min intervals from 10min focal observations. For Tammi's calf, the two incidences of play were trunk-behaviours. For N of observations per individual, see Table 3.5, Chapter Three. Binomial 95% CI.

6.4.2 Play Partner Availability

6.4.2.1 Wild African Calves

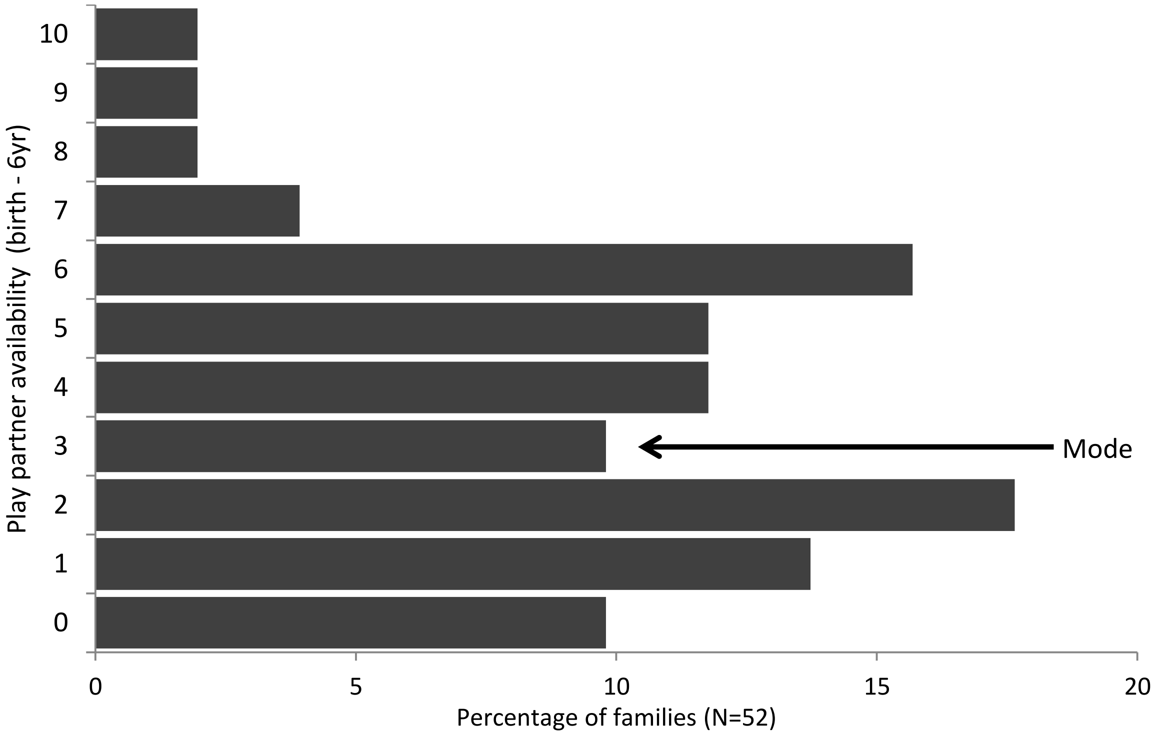


Figure 6.5 Percentage of Wild African Elephant Families with Numbers of Play Partners (<60 mo) Available. X and Y axis plotted in reverse to avoid confusion with x-axis of Figure 6.6.

Wild African calves$_{N=53}$ had a mean availability of 3.59 play partners <60 months in families (Figure 6.5). Captive African calves also had large numbers of potential play mates available (Figure 6.6) although access was often constrained to daylight hours. Captive Asian calves had at most three other calves <60 months and most had one or two potential partners <60 months (Figure 6.6).

Data on play partner availability were not collected for wild Asian elephants although group size data are presented in Figure 2.4 for Asian elephants and Figure 2.5 for African elephants.

6.4.2.2 Individual Captive Calves

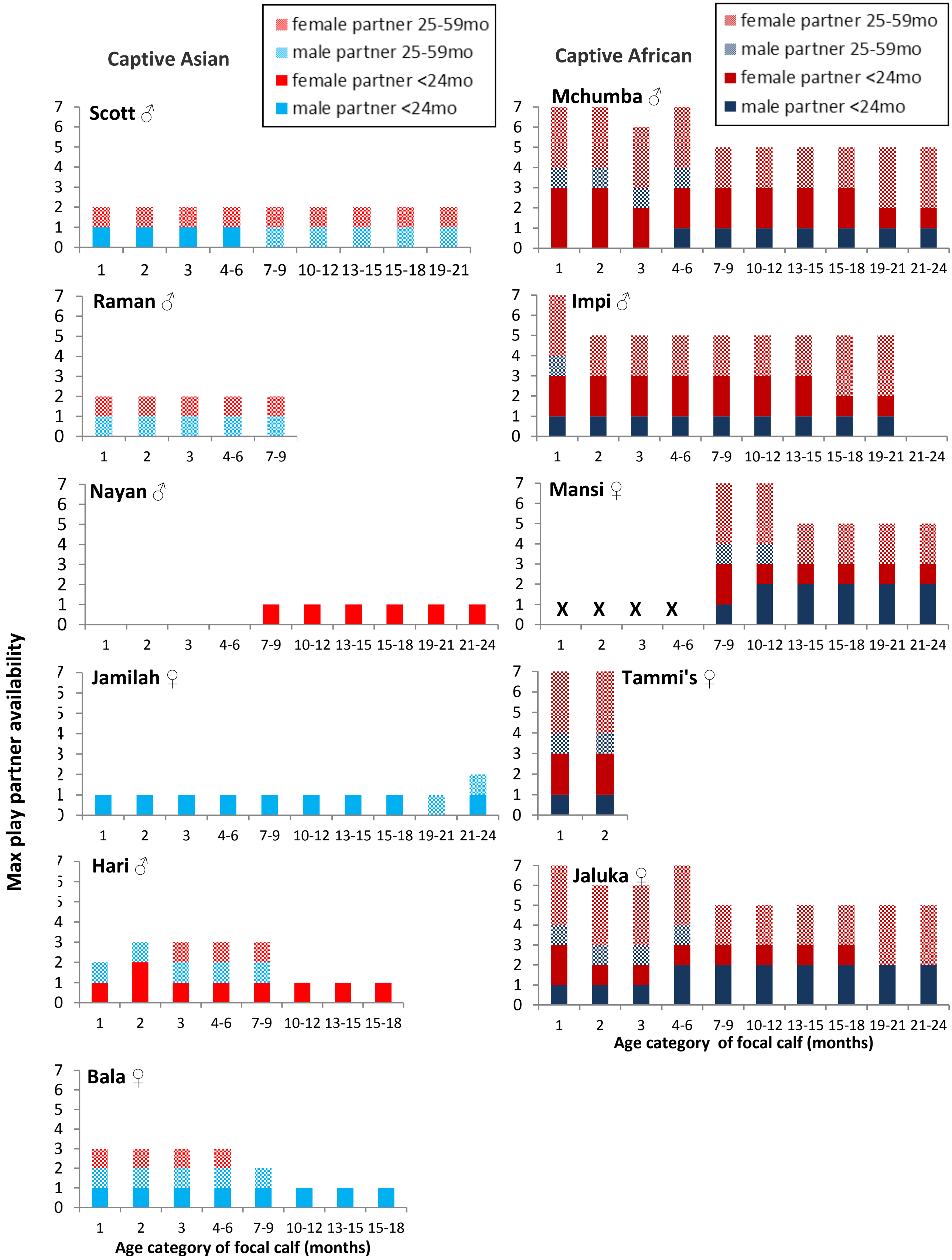


Figure 6.6 Maximum Play Partner Availability for Individual Captive Calves by Age. Play partners <24 mo and 25-59 mo and split here by sex. **X** represents no data available as opposed to no partners.

6.4.3 Play and Suckling Interactions

If energy for play is derived from milk during infancy, then play rates would be expected to correlate with suckling and possibly decline during weaning. However, as described in Chapter Four, a positive correlation was found between time spent suckling and LEGO-play only in captive female African calves (*p*<0.001) while for all other contexts, suckling and play were unrelated (Table 4.6, Chapter Four).

Wild Calves

For male wild African calves, no clear ‘weaning trough’ in play was observed, although wild Asian males tended to show a drop at 19-24 months as well as 31-36 months.

In female wild Asian calves, there did appear to be a ‘weaning trough’ around 31-36 months somewhat later than the decline for wild African females. However, this effect may be due to a low number of scans for older age categories (Figure 6.7).

Captive Calves

For each captive calf, and across captive means, percentage of time in play was unrelated to suckling interactions at each age (Figures 6.7; 6.8; 6.9). For some individual calves, the two percentages were very roughly associated such that if time spent in one activity increased, the other decreased. This was clearly seen in Bala, Hari, Raman and Mchumba (Figures 6.8; 6.9).

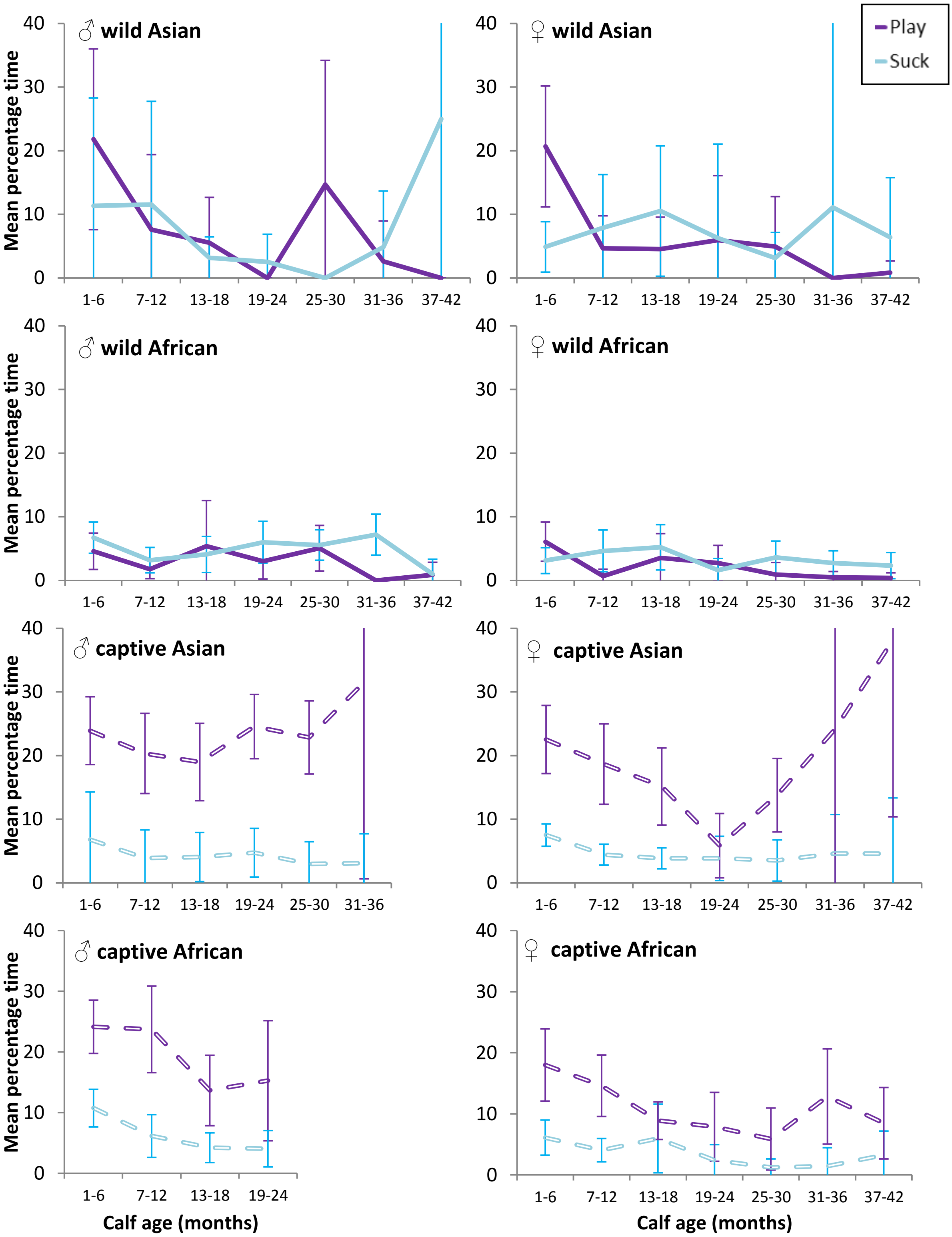


Figure 6.7 Mean Time in LEGO-Play and Suckling Interactions by Context and Sex for Calves (from birth to 3.5 years). See Table 3.6, Chapter Three, for N. ±95%CI.

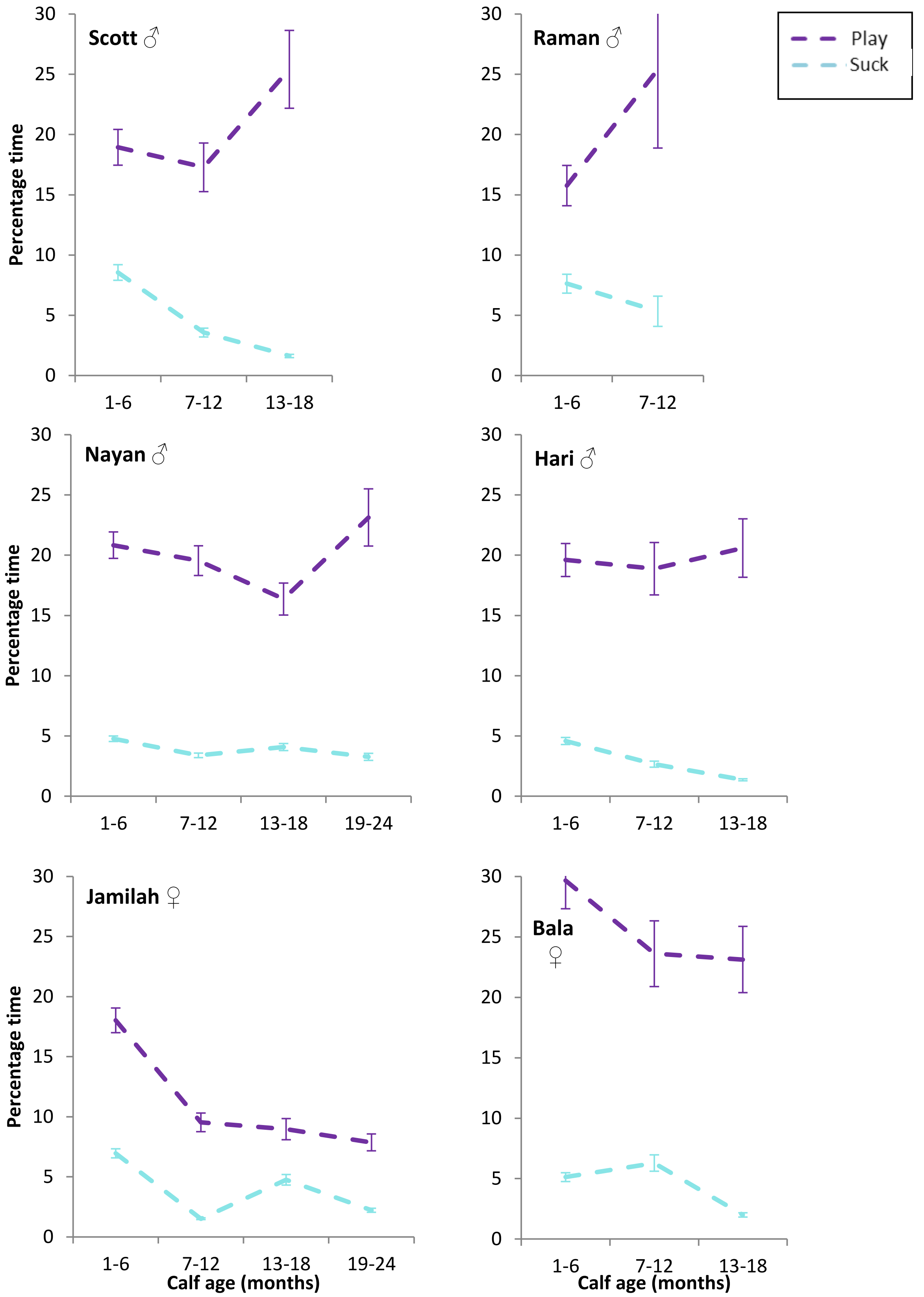


Figure 6.8 Percentage Time in LEGO-Play and Suckling Interactions for Individual Captive Asian Calves (from birth to three years). Data from scans at 5min intervals from 10min focal observations. For N of observations per individual, see Table 3.4, Chapter Three. Binomial 95%CI.

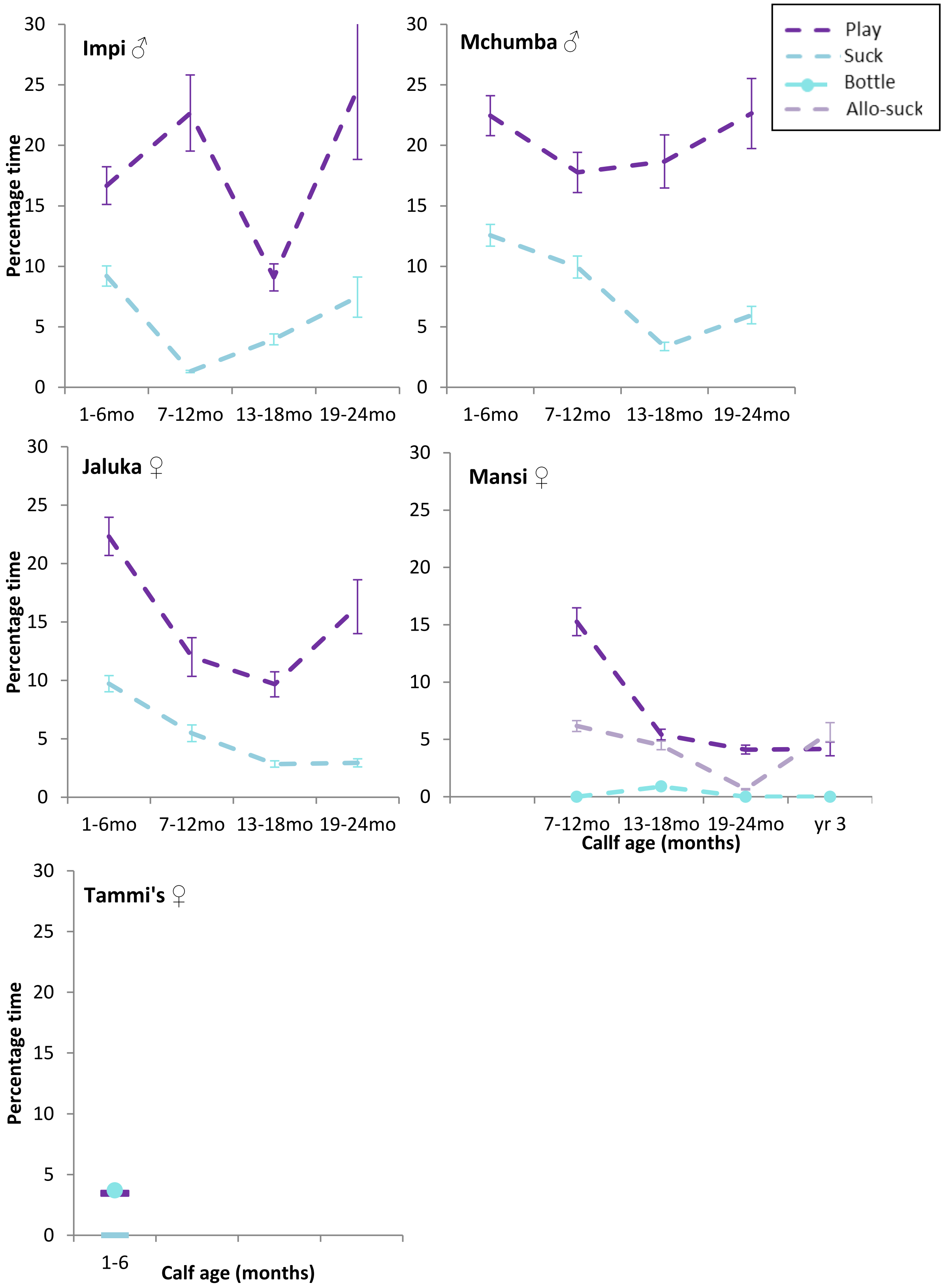


Figure 6.9 Percentage Time in LEGO-Play and Suckling Interactions for Individual Captive African Calves (from birth to three years). Data from scans at 5min intervals from 10min focal observations. For N of observations per individual, see Table 3.5, Chapter Three. Binomial 95%CI.

6.4.4 Play and Independent Feeding

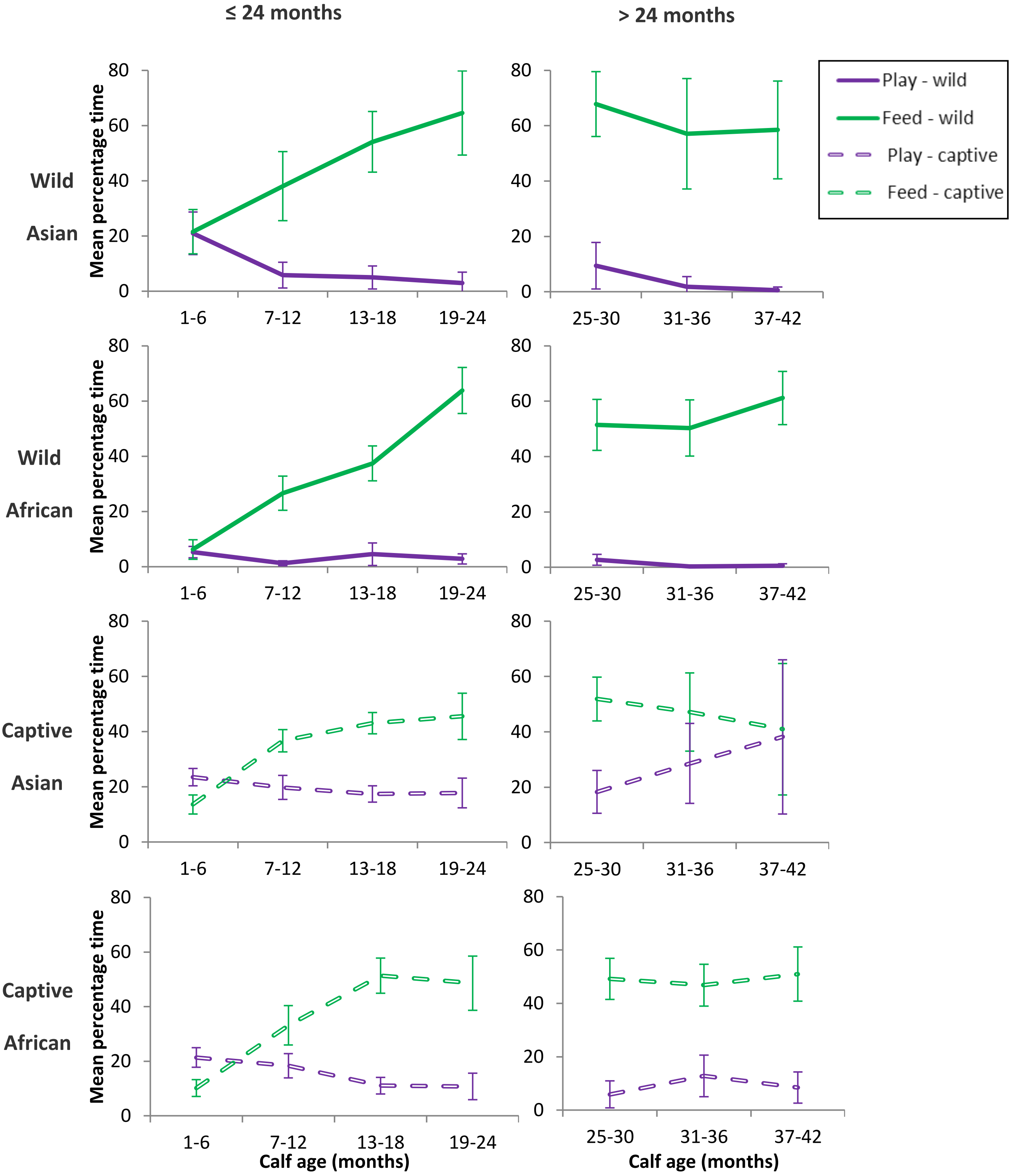


Figure 6.10 The Relationship between the Mean Percentage of Time in LEGO-play and Independent Feeding by Context (from birth to 3.5 years). Charts separated within context, for ≤24 mo and for >24 mo. See Table 3.6, Chapter Three, for N. ±95%CI.

6.4.4.1 Wild and Captive, Asian and African Calves

As described in Chapter Four, time spent in independent feeding increased with age. Independent feeding was negatively correlated with LEGO-play in all contexts and for both sexes, with the exception of male wild African calves where time spent feeding was unrelated to LEGO-play overall (Table 4.6, Chapter Four).

As the first 24 months were assumed to be the period of dependence on mothers for energy intake, rather than feeding independently, I split the time periods into <24 months and >24 months (Figure 6.10). Wild Asian calves followed similar patterns for play and independent feeding as wild African calves. Time spent in independent feeding increased with calf age and negatively co-varied with play for the first 24 months of life (Figure 6.10). For calves older than 24 months, this inverse relationship weakened and the two behaviours became more concordant. The exception might be captive Asian calves after 24 months which appeared to sustain the negative association between feeding and play.

6.4.4.2 Individual Case Studies

Individual Captive Asian Case Studies

For the two captive female Asian calves, Jamilah and Bala, feeding also negatively co-varied with play (Figure 6.11) and this followed a very similar pattern to the wild Asian and African calves (Figure 6.10), especially so for Jamilah. However, this relationship between the percentages of time spent independent feeding and in play was not observed as clearly in the individual males (Figure 6.11).

Individual Captive African Case Studies

Jaluka, a female captive African calf, also followed the same relationship as the wild Asian and African calves, with her time spent in independent feeding increasing and negatively co-varying with play (Figures 6.12; 6.10). Although at 19-24 mo her time spent in play increased again.

Insufficient data were collected on the other two females to detect this pattern in the younger age categories (Figure 6.12). Nonetheless, Mansi showed the same relationship as wild Asian and African calves from seven months to three years (Figures 6.12; 6.10).

The male captive African calves again both showed much less clear relationships between feeding and play (Figure 6.12). Impi’s independent feeding rates roughly mirrored his play rates although play increased in his first year, while Mchumba’s play rates remained more constant.

