THE BEHAVIOURAL ECOLOGY AND MOVEMENTS OF ADOLESCENT MALE AFRICAN ELEPHANT (*LOXODONTA AFRICANA)* IN THE OKAVANGO DELTA, BOTSWANA

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ABSTRACT

African elephant bull society is a complex hierarchy, which changes with rank, sexual state and age. Adolescence is considered the most changeable and influential stage, and has implications for elephant conservation and management, particularly translocations, human-elephant conflict and elephant space requirements. To investigate the social changes during adolescence and the process of independence, data were collected on the behaviour, social interactions, habitat selection and movements of male elephants in the Okavango Delta, Botswana. Five adolescent wild male elephants were fitted with satellite collars to measure habitat utilization, home range and daily movements. Data were collected on male and female elephants utilizing the study area to compare habitat utilization on a local scale to that collected over a larger area from the continuous satellite tracking. In addition three captive-raised adolescent male elephants and a young female were released into the wild. They were fitted with satellite collars and monitored from the ground and air.

My study shows that adolescence in the male African elephant is a highly social period of change and exploration as they integrate into male society and utilize new areas. Adolescent males exhibited higher levels of social behaviour than males of other age-classes, whilst the highest rate of vocalization was seen in >36yr males. Adolescent males (10-20 years) were seen in larger social groups than males of older age-classes and, within social groups, adolescent males preferred to be closer to older elephants than individuals of similar age.

The tendency of the young bulls to be closer to other elephants highlighted the influence of other bulls, and in particular older bulls, on the continued social development of adolescent males once they have left their natal herd.

In addition the research showed that wild-born captive elephants can be rehabilitated and released into the wild. Whilst they spent more time alone and in smaller social groupings, they did not differ significantly from their wild counterparts in their rate of social interactions.

The Okavango Delta provides important resources for elephants; however, the preferred resources are not widely available. The male elephants were predominantly grazers during the rainy season, browsers during the flood season and relied on a more diverse diet during the dry season. Habitat utilization and daily distance travelled was affected by season. Any proposed restriction of habitat availability or decrease in resource quality would have implications for the future of the Delta elephant population and potential human conflicts.

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In memory of my matriarchs, my mum Edith and Nana, Nina.

In thanks to Randall Jay Moore

"There is no holding nature still and looking at it"

Whitehead 1920

AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the regulations of the University of Bristol.

The analyses of the randomisation test in Chapter 4 and the nested GLM with Poisson distribution in Chapter 5 regression was carried out by Dr. Michael Pocock.

With those exceptions I declare that the work in this dissertation is my own, none of which has been submitted for any other academic award elsewhere. The views expressed in this dissertation are solely my own and do not represent those of the University of Bristol.

SIGNED: ……………………….. DATE: August 2006

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ABBREVIATIONS

AIC	Akaikes Information Criterion
ANOVA	analysis of variance
DWNP	Department of Wildlife and National Parks
EBS	Elephant Back Safaris
GLM	General Liner Model
GPS	global positioning system
HOORC	Harry Oppenheimer Okavango Research Centre
hr	hour
km	kilometres
m	metres
MCP	Minimum Convex Polygon
mm	millimetres
n	sample size
NN	nearest neighbour
NP	national park
^{o}C	degrees centigrade
P	probability
SE	standard error
WMA	Wildlife Management Areas
χ^2	chi-squared test statistic
yr	year

Chapter 1
Introduction

Across an animal's life span, its behaviour plays a crucial role in development. Animals modulate their behaviour to disperse and identify conspecifics, to find and compete for resources, to avoid predators, to reproduce and to care for offspring. Behaviours change with age and therefore represent their developmental period. One of the most important life stages is the period of adolescence, because this is a time when individuals acquire skills and develop relationships that may be of both immediate and long-term benefit to their survival and reproductive success.

1.1. Adolescence

Pereira & Altmann (1985) described adolescence as "the interval between the onset of puberty and the beginning of effective reproduction". Setchell (2003) refers to it as "the period between puberty and the attainment of full adult size and appearance". In humans it refers to the period between childhood and adulthood, characterised by a growth spurt, development of secondary sexual characteristics and cognitive development (Krisman-Scott *et al.* 2002). Bogin (1999) suggests that only humans and perhaps some apes, have an adolescent stage of growth and of life history, and that highly social mammals, such as the social carnivores (wolves, lions, hyenas), elephants, many cetaceans (porpoises, whales) and most primates only have a juvenile period, between infancy and adulthood.

However adolescence is a term often referred to in mammalian studies and whilst the distinction of adolescence is not as clearly defined there are certain behavioural characteristics observed in many mammals that can be attributed to the period of 'adolescence'.

Adolescence is a critical period during the behavioural development of mammals (Macri *et al.* 2002). During this period of development, individuals have a strong inner

drive to explore (Poirer & Smith 1974; Galef 1981) and are prone to take risks associated with this behaviour (Galef 1981; Compas, Hinden & Gerhardt 1995; Madu & Matla 2003). Macri *et al.* (2002) found that adolescence in mice is characterised by an elevated drive towards exploration of unknown environments regardless of the risks. Epidemiological data indicate that human adolescents are more involved in reckless behaviour than adults (Berndt 1979). This trend can also be seen in rodents, where adolescents differ markedly from adults in their spontaneous behaviour (Laviola & Adriani 1998; Spear 2000), in that they show more playful and affiliate behaviour (Bernstein, Judge & Ruehlmann 1993; Laviola & Adriani 1998) and are more explorative (Galef 1981).