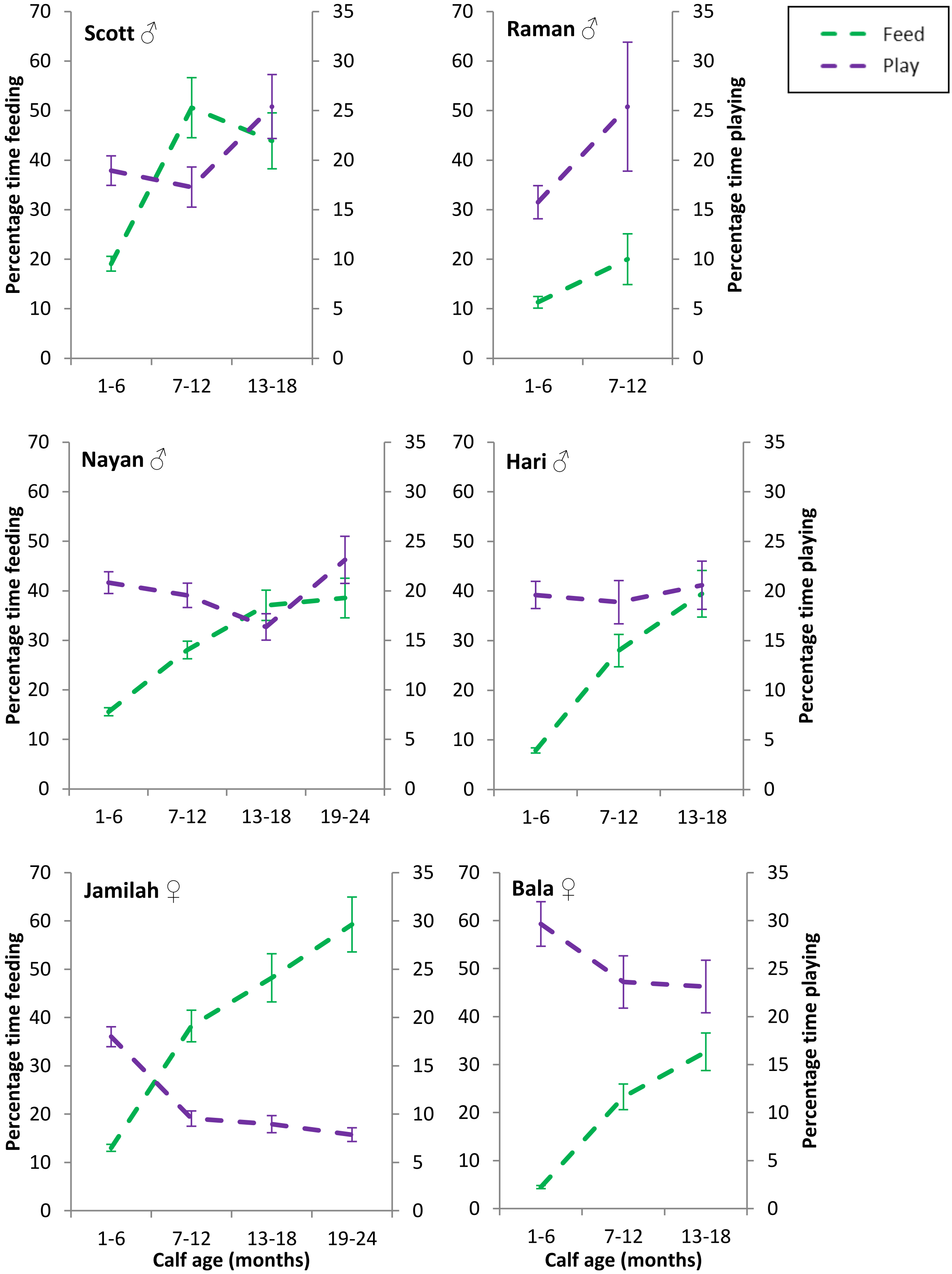


Figure 6.11 Individual Captive Asian Calves: The Relationship between the Percentage of Time in LEGO-Play and Independent Feeding (from birth to three years). For N of observations per individual, see Table 3.4, Chapter Three. Binomial 95%CI.

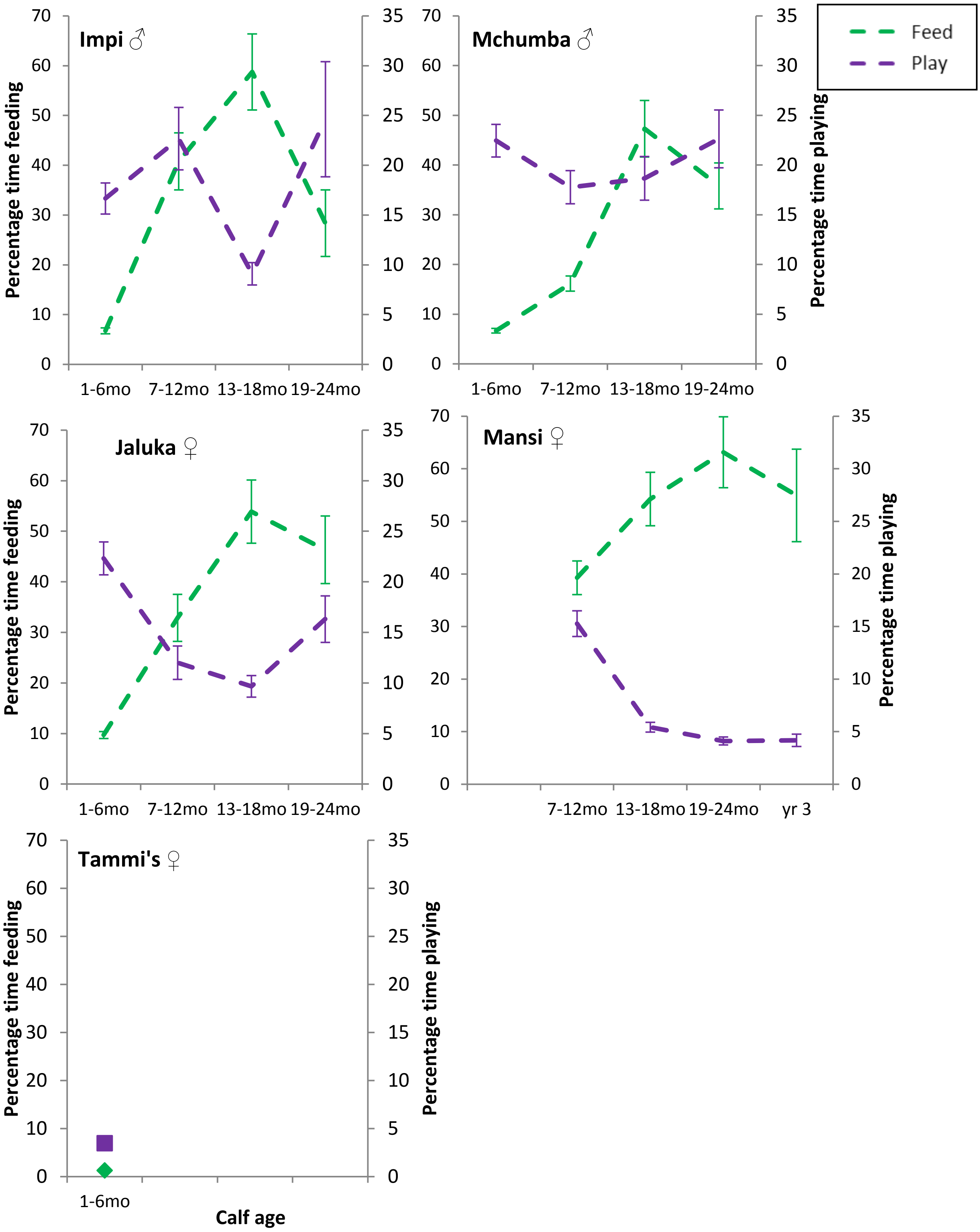


Figure 6.12 Individual Captive African Calves: The Relationship between the Percentage of Time in LEGO-play and Independent Feeding (from birth to three years). For N of observations per individual, see Table 3.5, Chapter Three. Binomial 95%CI.

6.5 Discussion

As with previous Chapters, individual calf ID was also a significant factor in the analysis of non-social play and LEGO-play, therefore contributing to the overall pattern of these data. Once again, calf age and context still significantly influenced behaviours over and above the effect of the individual, despite this considerable contribution of individual (calf ID) to the variance patterns in the tests. However, as stated before, results should be interpreted with caution due to individual variance, non-normal distributions and small samples.

Captive calves spent between 5-25% of their diurnal time in play. Wild calves played at 0-20% of their day and wild Asian and captive calves engaged in roughly equal proportions of social and non-social play. For all calves, non-social play (and therefore LEGO-play) declined with age, although no clear relationships were found between time spent in LEGO-play and energy from lactation. Play was inversely related to time spent feeding in the first 24 months of life.

Time in Play Changes with Age

Play persists into old age and adults play in many species, including elephants (Lee & Moss, 2014), chimpanzees, humans (Mendoza-Granados & Sommer, 1995), dogs (Bradshaw, Pullen & Rooney, 2015), wolves (Cordoni, 2009) and kangaroos (*Macropus* species, Watson, 1998). However, juveniles, the focus of this study, tend to spend more time and energy in play than do adults (e.g. common marmosets, Stevenson & Poole, 1982; Voland, 1977).

For wild elephant calves, the decline in both play types with increasing age in the first 12 months of life was more apparent in Asian than African calves, and play was less frequent in early life for African calves.

Sex Differences in Play

Although the sexes did not differ overall in any of the play types, sex did affect time spent in social play (in interactions with context, with age, and with age within context). These findings are in keeping with previous research that rough and tumble or escalated-contact social play usually occurs among males. This form of play is thought to be a "*unique motivated behaviour that is widespread throughout the mammalian order*" (Cooke & Shukla, 2011, p. 459).

Young male elephants use play as an opportunity to experience diverse and novel social partners outwith their own family (Lee & Moss, 2014). This play is important in training animals to deal with the unexpected in their environments (Kuczaj, Makecha, Trone, Paulis & Ramos, 2006; Špinka et al., 2001). Seeking out novel age-mates for social opportunities that are not available through usual companions has been shown to be important in other species such as chimpanzees (Hayaki, 1985) and dolphins (Kuczaj et al., 2006; Paulos et al., 2010). Male elephants may be using these play interactions with strangers as risk-learning in what are low-risk encounters, which prepares them for potentially dangerous encounters at later ages (Burghardt, 2006; Miller & Byers, 1998).

Play partner availability in captivity may still be important in terms of the limiting dynamism and novelty, despite the limited number of peer partners available in captivity – compared to the wild – having no apparent effect on limiting the *time* that calves spent in play. For example, I suggest that, a play partner for a one year old male calf of a male calf who is another year older, would offer a different quality and type of play interactions than would a female play partner who is three months old. Reduced challenges and limited learning opportunities (e.g. males unable to engage in risk-learning in low-risk encounters) may result from the lack of novelty and dynamism in social partners in captivity. Diversity of play partners available in captivity is therefore likely to be important for both male and females calves.

For females, the spike in mean time spent in social play (and therefore mean LEGO-play) for captive Asian calves at 3-5 years might be explained by behavioural changes at this age when females start to engage in allomothering play with younger calves. For example, Jamilah and Gheta may have become focused on allomothering activities with the births of Hari and Bala, and Raman, respectively. The observed dip in time spent in play by captive Asian females at 19-24 months might be explained by the absence of Bala, a particularly playful female, after 18 months.

This potential allomothering pattern in play was not as clear for other contexts although there were small increases in social play at 3-5 years for wild Asian and captive African calves. (Again, the latter might be influenced by the inclusion of Etana and Uzuri as playful older juveniles who were not included in earlier age categories).

For wild Asian males aged 19-24 months, no play was observed. This was possibly due to abnormally undernourished calves in this age category, such as [cBitsy_09] (10 of 17 focals). An illustration of the effects of starvation on play and development is presented in Appendix E.

Further data biases may exist due to the low number of individuals studied in captivity. Here, personality may influence patterns of behaviours. For example, Bala was a particularly energetic newborn calf (large and often active) and one of only two captive female Asian calves studied. These females differed greatly in their play time, and Bala's time spent in play was more similar to individual male calves. Whether males or females are more 'playful' remains to be determined but there is no evidence of sex effect from my captive research. Males seek novelty and contests in play but females may use play, especially allomothering, to bond within their families. Therefore while partners and play types might vary by sex, there may be no reason for time spent in play to vary between the sexes. Male and female calves in captivity consequently need different experiences and challenges.

Lee and Moss (2012) describe that female elephants retain an element of their playfulness into old age together with other personality traits including gentleness, constancy and leadership. In young females, the trait of leadership co-varies with play and it was suggested that playfulness may reflect a females' leadership potential as it may be an indicator of popularity, competence and sociability, as valued by the other females in the family (Lee & Moss, 2014). Personality, including playfulness, and age of the family's matriarch also shapes the family's tendency to be sociable (Lee & Moss, 2014).

Play and Independent Feeding

As calves age, independent feeding increased and takes up more of their time, thus leaving less time for play. Lee and Moss (1986) found independent feeding increased between 4-24 months "*to a level ca. 55% of daily*" activity budget (p. 355).

Comparable to my results across contexts, Lee and Moss (2014) also found that in the first 24 months in wild African calves, time spent in independent feeding increased with calf age, and negatively co-varied with play. After this age, no relationship was found between play rates and age-specific energy intake. They suggested that in the younger calves, "*playful calves were buffered against at least some of the energy costs of play*" (Lee & Moss, 2014, p. 148).

In captive white-tailed deer (*Odocoileus virginianus*), fawns have been observed to increase independent feeding to compensate for lower milk intake (Muller-Schwarze et al., 1982). Muller-Schwarze and colleagues (1982) investigated the effect of food shortage on play by experimentally inducing a 33% milk shortage to fawns (from approx. 3-7 weeks old). Following the reduction in milk, the fawns continued to play although at a reduction of 35%, alongside a reduction in general activity budget of 9%. The fawns also increased time spent grazing by 62%, which Muller-Schwarze and colleagues (1982) believe demonstrates energetic compensation and although play was reduced, its persistence here highlights the importance of play.

As mentioned earlier, playfulness has been positively correlated with survival. In the first two years of life, play rates in wild African elephants were associated with survival rates after weaning (although pre-weaning survival was not enhanced, Lee & Moss, 2014) and playfulness was also positively associated with survival to independence in wild brown bear cubs (Fagen & Fagen, 2009). For bear cubs, the effects of playfulness on probability of survival were 1-9 times higher than effects of maternal care or food availability.

During periods of environmental disturbances, young animals have been shown to play less, including juvenile wild African elephants (>3 years) during drought versus non-drought years (Lee & Moss, 2014) and Californian sea lion pups (*Zalophus californianus*) during El Niño events versus non-El Niño years (Ono, Boness & Oftedal, 1987). Periods of reduced maternal food availability were associated with poor growth rates and increased early mortality in these calves (Lee et al., 2013) and pups (Ono et al., 1987). Elephant calves also suffered from reduced lifetime fitness (Lee et al., 2013).

Play and Weaning

However, Lee and Moss (2011) found no significant differences between normal and drought years, or between seasons, for play rates in wild African calves in their first two years. They proposed that mothers of these calves could have been buffering the extra costs of calf play through lactation. I found positive correlations between suck and LEGO-play only in captive female African calves (Table 4.6, Chapter Four). This result is questionable since only one of the three captive African calves was mother raised, and the other two were bottle fed, creating a spurious mean for suckling times.

Lee and Moss (2014) suggested that play would decline during the processes of weaning. However, the "*lack of an association*" between suckling interactions and play in calves indicates that frequency of play may be unrelated to the energy gained from maternal milk in early life (p. 147). Weaning and correlated play declines have been found in other ungulates (cattle, Duve, Weary, Halekoh, & Jensen, 2012; antelope, Miller & Byres, 1991) particularly during separation (artificial weaning) and are indicative of either depression/anxiety or lack of energy, or both. However, Donaldson et al. (2002) hypothesised that play experience gained during development might be used as a coping mechanism, particularly during weaning in domestic piglets, with no evidence from other species.

Play and suckling interaction themselves tend to be behaviours of short duration, however, and they may have been underrepresented in scans, particularly in the wild Asian calves. It is also important to note that when no play or suckling interactions were scored, this relates to no visible play or suckling interactions within observations, and may not represent an absence of these behaviours at the specific ages.

In wild African play data ‘weaning troughs’ have been described, in female calves 25-36 months and at later ages in male calves at 37-48 months (Lee & Moss, 2011). However, the low points seen in the wild Asian play may either be due to similar ‘weaning troughs’, in which case they occur at earlier ages in wild Asian calves than wild African calves; or these may indeed not been true ‘troughs’, but instead were caused by low sample sizes. Only 10 and 15 scans were collected on 31-36 month female and 37-42 month male calves, respectively, which may explain the variance seen in the play data, rather than a true cessation of play in these groups across the population in Uda Walawe.

In the case of the play-less male calf, [cBitsy_09] in Uda Walawe (see Appendix E), his lack of play was due to him, and his mother, being extremely undernourished. It is believed that [cBitsy_09] did not have the resources to spare to engage in play (nor may he have been feeling in high spirits (Bateson & Martin, 2013)). However, if [cBitsy_09] was removed from analyses as an outlier, males in the 19-24 month category still showed no play.

Play Types in Wild and Captive Calves

Lee and Moss (2014) state that sociality in elephants is intricately linked to both their survival and play and that animals who play more have longer lifespans. My results, both in captivity and the wild, support their findings that elephants play in many different ways and that these vary in type with calf age and sex (Lee & Moss, 2014).

I hypothesised that wild calves would play more, due to novel environments and naturally larger play partner choices. The reverse was true, however, and captive calves spent more time playing than did wild calves. This pattern was found in both species, in both social and non-social play (and consequently, LEGO-play). Studies in other species support this finding that play is less frequent in wild populations than in captive groups (e.g. common marmosets, Stevenson and Poole 1982). Abundant energy and no constraints due to needing to forage or move mean more time for play is available in captivity.

This result has potential welfare implications since play behaviour is a candidate for use as an indicator of good welfare and positive emotions (Boissy et al., 2007). Studies on other species in captivity show an increase in their play when given larger or more complex environments (e.g. domestic piglets, Chaloupková, Illmann, Bartoš & Špinka, 2007; American mink kits, Vinke, van Leeuwen & Spruijt, 2005), yet play has also been shown to "*increase in stressful situations, in response to reduced parental care, or as a rebound after a period of deprivation and therefore does not consistently reflect favourable environmental conditions*" (Held & Špinka, 2011, p. 981). Interpretation therefore needs to be treated with care and Veasey (2006) suggests that no indicator should be solely relied upon. Other indicators, such as corticosteroid, should be used alongside other tools to assess welfare (see Table 1.1, Chapter One).

This study's results of increased play in captivity may, however, suggest that the captive study calves had their proximate needs met (Dawkins, 1990) and were in a 'relaxed' state in the sense of being free from challenges such as hunger, predation or heat stresses (e.g. Held & Špinka, 2011; Martin & Caro, 1985). While, the results in terms of percentage time in LEGO-play could indicate good welfare and energy balance in captive elephant calves up to the age of 60 months, further discussion is required: "*a better fundamental understanding is needed … in order to be able to explain … whether and how play might be applied as a tool to improve welfare*" (Held & Špinka, 2011, p. 891).

Nevertheless, two of the African case study captive calves (Tammi's calf and Mansi) were not free from other stressful challenges of severely reduced parental care or prolonged illness in the study period. Both calves suffered from stomach problems due to bottle feeding, although Mansi's bloating and diarrhoea were chronic while Tammi's calf succumbed to acute malnourishment. I therefore suggest that these two calves suffered from poor welfare, to varying degrees due to these stressors. However, although their percentages of time spent in play were lower than the other individual captive African calves, their time in play was still comparable or higher than their wild conspecifics. This highlights the great importance of taking care while interpreting play on its own as an indicator of good welfare.

The next prediction, that captive calves use behaviour such as non-social play to compensate for the lack of social partners, was also unsupported. Surprisingly, both social and non-social play in captivity were higher than that in the wild for both species.

In wild African calves, almost all of the play was social. Lee and Moss (2011) found that lone or object play (the two components I defined as non-social play) were rarely observed after the first 12 months in wild African calves. In contrast, wild Asian calf play contained both social and non-social forms. These differences in the wild might be explained by differences in the group sizes and greater numbers of calves in family groups among African elephants, especially those in Amboseli. A six month old African calf in Amboseli would likely have three other play partners available within its group for social play, whereas the Uda Walawe Asian calves have lower play-mate availability (Figure 2.4). While this difference may explain the social and non-social differences, the wild African calves still played less overall, suggesting either time or energy constraints. It was notable that wild Asian calves spent more time in suckling interactions than did wild African calves.

Captive calves grow up with even fewer, if any, available peer or age-mate play partners compared to wild Asian or African calves. It is therefore interesting that the play data demonstrated that both captive Asian and African calves engaged in play types and rates similar to wild Asian calves (although still higher). These results suggest that while play type is a function of group size and play partner availability, the time spent in play is less influenced by these constraints.

Familiarity of playmates in captivity could possibly have an effect on play types or frequency. Male wild African calves play with unfamiliar age-mates more than female calves do (Lee, 1986). It would be interesting to investigate if this were true in wild Asian calves, but it was beyond the scope of this study with poor visibility and the still-developing knowledge of the calf identities in the study population in Uda Walawe. Familiarity of playmates in captivity may also pose a further welfare question, of whether the social needs of male calves to explore and meet unfamiliar others can be met by small, constrained and invariant partners.

Nayan, a captive Asian calf was the only calf in his group until the age of seven months (at which point, Jamilah, was born). From birth to six months old, Nayan showed unexpectedly high rates of social play. Although not socialising with any calves in the first six months of his life, he played with other group members, notably the old adult female

Sheba, who although unrelated to the group, played the role of 'grandmother. Sheba was observed in play with Nayan, doing 'head-stands' beside him and allowing him to climb up against her head. Sheba's head-stands may have initially been a keeper-directed trained behaviour from free-contact training but were translated into a play context when a calf became available. That an old female is willing to play is not unexpected; rather her choice of a calf was.

It is also worth noting that social play, whether with peers or others in the group, can only occur when playmates are both available and also willing to play. So while captive calves had fewer partners available, these partners might have just had nothing to do but play.

For both captive and wild calves, non-social play in the form of object play, may provide animals with the opportunity to develop tool use through experimentation in addition to promoting motor skills and dexterity. An example of this was seen in Nepalese tourist camp Asian elephants' use of and modification of branches to use as fly switches (Hart et al., 2008).

Vicino and Marcacci (2015) designed an Integrated Play Index for captive elephants, dividing play into four categories of 'intensity', with the intention for its use as a potential measure of welfare. Their four categories represent arbitrary intensities which are used as continuous variables even though they are demonstrably ordinal. Furthermore these categories have not been validated against other indicators as welfare measures.

Their study may not be useful in comparing across elephants either, as both lone and object play were excluded from its design. This exclusion of non-social play is particularly important since I found greater levels of non-social play in captive calves and wild Asian calves than in wild African calves. As discussed earlier, my finding may be a function of group sizes and consequent partner availability. I would expect a higher ratio of social to non-social play if peer play partner availability increased, and conversely, a lower ratio in smaller groups. We should be wary of using play as a welfare indicator without using the spectrum of both social and non-social play behaviours, especially across the ranges of group sizes we find elephants in worldwide.

The use of play as an indicator of welfare depends on its occurrence in the absence of compromises but its presence alone is inadequate. The patterning (combination, order and duration, shifting between play types), intensity, quality and diversity of play types and partners is far more indicative of the wealth of the experience from play, in contrast to arbitrary categorisation of intensity alone (e.g. Vicino & Marcacci, 2015). It is the absence of play (Mendoza-Granados & Sommer, 1995) rather than any measure of intensity that indicates compromised welfare.

Why is Play So High in Captivity?

Although it was shown that play was more frequent in captivity than the wild, this study does not look into the quality of those behaviours nor at the partner preference or partner choice. When immature behaviours are prolonged into later ages, problems can arise on account of not learning age-appropriate behaviours (Bradshaw et al., 2005).

Captive African calves play sparring at Howletts. Females Etana and Uzuri at the back; male and females case study calves in the foreground, Mchumba and Jaluka.

As calves generally spent less time in captivity independently feeding than wild calves did, it could be postulated that this was due to higher quality easy-access foods in captivity. This possibly resulted in a reduced drive or amount of time needed to collect a high quantity of foods due to the greater availability of the high-quality foods. Studies by Lindsay (2011) and Eisenberg and Lockhart (1972) have shown independent feeding occurring in the wild at levels above 16 hrs of the day which obviously reduced time available for activities such as play (see Table 4.1, Chapter Four). In addition to debates over the obese elephants in captivity (Clubb & Mason, 2002), this then also opens the question of ‘what to do with your day if you do not need to collect and process food?’ Calves in captivity are perhaps filling this ‘spare time’ with play for the first two years and in doing so may elude boredom (see Footnote in Section 1.4). This spare time may also explain why calf play does not drop off to the same levels as wild calves at 3-5 years. High-quality foods, which do not require extensive periods of time to collect or process, do not necessarily equate to better care and welfare of captive elephants, since feeding is the primary behaviour in terms of activity budget time for wild elephants. I discuss the importance of providing elephants in captivity with the opportunity to replicate wild activity budgets in terms of time spent feeding in more depth in the next Chapter (Discussion Chapter Seven).

Across ages and contexts, social play occupied 3-9% of calves' diurnal activity budgets while they spent an additional 1-11% time engaged in non-social play. Most LEGO-play was observed in captive Asian calves, while the least LEGO-play was observed in wild African calves.

Family size, the availability of similar aged social partners within a family, and the demography of the population as a whole, all influence opportunities for social play in elephant calves (Lee & Moss, 2014). Social play in rats was found to increase when they were placed in small cages (Siegel & Jensen, 1986) and Burghardt (2006) suggests that increased availability of nearby play-partners, due to forced increased proximity resulting from small unstimulated environments, may facilitate social play (despite lack of novelty of play-partners) (p. 142). Non-social play may also be used by captive animals to combat boredom in stimulus deprived environments which lack novelty and variability (Burghardt, 2006).

Both social and non-social play may be directly influenced by the availability of energy through suckling or independent feeding. In addition, both play types may vary as a function of the presence of predators or other risks in environment such dangerous terrain or extreme weather (Lee & Moss, 2014).

Play remains a behaviour which, while easy to detect, has multiple functions during development and these change with age (Bateson & Martin, 2013). No single function will adequately describe why and when elephants play, neither in the wild nor in captivity. Thus resolving play's contribution to welfare in captivity remains elusive.

Chapter 7: Discussion

Captive African mother, Masa, resting whilst her calf Mchumba plays beneath her. Photograph taken 21st March 2011.

7.1 Abstract

This thesis related the diurnal activity patterns of calves, and mother-calf interactions, to typical processes of development. Baseline information on these processes and rates of change with age were established from wild elephant calves during early life, thus allowing a comparison between these observed behaviours and those of animals in captivity. Calves were observed across an age range of birth to five years, with a key focus on early development (up to 24 months).

These wild-captive comparisons had five key aims:

1. Chart normative maintenance activities (feeding, resting, moving) for captive and wild calves and their mothers. This thesis represents the first detailed study of wild Asian calves.
2. An examination of stereotypies in adult captive elephants in relation to potential stressors from changes in group structure resulting from births or losses.

3. Assess the social experience of elephant calves in captive and wild environments by exploring calf interactions with mothers and others, calf and mother activity synchrony, and the potential for both mothers and non-mother neighbours to be close to and interact with calves.
4. Chart the types of play seen across ages and investigate whether play in captive and wild environments could be used as a potential indicator of welfare.
5. Develop decision options associated with recommendations for the rearing of calves in captive contexts in order to optimise their long-term welfare.

Summary

Findings indicated that maintenance activities of independent feeding, resting and moving occupied the majority of activity budgets across contexts for both mothers and calves. In the first two years of life, wild calves spent ~70-80% whilst captive calves spent ~60% of their day engaged in basic diurnal maintenance activities. Wild mothers of both species spent >70% of their day feeding and ~10% resting and moving, irrespective of calf age. Wild mothers of both species spent more time feeding than did captive mothers, and wild Asian mothers rested less than either wild African or captive Asian mothers.

Across contexts, for calves, time spent feeding increased consistently in the first five years of life, resting time decreased, and moving decreased slightly or remained the same. Although time spent moving varied least with context, wild Asian calves engaged in most feeding and captive Asian calves rested the least.

Although abnormal behaviours were observed in captive elephants, the percentage time spent performing stereotypies showed no relationship with season or in response to transfers, births and deaths of other group members.

Some activities were synchronised between mothers and calves, but without any consistent patterns with age or context although wild African calves showed the greatest synchrony. Captive calves were found to be more independent than wild calves in terms of time spent in close proximity to their mothers. This could be due to captive calves having more opportunities to choose activities and locations irrespective of their mother’s activity. However, across all contents, calves became more independent with age and spent more time at a greater distance from their mothers. Suckling interactions also showed expected age-related declines although not significantly over the first five years. Calves in their first six months interacted socially significantly more than older ages did.

While non-play social interactions were diverse, they were least common in wild African calves.

Wild Asian and captive Asian and African calves engaged in roughly equal proportions of social and non-social play, while most wild African calf play was social play. Play ranged from 5-25% of time in captivity and 0-20% in the wild, and declined with age across all contexts. Most LEGO-play was seen in captive Asian calves while wild African calves engaged in play the least, despite having the greatest number and diversity of play partners available. While play, at least in its absence, is a potential indicator of poor welfare for many species, the presence of play cannot be interpreted as a wholly positive behaviour. It may nonetheless improve welfare by functioning as a displacement activity for understimulated captive elephants.

No clear relationships were found between time spent in play and energy from milk, at least as measured by time spent in suckling interactions. Play was, however, inversely related to time spent independently feeding in the first two years of life. Both results suggested that maternal energy via lactation did not limit play early in life but that energy acquired independently affected play.

These results emphasise the importance of ecological contexts (e.g. moving to obtain food) for basic activity patterns and that the demands of feeding and travel constrain opportunities for other behaviours.