Although adolescence can account for a significant proportion of a males reproductive lifespan in sexually dimorphic species (macaques, *Macaca mulatto:* Bernstein, Judge & Ruehlmann 1993; sperm whales (*Physeter catodon*): Whitehead & Weilgart 2000; mandrills, *Mandrillus sphinx:* Setchell & Dixson 2002), few studies have concentrated on adolescent development.

1.2.   Difference between the sexes

In sexually dimorphic mammals the characteristics of adolescence are visual as well as behavioural as they strive to attain adult size and secondary sexual characteristics (Setchell 2003). In polygynous species it is generally the males that are larger. Competition in polygynous species has set a premium on characteristics that assist polygynous males in locating and mating with receptive females, and lifetime reproductive success is closely related to growth in sexual dimorphic species and the development of weapons (Darwin 1888; Le Boeuf 1974; Clutton-Brock, Guinness & Albon 1982; Lincoln 1994; Poole 1994; Watson 1998; Connor, Read & Wrangham 2000; Whitehead & Weilgart 2000). Where breeding is related to size, early growth rate is likely to exert an important effect on adult breeding success, leading to increased neonate size, faster postnatal growth rates, extended period of lactation, later weaning and a prolonged period of growth (Reiter, Stinson & Le Boeuf 1978; Clutton-Brock, Albon & Guinness 1981, 1985; Lee & Moss 1986; Clutton-Brock 1994; Martin, Willner

& Dettling 1994). Also, sexual maturity and first breeding in many polygynous males are not synonymous. It has been postulated that the pre-reproductive but sexually mature periods in many primates may be longer, to enable the males to learn about their physical and social environments prior to attempting to reproduce (Poirier & Smith 1974; Bogin 1999). It also increases opportunities to learn various skills and may enable a longer period of brain growth needed for the association areas of the cerebral cortex to mature (Savin-Williams & Weisfeld 1989). Thus, the beneficial effects of this learning process to adult reproductive success, may justify delaying reproduction (Walters 1987). However, there are costs involved as juveniles divert the calories which would ordinarily be used for quick growth to learning purposes. When resources are in short supply the effect on the growth rates can have substantial long-term costs. Food shortages suppress the growth rates of males more, as they tend to have higher energetic requirements, and so males show higher levels of mortality during this period (Walters 1987; Clutton-Brock 1994; Lee & Moss 1999).

As hormonal and physical maturation proceeds, behavioural differences also become apparent as individuals continue to make the transition from maternal association to integration into adult community or dispersal (Pereira & Altmann 1985; Setchell 2003). The physical and behavioural differences between sexes when immature are related to differences in adult behaviour, especially among sexual dimorphic species (Fagen 1981; Clutton-Brock, Guinness & Albon *et al.* 1982). Sexual differentiation is evident in the behaviours of many polygynous mammals and includes their social interactions, partner choice in play, play type and eventually the dispersal of one sex (Reiter, Stinson & Le Boeuf 1978; Lee & Moss 1986; Watson 1998).

Many sexually dimorphic mammals show social and spatial segregation. Spatial segregation can occur on a local scale, where males and females utilize different foods or habitats, or on a larger scale where males and females utilize different ranges when not breeding (Villaret & Bon 1995; Whitehead & Weilgart 2000). Four principal hypotheses have been proposed to explain why sexual segregation, both social and spatial, occurs: (i) the predation risk hypothesis suggests that males are less vulnerable to predation than females and their offspring. Therefore, females choose habitats that are primarily safe from predators whereas males are free to seek habitats with high food

availability (Main, Weckerly & Bleich 1996; Ruckstuhl & Neuhaus 2000). (ii) The forage selection hypothesis predicts that the sexes segregate because body size dimorphism leads to different energy requirements and thus food selection. As metabolic rate is allometrically related to body weight, decreasing with increasing body weight (Kleiber 1961), the smaller sex requires more food or selects higher forage quality (Gross 1998). In addition, females have higher energy demands whilst pregnant and lactating, along with an increased demand for nitrogen, sodium and calcium (Clutton-Brock, Guinness & Albon 1982; Iason, Duck & Clutton-Brock 1986). (iii) The social preference hypothesis proposes that the segregation of the sexes is caused by the social affinities of males, whereas early preference for same-sex peers could cause the formation of male and female groups (Villaret & Bon 1995; Bon & Campan 1996). (iv) The activity budget hypothesis suggests that differences in activity budgets and movement rates are key factors of sexual segregation (Main, Weckerly & Bleich 1996; Ruckstuhl 1999; Ruckstuhl & Neuhaus 2000). Size dimorphism leads to differences in energetic requirements and metabolic efficiencies. This hypothesis differs from the forage selection hypothesis in that the sexes show different activity budgets even when feeding on the same forage plants in the same habitat. Thus the synchronization of activity in mixed-sex groups maybe energetically too costly to maintain.

Whatever the causes of sexual segregation, adults of many sexually dimorphic species live segregated except for short periods when breeding. During breeding males spend an enormous amount of energy and time searching, following and fighting for females in oestrus (Clutton-Brock, Guinness & Albon 1982; Poole 1982, 1989b; Whitehead & Weilgart 2000). The study of the ontogeny of behaviour in young, growing animals, their activity budgets, group choice and social preferences may help to detect the mechanisms underlying sexual segregation (Ruckstuhl 1999; Ruckstuhl & Neuhaus 2000).