A Decision Tree was conceived to develop decision options and recommendations for keeping and breeding elephants in captivity. This concept and its subsequent options and recommendations will be presented and discussed in depth here. The benefits that a calf potentially brings to captive companions, e.g. multi-generational matrilineal groups, enabling social bonding and reducing abnormal behaviours, were considered against space required for families to grow and divide naturally over time, as well as ensuring that captive-bred males are appropriately cared for over their potential 60+ years lifespan.

7.2 Elephant Welfare in Captivity

Even the spellbinding images of the Natural History Museum’s Wildlife Photographer of the Year cannot escape the global challenge of poor captive elephant welfare when one looks a little closer. Old scars from aggressive ankle bracelets are just visible on Jeff

Yonover’s (BBC Nature, 2012) enchanting winning image of Rajan snorkelling, a 60 year old ex-logging Asian elephant.

In order to address elephant welfare in captivity, we need to separate some of the interlinked ethical and welfare issues which surround the mammoth challenge of keeping elephants without compromising their welfare. A simplified Ethics and Recommendations Decision Tree for Breeding Elephants in Captivity (‘Decision Tree’ hereafter; Figure 7) was conceived to enable this. The purpose of the Decision Tree is to provide a decision support tool to tease out choices and to allow us to focus on the fifth aim of this thesis: to develop decision options associated with recommendations for rearing of calves in captive contexts in order to optimise their long-term welfare.

Numbered boxes will be used throughout this Chapter to permit referral from the Decision Tree back to the Discussion text, and their numbering will correspond to that presented in the model. Boxes permit the presentation of welfare recommendations alongside recommendations from previously published reports, with occasional modifications and extensions to previous suggestions, based on my observations.

The Decision Tree is primarily aimed at stakeholders, zoo curators, elephant managers and keepers, elephant and welfare scientists – including the UK Elephant Welfare Group – and the UK government – particularly the Secretary of State Standards for Modern Zoo Practices (SSSMZP). I envision its use as a discussion point for the Elephant Welfare Group and with elephant keepers at workshops to enable future plans for improving welfare to continue to evolve. Zoo curators and elephant managers may find it a useful tool for planning their facility’s Long Term Management Plans (LTMP) - aimed to cover >30 years – which they must produce for the SSSMZP. LTMPs include both the purpose of the collection (breeding, bachelor, retirement) and how this relates to long-term enclosure development planning, as well as exit strategies should the collection no longer chose to keep elephants. Facilities are also expected to develop a bull profile for male calves from the age of four years onwards, reviewing this every six months (Defra, 2017).

To develop this Decision Tree, I start in the top ‘canopy’ with the first overarching ethical question: ‘Should we keep elephants in captivity?’ Ethically we cannot justify the removal of wild elephants into captive environments given the enormous difficulty in providing them with their complex requirements, such as appropriate social groupings and suitable spaces, alongside our long history of failures to meet the many needs identified for elephants in captivity.

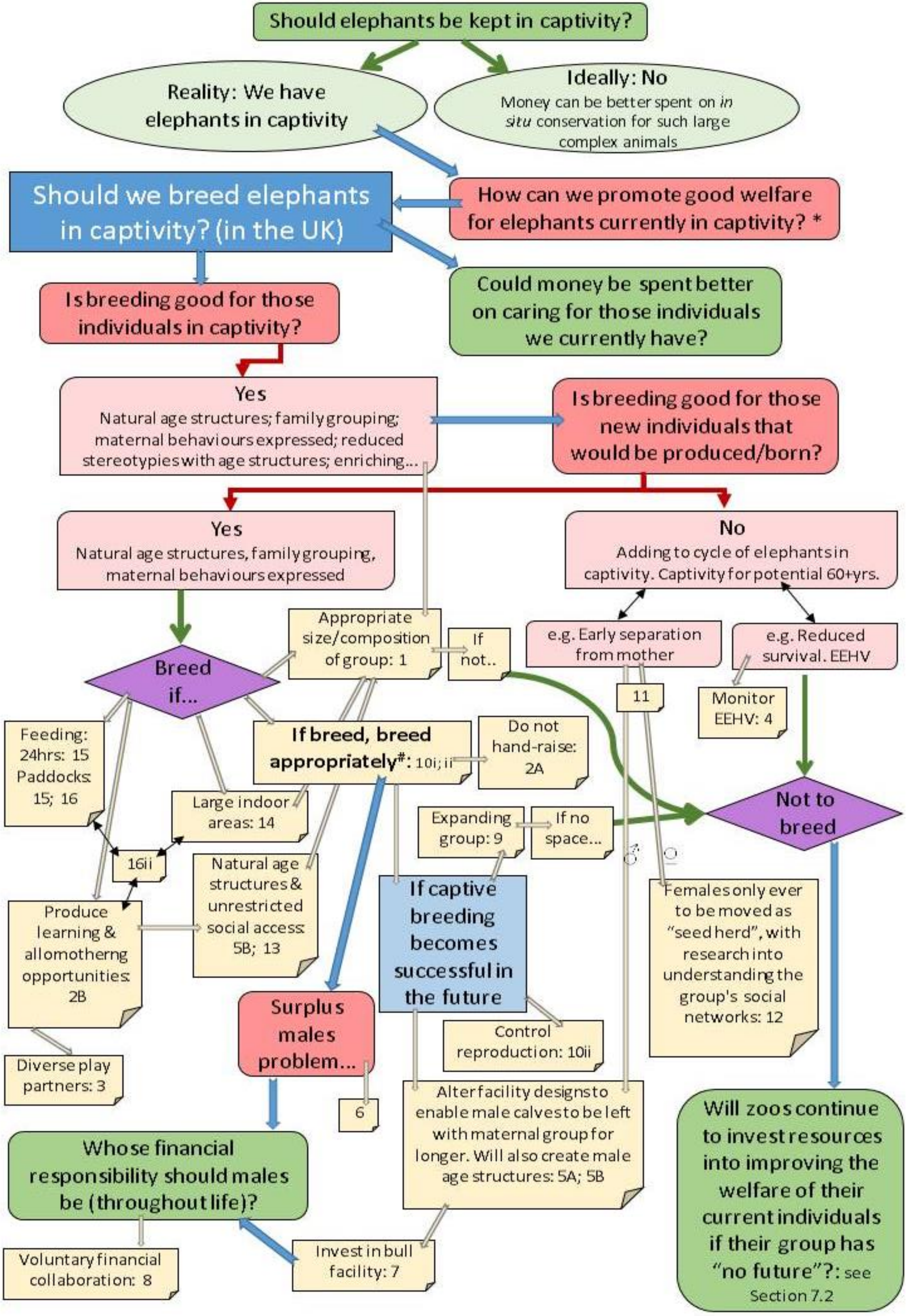
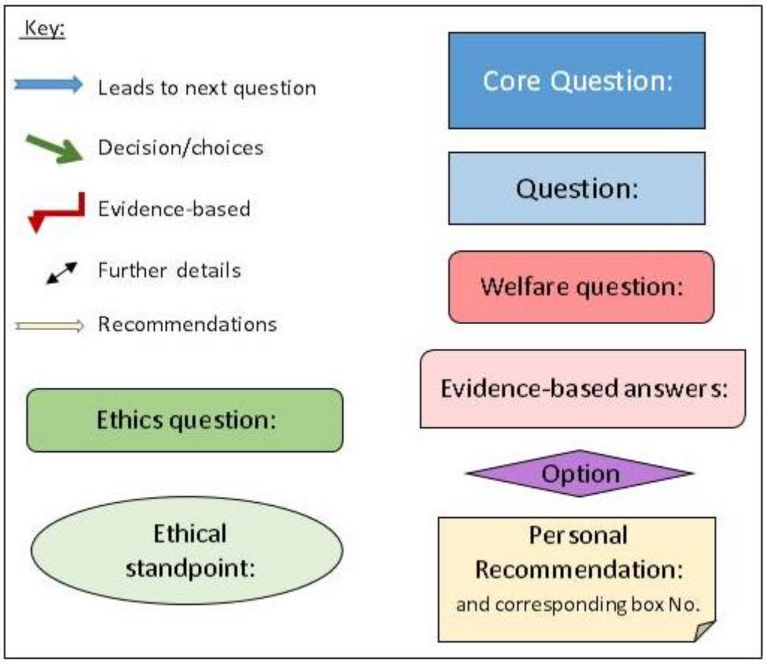


Figure 7 Ethics and Recommendations Decision Tree for Breeding Elephants in Captivity. See corresponding boxes throughout Chapter Seven for further details. Recommendations are from this thesis and other research: BIAZA, 2010; Kendall et al., 2016; Clubb & Mason, 2002. *For further discussion see Section 1.4; 1.7.2; 7.9 (Future Separations of Captive Groupings); 7.10; 7.11. EEHV=Elephant Endotheliotropic Herpesviruus. #Breed sufficient numbers to retain age and social-structures, which provide diversity, novelty in partners and learning opportunities.



It is certainly morally wrong to keep wild animals in captivity for human entertainment. But what about for education or conservation? Although zoos play the role of fundraisers and raise conservation awareness, it is unlikely that breeding populations of UK elephants will be returned to the wild (no one has done this to date). If zoos are to have a future, perhaps we should be focusing on only keeping species that are less compromised by captive environments to attract visitors to fundraise for conservation projects. Technologies such as film or virtual reality (e.g. Lonely Whale 4D VR Experience, www.lonelywhale.org; Born Free's Gorilla Safari VR, www.vEcotourism.org) could be used instead to educate the public about species that are not well-matched to live a life worth living in captivity due to their complex life histories.

France has already made huge steps in this direction with their historic advance earlier this year (May 2017) when they announced a new ban on captive breeding of bottlenose dolphins and orca. The ban prohibits keeping whales, dolphins and porpoises in captivity, with the exception of orcas and bottlenose dolphins already held in authorised facilities. Exchanges and importations are also now prohibited and pool sizes need to be expanded within a three-year deadline (BBC, 2017; Phys.org, 2017).

It may, therefore, be easy to state that the UK should take a leaf out of France's book, and ban captive breeding of elephants. However, for both whales and elephants, we may face facilities begrudging future financial investments designed to improve the lives of current individuals held in captivity if zoos no longer see the need for long-term (multi-generational) management plans (e.g. by developing enclosures).

The economic questions must therefore also be addressed. Why invest £2m in a state of the art whale facility when there may be no whales there in ten to thirty years' time (once the current individuals have reached the end of their lifespan; e.g. median life expectancy 28.8 years across four Seaworld facilities, orcas$_{N=65}$, Robeck, Willis, Scarpuzzi & O'Brien, 2015). To be financially sustainable, zoos need to be able to justify financial investments – and their existence is important for conservation of other specific species where success should be celebrated (e.g. Arabian oryx, *Oryx leucoryx*, reintroductions with Fauna & Flora International; Partula snails, *Partula spp*, at Edinburgh Zoo; Bali starlings, *Leucopsar rothschildi*, at Chester and Edinburgh Zoos).

We should be making ethical decisions when prioritising which species we (start or continue to) manage in *ex situ* breeding programmes by considering their attainable welfare standards in captivity and the related financial costs (versus *in situ* conservation) as well as their conservation status. Ethically, no elephants should be in captivity. While keeping elephants in captivity may not be in the elephant's best interest in terms of their welfare (or even as ambassadors for conservation (BIAZA, 2010)), there are already elephants living in captivity and we have a responsibility to these animals, in the UK and worldwide. Since we already have elephants in captivity, our next question should be, 'how can we best provide for the welfare of those individuals currently in captivity?'

A number of recommendations for the care and management of captive elephants have been made in recent reports (2008-2016). Interim recommendations were first made by Clubb and Mason (2002) which initiated subsequent research in the US (e.g, Greco, Meehan, Miller, et al., 2016; Holdgate et al., 2016; Meehan, Hogan et al., 2016; Prado-Oviedo et al., 2016) and the UK (Clubb et al., 2009; Harris et al., 2008, 2010; Hartley, 2016; Hartley & Stanley, 2016; Williams et al., 2015). As a result, Clubb and Mason's recommendations supplemented, or sometimes replaced the "*EAZA and AZA guidelines, and the forthcoming ones from the Zoo Federation of Great Britain and Northern Ireland*" (Clubb & Mason, 2002, p. 251). Their original suggestions included:

- that young male calves should remain with their mothers until the age of dispersal in the wild (10-15 years) "*unless problems with aggression arise within the group*" (p. 251);
- that female calves should remain with their mothers for life;

- that females, during parturition, should not be separated from the herd or chained, particularly inexperienced females;
- that recommendations about diet and nutritional intake be revisited;
- that enrichment should be provided indoors and outdoors in the form of foraging devices, rubbing/scratching posts, pools, mud wallows etc.;
- that elephants should be kept indoors for a maximum of a few hours per day, unless indoor space per elephant meets minimum recommendation of outdoor space.

Another consideration regarding welfare has been to give captive animals the opportunity to express their natural behaviours (e.g. mating, parenting, alloparenting and play) by encouraging breeding in captivity. Breeding itself may provide current captive animals with enrichment, more appropriate social and kin groupings, and may encourage diverse activities such as play (Yeates, 2010). Our line of questioning then leads us to the main question surrounding this thesis: ‘Is breeding good for those individuals we have in captivity?’

Clubb and Mason (2002) went on to recommend 1) empirical research into “*factors responsible for the poor welfare of zoo elephants*”; 2) “*until these factors are identified, that zoo breeding and importation be stopped”*; 3) “*only zoos that then solve these problems should be allowed to keep elephants in the future*”; 4) “*pending these further investigations, zoos should follow interim guidelines* [described above] *(in addition, or as an alternative, to those of the EAZA and AZA) to improve elephants’ social and physical environments*” (p. 252). It was in this context that my research in this thesis was undertaken.

BIAZA’s (2010) Elephant Husbandry Guidelines provide further recommendations for captive management. Some of their management guidelines are mandatory for facilities with BIAZA membership (as signified by the emphasis ‘MUST’) whilst others are suggested as best practice. Amongst others, these BIAZA (2010) guidelines include:
Social Grouping:

- *“Zoos MUST strive to keep a minimum group size of four compatible cows older than two years”* (p. 41).
- “*Zoos SHOULD STRIVE to ensure that for not less than 16 hours in any given 24-hour period, save in exceptional circumstances, compatible females have unrestricted access to each other. Thus whilst elephant facilities MUST retain the potential to separate elephants as required, routine and prolonged separation of compatible cows MUST not be practised”* (p. 41).
- *“Zoos MUST strive to keep animals in unrestricted social groupings at night*” (p. 47).

Housing and Environment Regulations:

- *"All elephants MUST have indoor and outdoor facilities and when weather conditions allow, they should have reasonable access to both over a 24-hr period (i.e. the animals should not be shut in overnight under normal circumstances)"* (p. 48).
- *"The inside area MUST allow* [a minimum of] *200m^2 for four animals and should increase by 80m^2 for each additional animal over two years of age"* (p. 48).
- *"The inside area therefore MUST be designed for such a herd, ensuring the elephants can move freely as a group and be able to move, turn and lie down"* (p. 49).
- *"The minimum indoor stall size for a bull MUST be at least 80m^2"* (p. 51).
- *"An outdoor enclosure MUST be 2,000m^2 with another 200m^2 for every additional cow (over two years of age) over a herd size of eight females. Ideally no outside area, designed for cows and bulls, should be less than 3,000m^2 in area and should allow some flexibility should separation be needed. The outside bull pen MUST be no smaller than 500m^2"* (p. 53).
- *"The indoor and outdoor environment MUST be positively challenging to the animals and should contain devices and structures which enrich the environment and encourage* natural behaviour" (p. 53) and in particular space to move (Kane, Forthman & Hancocks, 2009) encouraging exercise and good foot care.
- *"The EEP* [European Endangered Species Programmes] *recommendations on transferring the whole maternal group rather than splitting it up MUST be adhered to"* (p. 105). [This EEP Breeding Management recommendation, which is mandatory, states that young animals should remain with their family group for several years and should not be transferred at less than five years old. If this does happen however, then the infant should be accompanied by at least one other member from the group they were born into]. "*There are now incidences of young bulls disrupting the herd before the age of five. Therefore this may need to be reviewed on a case by case basis"* (p. 102).

An additional recommendation was also made regarding the use of sand flooring. BIAZA (2010) reports that all the births which have taken place on sand flooring have been successful in terms of the time that a calf takes to recover from birth and first stands (under six minutes, A. Roocroft, pers. comm.). It is thought that calves born onto sand are able to stand up sooner than those born onto concrete (or rubber) because the birthing fluids drain into the sand (BIAZA, 2010). On hard surfaces, newborn calves slide around more (BIAZA, 2010) without being able to gain enough traction to stand, and are also at risk of sliding great distances after being kicked by their mother when she tries to remove the birthing sac with her feet (pers obsv.). Sand also minimises foot problems which were common in all UK populations (Harris et al., 2008).

At the time of study, Howletts and Whipsnade had some non-compliance issues with the BIAZA guidelines while Chester had near-complete compliance. While some of these issues have since been addressed at all zoos (see Section 7.12, Zoo-Specific Advances and Recommendations, for more details), and Chester now has full compliance, a few of these concerns still remain at Howletts and Whipsnade.

At the time of data collection, Chester was unable to ensure that all compatible females had unrestricted access to each other, as a consequence of incompatibility between adult female Jangoli and the newly introduced male Aung-bo. This issue was resolved with Jangoli's removal to another facility (see Case Studies, Section 5.4.6). During the period of study, neither Howletts nor Whipsnade provided their elephants with free-access as both facilities locked their elephants in overnight (in sub-groupings) from around October to April when temperatures dropped; neither facility had the capacity to allow their groups to move freely; both had concrete flooring; and the inside areas were too small at both sites, for both the female groups and for the bull houses. Changes made to these facilities since data collection include the installation of refrigerator flaps to housing at Howletts (see Chapter Two, Section 2.4.3), and an entirely new sand floor indoor facility for the females at Whipsnade.

Captive elephant keeping in the UK has improved since the Clubb and Mason indictment (2002) with investment in discussion, research and change implementation. Many zoos are achieving noteworthy and positive advancement in their elephant care and are already applying many of the recommendations mentioned above, although there is still considerable variation. A few of the major innovations include the aforementioned sand flooring, advancement in enrichment (see Section 7.11), free choice of location and partners, and improvements in working towards more natural social groupings.

While some current elephant breeding groups may be making positive advancements, there are plans for others to breed in facilities that are simply unacceptable. In this context, these are facilities still using artificial insemination, while holding no bull of their own; keeper managed births; concrete floors; and limited group structure. Management strategies may be exacerbating the issues of social constraints. This could be either through physical constraints on movements and association or through keeper constraints rather than the choices of the elephants.

I shall refer to some of the above recommendations in further detail later in this Chapter, as I discuss elephant welfare indicators, learning from elders, advancement in enrichment and allowing individuals choice rather than having humans make those choices. I shall present these alongside my own recommendations, some of which result from this research.

Box 1 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 1

i) If captive facilities are unable to provide elephants with social structures with ample kinship, age-graded grouping and plentiful learning opportunities, then the best practice is not to captive breed elephants. If facilities are not delivering these aspects within their captive elephant care regimes, then there are no benefits to the elephants, only financial benefits to zoos, or a possible outlet for education and conservation.

ii) Only facilities which are large and complex enough to support appropriate group sizes and compositions should be permitted to breed. (At a minimum this should include housing their own adult male; see Recommendation 6).

Although the production of calves via captive breeding appears to result in activity budgets for age and sex that are comparable with the two reference wild populations, calves in captivity are still faced with additional challenges such as removal from their mothers at an early age, high mortality risk and social constraints on learning opportunities. Unless these issues are resolved then we should recognise that keeping and breeding elephants in captivity cannot satisfy their social and physical needs.

7.3 Welfare Indicators

Developing behavioural welfare indicators poses some specific problems of generality as elephant are individuals, each with differing ‘normative’ behaviours due to personality, age and life experience. Individuals may not express the same behavioural repertoire, irrespective of their welfare status, environment or social group.

Although there is much discussion about relevant comparator groups for assessing welfare in captivity (e.g. captive elephants across sites, Hutchins, 2006), in terms of animals with complex behaviour such as elephants, we should be using wild conspecifics as a baseline for normality, instead of the ‘best’ captive counterparts (see Introduction Section 1.3.3). Even if we could give captive elephants everything we determined that they ’needed’ (e.g. adequate space, appropriate social groupings, choices about what to do, where to be and who to be with), the majority of current captive individuals have atypical histories and early experiences, or at the very least, socialise with and learn from others who are also atypical.

Many indicators are used in the attempt to measure elephant welfare although these measures are often difficult to interpret (Mason & Mendl, 1993); see detailed discussion in Chapter One. Reactivity to stressors is one particular aspect of welfare assessments. During welfare assessments in relation to stress, it is important to differentiate between chronic and acute stress. With chronic stress, animals are repeatedly or constantly exposed to stressors and are limited in their capacity for appropriate responses (both behavioural and physiological). Acute stress, by contrast, is an event of short duration that may allow the potential for a response either during or after the stress, if animals have been able to develop a reactive capacity. Thus, there is some debate about differentiating between positive and negative stresses. While Broom (2002) states that, "*The term stress is best limited to adverse effects on individuals, rather than equating it to stimulation or to a certain kind of response. Thus stress always means poor welfare*", others maintain that some stressful encounters contribute to the psychological and physiological welfare of an animal (p. 4). Examples of situations causing eustress include exploring novel enrichment or mating. Jacobs (2011) reported low baseline cortisol metabolite concentration levels in three old female captive African elephants which surged when they were given free access to their paddock at night for the first time in their lives. This may indicate under-stimulated animals who are bored in their environment and has further welfare implications in that these individuals may have little capacity to deal with short-term stress or arousal since their baseline hormonal reactivity was low most of the time and surged when aroused (Jacobs, 2011). In summary, we need to distinguish between the consequences of a life of constant or chronic stress (anthropogenic noise, constant human presence, management, separations) and a general lack of arousal which would be expected to lead to a capacity for normal stress responses experienced in the wild (predators, other species, stranger elephants, hunger, thirst, long-distance movement; e.g. Foley, Papageorge & Wasser, 2001). Wild elephants are not 'unstressed', but they are seldom bored.

7.4 Calf Development

My results indicate that captive elephant calves (less than 24 months old) engage in similar activities for comparable proportions of the day as wild calves. However, this apparently 'normal' activity budget in captivity is only seen in calves who were raised by their mothers. Elephant mothers are therefore acting as important buffers to calves and these calves are protected by their mothers from the effects of problematic captive management, such as night separations, small enclosures, sterile environment, training etc., in their first 18-24 months of life.

Box 2 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 2A

Do not hand-raise calves in captivity since mothers are important buffers for calf development. Facilities should, therefore, prepare for calf loss. European studbook records showed that attempts have been made to hand-raise four African (N livebirths=48, 1982-2013 records) and four Asian (N livebirths=83, 1992-2013 records) calves although hand-raising attempts have only been successful in one African calf (and no Asian calves; Hartley & Stanley, 2016). This African calf was presumable Mansi from Howletts (who was rejected, reaccepted and then orphaned at 16 weeks). Although Mansi's hand-rearing has been 'successful' in that she has survived to date (Oct 2017), she may have suffered from stressful challenges of severely reduced parental care and from poor welfare due to prolonged stomach problems from bottle feeding (chronic bloating and diarrhoea; see also: Section 5.4.6 Case Studies).

Recommendation 2B

Provide opportunities to learn. Mothers will make mistakes when learning: allow them this opportunity. Chaining mothers results in stress caused by isolation and it has been suggested that this stress may lead to dystocia by suppressing the production of oxytocin (Clubb et al., 2009; Hartley & Stanley, 2016; Mason & Veasey, 2010). Chaining should therefore not be used at birth and full access should be given to important and compatible family members – it will be beneficial to involve experienced females, and beneficial for inexperienced females to be involved, to provide them with vital opportunities to learn.

From a perspective of the temporal pattern of behavioural development, few differences were found between wild and captive calves. I did, however, find increased time spent in play among captive calves (<24 months). This may be indicative of good welfare of the captive study calves (with the exception of bottle-fed Tammi's calf and Mansi) as Lee and Moss (2014) showed that wild African calves that had low rates of play, had higher mortality rates persisting even into adulthood.

Play as a welfare indicator was discussed in Chapter Six where I proposed that play, up to a certain level, is an indicator of good welfare in calves. While an absence of play can be an indicator of suboptimal welfare, excessive play could also pose a potential issue. Time in play above certain levels, especially in calves who have started to eat solids, may begin to indicate a lack of time spent foraging. This may not necessarily be through lack of opportunities to forage but through disinterest. Given that these calves were fed an energy-dense diet, their motivation to spend time foraging may have been limited (see below), and as an alternative, they engaged with their environment and others via play. 'Too much play' by comparison to wild calves is unlikely to be detrimental to calf development, but rather if excessive use of one type of behaviour is shown, then in compensation one or more alternate activities must be expressed at lower levels.

Additionally, perhaps the diversity and nature of play types and play partners are more important than actual time spent playing. If males do not have opportunities to explore 'strangers' in play as juveniles, then do they engage in more aggressive interactions later in life with more risks? Likewise, if females do not have the opportunity to engage in allomothering play or in allomothering at all, then does this mean that survival of their own calves is at further risk, due to maternal incompetence?

Box 3 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 3

Captive facilities need to provide calves with a diversity of play partners. Captive calves have limited diversity in social partners compared to the wild. Social experiences in captivity lack novelty and dynamism (which are critical for wild calves of both species) and results in reduced challenges and limited learning opportunities.

However, captive calves also have fewer choices over proximity to others due to enclosure constraints (i.e. they cannot leave their enclosure) and therefore appear to interact with others more than wild African calves do.

Future Study:

While this study found the pace and tempo of calf development in captivity to be comparable to wild counterparts and therefore 'normal', this was only the case as long as calves and their mothers survived the first 18-24 months. We can thus ask what happens to the calves after this age? What proportion of captive-born individuals will show stereotypies and at what ages? How can these be related to early development or by contrast to later management decisions? I suggest that juveniles aged around 4-6 years may be the age group where behavioural issues associated with abnormal behaviour and atypical activity patterns, seen in almost all captive adults, may arise due to management issues of weaning, separation and translocation. It will now be important to investigate differences in behavioural development between wild and captive calves in this later age group, especially in relation to husbandry and management decisions. The collection of calf behavioural data originally focused on the most physically and socially vulnerable age of <24 months (e.g. Lee & Moss, 1986). With hindsight, I would widen the data collection to include these older immatures who are likely to be experiencing behavioural issues more directly associated with captivity. This study suggests that maternal buffering is important in creating normative behaviour in the early years of life, but we know that abnormal behaviour, poor social and parenting skills, and reduced lifespan are the result of captivity – how and when these consequences arise remain to be determined.

7.5 Biases of Samples and Controls

Some control issues were insurmountable. Questions were raised as to whether wild Sri Lankan elephants differed genetically from captive Asian elephants and if any differences observed in data could be due to this variation. While Sri Lankan elephants are a unique subspecies, captive elephants are a general mix of subspecies which may have then been bred in captivity for several generations, for example up to three generations at Chester. Management differences between UK zoos were likely to have had a much greater influence in the study than the differences between subspecies. I collected data on as many elephant calves as possible in the study period across various UK zoos, to lessen a potential effect of these variables.

The project’s limited sample sizes and distribution constrained the choice of analyses, primarily due to the limited number of births and survival of newborns. Only seven Asian and six African calves were born in the UK from May 2010 to Aug 2013 (N surviving past their first day of life: five Asian, five African). Therefore all captive Asian and African calves born in this period who survived the first day of birth were studied; a larger sample size for captive calves could not have been collected within the UK in the time period available for a study which also sampled wild calves.

It must also be noted that this study could only be carried out at unique facilities which had been most successful at breeding elephant calves. Hence, the three captive study sites were where all UK calves (who survived their first day of life) had been born, from May 2010-Aug 2013. While the captive study calves had similar social and behavioural development to their wild counterparts, the facilities where calves were observed were those that had the most calves and were not necessarily a typical sample of UK facilities holding or trying to breed elephants. The captive African study site comprised of 3 male and 10 female elephants; and group sizes for the captive Asian study site ranged from 2-5 males and 5-6 females (all ages, in 2014; see Figures 2.10, 2.13 and 2.15 for age of these individuals per study year). Group sizes at these three sites perhaps deviated least from the wild, compared to the smaller group sizes found at the other four UK facilities which were also trying to breed elephants (range across four sites in 2014, all ages: Asian 0-1 male, 4-5 females; African 1 male, 2-3 females). Lower birth rates at these four facilities compared to the three study facilities (5 and 13 births in total between 2010-2014 including stillbirths, respectively) also contributed to fewer potential peer-matched play partners available to any calves born there. Therefore, the behavioural data collected on captive calves in this study may not be representative of all captive-born calves in the UK, but rather, may represent calves born at facilities with the best group sizes, sex-structures and age-structures available across the UK.