1.3. Play

Despite several decades of study, the adaptive purpose of play is still unclear and numerous hypotheses have been put forward to explain its function. These include the

enhancement of cerebral growth (Ferchmin & Eterovic 1979), increased cardiovascular fitness (Gomendio 1988), development of motor skills (Caro 1988), development of social skills (Bekoff 1978), problem solving (Fagen 1981), risk assessment (Thompson 1998), coping with stressful situations (Spinka, Newberry & Bekoff 2001) and the formation of social bonds (Baldwin 1982).

Caro (1988) has concluded that play is 'all locomotor activity performed postnatally that appears to an observer to have no obvious immediate benefits for the player, in which motor patterns resembling those used in serious functional contexts may be used in modified forms'. Play is often classified into three main categories: (i) object play, involving the manipulation of inanimate objects (ii) locomotor play, which consists of activities such as running, and (iii) social play, which involves two or more individuals that respond to each other's actions (Fagen 1981). These often occur simultaneously and so classification can be difficult. The consensus as to the importance of play is divided, but it appears to incorporate many physical components of adult behaviour patterns, such as aggression and mating, but lacks the immediate functional consequences (Walters 1987).

In most mammalian species play begins at infancy, peaks when juvenile and decreases with age, occurring rarely once an individual is adult (Poirier & Smith 1974; Fagen 1981; Humpreys & Smith 1987; Walters 1987; Pellis & Pellis 1990; Hall 1998). Many of the sex differences displayed later in life are evident in the play and other social interactions of young animals. For example, play in young males tends to be more aggressive and fight orientated (Smuts 1987; Waters 1987). Males also play more frequently (Reiter, Stinson & Le Boeuf 1978; Berger 1980; Lee 1983; Pellis & Pellis 1990, 1998; Rothstein & Griswold 1991) and play more with older animals than females (Lee 1983; 1986). This may increase proficiency in adult behaviours and so increase survival and mating success. Miller and Byers (1998) speculated that the interaction of young pronghorns (*Antilocapra americana*) with older bucks whilst playing enabled them to learn better techniques from the older more skilled partners.

Sparring, or play fighting, is one of the more common social play activities observed in eutherian mammals (Fagen 1981) and in some marsupials (Watson 1998). Whilst sparring is physically very similar to fighting, it rarely results in injury and the

movements tend to be slower (Miller & Byers 1998), less aggressive (Pellis & Pellis 1998) and in shorter bouts (Thompson 1998 for review). Play is more common in males than females (Fagen 1981; Humpreys & Smith 1987; Rothstein & Griswold 1991; Watson & Croft 1993; Clutton-Brock 1994; Biben 1998; Miller & Byers 1998; Watson 1998 Synder *et al.* 2003). In polygynous mammals it is important in the formation of a dominance order that influences current and/or future competition for resources (Poirier & Smith 1974; Humpreys & Smith 1987; Paquette 1994; Biben 1998; Miller & Byers 1998). It is motor training for future interactions (Caro 1988) and develops social skills (Harlow 1969; Bekoff 1978; Brown 1988), including the assessment of conspecifics' abilities (Poirier & Smith 1974; Biben 1998; Miller & Byers 1998), subordination (Biben 1998) and in certain social societies the cohesion of groups (Poirier & Smith 1974; Fagen 1981). Fighting ability and therefore dominance, increases a male's mating success (Clutton-Brock, Guinness & Albon 1982; Poole 1989a,b) As a consequence sparring among young males and interacting with conspecifics may influence an individual's long-term survival and reproductive success.

1.4.   Dispersal

Dispersal from natal groups to avoid inbreeding and competition with related individuals and to increase breeding success usually takes place at adolescence (Packer 1978; Dunbar 1987; Pusey & Packer 1987; Alberts & Altmann 1995; Macri *et al.* 2002). Consequently, it is important in understanding the many population processes, such as an individual's life history, population dynamics and species distribution. When adolescent animals disperse into new areas they must gather information about the social and ecological environment. Males may achieve this by joining up with other social groups in the new area.

Dispersal is described as the 'Movement of an organism or propagule from its site or group of origin to its first or subsequent breeding site or group' (Shields 1987). Hazards associated with emigration include increased risks of exposure, predation and disease. Lack of familiarity with an area may reduce foraging efficiency and increase the risk of predation (Isbell, Cheney & Seyfarth 1990; Higley *et al.* 1996). Also,

resident conspecifics attack strangers more severely than familiar individuals (Moore & Ali 1984; Isbell, Cheney & Seyfarth 1990).

In most polygynous and promiscuous species of mammals, males are the predominant dispersers (Greenwood 1980; Dobson 1982; Bernstein, Judge & Ruehlmann 1993; Pusey & Packer 1987; Alberts & Altmann 1995; Soulsbury 2005; Loe *et al.* 2006), usually leaving their natal group at puberty. However there is much variation in the age and stage of maturation that males leave, with hamadryas baboons (*Papio hamadryas*) leaving before puberty whilst savannah baboons (*Papio cynocephalus*) leave after. The period of transfer, once they have left their natal group or area, is associated with movement and exploration, until the animal settles in a new area (Andreassen, Stenseth & Ims 2002). How individuals orientate themselves within a landscape during this transfer phase is perhaps the main behavioural question and theories include the use of olfactory (Raimondi 1988; Andreassen, Stenseth & Ims 2002), visual (Zollner & Lima 1997, 1999; Andreassen Hertzberg & Ims 1998) or auditory stimuli (Andreassen, Stenseth & Ims 2002). It is probably a combination of factors that affect the decision made during transfer, not least the information gained through associating with conspecifics (Macdonald & Johnson 2001; Stamps 2001). Whilst settling into a new area, individuals cannot fully exploit a habitat, as time and energy expended in exploration and socializing detracts from activities to increase their bulk. If gathering information about an area will increase an individual's long-term fitness, then learning about an area from conspecifics may reduce some of these costs. 'Conspecific attraction' is a term attributed to the tendency for animals to disperse into areas already occupied in spite of unoccupied areas of equal quality being available, and has been observed in solitary, territorial and colonial animals (Stamps 1988, 2001; Setchell 2003). Dispersers may begin searching for a new habitat while still residing in the old one with increased peripheralization from the adult female social network and forays away from their natal groups with conspecifics seen in many mammals (Boelkins & Wilson 1972; Walters 1987; Hayaki 1988: Pocock, Hauffe & Searle 2005; Sharpe 2005) may serve as information gathering exercises about potential dispersal sites.