Although the final captive sample size is small and therefore subject to individual variation as well as sex differences, consistent age-specific patterns of behavioural development were constructed from these individual observations. This allowed for the behavioural development of captive calves to be compared against the baseline data collected on both wild Asian and African calves.

Variation in methodology was problematic as longitudinal behavioural data were collected from captive calves, and mixed cross-sectional and longitudinal data were collected from wild calves. While I attempted to account for this effect in the statistical models and avoided aggregating by groups rather than by individual, some effects due to the strong influence of individual is to be expected in analysis.

Biases may exist in the data because wild Asian calves were only studied in the dry season whereas all other contexts were studied in each season. However, between 2011 and 2013, Uda Walawe’s dry seasons became progressively wetter, resulting in poorer visibility across the years due to increased vegetation. In wetter conditions (where puddles were plenty!), the elephants were more likely to stay in the forest areas, where they could not be observed, rather than walking amongst the grassy vegetation to the water holes and reservoirs. Due to the cross-sectional nature of data collection in Uda Walawe, these biases should affect all age categories equally.

Although the age categories of wild Asian calves available to sample should not have been biased by fluctuations in the severity of the dry seasons, dry seasons can have huge impacts on the behaviour and survival of individual calves. For example, Fernando (2015) reported that six starving elephants were captured by the Sri Lanka’s Department of Wildlife Conservation and brought to the Elephant Transit Home in the dry seasons in 2015. The same effect of altered activity patterns and increased mortality during droughts was noted in the wild African population (Lee et al., 2011).

While the wild calves studied experienced considerable seasonality this variation is inconsequential compared to the plummeting cold temperatures experienced by captive calves in the UK (e.g. England average annual temperature 1981-2010: minimum 5.9°C; maximum 13.5°C; Met Office, 2015). I personally experienced collecting behavioural observations of elephant calves in -4°C. However, data on captive calves were collected in all seasons and weathers over a five year period.

7.6 Calf Survival

Wild calves in both populations experience extreme dry seasons. In Amboseli, this resulted in significant increases in mortality with a 30% increase in the risk of mortality (Lee et al., 2011). While lack of food is not usually an issue in zoos in contrast to the wild calves, calf survival remains a major concern in captivity. Clubb and Mason (2002) stated that in order for zoo infant mortality to match that of Asian logging camp elephants, zoo mortality rates would need "*to be reduced by a factor of nine*" (p. 250).

While mortality data on wild Asian calves are sparse, and we do not currently have figures for calf mortality in Uda Walawe, Sukumar (1989) indicates high infant survival when calves experience good environmental conditions, with mortality rates of 5% in the first five years of life. Mortality rates of live-born captive calves dying before they reach five years have been cited in range country populations as <15% (see Table 7.1 below; Clubb et al., 2008; Taylor & Poole, 1998, Sukumar, Krishnamurthy, Wemmer & Rodden, 1997), and as low as 7.7% in Pinnawala (Pushpakumara, Rajapakse, Perera & Brown, 2016) while Mar et al. (2012) also report a higher 25.6% in Myanmar logging camps (see Table 7.1).

In contrast, zoo infant mortality rates were found to be higher in captive Asian elephants compared to those in Myanmar logging camps (see Table 7.1 below; Clubb et al., 2008). Studbook analysis (from 1986-2006) showed 21% of African$_{N=89}$ and 42% of Asian elephant calves$_{N=195}$ born in European zoos (and 45% of African elephants$_{N=49}$ in US zoos) died before reaching age five years (Sargusty et al., 2009). EEHV remains a significant factor in the mortality of Asian elephants in US and EU zoo populations. Kendall, Howard, Masters and Grant (2016) demonstrated that eight (21.6%) of all 37 deaths of captive Asian elephants born in the UK and Ireland died from EEHV from 1995-2013 (29.6% of all fatalities of calves that lived to be 12 months old). These eight deaths would have included Raman (died 2009), Nayan and Jamilah (both died 2013), but Bala and Hari's deaths (in 2015) would have not been included in their dataset.

While calf mortality in Asian elephants differs between captivity and the wild, Clubb et al. (2008) showed that calf mortality did not significantly differ for African elephants between European zoos and the wild Amboseli population (Clubb et al., 2008). In Amboseli, 19% (N=1551, male and female) of calves died their first two years of life (Lee, Lindsay & Moss, 2011) and 10.3% of female calves died in their first year (livebirths, all death causes; 9.1% from natural causes; Clubb et al., 2008; see Table 7.1 below). Infant mortality in their first five years of life was found to be 12.5% (42/336) in Samburu and Buffalo Spring National Reserve, Kenya (Wittemyer, Daballen, Rasmussen, Kahindi & Douglas-Hamilton, 2005).

Rates of infant mortality, both live-born and total (i.e. premature and stillbirths) were higher for primiparous females for Asian and African elephants both in zoos, in the wild in Amboseli, and in Myanmar logging camps. In African zoo elephants recently improved adult survivorship has also been shown although juvenile or zoo-born infant survivorship has not improved. Neither adults, juveniles or zoo-born infants of Asian zoo elephants have seen improvements in survivorship recently (Clubb et al., 2008).

Box 4 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 4

In order to improve calf survival, Kendall and colleagues' (2016) recommendation should be followed: that young Asian elephants at risk of EEHV (1-8 year olds) should be monitored to detect subclinical viremia early, using blood samples (polymerase chain reaction analysis), in order for treatment to be given before the appearance of visible clinical signs.

Table 7.1 Asian and African Elephant Calf Mortality Rates in Different Populations [a]Taylor & Poole, 1998 (data from 1996 questionnaire); [b]Mar et al., 20012 (data from 1960-1999). [c]Kendall et al., 2016 (data from 1995-2013); [d]Clubb et al., 2008 (European studbook data up to 2005); [e]Hartley and Stanley, 2016 (European studbook data from 1992-2013 for Asian; 1983-2013 for African elephants); [f]Sargusty et al., 2009 (Studbook records for Asian elephants 1962-2006; African elephants (1965-2006); [g]Pushpakumara et al., 2016 (data from 1975-2013; [h]Wittemyer et al., 2005 (data from 1998-2003); [i]Lee, Lindsay & Moss, 2011 (1972-2003); [j]Mar et al., 2007; [k]AERP longterm records (data from 1974-2016).

Elephant population	Spp.	Captive / Wild	Mortality inc. stillbirths	Mortality of live-births			Stillbirth & Infanticide
			0-1yrs	0-1yrs	0-2yrs	0-5yrs	
Pinnawala 'Orphanage', Sri Lanka	*E.m.*	Captive				9.1%[a] (1/11) 7.6%[g] (5/65)	Stillbirths 4.4%[g] (3/68)
Myanmar logging camps	*E.m.*	Semi-captive	Female calves: 12.5%[d] (89/712)	Female calves: 9.3%[d] (64/687)		6.4-11.1%[a] (27/424 to 47-423) 25.6%[b] (250/975) 27%[j] (N=1020)	45 stillbirths[b] (N=1020)
Tamilnadu Forest Dept.	*E.m.*	Semi-captive				6.7% [a] (15/220)	
UK & Irish zoos	*E.m.*	Captive					21.6% stillbirths[c] (8/37); 5.4% infanticides (2/37) [c]
European zoos	*E.m.*	Captive	Female calves: 38.5%[d] (20/52)	Female calves: 20.5%[d] (9/44)		18.6%[e] (19/102) 41.5%[f] (81/195)	12.7% stillbirths[e] (15/118) deaths ≤1 day 27.7%[f] (54/195)
US zoos	*E.m.*	Captive				39.6%[f] (61/154)	deaths ≤1 day 21.4%[f] (33/154)
Amboseli, Kenya	*L.a.*	Wild	Female calves: Natural deaths 9.3%[d] (82/880) All deaths 10.3%[d] (91/880)	Female calves: Natural death 9.1%[d] (70/768) All deaths 10.3%[d] (79/768) Both sexes: All deaths 14.8%[i] (N=1551)	(Both sexes) 18.8%[i] (N= 1551)		1.6%[k] neonatal mortality (in first month of life; N= 2647)
Samburu & Buffalo Spring Reserve, Kenya	*L.a.*	Wild				12.5%[h] (42/336)	
European zoos	*L.a.*	Captive	Female calves: 20.6%[d] (7/34)	Female calves: 18.8%[d] (6/32)		18.6%[e] (11/59) 21.3%[f] (19/89)	8.2% stillbirths[e] (5/61 births) deaths ≤1 day 11.2%[f] (10/89)
US zoos	*L.a.*	Captive				44.9%[f] (22/49)	deaths ≤1 day 26.5%[f] (13/49)

7.7 Accelerated Development

In addition to these high mortality rates, calves in captivity appear to have accelerated rates of physical and possibly physiological development. Body Condition Scoring (BCS) indexes showed that 40% of captive African$_{N=132}$ and Asian elephants$_{N=108}$ in the US had elevated BCSs and a further 34% had BSCs suggestive of obesity (Morfeld, Meehan, Hogan & Brown, 2016). Hildebrandt, Goeritz, Reid, Dehnhard and Brown (2006) reported the early onset of sexual maturity in males in captivity when an adult male was not present and that Asian males as young as six years, and African males at eight years, had successfully sired offspring in captivity, whereas males of both species in the wild appear to successfully sire at the earliest age of 25-30 years (Poole, 1994; Sukumar, 1989).

Possible accelerated physiological development in captivity may be leading to management decisions of prematurely removing male calves from their mothers. In captivity, the choice to leave or remove a male calf from his group after his behaviour has begun raising concerns (high aggression towards other elephants, boisterous ‘accidents’ etc.) is a case of risk management and varies greatly from case to case. Captive male calves may physically mature early for their age, possibly caused by calorically dense diets and by limitations of opportunities to exercise, travel or wear themselves out in escalated-contact play, and lack of suppression from and exposure to age-appropriate older males, compared to wild male youngsters. Thus, finding appropriate ways to manage activities, body mass composition and exposure to older males could allow immature males to stay with their maternal group for longer, past the current recommended five years of age, postponing early separation from their mother and siblings.

Decisions regarding enclosure design (both size and complexity of allowing choices to ‘escape’ from individuals) and social groupings may be sufficient to manage young males rather than relying on veterinary solutions (see Lueders & Hildebrandt, 2014) or removal. Design solutions for keeping male calves with their mothers until older ages (as Clubb and Mason, 2002, suggest) are vital as the welfare of the rest of the group may also be compromised (e.g. young males attempting to engage in escalated-play with unwilling play partners) if facilities are not modified to allow individuals the space and ability to join and to leave or avoid others. Such modifications may help reduce problems with aggression.

Box 5A Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 5A

i) Do not fully separate males from their family group until eight years old by ii) designing facilities to enable male calves to be left with their maternal group for longer. Current mandatory EEP recommendations state that individuals should not be transferred before the age of five years with an added footnote and that "*There are now incidences of young bulls disrupting the herd before the age of five. Therefore this may need to be reviewed on a case by case basis*" (BIAZA, 2010, p.102). Clubb and Mason (2002) recommend that young male calves should remain with their mothers until the age of dispersal in the wild (10-15 years) with a similar caveat: "*unless problems with aggression arise within the group*" (p. 251). Keeping problematic, disruptive or aggressive male calves in groups may be unfeasible with present facility designs without compromising the welfare of other group members. Although it may still prove to be unfeasible for male calves to be left with their family until wild dispersal ages due to potential inbreeding with female siblings of similar ages, carefully designed expansions to breeding facilities would enable male calves to drift between adult males and their families, potentially reducing disruptive behaviour directed at the females and providing the young males with the choice of whether to spend their time with maternal groups or with other males in the facility. Groups should be allowed access to a male for mating and social experience as well as social respite from them and from each other. Providing young males with **social choices** on their own terms may not only permit males to stay with their maternal group for longer but will also provide them with opportunities for learning from the group's older male(s), producing future males with good sociability (A. McKenzie, Oct 2017, pers. comm; see also Section 7.9 below). These facility design changes and expansions are already being explored at Chester.

7.8 Social Grouping

The lack of social ‘breaks’ in captivity may be perpetuating age-inappropriate behaviour, particularly in the absence of a calf’s mother. Social constraints may also be limiting learning opportunities in captivity, both for male and female calves. These constraints include lack of kinship, lack of age-graded groups and lack of other calves and juveniles as available social partners. Many captive groups also lack experience of large musth males, and individuals lack mothering or allomothering experience. Thus while captive groups are atypically structured in terms of age, sex and experience, they are also inflexible, which is in stark contrast to the fission-fusion choices of social partners in the wild.

In the captive data analysed in this thesis, I did not test partner preferences as there were simply too few individuals available in groups for the calves to exhibit preferences. This is a huge constraint on acquiring the knowledge that is clearly available in the fission-fusion sociality of both wild Asian and African elephants (see Chapter Five). No unmanaged opportunities for choice or diversity of partners existed in captivity.

Box 5B Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 5B

Zoos should be aiming to keep age-structured groups to encourage learning opportunities and diversity of social partners. This is especially important for males and Recommendation 5A may support this development. Likewise, Recommendation 10 (see below; if breed, breed appropriately) would also facilitate this age-structuring. Greco, Meehan, Hogan and colleagues (2016) also showed that the age of social partners was important for captive Asian and African elephant welfare by demonstrating that spending more time in groups with juveniles (seven years or younger) had a protective effect reducing the risk of performing stereotypies.

Historically, importation from range-countries has been skewed towards females for both Asian and African elephants. Females were thought to be easier to handle and house and there are only a limited few facilities who are equipped to house adult males (Prado-Oviedo et al., 2016). In more recent years, females have also been imported for breeding programmes and Prado-Oviedo et al. (2016) demonstrated that 79% (158/200) of females from their captive study population with North America were imported, whereas only 34% (17/50) of males were imported. However, while importation is now rare, births in captivity are roughly 50:50 in sex and if zoos are to continue to breed, they therefore need to be evolving to solve the solution of housing surplus males born in captivity. The AZA Standards for Elephant Management and Care (approved March 2011) have recently been amended to state that all elephant facilities planning new construction or modifying existing facilities must contain areas suitable for adult males in plans. In 2012, 43% (29/68) facilities in the US already held males and 16% (11/68) held more than one male, including one facility which only kept a male social group (Prado-Oviedo et al., 2016).

Box 6 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 6

To begin to address the problem of surplus males in captivity, no A.I. should be permitted at a facility unless they already house at least one other male. Facilities should be housing, at a minimum, one adult male, which would at least provide any male calves with basic learning and social opportunities with another male.

Male Dispersal

In the wild, males leave their maternal group at an age that is highly individualistic. For example, in Uda Walawe, a nine year old adolescent may still be suckling whilst a six year old may have completely dispersed from his family (S. de Silva, pers comm. April 2016). Meanwhile, it has been shown in African elephants that males dispersing from their birth family might simply join another family, or shift from family to family, still spending 80% of their time with family groups (Lee & Moss, 1999). Males as young as four or five will leave the family for a few hours or days, but most males leave permanently between 12-16 years (Lee & Moss, 1999). These departures are not typically associated with mother-calf aggression although other family females may become intolerant (Lee, Poole, Njiraini, Sayialel & Moss, 2011).

A lack of social partners in captivity is not just a social problem for male calves, but for male adolescents and young adults too. Chiyo et al. (2011) found that males formed long-lasting strong partnerships, especially when engaging in high-risk behaviour such as crop raiding. Evans and Harris (2008) found that all ages of adolescent males showed a preference for older males (>36 years) as their nearest neighbour. Evans and Harris (2008) suggest that opportunities for males to learn from elders might come about from males being closer to these more experienced older adult males and highlight that this is also "*thought to be the case with pronghorns, Antilocapra americana (Miller & Byers, 1998), chimpanzees (Pusey, 1990) and savannah baboons (Pereira, 1988)*" (p. 784). While matriarchs are largely acknowledged as being the repositories of ecological and social knowledge (see McComb et al., 2001), Evans and Harris (2008) suggest that mature males are the source of this knowledge within bull societies.

Male Hierarchies

O’Connell's (2015) study further supports the idea that young males learn from their elders. O'Connell studied a ‘boys club’ of more than 200 African adult males in Etosha National Park, Namibia in the dry season of two wet and two dry years. The elephants in Etosha NP are dependent on permanent water holes for drinking and O'Connell reported that males expressed striking affiliative behaviours at the watering hole and that males were more affiliative than females while visiting these holes. She found that the stable male dominance hierarchies observed during dry years broke down during wetter years. When younger males had more choice of where to drink they no longer needed to defer to the dominant male. The hierarchy became non-linear as young males spent less time with their elders and their aggression increased along with testosterone spikes (Evans Ogden, 2014; O’Connell, 2015). These observations have implications for captivity and raise questions as to whether aggression rates in captivity are high because we currently do not recognise this male hierarchy. Captive males in the UK are not kept in large groups (maximum currently two independent males) and the oldest male kept in captivity is currently (2016) a 35 year old African (and 25 year old Asian) – therefore there are minimal male elders present to keep young male calves in check. Conversely, would we see this ‘hierarchy breakdown’ anyway in captivity because food and water are more available in captivity? In some facilities, there is still competition at feeding time if they have to feed from the same sites.

Due to the rising number of male elephants in captivity (current estimates are 50 across the EU, A. McKenzie, Oct 2017, pers. comm.), mostly as a function of captive breeding, BIAZA (2010) highlights the need to address keeping large numbers of males in captivity well in advance of these facilities being required. Such facilities are required now! In addition to being a practical solution for housing ‘surplus males’ (since breeding facilities currently need fewer males than females even though calves are born at roughly equal or male-biased sex ratios), such bull facilities would provide adolescent males with age-graded social partners, opportunities to learn from elders, to develop mating and fighting skills, and establish their relative rank (see Evans & Harris, 2008). Moreover, captive bull facilities would offer a unique experience for public education and conservation. After all, if the public are inspired by the immense size of individuals in female breeding groups, then logic follows that witnessing adult males would have an even greater potential to inspire the public.

Box 7 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 7

The EEP's mandatory breeding management recommendation states that "*It is of the utmost importance that a bachelor herd facility for several adult bulls be developed*" (BIAZA, 2010, p. 102). Looking to the future and asking where will young males born in captive breeding programmes live out their lives is vital if we are to continue breeding elephants in captivity. While the EEP warns that this "*facility should not primarily function as a surplus-male facility but as a component of the genetic reservoir of the population*," (BIAZA, 2010, p. 102) I argue that the wellbeing of these surplus males and their development of relevant social behaviours should, in fact, be our primary focus when designing such facilities. Furthermore, if these males are to play roles, later in life, in the genetic diversity of our captive populations then we need to ensure that we are not producing males with poor sociability.

This leads us on to the ethical question: Whose financial responsibility should males be, throughout their lives?

Box 8 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 8

Facilities should only be permitted to breed if they invest in the financial costs of their expanding groups by: holding a breeding male (Recommendation 6); retaining young males until at least eight years old (Recommendation 5A); and investing in any male calves they produce for the duration of the male’s lifetime.

One mechanism to enable zoos to invest in their males is for UK facilities to form a collaboration where all breeding facilities volunteer to financially contribute towards this collaboration with the shared goal of optimally caring for males who have been bred at these facilities. Each facility would set aside a monetary value contribution for every year (from birth) for each calf they produce: e.g. £5,000-£10,000. US zoos have tried this with $10,000 a year for surplus male great apes, however this contribution, was not voluntary and the group dissolved (L. New, Sept 2017, pers. comm.). For each year that a zoo cares for their own calf, the zoo would be encouraged to reinvest this into their own facility for enclosure and environmental enrichment adaptations. This reinvestment may help enable zoos to make changes to their facilities so they can keep males with their maternal group for longer (Recommendation 11). When a facility can no longer care for their ‘calf’ at their own facility, subsequent investment is then used as a ‘kitty’ to fund the facility where the individual is moved to. This financial contribution can be used to finance a much-needed bull facility for surplus bred males; and when a male is moved on to another breeding programme, the investment could follow him to aid development of this facility in terms of present enclosures; health care for the elephant; or keeper training and workshops for the team etc. This suggestion is clearly only a seed idea which requires much development itself. However, without it, there is no financial responsibility to build a bull facility and provide captive-bred calves, particularly males, with care throughout their lifetime. Zoos have a responsibility for the care of their animals and in situations where they have bred this animal this responsibility should extend into the full lifetime of the individual animal.

7.9 Removal of Individuals in Captivity

Box 9 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 9

Reproduction must be considered in the context of space needs for an expanding group and costs of sustaining and managing a calf over 60+ years whether male or female. Enclosure size and design should not set limits to group sizes. There is no 'optimal' family size – they can range from 2-50+. Facilities either need to be prepared for organic increases in size or to not breed. No facility without space to allow for family expansion should breed. No facility without guaranteed future funding to sustain all individuals should breed.

BIAZA (2010) states that the removal of individual elephants from a facility may be justified in situations where elephants have compatibility issues leading to individuals being kept separately for prolonged periods of time. The removal of adult female Jangoli was such a case, as discussed in Chapter Five, although she was not related to the rest of the group. However, Karishma was separated from her mother when she was eight years old and moved to Whipsnade (see below for further details).

Removal of Male Calves from Groups

In both cases where captive study calves were moved from their maternal group, both BIAZA and EEP guidelines were adhered to in that all four male calves (two Asian, two African) were five years or older (BIAZA, 2010). While five years of age is very young compared to the very youngest ages at which wild calves start to temporarily disperse, the zoos also elected to transfer the young animals in pairs meaning that they were accompanied by another calf of the group they were born into (BIAZA, 2010). In the most recent of these transfers (Nov 2016, Whipsnade), Scott (aged 5 years 1 month; born Oct 2011) was moved along with his elder half-brother (Ned, 5 years 7 months, born April 2010). While their ages fell within guidelines, this split resulted in isolating a 26 month old male calf, Sam (born Sept 2014 to the same mother as Scott: Azizah) from interactions with young males either: until he is himself transferred from his family group to potentially live with older male non-adults and adults; or until new male calves are born into the Whipsnade group. Nevertheless, in this situation Sam was at least left with the company of two female non-adults: an older 7 year 4 month old (Donna, born July 2009) and a 5 month old calf (Elizabeth born June 2016).

Howletts have succeeded in keeping their male calf Mchumba (born Jan 2011) with his family group to the present age of 6 years 9 months (as of October 2017). Likewise, Impi (born June 2011), although orphaned, has remained with his familiar group members (including his grandmother, ‘uncle’ Mchumba, ‘aunt’ Jama, and two older sisters, Etana and Janu) until the present age of 6 years 4 months (as of October 2017).

Due to EEHV, Chester has not had male calves survive past the age of three years (since Tunga, born Oct 2004).

Box 10 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 10

i) If breed, breed appropriately, meaning breed sufficient numbers to retain appropriate age and social-structures. This will also provide diversity, novelty in partners and learning opportunities. Females in the wild are often synchronised in breeding (due to social, nutritional and seasonal factors; Lee et al., 2011) so endeavour to have several females cycle and mate simultaneously. This will produce a) females sharing care of calves; b) cohorts of young calves to interact and play with, and to learn from each other (Chapter Five; and enabling Recommendation 5B: age-structured groups).

ii) It is essential to highlight that this ‘if breed, breed appropriately’ recommendation should not result in unnaturally short inter-birth-intervals (IBI) and reproduction still needs to be controlled (once facilities are successful females can have a calf every ~30 months).

In Uda Walawe all five females with IBI <40 months (of 27 females with IBI records; 2005-2012) lost the oldest of their calf dyad within a year or less of the birth of the second calf (de Silva et al., 2013). Similarly, mothers of African calves who survived their first years of life in Amboseli had significantly longer IBIs (median 53 months) than did mothers of calves who died <24 months (median IBI 37 months; mothers$_{N=319}$; Moss & Lee, 2011). IBIs for calves who died after the birth of their younger sibling but before they themselves had reached five years (calves$_{N=17}$) were also similar to when calves died <24 months (median ~38 months) indicating that older calves were dying as a result of mothers conceiving again ’too early’ for their calves (p. 200). Those conceived ’too early’ after the birth of the older sibling were also at risk of being miscarried in Myanmar logging camps where stillbirths or abortions result if a female gets pregnant again just after she has given birth (Mar, 2007).

Psychological or physiological stress compromising immune system responses is also thought to be a risk factor for developing EEHV in elephants (Kendall et al., 2016). No EEHV fatalities have ever been confirmed in calves less than 12 months old (L. Howard, pers. comm. in Kendall et al., 2016). Could short IBI’s also be exacerbating susceptibility to EEHV by inducing early weaning due to the birth of a younger sibling, thereby producing an early onset of a) psychological weaning stress and b) physiological stress by decreasing immunity protection, for the older calf? Further empirical research is vital and mother-calf proximity should be managed to ensure

Removal of Females from Groups

In UK zoos, females are removed from their family groups much more rarely than are males. One such case was that of Karishma (Ned's mother). Karishma was born at Twycross Zoo and was separated from her mother when aged just under eight years and then moved to Whipsnade "*to breed* [as] *she was getting too boisterous in the group at Twycross which upset the other four elephants*" (J. Barber, Aug 2007, pers. comm.). Although rare in the UK, moving young females arises in captive contexts outside the UK. Last year Auckland Zoo imported an eight year old Asian female from Pinnawala elephant 'orphanage' where she joined their lone female. The zoo is currently (2016) in legal debates regarding importing a second juvenile (around four or five years old), Nandi, from Pinnawala. Pinnawala is successful at breeding calves, while all orphaned, lost or injured wild calves are now taken to the Elephant Transit Home, thus it is extremely likely that Nandi's removal from Pinnawala will involve her separation from her mother, and will certainly involve her separation from a vast array of elephants both known and familiar to Nandi. Although Anjalee and Nandi may well become "*extraordinarily powerful ambassadors for wildlife and the natural world*," as stated by Auckland Zoo director Jonathan Wilcken (Auckland Zoo, 2016), it is perplexing that he goes on to state, "*we are very excited about Nandi joining Anjalee and Burma to become part of a future sustainable breeding herd,*" when these females are being moved from successful range state breeding facilities to a facility with no males and no experience of breeding (para. 10). At the very least, females should be moved as maternal groups.

Box 11 Recommendations from Decision Tree. See Decision Tree, Figure 7.

<ins>Recommendation 11</ins>

Keep calves in female groups for as long as possible. Ideally, this would be to eight years in males (Recommendation 5A) and females should remain with their mothers for life (however, see Recommendation 12). This will also enable recommendation 5B, by assisting in retaining age-structures within a group.

These two transfers from Pinnawala also provoke a controversial debate over whether resources could be better spent elsewhere to conserve elephants in Sri Lanka, rather than through expensive A.I. and captive breeding or redeveloping a facility. The economic cost/benefit decisions need to involve a careful evaluation of welfare issues. Although the welfare of the original lone female, Burma, at Auckland Zoo is likely to improve with her new facility and some conspecific company, is it acceptable to be removing young females from their maternal group?

Future Separations of Captive Groupings

BIAZA (2010) "*recommended that, in zoos that are successfully breeding elephants, the herd is allowed to grow to a point where it is necessary to reduce its size only because of the physical limitations of the zoo or because the herd has reached a social 'critical mass'. Such an upper limit will depend on the nature of the individuals within the group, however a number of five to ten animals is realistic. If a reduction in herd size does become necessary then compatible female pairs (or preferably trios or more) should be moved together to other facilities in accordance with EEP recommendation*" (p. 42). Rather than recommending "*social 'critical mass'*" as justification for dividing successfully growing captive groups, as BIAZA (2010) has, I suggest that zoos need to invest and design future housing for elephants to take into account the possibility of expanding group sizes if future breeding attempts are successful. Clubb and Mason's (2002) recommendation that captive female calves should remain with mothers for life should be a requirement, especially if we are attempting to enable behaviours seen in the wild. If zoos do achieve successful captive breeding with sustainable rates of increase, then it is inevitable that some group sizes outgrow the holding capacity of their facility. To limit the need for groups being split, and to manage larger multi-generational groups, any breeding facility should have in place strategic plans for future housing to accommodate these rising numbers, or at least, have the prospects for expansions within their designs. However, while captive breeding still faces so many issues, and is not yet self-sustaining, it is unlikely that breeding facilities will prioritise this planning and related financial commitments. Nevertheless, its importance must be held in mind when future plans are discussed.

Box 12 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 12

If group sizes outgrow the holding capacity of a facility, subsets of females should only be moved *togethe*r as seed herds. Research is currently investigating social bonds within the group at Chester and Dublin Zoos (e.g. Williams et al., 2015; R. Wazara PhD project, ongoing) in order to provide a management tool for future decisions of where to make the split in the group to form the seed herd. I recommend that in the interim while we do not have a solution to increasing group sizes with current facility designs, that this research is a prerequisite of all successful breeding facilities to garner social network knowledge of their elephants in order to limit damage to social bonds when female groups are divided.

In the recent research on welfare issues in the US captive elephant population, Greco, Meehan, Hogan and colleagues (2016) characterise social variables as predictors of stereotypic behaviour. The amount of time an individual was housed alone increased the risk of stereotypic behaviour whereas variables which decreased the risk were: the percentage time spent with keepers and a unique variable of Social Group Contact – a measure which "*reflects the fact that, in most zoos, herds are divided into various sub-groups, and that individual elephants generally spend time in more than one of these subgroups*" (Greco, Meehan, Hogan et al., 2016; Meehan, Mench, Carlstead & Hogan, 2016, p. 6). It was also shown that female African elephants were at greater risk of being hyperprolactinemic (an endocrine dysfunction linked to acyclicity and a known cause of infertility in women; Brown, 2000) as the number of social groupings increased (Meehan, Hogan, et al., 2016). (Blood samples from Asian elephants were not analysed for serum prolactin since hyperprolactinemia predominantly affects African elephants - 28% of the US study population, compared to 3% in the Asian study population (Brown et al., 2016)). Brown et al. (2016) suggest "*social stability and feeding and enrichment diversity may have positive influences on hormone status*" (p. 2). They propose this link between social grouping and hyperprolactinemic could be due to prolactin's role in stress responses, especially socially related stressors. They go on to suggest that "*for female African elephants, not being in a stable social group may be a stressor that elicits an increased prolactin response*" and that "*management practices that include dividing the herd into multiple social groups and housing elephants in a variety of social configurations may yield a more demanding social environment to which they respond with elevated prolactin*" (Brown et al., 2016, p. 17). These social variables therefore have welfare implications for single housed females and for larger groups who are separated or subdivided, by people rather than their own choices, for prolonged periods of the day or night, especially for African elephants, in terms of reproductive health and success.

Box 13 Recommendations from Decision Tree. See Decision Tree, Figure 7.

Recommendation 13

BIAZA's (2010) recommendation of unrestricted social access for compatible females across 24hr periods (or as close to 24hr as possible given day-to-day management such as cleaning enclosures, training or health care), with areas designed to allow female groups to "*move freely as a group*" (p. 49; see Section 7.2) needs to be followed. This would also permit choice of social partners in an age-structured group (see also Recommendation 5B) and Greco, Meehan, Hogan and colleagues (2016) demonstrated, for both captive Asian and African elephants, that spending time housed separately increased the risk of performing higher rates of daytime stereotypies (summer and winter observation, African$_{N=47}$, Asian$_{N=42}$, at 39 US facilities).

7.10 Housing Complexity in Captivity

In addition to social richness, housing complexity has also been shown to play a key role in welfare in captivity. Studies have shown housing to have impacts on learning, social conflict, stereotypies and even reproductive behaviour. For example, wombats in captivity, like elephants, suffer from high levels of stereotypies (pacing) and are often obese, with low reproductive rates and expressing severe aggression. Smaller wombat enclosures were correlated with increased social conflict and decreased natural grazing (Descovich, Lisle, Johnston, Nicolson & Phillips, 2012). Research on captive American mink has shown that impoverished environments may impair development while stress was also found to suppress key hormones and reduce reproductive behaviour, both leading to reduced reproduction (Buob et al., 2013; Dallaire, Meagher & Mason, 2012; Meagher & Mason, 2012). When enrichment was provided to mink (as golf balls, 'sniff' balls, plastic chains and tube toys), rates of play increased, screaming (when handled) reduced, and reproductive success increased in terms of changes to mating behaviour and increased litter sizes (Meagher et al., 2012; Meagher & Mason, 2012).

Furthermore, the presence of social partners may be important for cognitive development; experiments in dairy cows showed that calves raised individually performed poorly on a reversal learning task (approximately 20% success by the end of the experiment, for 24 sessions) compared to those raised in social housing (100% demonstrated reversal learning (Gaillard, Meagher, Von Keyserlingk & Weary, 2014). Dairy calves reared in the individual housing also failed to habituate to a novel object (ball). These studies suggested that contact with social partners improves the calves' ability to adjust to new conditions (Gaillard et al., 2014) which has welfare implications.

In relation to spatial requirements, Harris et al. (2008) showed that elephants with 40-80m^2 per elephant expressed significantly less stereotypic behaviour than those with less space. However, it is important to note that in captive housing, complexity of space and making the most of it is more important that simply space for the sake of it (Meehan, Hogan. et al., 2016). There is an exception here, however, space gives animals in captivity the opportunity to get away from each other. Nevertheless, this may not necessarily always be physical distance, and with careful use of the space available to facilities, animals may still be able to 'feel' like they have had social respite. One such example is the polar bear enclosure at the Highland Wildlife Centre, Scotland, where visual barriers have been designed into the rolls of the landscape, providing areas where bears can take social breaks if they chose to.

In the UK, elephant facilities would ideally have enormous indoor enclosures due to the inclement weather (see Section 7.5 above) and need for elephants to spend large portions of time indoors in the winter. Although it is argued that this is expensive, Blair Drummond Safari Park recently provided their African elephants with a new, relatively inexpensive indoor building using agriculture warehouses, which now also permits access to their outdoor paddock, at the elephants' choice. Previously, three adult females shared a partitioned area divided into areas of 50.9m^2, 50.9m^2 and 39.8m^2 at night (Jacobs, 2011), and at its worst, keepers were not able to give them access to their outdoor paddock for weeks or even months in winter. Blair Drummond Safari Park has highlighted how huge differences to the lives of captive animals can be made with relatively inexpensive but appropriate changes of housing conditions and management. In the research by Meehan and colleagues (2016) on the captive US elephant population, social and management factors were found to be important for multiple indicators of welfare whereas they found exhibit space to be a less influential factor than they expected.

Box 14 Recommendations from Decision Tree. See Decision Tree, Figure 7.

<ins>Recommendation 14</ins>

Considering both the inclement British weather and the need for facilities to keep their elephants indoors for long periods during cold weather, and following Mason and Clubb's (2002) recommendation that elephants should be kept indoors for a maximum of a few hours per day unless indoor space per elephant meets minimum recommendation of outdoor space ("*2,000m^2 with another 200m^2 for every additional cow (over two years of age) over a herd size of eight females*"; the "*bull pen MUST be no smaller than 500m^2*"; BIAZA, 2010, p. 53), all UK elephant facilities should have large indoor enclosures and the ability to avoid the cold.

7.11 The Importance of Forage Opportunities in Captivity

Providing captive elephants with opportunities to feed at rates similar to those in the wild may be even more important to welfare in captivity than has previously been recognised. I justify this suggestion using similarities between elephants and horses in digestive physiology. Horses are termed ‘trickle feeders’ in that they eat small quantities of food at a time, spending around 12.5 ±2.5 hours eating and foraging per 24-hours with intermittent rest periods (Ellis, 2010). Elia, Erb and Houpt (2010) also report that stabled horses spent 61.5% (29-76% range; N=8 mares) of time in 24-hour periods when fed *ad libitum* orchard grass hay, while Sweeting, Houpt and Houpt (1985) report 70.1 ± 8.6% feeding during observations at 10am-12pm and again at 2pm-4pm (N=8 stabled mares; 117hrs data collected). This term can therefore also be applied to elephants. A further comparison between horses and elephants is that they both lack gallbladders (Agnew, Hagey & Shoshani, 2005). In horses, hydrochloric acid (HCl) is produced continuously into their stomachs (unlike in animals who have gallbladders, who only produce HCl when they eat), and saliva then prevents the gastric tissues from being damaged by the digestive acids (Boswinkel, Ellis & van Oldruitenborgh-Oosterbaan, 2007). It is thought that this saliva protects these tissues from ulceration, a disorder prevalent in performance horses (Boswinkel et al., 2007). However, horses only produce saliva during mastication (Alexander, 1966) and this in turn has led to the horse feeding guidelines of providing 24-hour access to forage. One recent study even showed that horses$_{N=8}$ chewed more times when eating a diet of hay (43,476 chews/day) compared to when eating a pellet diet (10,036 chews/day) (Elia et al., 2010). The lack of foraging opportunities for stabled horses leads to reduced time spent chewing which in turn leads to negative impacts on the digestive system including greater risk of ulcers and increased risk of colic (Ellis et al., 2015). It may then be possible, by the same logic, that in providing captive elephants with access to calorically dilute foods, 24-hours a day, we could possibly see a reduction in cases of colic in captivity by fostering increasing periods of saliva production and subsequently diluting stomach acid levels (Murray & Eichorn, 1996). Further research into elephant saliva production would clearly be required and this would obviously prove more of a logistical challenge in captive elephants than horses. Colic, along with obesity, is a major concern for captive elephant care (Hatt & Clauss, 2006) and two of the African elephants from the captive study population (Umna and Juva) died (aged 13 years, and 6 years 3 months, respectively) due to colic in the study period.

Furthermore, regarding the potential parallels between elephants and horses and the importance of time spent feeding in captivity, it has been suggested that lack of foraging opportunities for stabled horses could lead to the development of abnormal behaviours (Ellis et al., 2015). The behavioural urge for horses to spend a percentage of their activity budget on food ingestion (Ellis et al., 2015) may be the motivation behind horses foraging in bedding and ingesting wood shavings or faeces when few foraging opportunities have been provided (Boswinkel et al., 2007; Curtis, Barfoot, Dugdale, Harris & Argo, 2011; Elia et al., 2010). While coprophagy is a natural behaviour for young animals to enable individuals to populate their guts with relevant bacteria and was seen in elephant calves both in the wild and captivity, it was also seen across ages in captive African elephants. This abnormal behaviour in adults may thus stem from the lack of foraging opportunities in captivity and from the motivation of elephants to forage at their natural rates. A tendency towards coprophagy by non-infants was not seen in captive Asian elephants, however. Captive Asian elephants appeared to give faecal matter a wide birth and stepped around it, whereas African elephants would walk straight through it and even throw it on themselves sometimes. This could perhaps be related to the differences in their faecal matter in terms of consistency and shape (Asian elephant faeces tend to be more coherent boli and less moist; pers. obsv.) or have deeper roots in their natural ecology.

In addition to coprophagy and a behavioural drive for both horses and elephants to forage, it has also been suggested that gastrointestinal irritation in horses could be the motivation for the development of another abnormal behaviour: crib-biting (Moeller, McCall, Silverman & McElhenney, 2008). This is an oral stereotypy, whereby a horse uses its teeth to take a hold of a fixed object and draws air into its cranial oesophagus (McGreevy, Richardson, Nicol & Lane, 1995). Moeller et al. (2008) suggested that crib-biting and wind-sucking increase saliva flow and buffer the stomach. This may shed light on the unusual abnormal behaviour of Mansi, the bottle-fed captive African calf in this study. Mansi often appeared to be uncomfortable due to trapped wind, presumably due to her bottle-feed and was at times, effectively observed doing a ‘handstand’ with at least one of her back legs raised and with her weight on her forelegs. It was thought that this was to relieve gas (N. Boyd, January 2011, pers. comm.). Mansi was also often seen sucking her trunk, which may have been a form of wind-sucking as she often appeared particularly bloated at these times (pers. obsv.). I suggest that Mansi wind-sucked in order to relieve gastrointestinal irritation by increasing her saliva flow, particularly when solids were introduced to her diet. However, it must be pointed out that Mansi may have simply been sucking her own trunk in order to self-soothe since her mother was not present to provide this calming effect. Sucking her trunk could have also been a sign of pain since Shrestha and Gairhe (2006) have reported captive Asian elephants in Nepal biting the tip of their trunk and employing abnormal postures when in pain due to colic.

If saliva is only produced by elephants when masticating, as discussed above, then this may also shed some light on differences observed between wild and captive elephants. Parotid salivary glands in elephants are located behind the ear canal (Dumonceaux, 2006) and are more developed in the wild than in captive elephants, conceivably due to wild diets containing more browse and thus requiring more saliva than captive diets (N. Masters, September 2016, pers comm.). In fact, it may not be that wild diets simply require more saliva, but that wild diets also stimulate the production of more saliva, by means of chewing more. Research showed an absence of detectable alpha-amylase levels in African elephant saliva, thus negating a digestive role for the saliva (Raubenheimer, Dauth, Dreyer & de Vos, 1988). The authors instead suggest that the role of the saliva in African elephants is a function of the sheer volume with which it is secreted, in order to lubricate the masses of ingested grasses, leaves and bark so as to aid swallowing (Raubenheimer et al., 1988).

7.12 Zoo-Specific Advances and Recommendations

In recent years Chester have been working towards improving the hours that elephants spend feeding. In 2016, keepers use combinations of feeders to encourage more natural muscle use and increased time spent foraging (Edwards, 2016).

Sithami using join-flex feeder at Chester. Video still from footage filmed by Andrew McKenzie. (For video clip, see https://business.facebook.com/elephantbusiness/videos/1203527596348737/).

The use and spread of creative ideas such as those implemented at Chester could also encourage public engagement and promote more natural activity budgets of elephants at other facilities too. Howletts have a particular opportunity to utilise joint-flex-tube feeders (tunnel or L-shaped tubes with a barrier preventing the elephants from getting inside, used to encourage individuals to bend down and stretch to reach food items) since the elephants already bend down and reach for boundary vegetation growing at the other side of paddock fences. Positioning joint-flex-tubes alongside public viewing areas may develop public engagement as well as encourage more of this naturalistic behaviour, especially in smaller individuals who cannot reach the vegetation. As a result of developing these feeding techniques at Chester, elephants have the opportunity to feed almost 24-hours a day (A. McKenzie, Sept 2016, pers comm.).

Adult African male, Jums, as Howletts flexing his front wrists to reach vegetation on the opposite side of the grass paddock boundary fence. Photograph taken 17th May 2012.

Box 15 Recommendations from Decision Tree and Grass Paddock Recommendation for Chester Zoo. See Decision Tree, Figure 7.

Recommendation 15

Twenty-four-hour feeding opportunities, with low quality high-fibre food, should be provided throughout the enclosures, to encourage both trickle-feeding and exercise. However, this 24hr feeding system must be set up to avoid disturbing sleeping elephants (A. Roocroft, Oct 2016, pers. comm.) and therefore sleep studies are important to gauge and verify the appropriate timings of automatic feeders (e.g. Williams et al., 2015).

Recommendation for Chester Zoo

A further recommendation of this thesis is for Chester to also provide elephants with grass paddocks to further encourage natural feeding behaviours because captive African elephants kept on grass have been shown to spend 75% of their time feeding (Rees, 1977). Furthermore, the team at Chester have also stated that they would now like to increase grazing for their Asian elephants (Edwards, 2016).

Box 16 Recommendations for Howletts WAP. See Decision Tree, Figure 7.

Recommendations for Howletts WAP

i) Indoor feeding systems should be designed and installed at Howletts to provide elephants with feeding opportunities (around the clock) when the elephants are denied access to their outdoor grass paddocks (e.g. overnight during inclement weather).

ii) During data collection, the elephants at Howletts were not given free-access to one another as they were locked overnight in subgroups from around Oct-April. However, the recent installation of refrigerator flaps to the indoor enclosure doorways now allows females and calves to move freely and chose who to spend time with. Nonetheless, these indoor houses at Howletts still have concrete flooring, and neither the female group housing nor the bull house meet the BIAZA (2010) guidelines in terms of minimum space. This thesis recommends that Howletts invests in designing and building new indoor enclosures for both the female group and for the male. These facilities should include sand flooring and should, *at a minimum*, reach BIAZA (2010) guidelines for size. New indoor facilities should also take into account Recommendation iii, below.

iii) While the addition of refrigerator flaps at Howletts permitted free access between females and calves, a further consequence may have been to enable Howletts to keep male calves with their mothers for longer. This simple enclosure modification is facilitating Howletts to follow Clubb and Mason's (2002) recommendation: that young male calves should remain with their mothers until the age of dispersal in the wild (10-15 years) "*unless problems with aggression arise within the group*" (p. 251). Male calf Mchumba is almost seven years old and still with his mother with no reported problems of aggression (N. Boyd, Oct 2017, pers. comm.). This achievement should be commended and it is therefore of great importance that Recommendations 5A and 5B be integrated into any future enclosure designs at Howletts to allow this success to continue and evolve. These facility designs will produce future males with good sociability by permitting young males to drift between adult males and their families, enabling age-structured groups to exist, and by providing males with social choices (see Box 5A and 5B for further details).

While Whipsnade provides elephants with grass paddocks and walks to other vegetated areas around the zoo, the elephants spent a large proportion of their time either in the sand paddocks or indoor concrete housing (e.g 46% for Scott, for 465 25 min scans from

10:30am-4:30pm; and 38% of this was in sand-paddocks). While it has been suggested that sand is significantly better as substrate flooring for captive elephants than concrete (BIAZA, 2010), in outdoor paddocks grass can provide a richer and more complex environment in terms of opportunities to forage and to mud wallow. At Whipsnade, the smaller outdoor sand paddocks were used in particularly wet weather, to ensure the grass was not damaged by the elephants and to prevent elephants slipping and falling. However, the site often suffers from poor wet weather and at the time of data collection several recommendations were made.

Box 17 Recommendations for Whipsnade Zoo

Recommendation for Whipsnade Zoo

i) Allow elephants access to grass paddocks on more days of the years in less inclement weather. Although calves also engaged in social-play in the sand paddocks, adults were not observed in play on the sand paddock or indoors (pers. obsv.). However social play was observed in adults on the grass paddocks and greater access to these large grass paddocks may encourage more social-play in adults, as captured in these images below of Lucha, Scott and Ned in a typically wet summertime.

Since data collection was completed, Whipsnade have designed and built a new indoor enclosure for their females and calves. This new housing has addressed the issues in Recommendation 16ii below:

ii) During the study period future housing developments were in dire need in order to resolve the requirement of larger indoor housing, without concrete flooring where compatible individuals can mix at night. Options needed to be explored in designs which kept incompatible females separated but allowed calves and smaller individuals to roam freely between social groups. Suggested designs to permit access to smaller individuals only were similar to those used for P.C. calf training at Chester and Dublin Zoo.

Since data collection was completed, Whipsnade now allows the groups to stay outdoors in the grass paddocks at night in good weather, and even permitted Azizah to give birth outdoors (October 2014). This was the first group-birth within Whipsnade's elephants and provided young Gheta with vital experience which will be essential when she comes to breed herself (see recommendation 2B). Whipsnade now provides the group with large indoor enclosures (which now meet the BAIZA standards, 2010) and sand flooring. These housing improvements should result in improved welfare by providing more complexity to the elephants' environment, offering them greater social access at night, as well as more space and improved health (e.g. relieving chronic foot problems with sand replacing concrete especially for Azizah, N. Masters, Oct 2017, pers comm.).

Unrelated adult female Mya engaged in social play with male calves Scott and Ned during a rainstorm at Whipsnade. Photographs take May 2012.

All three captive study sites therefore now provide elephants with outdoor access (and two of these provide most of the elephants with free access between indoors housing and outdoor sand paddocks giving the elephants the opportunity to choose). Considering the female elephants at Howletts were previously divided into four separate houses with no interaction between the houses (up to 19 hours a day on occasion in cold months), the addition of refrigerator flaps installed to external doors on housing is a great example of how even inexpensive and simple changes to housing can have incredible impacts on the welfare of individuals in terms of choice (of where to be and who to be with), social complexity and therefore potentially at least, wellbeing and welfare.

Captive facilities are now exploring housing design which allows even more complexity in social groups by permitting males to remain with the group, for 24-hours, indoors and outdoors. Dublin Zoo is the forerunner of this development and appears to have great success with the male, Upali, even choosing to sleep with the group at night. This progress should be celebrated, especially in light of the fact that even a few decades ago male elephants were described as living solitary lives "*with few social bonds*" (Poole, 1994 p. 331).

7.13 Concluding Remarks

Each calf born in captivity has the potential to spend the next 70 years in these conditions; facilities have an obligation to ensure that these conditions are neither psychologically or socially damaging for survivors, nor detrimental in terms of mortality, risks and low reproductive potential, over the very longest term to the animals under their care.

The recent body of literature on captive elephants and this study support the recommendations proposed by Clubb and Mason (2002) (see Section 7.2, Elephant Welfare in Captivity) that 1: we should continue investigating empirical research into "*factors responsible for the poor welfare of zoo elephants*" (p. 252). The second and third recommendations (2: ***"until these factors are identified, that zoo breeding and importation be stopped"***; 3: "*only zoos that then solve these problems should be allowed to keep elephants in the future*") were discussed together. Ethically there is no justification for importation of elephants from the wild. Importation has its place in elephant conservation for temporary and veterinary purposes (e.g. rehabilitating lost and injured calves) but, in terms of ethics, the degree to which the individual's wellbeing is compromised (from the wild to captivity) cannot be balanced by its contribution to *ex situ* conservation breeding programmes, particularly when we still face so many problems at present with successfully producing viable offspring in captivity. In terms of captive breeding, rather than a blanket ban on breeding, a slight revision is suggested: that only zoos that are actively solving some of the key problems discussed here (e.g. breeding lots simultaneously to produce natural age structures; developing enclosures to enable keeping male juveniles for longer periods; investing in bull facilities) should be permitted to be breeding elephants at present; and that all breeding at other facilities should be halted (e.g. facilities where strategies are not currently in place to house males; plans for growing families etc.). We also need to face the difficult recommendation that those zoos who are falling short of guidelines and Clubb and Mason's (2002) fourth recommendation (4: "*pending these further investigations, zoos should follow interim guidelines (in addition, or as an alternative, to those of the EAZA and AZA) to improve elephants' social and physical environments*", p. 252) should not be allowed to keep elephants, and that alternative facilities achieving higher welfare standards need to be found for these elephants. Investing in the care of such large and complex animals in captivity is a huge burden and it may be time for some facilities to face the difficult decision to follow the example of Twycross Zoo (UK) and 'go out' of elephant keeping, and invest their zoo's resources elsewhere. However, what to do with the 'abandoned' elephants remains a problem.

Although it appears that young calves in captivity (up to 24 months) raised by their mothers show patterns of social and behavioural development that are similar to those seen in wild calves, we are still a long way from successful captive breeding in terms of calf survival. It is important to reiterate here that, in 2016, only two (14%) of the 14 main captive study calves, born from 2010-2013, were both alive and not orphaned. It also should be recognised, as was clear from the analyses of wild and captive calf behaviour, that each calf is an individual, with variation in personality, arousal, reactions to stressors, physical growth and maternal experiences. As such, in the limited sample of captive calves examined here, and those likely to be present in the future, drawing robust conclusions about developmental rates and processes and their long term consequences will remain problematic (see Section 7.5, Biases of Samples and Controls).

At current mortality rates, as shown above, unsuccessful captive breeding could be viewed as a drain on facility and maternal resources. In the absence of well-developed strategies to manage male calves born in captivity (around 50% of calves), producing more individuals to become socially isolated cannot be tolerated. The potential benefits that a calf brings, such as developing normative multi-generational matrilineal groups, enabling positive social bonding stimuli from calf presence and thus reducing abnormal behaviours, need to be balanced against ensuring adequate space for families to grow and to divide naturally with time. At this stage, none of these ‘problems’ has been solved. We should either be prepared to meet these needs or, as stated earlier in this Chapter, we should be prepared to stop breeding elephants in captivity.

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APPENDIX A: Details of Rehabilitated and Released Juveniles from the Elephant Transit Home

Table A1 Number of Juvenile Elephants Released from the ETH and the Maximum Number of ETH Orphans of Reproductive Age during Study Period (2011-2013). Table adapted from [a]Miththpala, 2009. [b]Fernando et al., 2011; [c]ETH, n.d.. *These include Sandamali/[Indika] and Maththali, both now confirmed mothers. Prior to 2010, all juveniles were released in Uda Walawe; from 2010 onwards juveniles were also released to other locations inc. Lunugamwehera NP. Estimated age in study periods assumes ~5 years old at release. For age at first birth, see Table 1.2 in Introduction Chapter; also de Silva et al., 2013; de Silva, Ranjeewa & Weerakoon, 2011; Ishwaran, 1993.

Release Year (aged ~5yrs)	N total p/yr	N Males	N females	Est. age range (yrs) of any rehabilitated/ released calves at start of study period (2011) – end of study period (2013)	N rehabilitated/ released females old enough to have produced their first calf (≥~12yrs) by study period
1998[a]	4	3	1	18-20	1
2000[a]	5	1	4*	16-18	4*
2002[a]	8	3	5	14-16	5
2003[a]	11	4	7	13-15	7
2004[a]	11	7	4	12-14	4
2006[a]	9	4	5	10-12	≤5
2007[a]	10	4	6	9-11	0
2008[a]	8	2	6	8-10	0
2009-2011[b]	10	-	-	5-9	0
2012-2017[c]	27	-	-	5-6	0
Total:	103 [c]	Minimum 28	Minimum 38		21-26

APPENDIX B: Counts of Behavioural Observations on Elephant Calves

Table B1.1 Count of 10 min Focal Observations for Wild Asian Calves, by Sex and Age Category. Unknown sex and ages excluded from analyses.

	Age category					
Calf Sex	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	30	24	43	21	42	**159**
Female	90	32	50	22	68	**262**
Unknown	7	2	1	2	9	**21**
Overall	127	58	94	45	109	**443**

Table B1.2 Count of 10 min Focal Observations for Wild Asian Calves per Field Season by Sex. Unknown sexes only used in analyses when all sexes were combined.

Sex	Field season			
	2011	**2012**	**2013**	**Total**
Male	63	56	40	**159**
Female	87	94	83	**264**
Unknown	8	3	10	**21**
Total	**158**	**153**	**133**	**444**

Table B1.3 Wild Asian Elephant Calf IDs, Birth Months, Sex and Age during 2011, 2012 and 2013 Study Periods in Uda Walawe National Park. Ages calculated using birth estimates and Julian calculations.