A male in a polygynous society could benefit from staying in his natal group due to the decreased predation risk, the assistance from his relatives in breeding competition

and by increasing his inclusive fitness by assisting them (Whitehead & Weilgart 2000). Whilst matrilineal societies do meet up with other groups from time to time, these interactions are often with related females (Moss 1988), so his breeding opportunities would be low. As reproductive success is related to size in dimorphic species, feeding and continued growth past sexual maturity is important. Sociality does not increase a male's feeding rate in sperm whales and large males are able to defend themselves against predation (Whitehead & Weilgart 2000); therefore, a male should leave its family unit if he can enhance his breeding success. By dispersing into male only areas, adolescent males could be avoiding competition with females, as females are often restricted to certain areas by the needs of their young (Whitehead & Weilgart 2000; Stokke & du Toit 2002). In sperm whales, adult males become more solitary and migrate towards the poles. However, there are costs involved with this strategy as studies on various mammals have shown that foraging efficiency is increased by familiarity with the area and the phenology of food sources, and so the benefits of increased breeding success must compensate (Waser & Jones 1983; Pusey & Packer 1987; Stamps 2001). Delaying dispersal until they are older and therefore larger would benefit the males, but could be a cost to the other herd members. Many animals show 'habitat imprinting' upon dispersal, whereby stimuli they have been exposed to early in life increases the probability that an individual will select similar habitat in an unfamiliar area (Stamps 2001). It is thought that this imprinting is most likely to occur during a particular age or developmental stage. Studies on birds and mammals have shown that the stimuli they encounter whilst juvenile affects habitat choice later on (Teuschl, Taborsky & Taborsky 1998).

1.5.   Change of social group

When an animal disperses from its natal group it will under go a change of social group. It may join an unrelated group of a similar social structure as in gorilla, *Gorilla gorilla* (Stewart & Harcourt 1987), and hamadyrus baboon, *Papio hamadryas* (Sigg *et al.* 1982). They may become nomadic as in lion (*Panthera leo; pers. obs.*) and interact with groups intermittently. Or they join a completely different social set up, as is the

case in many polygynous species where males will leave a society dominated by females and a matrilineal system and join a male society, only interacting with female groups occasionally such as Grant's (*Gazella granti)* and Thompson's (*Gazella thomsonii)* gazelles (Estes 1967) and red deer (*Cervus elephas;* Clutton-Brock, Guinness & Albon 1982). A male's social interactions whilst in his natal group and/or during forays prior to independence, when he may join up and associate with peers or older individuals (Walters 1987; Hayaki 1988), may well prove important in his decision on when and where to disperse. During the transfer phase of dispersal, he will meet up with more individuals that again could influence decisions on dispersal site.

1.6.   Adolescence in elephants

In comparison to adults and herds (Douglas-Hamilton 1973; Eltringham 1977; Poole & Moss 1981, 1982; Moss & Poole 1983; Western & Lindsay 1984; Dunham 1986; Lee & Moss 1986, 1999; De Villiers & Kok 1997; Moss 1988; McComb *et al.* 2001), adolescence in elephants has been mostly over looked and the relationships between physiological maturation and behavioural development during adolescence not well understood.

Adult African elephants (*Loxodonta africana)* are markedly sexually dimorphic in body size. Both male and female elephants grow continuously. However, whilst female growth levels off at around 25 years of age, males continue to grow at a similar rate past this age (Laws & Parker 1968). This is attributed to the delayed fusion of the long bones, which is more pronounced in the male. In females epiphyseal fusion of the long bones takes place between 15 and 25 years of age, whilst in the males it occurs between 30 and 45 years of age (Poole 1994). By the time fusion takes place a male elephant might be 3.30-3.60m at the shoulder and weigh up to seven tonnes (Moss 1996). Females rarely reach more than 2.70m and weigh about three tonnes when adult (Moss 1996). This prolonged growth in males is also evident in its tusks, which grow exponentially with age and by 50 years of age a male's tusks can weigh seven times those of a female (Poole 1994; Moss 1996). These characteristics of sexual

dimorphism, along with the occurrence of musth[1] in male elephants have evolved through intense sexual selection pressure (Poole 1994).

The sexes differ behaviourally as well. A fundamental difference is that whilst adult females live in tight-knit stable family groups (Douglas-Hamilton 1973; Fernando & Lande 2000), adult males live more solitary, independent lives with seemingly few social bonds. Female elephant society is built around an adult female and her offspring. It is reliant on females showing affiliation and cooperative behaviour with female kin throughout their lives. It extends beyond the immediate family to incorporate multi-tiered relationships with other related females. The basic social unit is the 'family', which is composed of several related females and their offspring. The 'bond' group is made up of one to five associated females, who are usually related and spend a large proportion of their time together and show synchronized behaviour. The final tier is the 'clan', which incorporates families and bond groups that utilize the same dry-season home range (Douglas-Hamilton 1972, 1973; Moss & Poole 1983; Moss 1988; Charif *et al.* 2005).

The differences in the behaviour of the sexes in elephants commence at birth with the male sucking more frequently and for longer than the female but moving away from their mothers earlier (Lee 1986). Play is generally in the form of sparring; unlike females, they also interact and play more frequently with family and non-family members (Lee 1986). This independence from their mother and the herd, and potential assessment of strength and status of a novel partner during play, can be related to the later dispersal behaviour of young bulls (Berger 1980; Lee 1986).

Early assessment of conspecifics is important in a fluid hierarchal social system where encounters are unpredictable and prior knowledge could avoid costly fighting (Moss & Poole 1983). Puberty in male elephants occurs between the ages of nine and fifteen (Short, Mann & Hay 1967; Hanks & McIntosh 1973; Lee 1986), whilst sexual maturity is reached at 17 (Laws 1969; Poole 1994). In the African elephant, puberty is

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[1] Musth comes from the Hindi word *mast,* meaning intoxication. In elephants this word describes the period of sexual activity, signified by high testosterone levels, urine dribbling, Green Penis Syndrome (a green colouration to the end of the penis and part of the sheath) and swollen temporal glands (Poole 1981).

not necessarily the trigger for a male to leave the herd, as the age at which a male leaves varies widely, with some departing at eight whilst others leave at 20 years. The majority depart at the age of 14 (Douglas-Hamilton 1972, 1973; Poole 1987a; 1994, 1996b; Lee & Moss 1999).

Not only are the sexes of elephants segregated socially, they are also segregated spatially. This segregation can occur locally with the utilization of different food (Stokke & du Toit 2002; Shannon, Page & Duffy 2006) and also over a much larger scale with the occurrence of herd and bull areas (Laws, Parker & Johnstone 1975; Moss & Poole 1983; Moss 1988; Whitehead & Wielgart 2000). This spatial segregation starts to take place at adolescence. The process of becoming independent in male elephants may take anything from one to four years (Lee & Moss 1986), with newly independent males following several different courses to social maturity. Some leave their herd and join up with another family for a couple of years, others go off to bull areas and join up with groups of bulls, whilst some stay in the female area and move from family to family (Poole 1996a). It is likely that young bulls do not immediately settle into a new area but go through a period of transfer, characterised by exploration of areas, unsettled movements (Andreassen, Stenseth & Ims 2002) and higher social interactions than older bulls (Whitehead & Weilgart 2000).

By their early twenties male elephants have dispersed from their natal herd and entered a highly dynamic situation of changing sexual rank, state, behaviour and associations (Hall-Martin 1987; Poole 1989a; 1989b, 1996b), whilst the females remain in their natal herd (Douglas-Hamilton 1973; Fernando & Lande 2000). The social interactions of males are dependent on their use of a large variable habitat, age, sexual state and possibly their degree of relatedness (Moss & Poole 1983). Although sexually mature in their teens, male elephants are unlikely to father their first offspring until 30 to 35 years of age, after they have experienced their first period of musth at around 29 years. They reach their sexual prime at 45 years of age (Poole 1994).

Unlike other polygynous males, elephants do not try and dominate a group of females and form a harem such as elephant seals, *Mirounga angustirastris* (Le Boeuf 1974) and red deer (Clutton-Brock, Guinness & Albon 1982), or form leks, like the Ugandan kob, *Kobus kob thomas* (Blamford 1992) and fallow deer, *Dama dama*

(Clutton-Brock *et al.* 1988). The interbirth interval in female elephants is 4-5 years (Douglas-Hamilton 1972; Moss 1988) and thus adult females come into oestrus infrequently. Therefore a male elephant will be reproductively more successful if he spends his time increasing his bulk and then searching for receptive females over a wide area, as in sperm whales (Whitehead & Weilgart 2000). In sperm whales and in elephants, once the males have become independent of their natal group they move away from the areas frequented by females into 'bull areas' (Laws, Parker & Johnstone 1975; Moss & Poole 1983; Moss 1988; Whitehead & Wielgart 2000). This behaviour may occur to avoid intersexual competition, as females are restricted to certain areas due to young (Stokke & du Toit 2002), at a time when the males need to increase their bulk to enhance intrasexual competition at adulthood (Whitehead & Wielgart 2000).

Male elephant society is based on a dominance hierarchy, where older, larger males are dominant and secure most mating opportunities (Poole 1987b, 1989a). In order to increase mating success, young males must grow as fast as possible and establish their position in this hierarchy. Social knowledge acquired through social interactions whilst in their herd, in particular sparring with non-herd members, will help adolescent male elephants integrate into bull society. However, once independent, they are likely to encounter new males as they explore more areas. Socializing with older conspecifics may provide the means by which dispersing males pick up cues as to the location of good areas to utilize. By 'learning' from other individuals in this way they decrease the time they must expend gathering information, and can expend energy on bulking up and socializing. Socializing takes time away from feeding and so there is a continual trade off between gleaning information about the dominance of others against reaching their growth potential fastest. This trade off will be influenced by habitat and food quality and an individual's physical condition (Caro 1988; Sharpe *et al.* 2002).