Calf ID	Birth year	Birth month	Julian birthdate	Calf sex	Mother ID	Mother wild (W) or ETH?	Calf studied in 2011	Age of calf in June-July 2011 (months)	Calf studied in 2012	Age of calf in June-July 2012 (months)	Calf studied in 2013	Age of calf in May-July 2013 (months)
[c078_06]	2006	1	1033	?	[078]	W	2011	67-68				
[c205_06]	2006	10	1042	F	[205]	W	2011	56-57				
[c136_07]	2007	1	1045	M	[136]	W	2011	53-54				
[c177_07]	2007	3	1047	F	[177]	W	2011	51-52				
[c026_07]	2007	7	1051	M	[026]	W	2011	47-48				
[c301_07]	2007	11	1055	M	[301]	W	2011	43-44				
[c129_08]	2008	2	1058	F	[129]	W	2011	40-41				
[c800_08]	2008	2	1058	M	[800]	ETH	2011	40-41				
[c312_08]	2008	5	1061	F	[312]	W	2011	37-38				
[c218_08]	2008	6	1062	F	[218]	W	2011	36-37				
[c256_08]	2008	7	1063	M	[256]	W	2011	35-36				
[c830_09]	2009	3	1071	F	[830]	W	2011	27-28				
[c331_09]	2009	4	1072	F	[331]	W	2011	26-27				
[c117_09]	2009	5	1073	F	[117]	W	2011	25-26				
[c431_09]	2009	5	1073	M	[431]	W	2011	25-26				

Calf ID	Birth year	Birth month	Julian birthdate	Calf sex	Mother ID	Mother wild (W) or ETH?	Calf studied in 2011	Age of calf in June-July 2011 (months)	Calf studied in 2012	Age of calf in June-July 2012 (months)	Calf studied in 2013	Age of calf in May-July 2013 (months)
[c832_09]	2009	5	1073	M	[832]	ETH	2011	25-26				
[c310_09]	2009	6	1074	F	[310]		2011	24-25				
[c210_09]	2009	7	1075	F	[210]	W	2011	23-24				
[c147_09]	2009	8	1076	F	[147]		2011	22-23				
[c149_10]	2009	12	1080	?	[149]	W	2011	18-19				
[c187_10]	2010	3	1083	M	[187]		2011	15-16				
[c429_10]	2010	6	1086	F	[429]	W	2011	12-13				
[c076_10]	2010	7	1087	?	[076]		2011	11-12				
[c173_10]	2010	8	1088	?	[173]	W	2011	10-11				
[c219_11]	2011	1	1093	F	[219]	W	2011	5-6				
[c104_10]	2010	1	1081	?	[104]		2011	17-18				
[c173_11]	2011	1	1093	?	[427]		2011	5-6				
[DEV_11]	2011	3	1095	F	N/A	ETH	2011	3-4				
[c324_11]	2011	4	1096	F	[324]		2011	2-3				
[c198_11]	2011	7	1099	M	[198]	W	2011	0				
[c025_09]	2009	4	1072	F	[025]	W	2011	26-27	2012	38-39		
[c237_10]	2009	12	1080	M	[237]	W	2011	18-19	2012	30-31		
[c039_10]	2010	4	1084	M	[039]	W	2011	14-15	2012	26-27		
[c809_10]	2010	4	1084	F	[809]		2011	14-15	2012	26-27		
[c056_10]	2010	6	1086	F	[056]		2011	12-13	2012	24-25		
[c005_10]	2010	7	1087	M	[005]	W	2011	11-12	2012	23-24		
[c833_10]	2010	11	1091	M	[833]		2011	7-8	2012	19-20		
[c001_11]	2011	1	1093	F	[001]	W	2011	5-6	2012	17-18		
[c002_11]	2011	1	1093	F	[002]	W	2011	5-6	2012	17-18		
[c142_11]	2011	5	1097	M	[142]	W	2011	1-2	2012	13-14		
[c145_07]	2008	6	1062	F	[145]	W			2012	48-49		
[c119_10]	2010	1	1081	M	[119]	W			2012	29-30		
[c064_10]	2010	3	1083	M	[064]	W			2012	27-28		
[c824_10]	2010	9	1089	M	[824]	W			2012	21-22		
[c802_11]	2011	1	1093	?	[802]				2012	17-18		
[c062_11]	2011	3	1095	M	[062]				2012	15-16		
[c271_11]	2011	4	1096	F	[271]	W			2012	14-15		
[c816_11]	2011	8	1100	F	[816]				2012	10-11		
[c178_11]	2011	12	1104	F	[178]	W			2012	6-7		
[c301_11]	2011	12	1104	M	[301]	W			2012	6-7		
[c431_12]	2012	3	1107	M	[431]	W			2012	3-4		
[c474_12]	2012	3	1107	F	[474]	W			2012	3-4		
[c839_12]	2012	3	1107	M	[839]	W			2012	3-4		
[c239_12]	2012	4	1108	F	[239]	W			2012	2-3		
cAfrCol_12	2012	5	1109	M	N/A	ETH			2012	1-2		
[c218_12]	2012	6	1110	F	[218]	W			2012	0-1		
[c245_12]	2012	6	1110	F	[245]				2012	0-1		

Calf ID	Birth year	Birth month	Julian birthdate	Calf sex	Mother ID	Mother wild (W) or ETH?	Calf studied in 2011	Age of calf in June-July 2011 (months)	Calf studied in 2012	Age of calf in June-July 2012 (months)	Calf studied in 2013	Age of calf in May-July 2013 (months)
[c838_12]	2012	6	1110	M	[838]	W			2012	0-1		
[c877_09]	2009	12	1080	F	[877]	W	2011	18-19			2013	41-43
[c073_10]	2010	3	1083	M	[073]	W	2011	15-16			2013	38-40
[c812_10]	2010	8	1088	M	[812]		2011	10-11			2013	33-35
[c214_11]	2011	1	1093	M	[214]	W	2011	5-6			2013	28-30
[c120_11]	2011	3	1095	F	[120]		2011	3-4			2013	26-28
[c866_11]	2011	6	1098	M	[866]	W	2011	0-1			2013	23-25
[c225_10]	2010	1	1081	F	[225]	W	2011	17-18	2012	29-30	2013	40-42
[c278_10]	2010	4	1084	M	[278]	W	2011	14-15	2012	26-27	2013	37-39
[c196_10]	2010	7	1087	F	[196]	W	2011	11-12	2012	23-24	2013	34-36
[c276_11]	2011	2	1094	F	[276]	W	2011	4-5	2012	16-17	2013	27-29
[c151_10	2010	6	1086	F	[151]				2012	24-25	2013	35-37
[c076_12]	2012	1	1105	M	[076]	W			2012	5-6	2013	16-18
[c405_12]	2012	1	1105	F	[405]	W			2012	5-6	2013	16-18
[c458_12]	2012	1	1105	M	[458]	W			2012	5-6	2013	16-18
[c834_12]	2012	1	1105	F	[834]	ETH			2012	5-6	2013	16-18
[c205_12]	2012	3	1107	M	[205]	W			2012	3-4	2013	14-16
[c828_12]	2012	3	1107	F	[828]	W			2012	3-4	2013	14-16
[c036_12]	2012	4	1108	F	[036]	W		-	2012	2-3	2013	13-15
[c174_12]	2012	4	1108	F	[174]	W			2012	2-3	2013	13-15
[c010_12]	2012	6	1110	F	[010]				2012	0-1	2013	11-13
[c853_12]	2012	6	1110	F	[853]	W			2012	0-1	2013	11-13
[c820_12]	2012	7	1111	M	[820]	W			2012	0	2013	10-12
[c051_07]	2007	4	1048	F	[051]	W					2013	73-75
[c198_09]	2009	4	1072	F	[198]	W					2013	49-51
[c434_08]	2009	5	1073	F?	[434]	W					2013	48-50
[c265_09]	2009	9	1077	M	[265]	W					2013	44-46
[c469_09]	2009	12	1080	F	[469]	W					2013	41-43
[c428_10]	2010	6	1086	M	[428]						2013	35-37
[c346_11]	2011	1	1093	?	[346]						2013	28-30
[c436_11]	2011	2	1094	?	[436]						2013	27-29
[c432_11]	2011	6	1098	?	[432]						2013	23-25
[c019_12]	2011	12	1104	M	[019]	W		-			2013	17-19
[c090_11]	2011	12	1104	M	[090]						2013	17-19
[c805_11]	2011	12	1104	M	[805]						2013	17-19
[c053_12]	2012	6	1110	F	[053]						2013	11-13
[c144_12]	2012	7	1111	?	[144]						2013	10-12
[c175_12]	2012	9	1113	F	[175]	W					2013	8-10
[c859_13]	2013	4	1120	?	[859]						2013	1-3
[c800_13]	2013	4	1120	F	[800]	ETH					2013	1-3
[c102_13]	2013	5	1121	F	[102]						2013	0-2
[c187_13]	2013	6	1122	F	[187]						2013	0-1

Table B2.1 Count of 60 min Focal Observations for Wild African Calves, Sampled from 1980-1984, by Sex and Age Category. N=130 calves.

	Age category					
Calf Sex	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	27	21	18	10	44	**120**
Female	23	20	15	14	60	**132**
Overall	50	41	33	24	104	**252**

Table B2.2 Wild African Elephant Calf IDs, Sex, and Age when Focal Sampled during Study Periods in Amboseli National Park. Ages calculated using birth estimates and Julian calculations. IDs of calves in bold and underlined were individuals who were also studied in 1980 and 1981 (and their corresponding ages at the time); all other ages relate to observations made in 1982-1984.

Calf ID	Calf sex	Age1 (mo)	Age2 (mo)	Age3 (mo)	Age4 (mo)	Age5 (mo)
AB2	F	23	29			
AE1	F	20	28			
AG2	F	21	30			
AM1	F	29	37			
AST	F	52				
BO3	F	4				
BEA	F	43				
BN3	F	8				
BO3	F	19				
DB3	F	23	11			
DE3	F	23	13			
DIZ	F	**1**				
EF2	F	22	27			
EQU	F	**4**	**7**	34	39	47
ES0	F	32				
FL3	F	5				
FM1	F	29	37			
FRA	F	**10**	**17**	45		
FY0	F	34	39	44	50	
GAR	F	37	39			
GOO	F	39	50			
GR3	F	4	12			
GWE	F	**12**	**21**	42		
IG3	F	6	18			
IO3	F	6	10			
JO9	F	42	51			
JS3	F	7	15	18		
KEL	F	**17**	45			
KK3	F	1	7	13		
LE3	F	5				
LN3	F	5	18			
LOO	F	35	45			

Calf ID	Calf sex	Age1 (mo)	Age2 (mo)	Age3 (mo)	Age4 (mo)	Age5 (mo)
LS2	F	17	29			
LT1	F	17	38			
LY0	F	37	39	49		
ME0	F	37				
MG0	F	30				
ML9	F	42	52			
MO3	F	11				
MR1	F	35	43			
OC1	F	26	34			
PA3	F	10				
PEA	F	**2**	**7**	35		
PIA	F	42	49			
PL2	F	11	20			
PO3	F	9	15			
PRU	F	50	53			
PY3	F	10	12			
QDU	F	40	52			
QE3	F	4	18			
QL1	F	23	33			
Q01	F	20	28			
QQ3	F	4	15			
SL2	F	12	21			
SR1	F	19	24	26	30	
SU3	F	5	13			
TAO	F	6	10			
TE2	F	18	21	29		
TI3	F	4	12			
TS3	F	3	10			
TSLO	F	**6**	**10**	35		
ULO	F	1				
VG3	F	5	9			
VIV	F	13	15			
VR2	F	14	23			
VV3	F	4	7	10		
WA9	F	42	50			
WE9	F	45	52			
WH2	F	8	23			
WMO	F	25	30			
WR1	F	34	42			
ZAO	F	26	50			
AL3	M	9	17			
BB3	M	4	9			
BE3	M	7	14			
BG9	M	51	60			

Calf ID	Calf sex	Age1 (mo)	Age2 (mo)	Age3 (mo)	Age4 (mo)	Age5 (mo)
BL3	M	2	16			
BSK	M	48				
CU3	M	4	14			
DOU	M	52				
DS1	M	17	26	32	37	
ECL	M	**2**	**6**	33	40	45
EO2	M	9	14	21	23	
EV9	M	41	44	50	56	
FC3	M	3				
FE3	M	9	12			
FR9	M	50	58			
GD4	M	5				
GE3	M	4	7	14		
GY3	M	8	15			
IN2	M	10	25			
IRA	M	36				
IS3	M	1	12	13	18	
JL1	M	19	28	32	37	
JY3	M	5	13			
JZ2	M	13	23	33		
KE3	M	5				
KEV	M	40				
KM3	M	6	9			
KN2	M	2	7	28		
KR3	M	10	14			
LEW	M	**14**	22	45	53	60
LR1	M	**3**	28	38		
LU3	M	8	17	19		
MN2	M	23				
PC9	M	42	48	59		
PHO	M	40				
PH3	M	8				
PN3	M	8	16			
PP4	M	2				
PR3	M	3	12			
RAO	M	**15**	23	46		
RB0	M	3	10			
RB3	M	5	12			
RE3	M	4	16			
REX	M	53				
RN1	M	24	26	36	39	
SET	M	**16**	**20**	47		
SN1	M	23	26	32	38	
TIO	M	**1**	**10**	39		

Calf ID	Calf sex	Age1 (mo)	Age2 (mo)	Age3 (mo)	Age4 (mo)	Age5 (mo)
TR2	M	11	15			
TUO	M	6	10			
VD3	M	3	8			
VE1	M	17	21	32	37	
VO3	M	4	13			
VOD	M	45				
ZEO	M	27				
ZL2	M	4	7	18		
ZN2	M	20	29	34		
ZOO	M	38	46	53		

Table B3.1 Count of 10 min Focal Observations for Captive Asian Calves, by Sex and Age Category. From the six core calves (Raman, Nayan, Jamilah, Hari, Bala and Scott).

	Age category					
Calf Sex	1-6 mo	7-12 mo	13-18 mo	19-24 mo	3-5 yrs	Total
Male	1891	924	564	165	0	**3544**
Female	873	423	318	135	24	**1889**
Overall	2764	1347	882	300	24	**5433**

Table B3.2 Count of 5 min Observation Scans for Individual Captive Asian Calves by Age Category. Scans at 5 min intervals from 10 min calf focal observations.

	Age category					
Calf ID	1-6 mo	7-12 mo	13-18 mo	19-24 mo	3-5 yrs	Total
Raman ♂	318	56	0	0	0	**374**
Nayan ♂	826	396	266	147	0	**1635**
Jamilah ♀	502	241	156	147	0	**1046**
Hari ♂	296	141	135	0	0	**572**
Bala ♀	289	144	132	0	0	**565**
Scott ♂	334	162	131	0	0	**637**
Gheta ♀	0	0	0	0	0	**0**
Ned ♂	0	0	0	0	0	**0**
Total	2575	1140	820	294	0	**4829**

Table B3.3 Count of 25 min Observations from Group Scans for Individual Captive Asian Calves by Age Category.

	Age category					
Calf ID	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Raman ♂	0	0	0	0	0	**0**
Nayan ♂	502	516	277	201	559	**2055**
Jamilah ♀	608	270	195	263	284	**1620**
Hari ♂	454	133	128	0	0	**715**
Bala ♀	314	133	130	0	0	**577**
Scott ♂	252	102	97	0	0	**451**
Gheta ♀	0	0	0	0	414	**414**
Ned ♂	0	0	61	164	171	**396**
Total	2130	1154	888	628	1428	**6228**

Table B4.1 Count of 10min Focal Observations for Captive African Calves, by Sex and Age Category. From the five core calves (Tammi's, Mansi, Mchumba, Jaluka and Impi).

	Age category					
Calf Sex	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Male	582	246	303	216	0	**1697**
Female	504	428	396	296	73	**1347**
Overall	1086	674	699	512	73	**3044**

Table B4.2 Count of 5 min Observation Scans for Individual Captive African Calves by Age Category. Scans at 5 min intervals from 10 min calf focal observations.

	Age category					
Calf ID	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Mchumba ♂	373	161	148	134	0	**816**
Mansi ♀	0	307	219	150	71	**747**
Jaluka ♀	380	73	141	136	0	**730**
Tammi's ♀	77	0	0	0	0	**77**
Impi ♂	162	74	126	67	0	**429**
Total	992	615	634	487	71	**2799**

Table B4.3 Count of 25 min Observation from Group Scans for Individual Captive African Calves by Age Category. Note the addition of Etana and Uzuri to the 3-5 yr age category in 25 min group scans.

	Age category					
Calf ID	**1-6 mo**	**7-12 mo**	**13-18 mo**	**19-24 mo**	**3-5 yrs**	**Total**
Mchumba ♂	311	249	115	90	0	**765**
Mansi ♀	0	258	211	182	76	**727**
Jaluka ♀	306	112	140	45	0	**603**
Tammi's ♀	51	0	0	0	0	**51**
Impi ♂	250	117	98	0	0	**465**
Etana ♀	0	0	0	0	756	**756**
Uzuri ♀	0	0	0	0	525	**525**
Total	918	736	564	317	1357	**3892**

APPENDIX C: Ethogram

Table C1 Ethogram of Elephant Behaviours. Developed in Nov 2006 by C.E. Webber & R. Fraser. This was combined, in Oct 2010, with P.C. Lee's 1983 ethogram, and was last revised in Oct 2011. The Ethogram was further condensed for video coding in Dec 2012.

Category	Key code	Modifier	Definition
MOVING (1)			(inc. "passing or approaching a specific individual, leaving, brisk walk" [Shermin 2009?])
	F	Forward	Moving head first from one location to another (at walk or trot).
	B	Backwards	Moving rear first from one location to another. Note if backing into anything i.e. others or objects.
	R	Running	Moving at a quickened pace from one location to another.
	S	Climbing	One or more leg raised on object bigger than elephant's own foot. Also includes climbing through fences and on logs, rocks or up a steep bank.
	C	Swimming / submerged	In water: may just be walking through the water (water level above knees), or feet off ground. Not playing. If other elephants are present, no physical interaction.
FEEDING (2)	b	Eating browse	The consumption of browse/woody/leafy vegetation
	H	Eating hay	The consumption of hay (note: provided by the keepers in captivity).
	f	Eating fruit/veg	The consumption of fruit/veg
	G	Eating grass	The consumption of grass.
	W	Feeding whilst walking	Feed walking; one-three steps/mouthful. [Note when also caching food (on head, in trunk, on tusks)].
	g	Foraging	The use of the trunk to displace ground matter for food or when picking up/ sweeping food from ground. Also includes the use of the trunk to investigate wall/rocky areas where food enrichment is often hidden. Sifting through grass, ground etc, shaking off foods, picking off, etc.
	m	Manipulating food / dig	Using trunk or feet to manipulate specified food source before placing it in their mouth, e.g. stripping bark, shaking off sand, washing.

	D	Drinking water	Using the trunk to take water to the mouth for swallowing. Can include "Drinking straw": Using the trunk to take water to the mouth for swallowing; or "Trunk-tip dipped": tip of trunk dipped in water/pool/puddle, then placed in mouth - usually calf (with no signs of "straw" action in this case, just wet tip with possible drips into mouth.)
SELF-MAINTENANCE/ COMFORT (3)	E	Defecating / urinating	The excretion of faeces or urine by an individual
	s	Shower sand / dusting	Comfort environment/Showering: The use of trunk to cover body with sand or dust by spraying or throwing.
	i	Shower water/ mud	Comfort environment/Showering: The use of trunk to cover body with water or mud spraying or throwing.
	;	Shower hay / grass	Comfort environment/Showering: The use of trunk to cover body with hay or grass by throwing.
	k	Shower other / snow	Comfort environment/Showering: The use of trunk to cover body with snow or other material by spraying or throwing.
	r	Rubbing self	Using legs to rub other legs or using inanimate objects to rub the body surface, backside or belly.
	wal	wallowing	Lying or rolling in mud.
SOCIAL INTERACTIONS (4)	T	Touching another elephant's body	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 involve nudging with trunk or head.
	j	Touch genitals	The use of trunk to touch another elephant's genitals
	K	Touch face	The use of trunk to touch another elephant's face
	X	Trunk to mouth	Placing trunk tip in another elephant's mouth
	t	Linking trunks	The inter-twining of trunks (whereas "Trunk wrestle" is in play, with more vigour).
	J	Trunk reach / smelling	Extend trunk (trunk reach) towards an object or another elephant to smell it. Trunk usually in "S" or "J" position.
	Z	Backs into /rubs against ele	Not play. Inc. pushes out the way (non-aggressive) & investigates
	M	Mounting	Raising front two legs onto the back of another elephant. (In calves this is usually PLAY mount instead).
	A	Alert – pause & scan, often with ears out & trunk sniffing	Head up, ears raised or out, trunk may be curled or raised, foot may be lifted off the ground. Can be listening.
	u	Charging (in calves playing this is chase)	Moving at a quickened pace with head lowered towards another elephant or object/bird etc. (For calves playing, this would be chase).

		v	Shoving	The use of front or back legs in strong/forceful motion towards another elephant.
		w	Kicking	The use of front or back legs in strong/forceful motion towards another elephant.
		x	Biting	The use of mouth to clamp down on a part of another elephant (e.g. tail, ear) or gate etc.
		y	Slap/hitting	Raising of the trunk to move downwards towards another elephant with velocity or hitting sideways towards another elephant with velocity (may or may not make contact)
		z	Assertive trunk contact (was "Dominance display")	Dominance display: “dominance or threat displays (trunk over another individual, tossing soil or vegetation over the back during a disturbance…” (de Silva, 2010).
PLAY (5)	Lone (L)	P	Lone play (P lone)	Solitary play, obviously not addressed at a conspecific, with no other elephant engaged in same or parallel activity.
		U	Trunk behaviour (P lone)	Use of the trunk that is not interaction with other elephants or objects around the individual. E.g. calf learning to control its trunk. May involve using calf’s own front foot and can be whilst walking.
		h	Rolling (P lone)	Elephant rolling their body in sand/hay/mud. Crawling/face-plant/rubbing backside on ground. (Can inc. climbing or rolling under another elephant, if not gentle-contact-play).
		p	Digging (P lone)	The Use of feet or trunk to dig in ground matter.
		Q	Spinning (P lone)	Spinning around, often with no apparent ‘direction’ in burst of running. Can involve use of foot, face-planting or kicking.
		q	Splashing (P lone) (inc. lone play swim)	Using trunk or feet to intentionally splash in puddle/watery mud/pool shallows (not using body or showering self but splashing looks intentional i.e. not just running towards something).
	Gentle-contact (G)	!	Push/rub against/lean on (P gentle)	Rub against another elephant (initiating contact). Push against: if another elephant push plays, calf backs into or rubs against other. Gentle contact play with another ele: (Interacting in a non-aggressive manner. Does not include tail swatting, linking or simple brushing of body surfaces.)
		“	Backs into/ shove gentle (P gentle)	(usually calf into an adult), with no or little response from other elephant. Can be initiating play but with no response [in between Fi & Pe] e.g. pushing or playing beneath with body contact, but with no response from another elephant.

		-	Gentle play in pool (P gentle)	Gentle playful interaction in a non-aggressive manner with other elephants in water. May involve trunk interactions. (Not when simply walking across/through water body)
		&	Trunk wrestle/twining (P gentle)	Gentle wrestling of the trunk or twining trunks, often with open mouths
		$	Rolling with elephant (P gentle)	Elephant rolling their body in sand/hay/mud. Crawling / face plant / rubbing backside on ground.
	Escalated-contact (E)	%	Climbing on/with ele / kneel on (P gentle)	Climbing on/with/kneel on another elephant.
			Escalated contact play with another elephant	Interacting in a non aggressive manner. Does not include tail swatting, linking or simple brushing of body surfaces.
		a	Spar (P escalated)	Spar vigorously.
		Y	Chase (P escalated)	One elephant follows, while another retreats
		*	Wrestle (P escalated)	Whole body engagement between partners, with vigour
		(	Play mount (P escalated)	Mounting while in play
		)	Push / shoving in play (P escalated)	Push or shove another elephant (using head or body)
		e	Bite or “mouth” in play (P escalated)	Biting another elephants
		d	Escalated play in pool/water (P escalated)	Rough play with other elephants in water. May involve trunk interactions, climbing, wrestling and other such activity (was Wpe).
	Object (O)	o	Playing with objects/ ball / browse (P object) (inc. fiddle with stick)	Using inanimate objects in a calm non-aggressive manner with foot or trunk, individually or with another elephants. May involve shoving or kicking object gently e.g. playing with browse may include, running into it, head-butting, kicking, pulling, wrestling it.
ENVIRONMENTAL EXPLORATION (6)		^	Environmental exploration (non-play)	Investigating. (inc. suckling rope/ poi or suckling keeper door / chase birds)
		I	Investigating ground / mud / water	May be for food, but with seemingly empty trunk. Includes calf learning to use trunk to drink - tip of trunk dipped in water/pool/puddle, then placed in calf’s mouth. No signs of “straw” action, just wet tip with possible drips into mouth
		{	Investigating object / grasses	Investigating inanimate object with trunk. May include gates/chains/posts etc. Touch, test with trunk, place in mouth but no chewing etc.
		+	Investigating faeces	Touching with trunk, or even rolling/ nudging with foot
		’	Eating faeces	Ingesting faeces

	/	Flehem	“Testing” urine using Jacobsen’s organ.
RESTING (7)	}	Standing/rest active	Standing in one particular place with little movement or interest in any other activity but with slight body movements, ear flaps, trunk swinging etc. (Upright & stationary, not in motion in any direction nor manipulating anything in the environment).
	[	Standing asleep	As "rest active" but with eye(s) visibly closed for prolonged period of time.
	#	Standing over calf	As ‘rest active’ but with some part of calf’s body/head/legs underneath while calf rests/sleeps.
	~	Leaning/ trunk, head or foot resting	Leaning: Using an inanimate object to support a portion of the individuals weight with little interest in any other activity. Trunk/head resting: When the trunk/head is placed over an object with no other actions present in an inactive state. Foot resting: Placing an individual foot onto an object with no visible purpose (different to investigating object).
	]	Rest lying / lying asleep	Lying: Lying on one side of the body and unless crouched, no weight on any of the limbs, with little movement (note position e.g. if on tummy, L /R side or crouching with stomach on ground). Lying asleep: As ‘lying’ but with eye(s) visibly closed for prolonged period of time.
OUT OF SIGHT (8)	8	out of sight	Behaviours taking place when the individual cannot be seen.
ABNORMAL (9)	9	Stereotypy	Repetitive unvarying behaviours, characteristic to a particular individual (rare to occur in new calf) which have no clear goal or function (Mason, 1991; Odberg, 1978).
	ssf	Throwing faeces (Abnormal behaviour)	Using the trunk to pick up and throw faeces up and over their own body (see ‘Dusting’, above).
OTHER (0)	O	Other (specify), e.g. "convulsions"	e.g. Kicking sand: Anxious (not the same as digging) – swinging legs, straightened, back & forth. e.g. Aggression: (both without and with body contact).
	<	Defensive huddling	A defensive strategy of drawing together to form a densely packed group/aggregation, often out of fear or to provide protection.
	>	Calf distress / major Tantrum	Calf runs from nipple to nipple, tries to block mother (hook trunk around leg or calf places body in front of mother) and gives distress bellows, roars and trumpets.
	KI	Keeper interaction	Interacting with zoo keeper, e.g. in training or healthcare sessions, following vocal commands from keeper, investigating keeper, accepting treat/medication/food from keeper.

	own nipple	Trunk to own nipple	Using their trunk to touch or pull at their own nipple.
	NSB	Drinking from bottle	(i.e. Mansi; Tammi's calf). Drinking milk from bottle provided by keepers
	Trunked-up	Trunk-to-tail	Walking as a group - Command from keepers. Can include walking/locomotion
	Suck own trunk	Suck own trunk	Non-playful sucking of own trunk tip, i.e. relaxed trunk.
SUCKLING INTERACTIONS (11)	@	Suckled from another elephant	As ‘rest active’ whilst being suckled, but may also be eating.
	L	Suckling left nipple	The use of the mouth to gain fluids from a suitable elephant’s teats. Left or Right nipple noted & timed for each nipple; if there was more than 60 seconds of pause, this was considered a new bout.
	N	Suckling right nipple	As above, with right nipple.
	c	Calf breaks nipple contact	Calf initiates its own break in contact with the nipple
	L/N	Suckling (when no record of L or R nipple)	
	V	Ma breaks nipple contact	Mother initiates a break in contact between herself and the suckling calf. E.g. by walking forwards or pushing the calf off her nipple by moving her foreleg back to block access to her nipple
	n	Touch nipple	Using the tip of the trunk to touch the nipple of another elephant (usually mother or alllomother in the case of calves).

Table C2 Group Behaviour Activity. Recorded at the beginning of each calf focal observation in the wild.