Fighting can be a costly business; hence its occurrence is thought to decrease over time as individuals become better established in the hierarchy and use more ritualized signals (Parker 1974, 1978; Smuts 1987). In elephants this is assisted by the honest signalling of their musth periods, whereby males announce a state of heightened aggression and intention to fight with temporal gland secretions, urine marking and vocalizations (Poole 1981a, 1987b, 1989a). Despite being in this highly aggressive state

of musth, contests are rare, suggesting that opponents are able to access the dominance of each other with relative accuracy (Poole 1989a).

In spite of several decades of research and hundreds of years of utilization and reverence by man, there is a lack of knowledge on the social development of male elephants. However, there is a need for an adequate understanding of the ontogeny of their adult behaviour. As, in most mammals, adolescence is a critical period during the behavioural development of male elephants (Macri *et al.* 2002). It is one that affects his social standing and therefore mating opportunities in maturity. As there is such a large variation in the length of adolescence, elephants provide a model for understanding the importance of adolescence in all polygynous mammals.

1.7. Aims of thesis

The primary objectives of this study were to investigate the behavioural and ecological changes that occur during adolescence in the male African elephant. Firstly, the density of male and female elephants utilizing the area was estimated to conclude whether it was a bull area, as found in other elephant ranges, or if the elephant population is re-colonizing historic elephant range. Then I wanted to assess the importance of social development during adolescence and the potential influence this may have on future reproductive success. Secondly, I investigated the dispersal patterns and exploration of adolescent male elephants to understand the importance of the Delta's habitat as a resource for adolescent males. Four wild born, elephants that were raised in captivity, were released to examine the impact translocation may have on the individuals as well as the resident population.

In addition, my research addressed applied management issues, both national and international. Botswana is considering culling the elephant population, yet there are no behavioural, utilization or movement data on the 20-30,000 elephants utilizing the Delta. Botswana's population is integrated with the Hwange/Matetsi complex in Zimbabwe (Dublin 1989) and crosses other international borders into Namibia, Zambia

and Angola (Craig 1996; Blanc *et al.* 2003). Therefore any management decision in one country could have an impact on the population in others, as has been the case in Kenya and Tanzania (Dublin & Douglas-Hamilton 1987). Information on density, population, habitat utilization and movements are basic requirements to make management decisions. Internationally, translocation is being increasingly used in the management and conservation of fragmented populations and problem animals; although it has varying degrees of success, due to a lack of understanding of the social and ecological requirements of elephants.

1.8.   Thesis structure

Chapter 2 is an overview of the main methods used throughout the thesis.

In Chapter 3 the theories of expanding habitat range, increasing population and the occurrence of 'bull areas' in the Okavango Delta elephants are investigated through monthly road surveys to access the demography and density of the elephants utilizing the study area analyzed in DISTANCE.

In Chapter 4, adolescent male African elephant behaviour and social interactions are investigated through the analysis of focal data collected on wild male elephants from five age groups. In particular their social behaviours, such as greeting and sparring and their social groupings, were compared to older males as well as their preferences for social groupings and nearest neighbour.

In Chapter 5, the movements of adolescent male elephants and the effect of age and sex on habitat selection and utilization in the Okavango Delta are investigated. This is achieved through the analysis of data from five satellite collared adolescent male elephants as well as observations on male and female elephants within the study area accessible from the ground.

In Chapter 6 the feasibility of releasing captive raised elephants into the wild and the potential impact of translocation on individual elephants as well as elephant populations were investigated by monitoring three released captive raised male adolescent elephants.

Chapter 7 looks at the social interactions, area and habitat utilized by a young captive raised released female elephant, following on from the previous Chapter.

In Chapter 8 the period of adolescence in male elephants and its important implications in the conservation and management of the African elephant is discussed. Also the importance of the Okavango Delta's habitats to the elephant population and future implications should ecological conditions change.

Chapter 2

Methodology

2.1.   Study area

The study was conducted in the Okavango Delta, Botswana, in southern Africa (Figure 2.1). National parks and game reserves cover over 17% of the land area of Botswana, with a further 21% administered as Wildlife Management Areas (WMAs) (Wheelwright *et al.* 1996). Safari hunting is permitted on a quota system within certain WMAs. The Okavango Delta is situated in the north-west of the country and is an alluvial fan covering 15,000km^2. It has been recognised as an area of 'outstanding universal value' by the World Heritage Convention and, in 1996, was listed as the largest Ramsar Site by the Convention on Wetlands of International Importance. The Delta is reliant on the water and sediment brought down by the Okavango River from tributaries in Angola (Figure 2.1). Whilst the majority of rain in Angola falls during the summer months, the peak flow through Mohembo and into the Okavango Delta is in April. The waters then take approximately four months to permeate through to Maun, the capital of the region of Ngamiland, where the highest flows are recorded in August (Mendelsohn & el Obeid 2004).

The study was centred on the research camp at S-19.40420, E22.56162 (digital degrees and minutes) in WMA NG26, which covers 500km^2 in the west of the Delta (Figure 2.1). Data were collected on the ground across an area of 215km^2 and across 2950 km^2 from the air. The study area was thought to be a 'bull area', where mature bulls go to gain weight and reserves of energy before coming into musth and then leave in pursuit of females (Laws, Parker & Johnstone 1975; Moss & Poole 1983; Moss 1988).
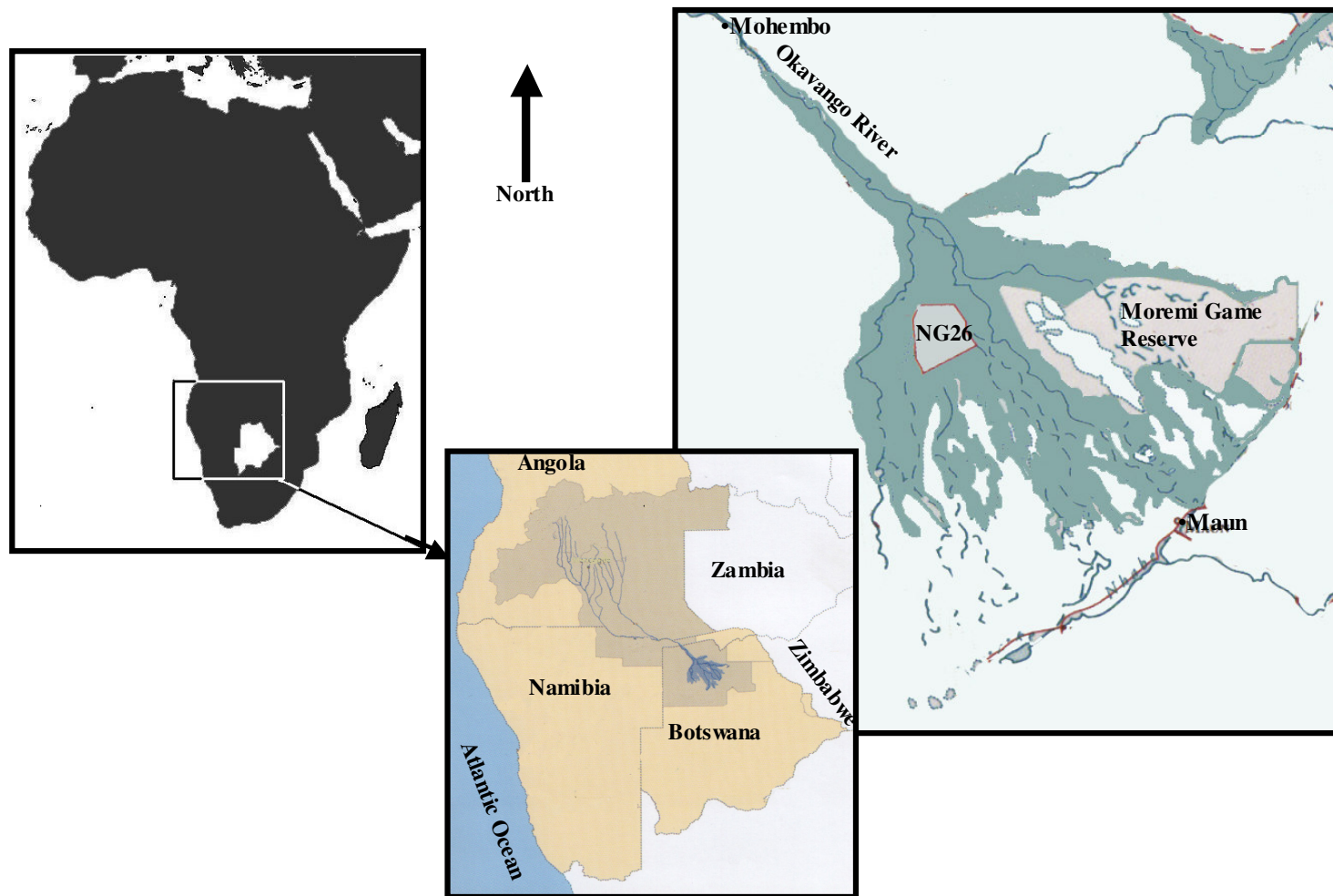
Figure 2.1: Location of the study area (Wildlife Management Area NG26) in the Okavango Delta, Botswana, southern Africa.

As rainfall varies considerably across the Delta (Mendelsohn & el Obeid 2004) and as there is an annual flood season determined by the rainfall in Angola, three seasons were recognised: the rainy season (November-March); the flood season (April-September); and the dry season (October). For the purposes of this study, mean monthly rainfall was estimated by averaging daily rainfall readings from the research camp and weather stations in both Mohembo and Maun (Water and Ecosystem Resources in Regional Development, Botswana) over three years (Figure 2.2). The start of the flood season was determined by the arrival and presence of standing water in the floodplains surrounding the research camp.

Within each 24hr period, three time periods were utilized; morning (06.00-11.59), afternoon (12.00-18.59) and night (19.00-05.59). During the study, temperature ranged from 2-42°C, with minimum and maximum mean monthly temperature ranges of 3-6°C and 22-38°C respectively (Figure 2.2.).