	Group Activity	Code
1	Feed whilst walking	FW
2	Feed standing	FS
3	Rest standing (inc. lying/leaning)	RS
4	Comfort / dust, mud etc.	CE
5	Interact	I
6	Drink	D
7	Walking	W
8	Alert to environment / predators, others	A
9	Mixed (if all adults doing something different)	MIX

APPENDIX D: Estimated Means of Percentage Time Figures from GLMM Tests used on Calf and Mother, Activities and Proximities

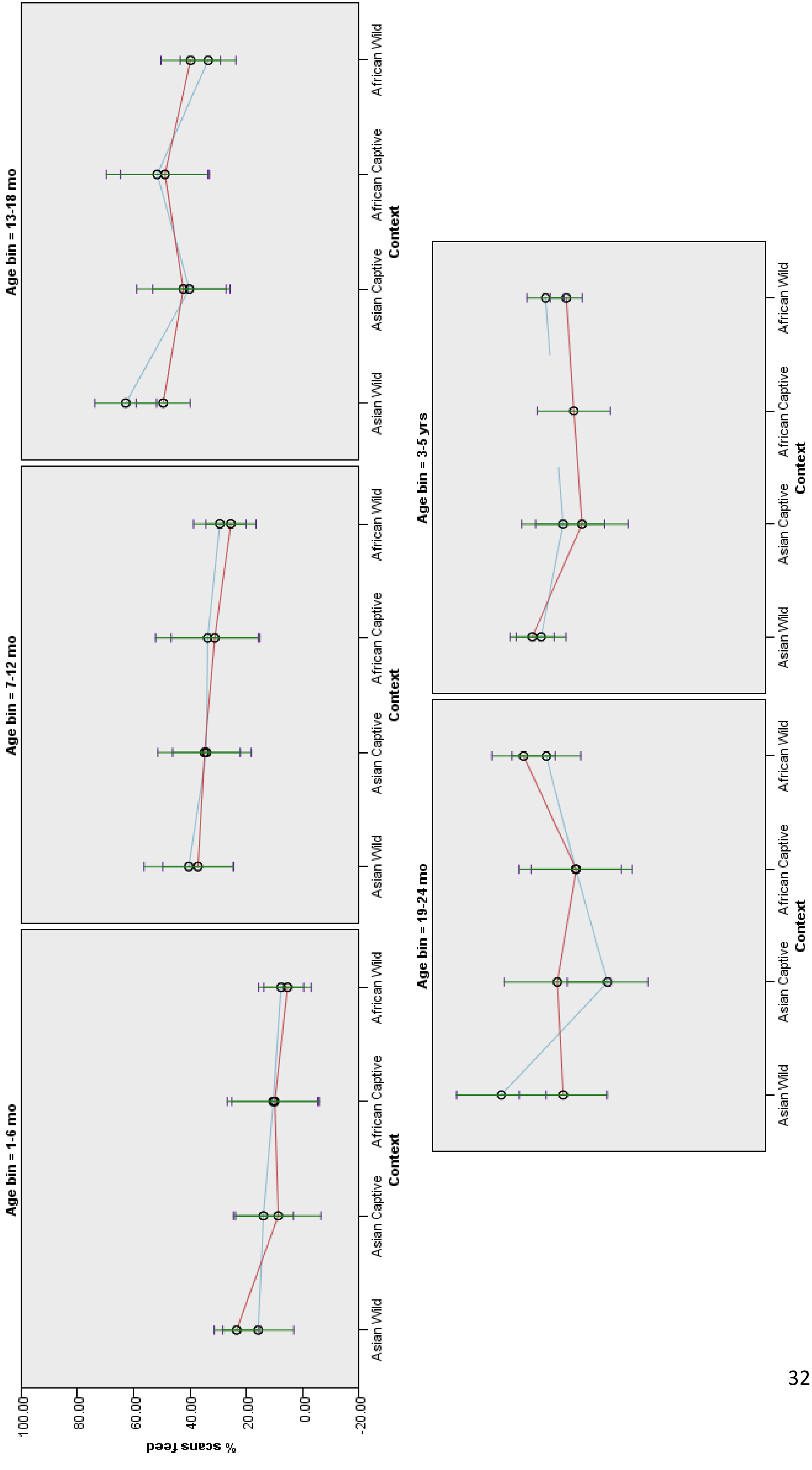


Figure D1.1 Estimated Means of Percentage Time Calves Independent Feeding. Calf sex by calf age category within context

Figure D1.2 Estimated Means of Percentage Time Calves Resting. Calf sex by calf age category within context

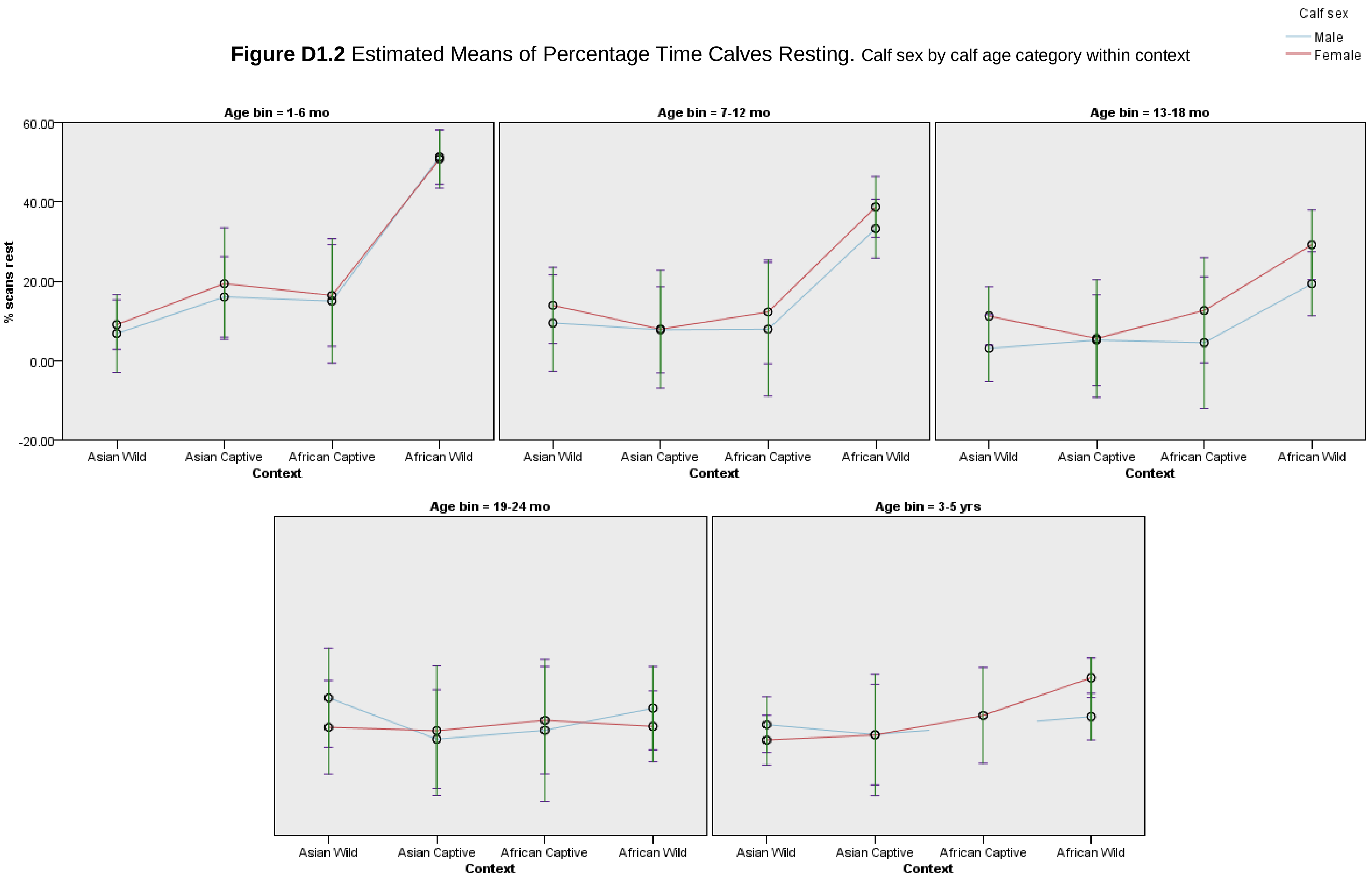


Figure D1.3 Estimated Means of Percentage Time Calves Moving. Calf sex by calf age category within context

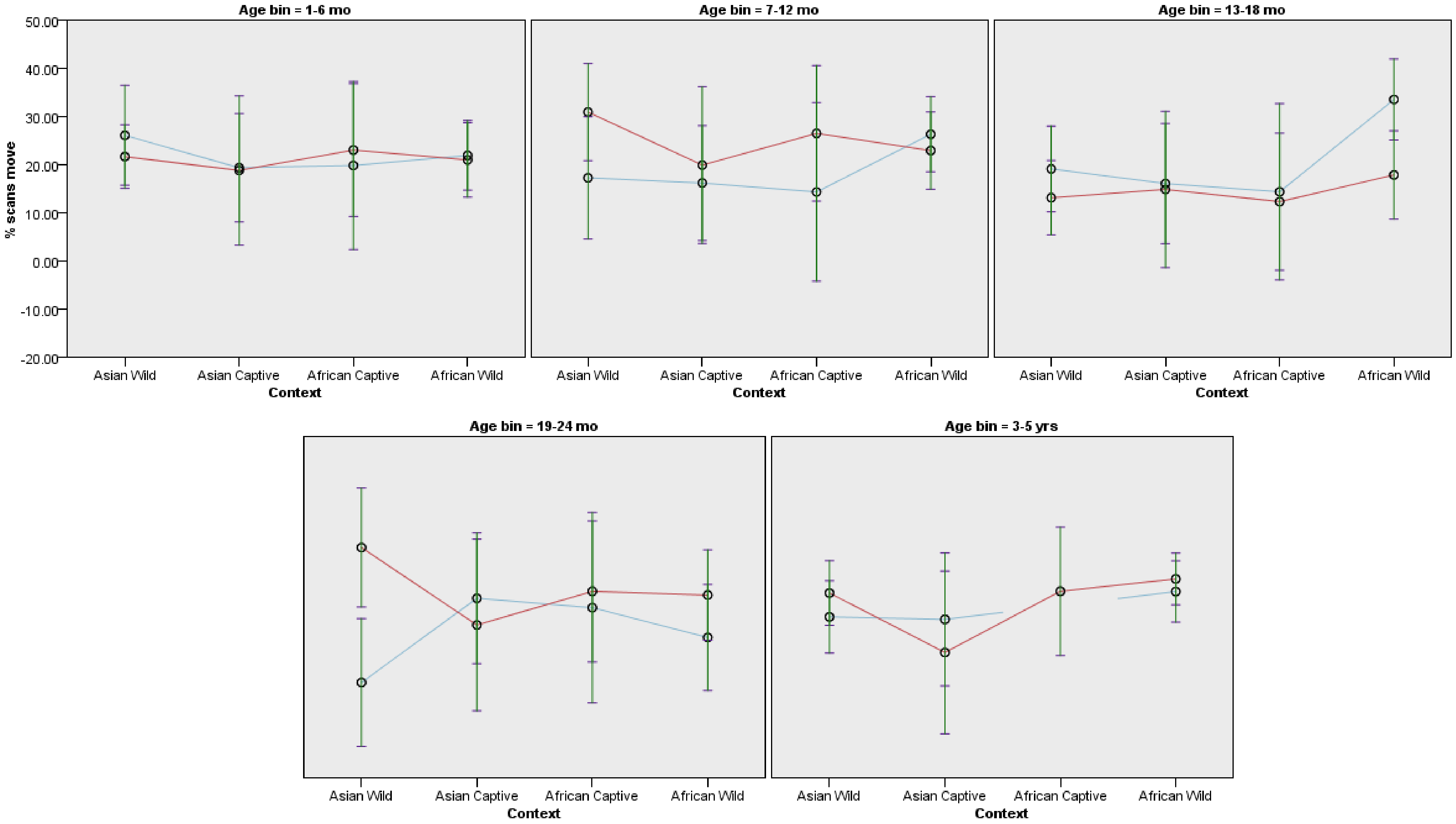


Figure D2.1 Estimated Means of Percentage Time Mothers Feeding. Calf sex by calf age category within context

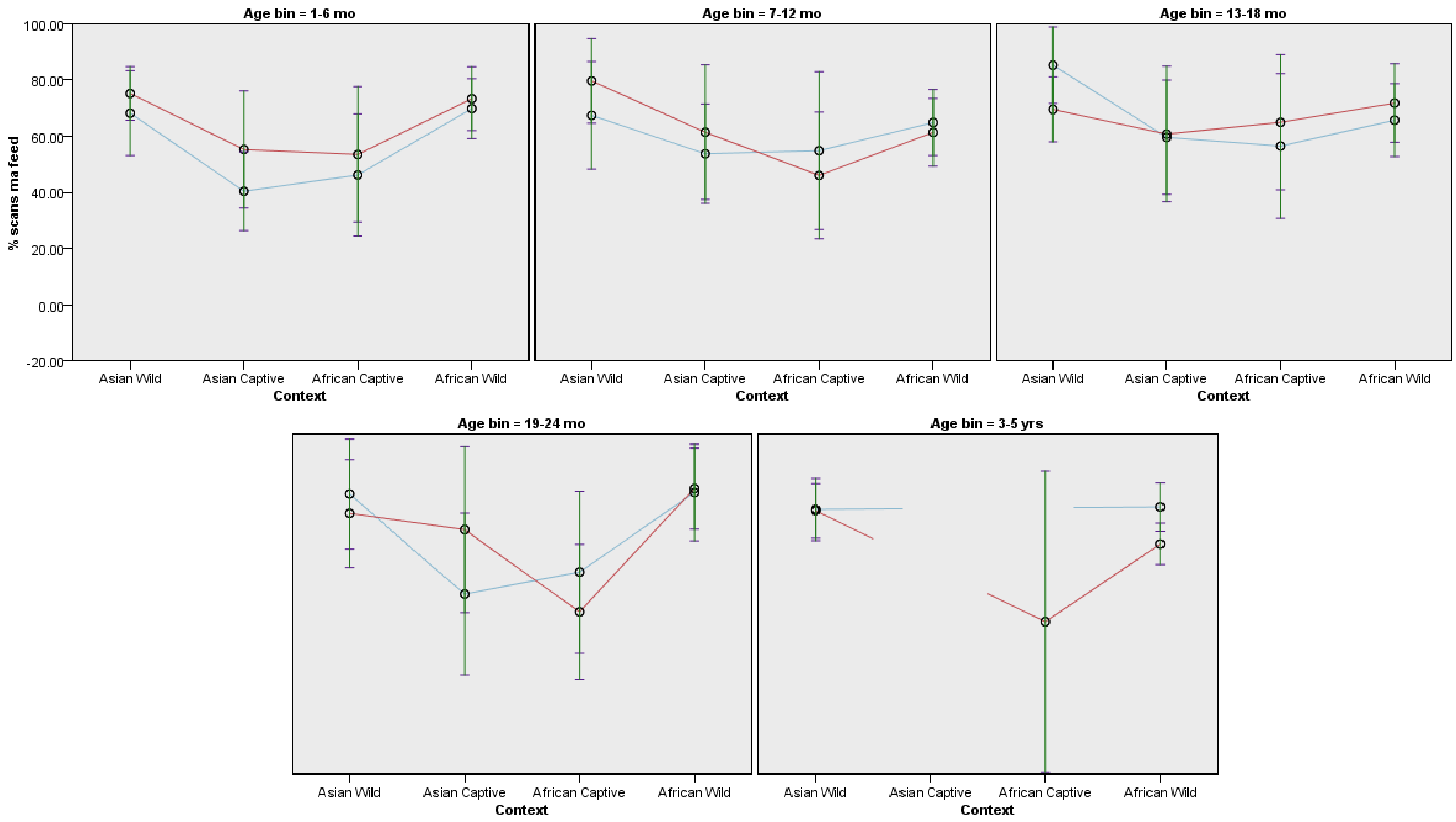


Figure D2.2 Estimated Means of Percentage Time Mothers Resting. Calf sex by calf age category within context

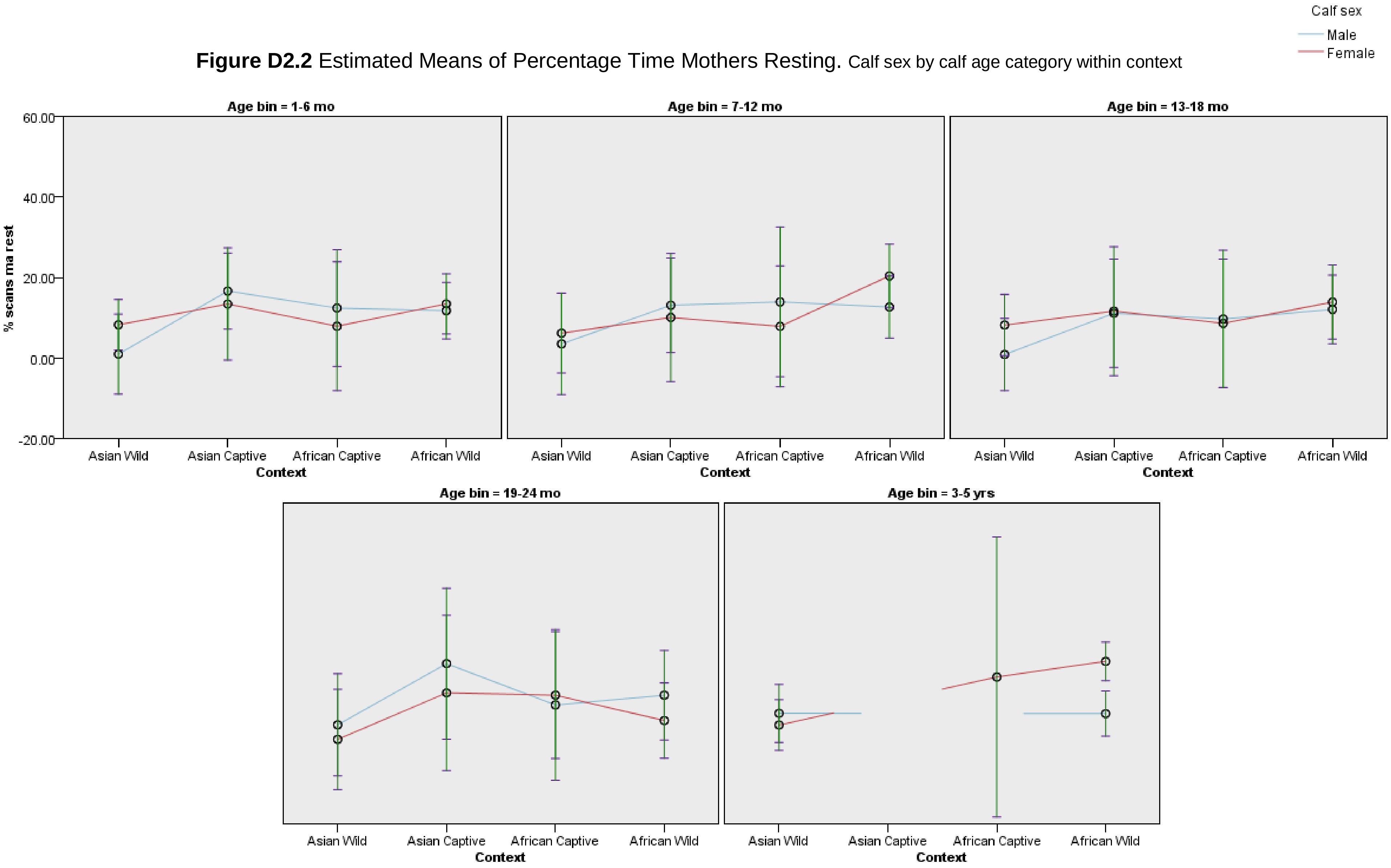


Figure D2.3 Estimated Means of Percentage Time Mothers Moving. Calf sex by calf age category within context

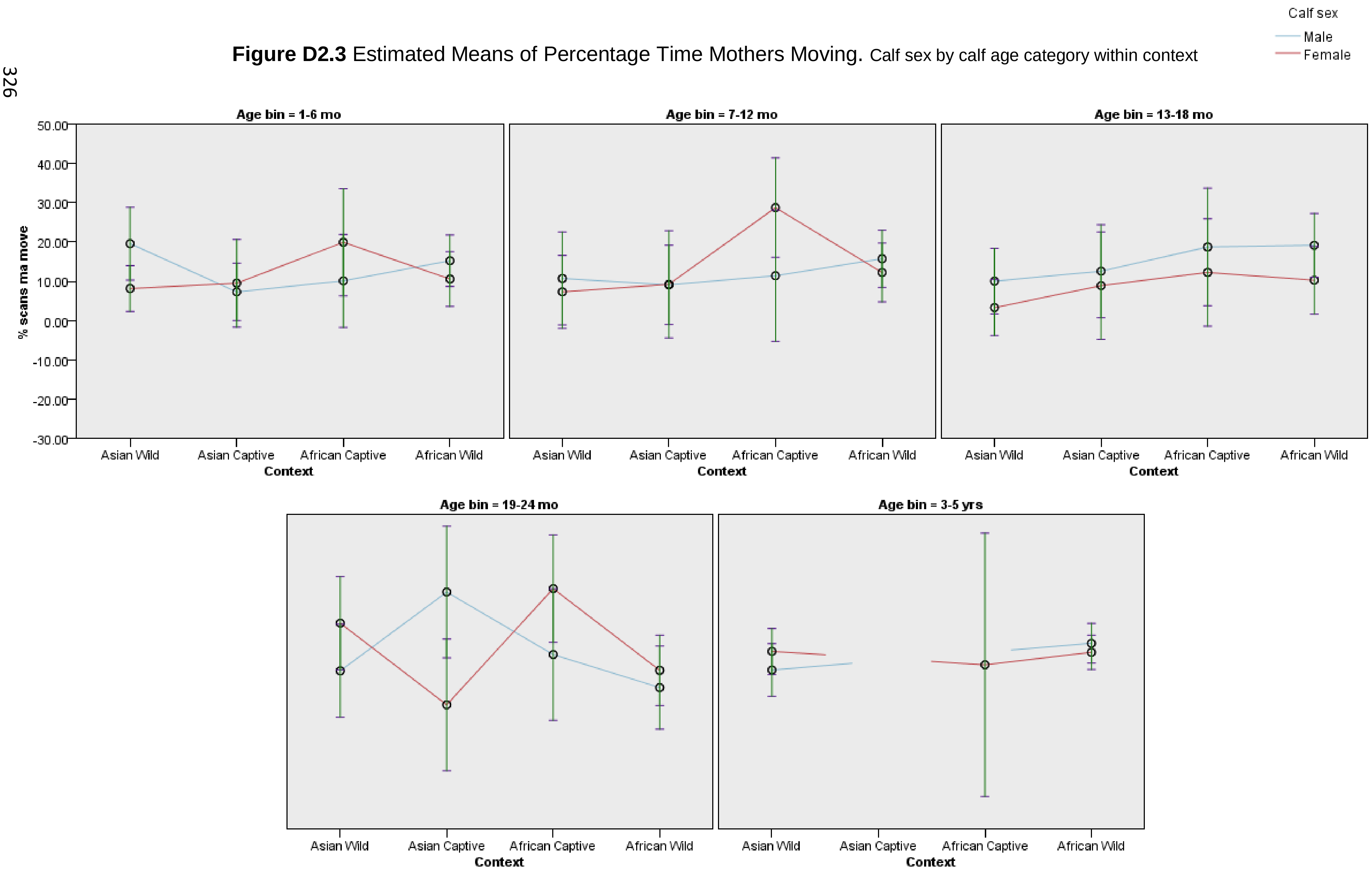


Figure D3.1 Estimated Means of Percentage Time Calves in Close Proximity to Mothers (<2M). Calf sex by calf age category within context

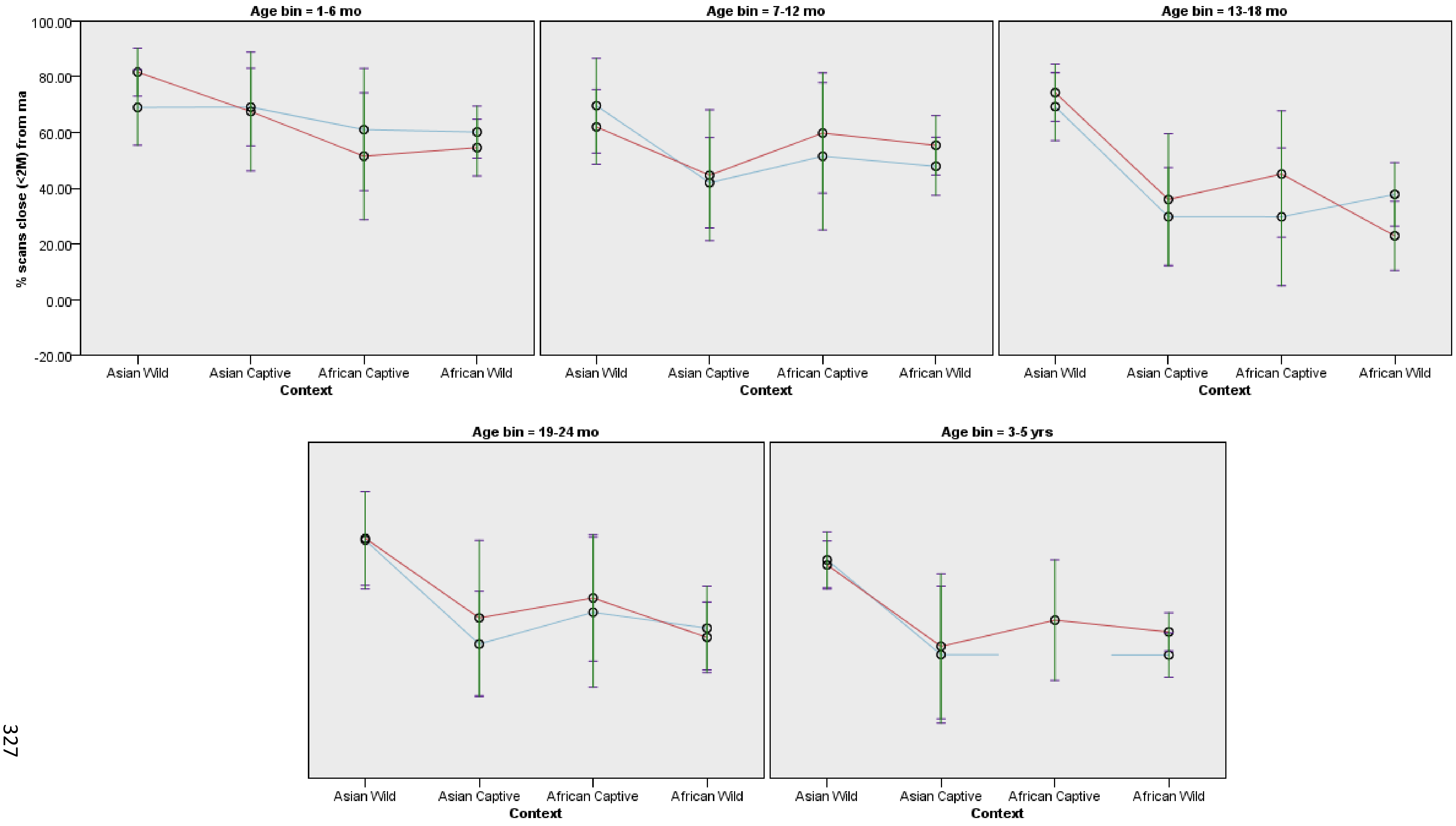


Figure D3.2 Estimated Means of Percentage Time Calves in Mid Proximity to Mothers (2-5M). Calf sex by calf age category within context

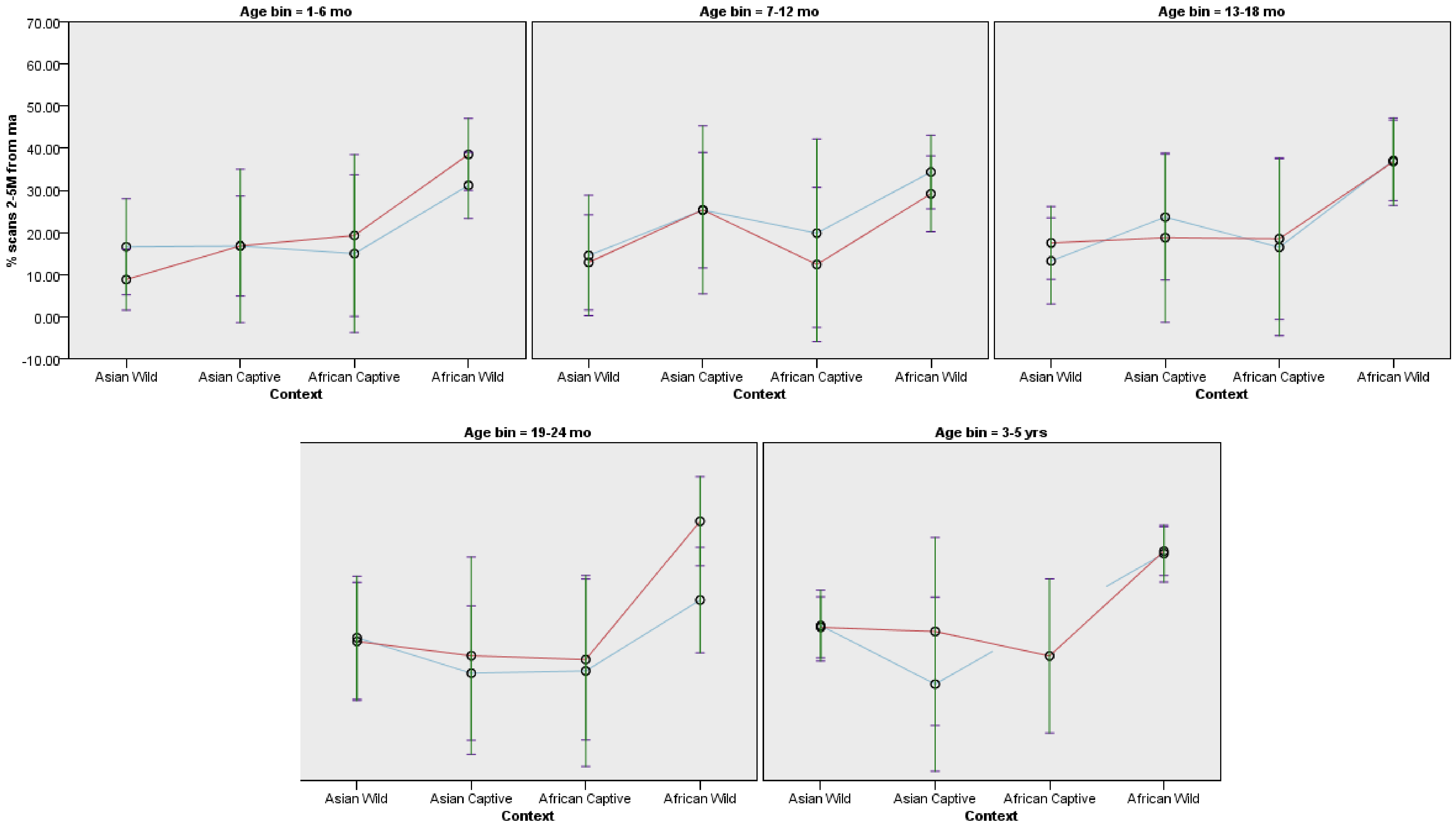


Figure D3.3 Estimated Means of Percentage Time Calves Far Proximity from Mothers (>5M). Calf sex by calf age category within context

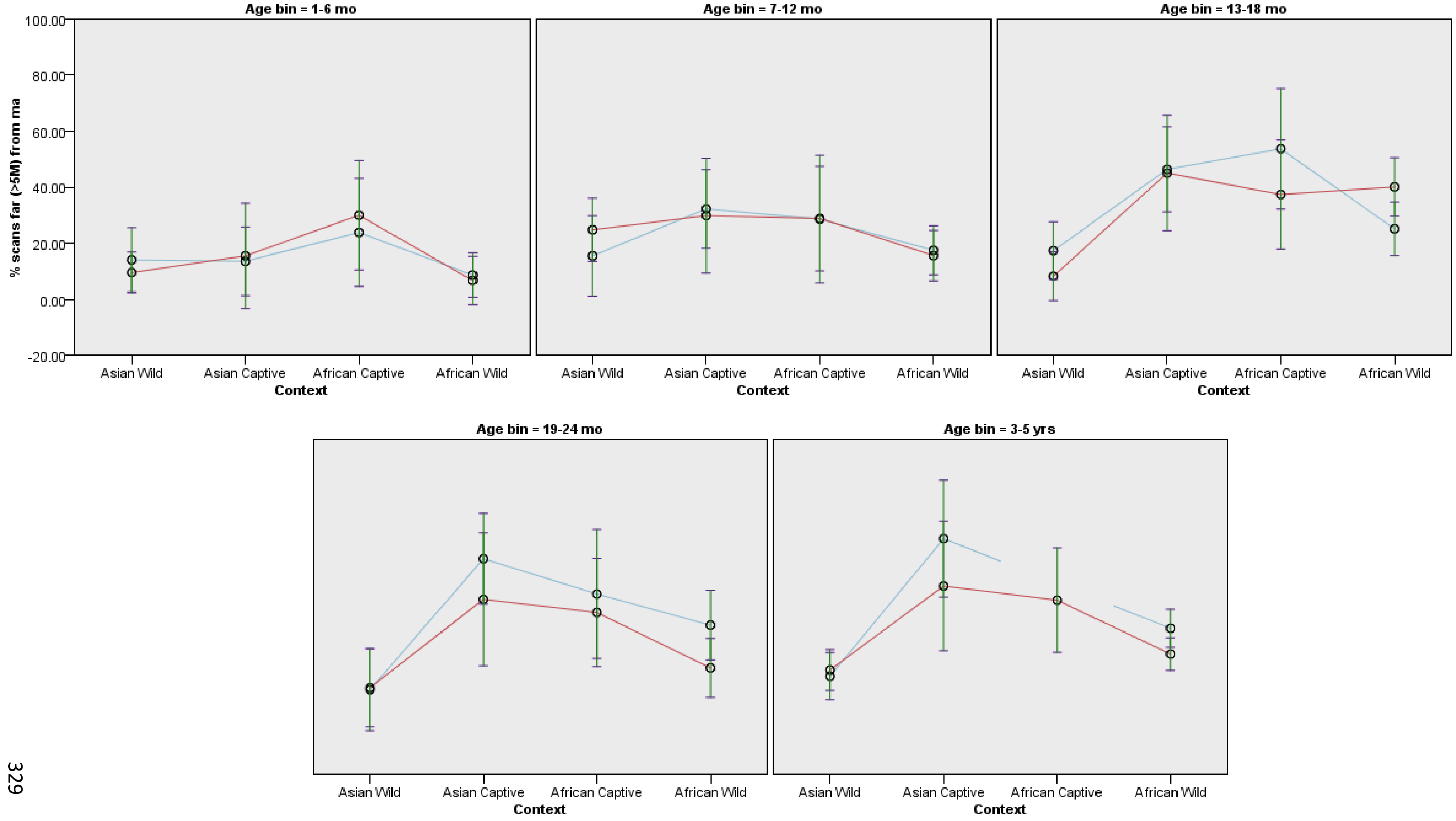
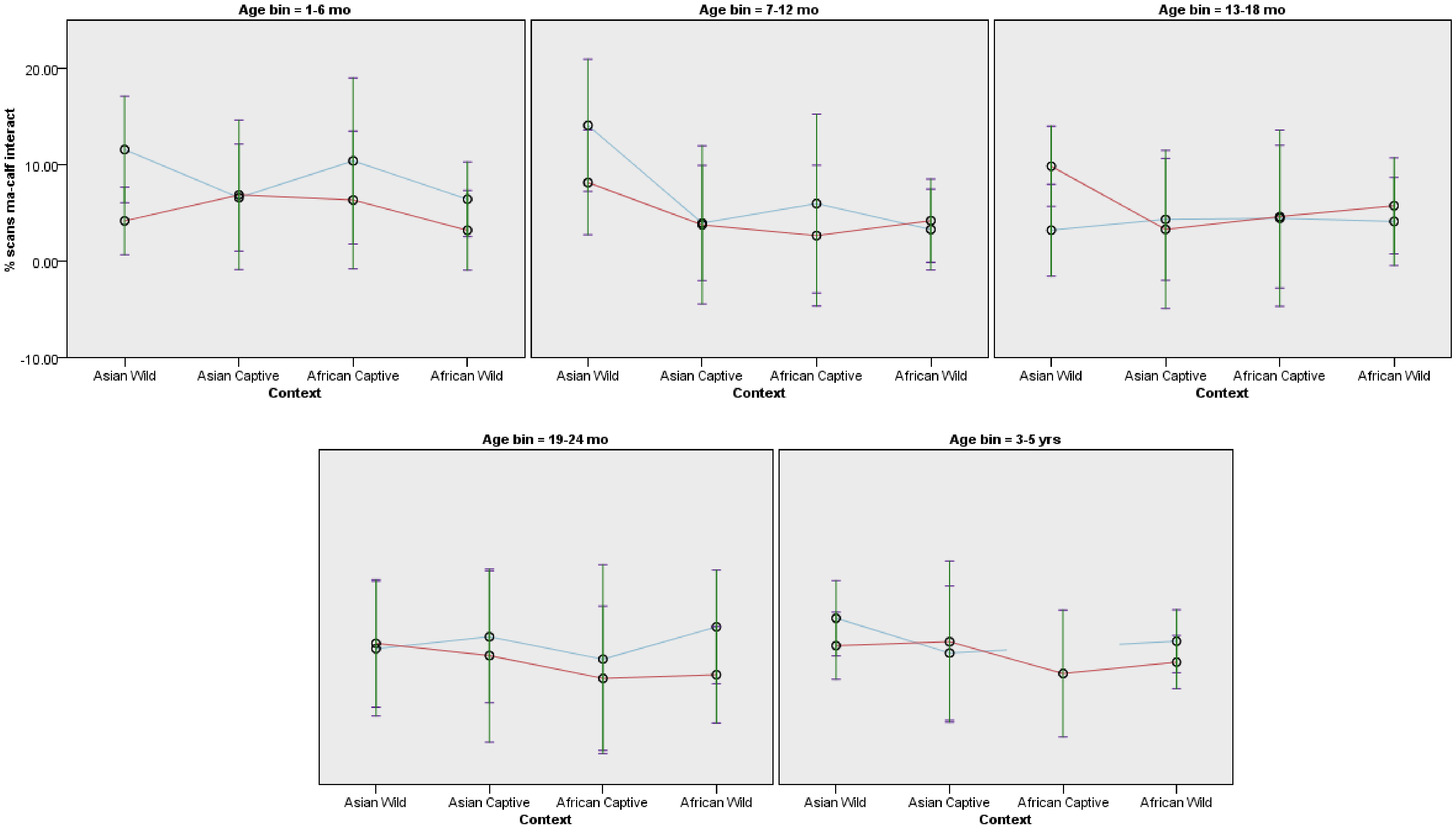


Figure D4.1 Estimated Means of Percentage Time Calves in Suckling Interactions. Calf sex by calf age category within context



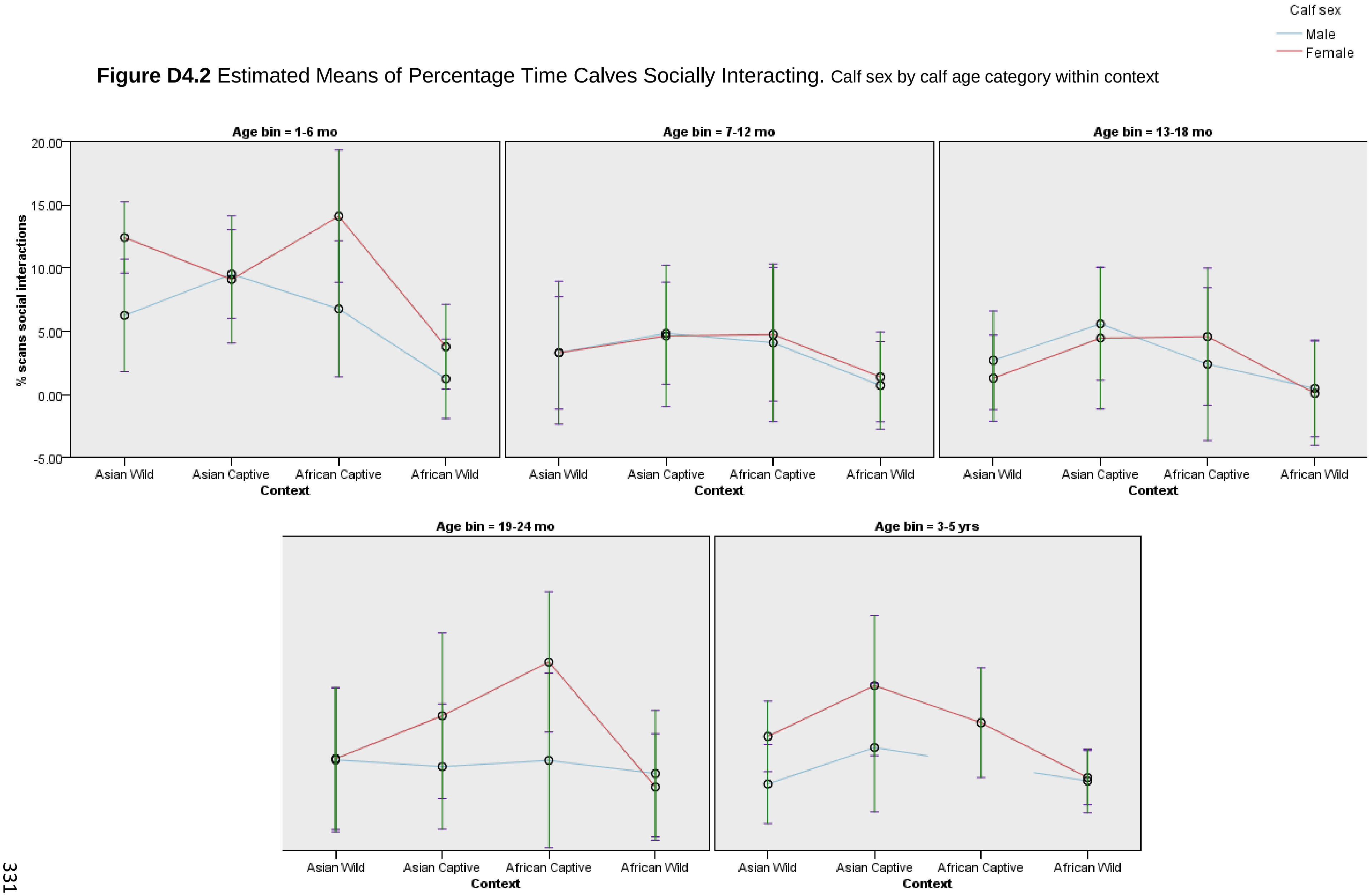


Figure D4.2 Estimated Means of Percentage Time Calves Socially Interacting. Calf sex by calf age category within context

Figure D5.1 Estimated Means of Percentage Time Calves in LEGO-Play. Calf sex by calf age category within context

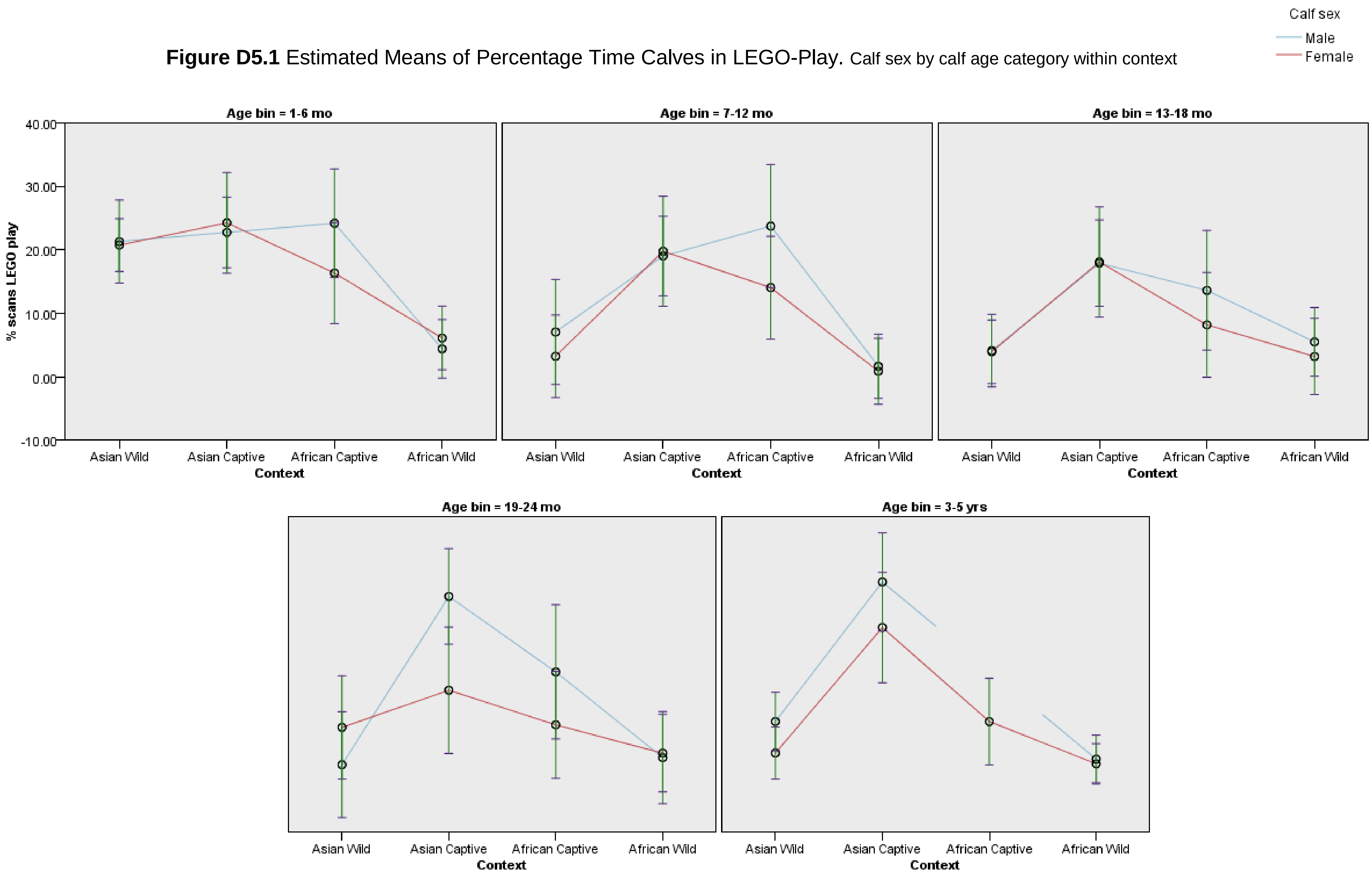


Figure D5.2 Estimated Means of Percentage Time Calves in Social Play. Calf sex by calf age category within context

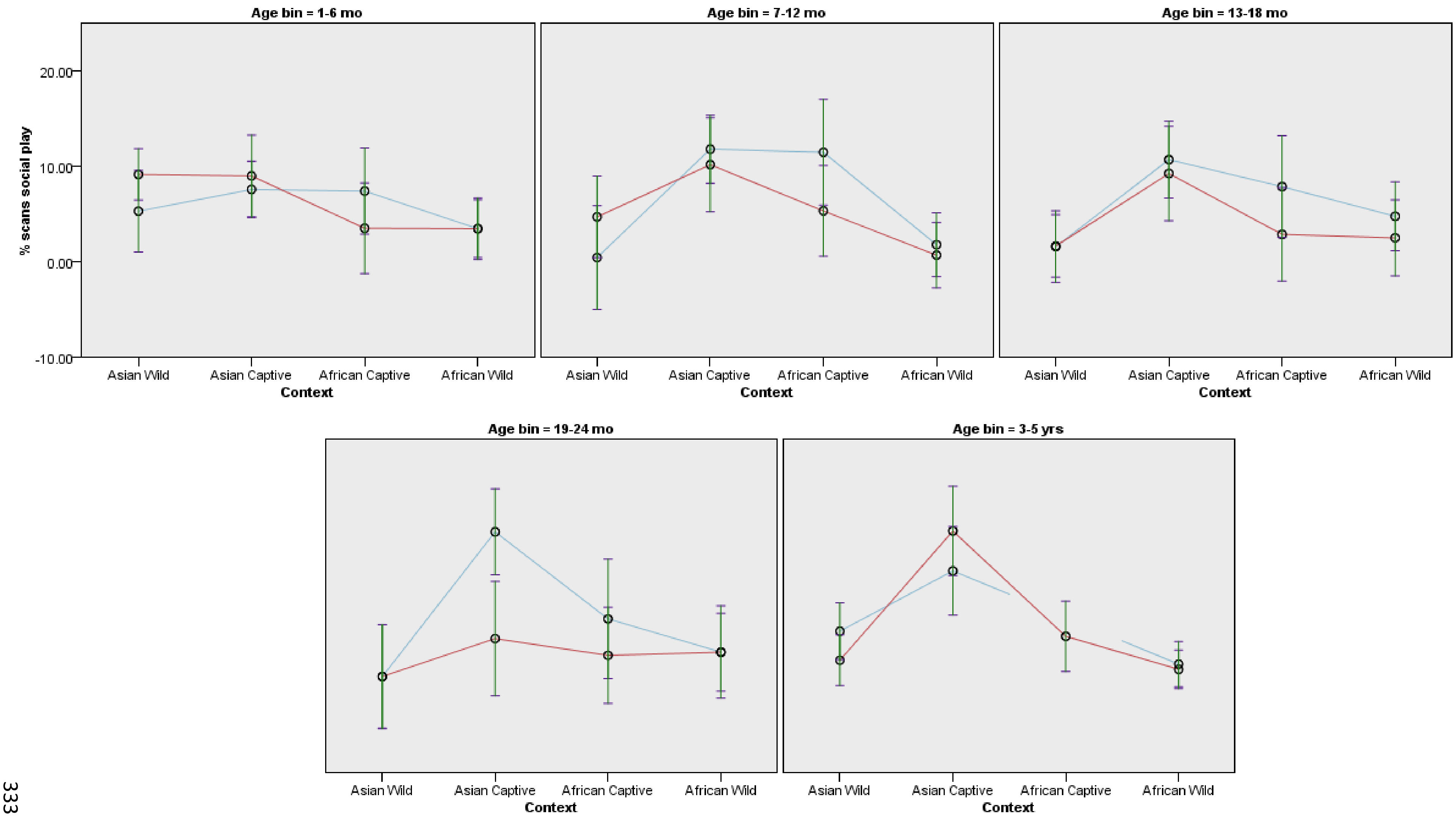
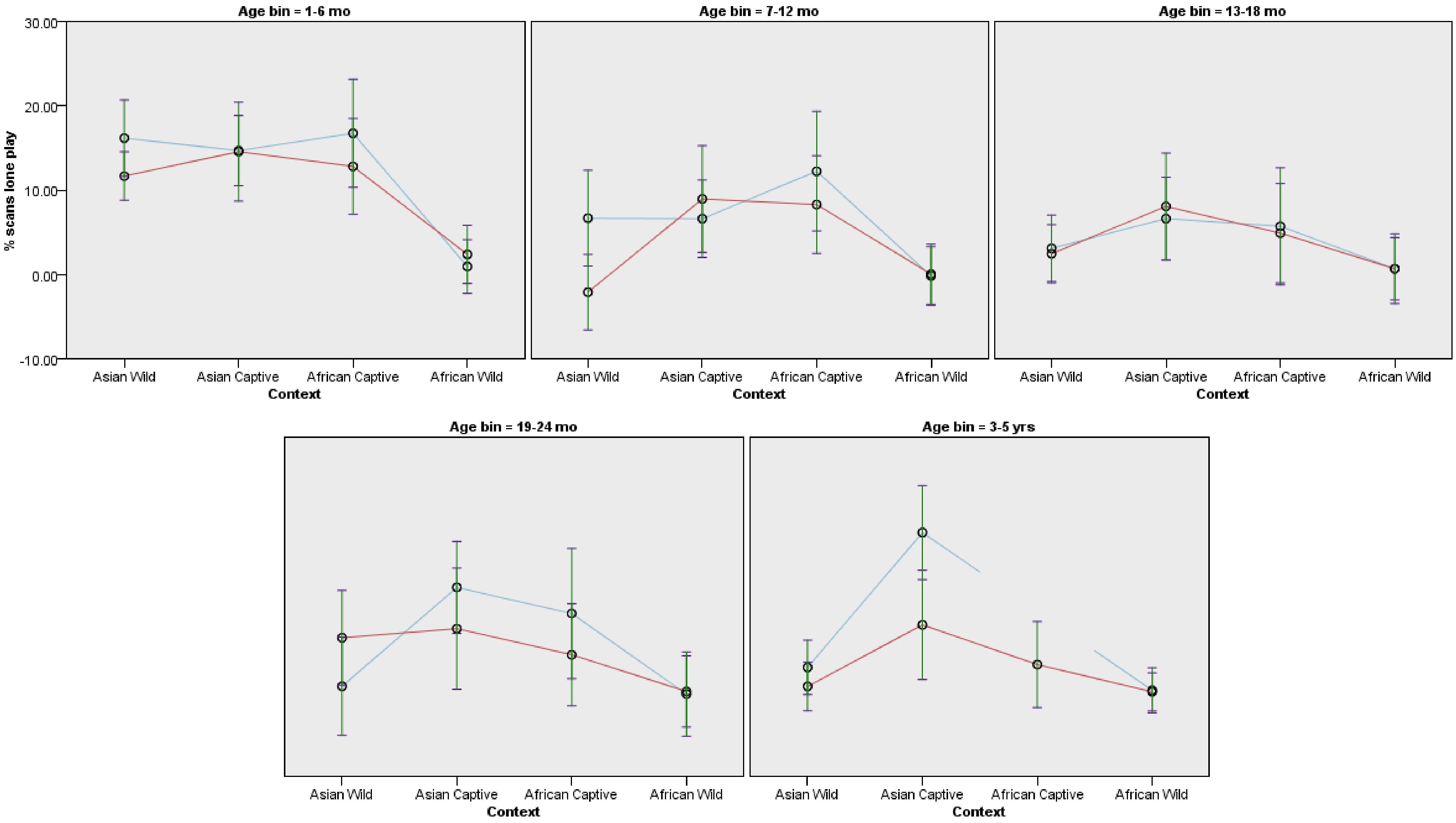


Figure D5.3 Estimated Means of Percentage Time Calves in Non-Social Play. Calf sex by calf age category within context



Appendix E: Illustration of the Effects of Starvation on Play and Development Using [cBitsy_09]

[cBitsy_09] represents one of the four wild male Asian calves in the 19-21 months age category (58.7%; (10 of 17) focals). No play was seen in any of [cBitsy_09]'s scan nor focal data and we suggest that this was due to [cBitsy_09] being an extremely undernourished, lethargic calf who was perhaps suffering from related health issues. It is believed that he therefore did not have resources to spare to play (didn't feel playful!!). His mother was also extremely undernourished (possible due to old age) and although she never rejected his sucklings, he was only ever seen suckling for a few seconds at a time, giving the impression that he was not successful in gaining much, if any, milk. On the first field day which he was observed, he was constantly calling with no response from his mother, though his mother was presumably an experienced mother due to her old age.

Figure E.1 Undernourished adult female, [Bitsy], and her 18 month old male calf, [cBitsy_09]. Photos taken 22nd June 2011.

The apparently stunted growth of this calf is also noticeable in Figures 6.15 and 6.16 taken on the 22nd of June in 2011 and 2012 at 18 and 30 months, respectively. This demonstrates the discussion of Lee et al. (2013) that in the first 24 months of life, maternal lactation “underlies variation in growth rates and individual survival”.

Neither [Bitsy] nor her calf have not been seen by the UWERP team since 3/July/2012, when LW carried out focals on [cBitsy_09]. Having not been seen in 2013, 2014 or 2015, it is presumed that they did not survive.

Lee & Moss (2014) demonstrated rates of play in wild African calves being limited in drought periods. Although not significant, they observed that younger calves reduced their play further than older calves who were independently feeding during these dry periods. More notably however, their study found calf play to be a predictor for probability of death. Calves who played less than expected for their age, were found to have a higher chance of dying after 5 years of age, “by comparison with survivors and those who died under 5”. Playful calves were found to have higher mean survival of 23.6 years (95% CI=20.4-26.8) compared to less playful individuals at 19.9years (95% CI=16.8-23.1) (Lee & Moss, 2014).

[cBitsy_09] Activity Budget:

Despite [cBitsy_09]’s undernourished state, he only appeared to have dropped play from his activity budget. At 19-21 months he spent 56% of time independently feeding; 16% inactive; 12% in locomotion; 12% in social interactions; and 4% of time in suckling interactions (N=28 scan points). Notwithstanding having never been observed in play, [cBitsy_09]‘s other activity rates were closely comparable with the wild: 58.73% feeding; 12.7% inactive; and 3.17% suckling interactions.

Figure E.2 One year on: Undernourished adult female [Bitsy] and her 30 month old male calf [cBitsy_09]. Photos taken June 2012.

It seems surprising that [cBitsy_09]'s rate of independent feeding was not higher than the mean since independent feeding was observed to increase in captive white-tailed deer fawns to compensate for experimentally induced lower milk intake (Muller-Schwarze et al., 1982). Although these fawns also reduced their time in play, their play at least continued to persist, in further contrast to [cBitsy_09].

It is possible that [cBitsy_09] may not have increased independent feeding in an attempt to compensate for the suspected lack of milk as at 19-21 months as he was already engaging in high rates. As adult wild Asian elephants are reported to spend more than 16 hours feeding (Eisenberg & Lockhart, 1972), it would not be expected for [cBitsy_09] to engage in even higher rates than this.

[cBitsy_09] Proximity to Mother

Notably, [cBitsy_09] spent more than twice as much time >5 metres from his mother at 19-20 months (39.29%; N=28 scan points) than the mean for male wild Asian calves at 19-24 months (19.30%). When observed the following field season, at 31-33 months however, his proximity to his mother proximity more closely resembled the mean (15.24%), although this was only with six scan points.

“There is mystery behind that masked gray visage, an ancient life force, delicate and mighty, awesome and enchanted, commanding the silence ordinarily reserved for mountain peaks, great fires, and the sea.”

—Peter Matthiessen
The Tree Where Man Was Born