2.2. Habitat types

The Okavango Delta has three distinct habitat zones: the panhandle, and permanent and seasonal swamps (Mendelsohn & el Obeid 2004). The panhandle is the beginning of the Delta, where most of the water flows along a single channel surrounded by broad areas of marsh. The permanent swamps form the core of the alluvial fan and surround the three main channels and distribute water across the fan; they cover much of the upper northern and central areas of the Delta, extending over 2,000-3,000 km^2. Seasonal swamps cover the remaining southern, western and eastern areas. The extent of the seasonal swamps varies greatly from year to year (4,000-8,000 km^2), and is dependent largely on the inflow from the Angolan catchment area. Plant communities in seasonal swamps are more diverse than elsewhere in the Delta because of the differences in flooding patterns, with different plant species favouring patches that differ according to the duration and depth of flooding.
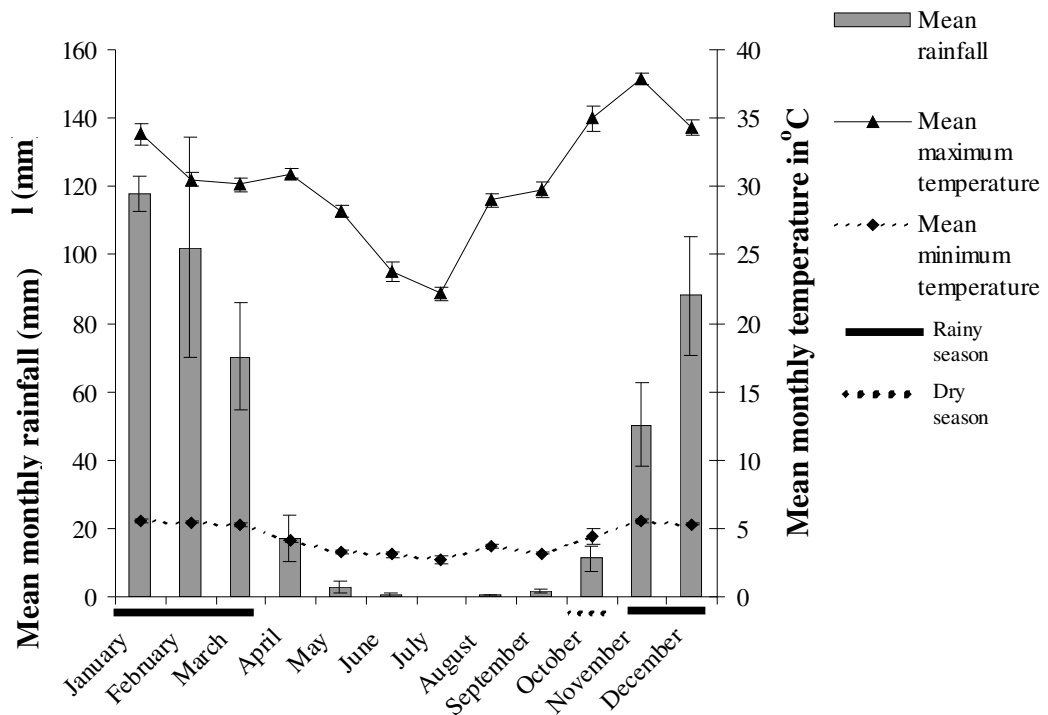
Figure 2.2: Mean (+SE) monthly rainfall and maximum and minimum temperatures. Rainfall figures were derived from data collected in the research camp and at weather stations in Mohembo and Maun; temperature data were collected at the research camp.

Habitat types were originally classified according to the Harry Oppenheimer Okavango Research Centre (HOORC) satellite vegetation map (Jellema, Ringrose & Matheson 2002). However, for statistical analyses, the number of distinct habitat categories were reduced to ensure sufficient sample sizes in each category. For the analyses of data derived from satellite collars, four habitat types were utilized; grassland/floodplain, mopane (*Colophospermum mopane*) woodland, other woodland (*Acacia* spp., *Combretum* spp., *Terminalia sericea*) and island vegetation (mainly consisting of *Hyphaene petersiania* or *Phoenix reclinata*) (Table 2.1). For the analyses of data derived from ground observations, five habitat types were utilized; grassland/floodplain, mopane woodland, other woodland, island vegetation and *Terminalia* woodland (Table 2.1). Data collection procedures are outlined below and in subsequent chapters.

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Table 2.1: Habitat types of the Okavango Delta according to the Harry Oppenheimer Okavango Research Centre satellite vegetation map (Jellema, Ringrose & Matheson 2002) with classifications used for the satellite collar data and the ground observational data.

HOORC vegetation classification	Classification for satellite collar data	Classification for observational data
Low open grassed scrubland on dune valley with *Burkea* spp. and *Baikiae* spp.	Grassland/floodplain	Grassland/floodplain
Low open grassed scrubland on dune valley with *Colophospermum mopane* and *Combretum* spp.	Mopane woodland	Mopane woodland
Low open grassland with tree scrubland on dune valley with *Terminalia* spp. and *Baphia* spp.	Other woodland	*Terminalia* woodland
Low open scrubland on dune crest with mixed species	Other woodland	Other woodland
Dense tree scrubland on dune side with *Burkea* spp. and *Baikiae* spp.	Other woodland	Other woodland
Low open grassed scrubland on dune valley with *Terminalia* spp and *Baphia* spp.	Other woodland	*Terminalia* woodland
Low open grassed scrubland in paleo delta with *Acacia* spp.	Other woodland	Other woodland
Low open scrub grassland with sage bush	Grassland/floodplain	Grassland/floodplain
Open tree scrubland on dune side with *Burkea spp.* and *Baikiae* spp.	Other woodland	Other woodland
Low open grassed scrubland on dune valley with *Terminalia* spp. and *Baphia* spp.	Other woodland	*Terminalia* woodland
Low open grassed scrubland in paleo delta with *Acacia* spp.	Grassland/floodplain	Grassland/floodplain
Densely vegetated paleo-riparian ridges	Other woodland	Other woodland
Low open grassed scrubland in paleo delta with *Combretum* spp.	Grassland/floodplain	Grassland/floodplain
Low dense thickets on former lake ridges with *Acacia* spp.	Other woodland	Other woodland
Low open grassed scrubland/treed grassland with *Acacia* spp. and *Terminalia* spp.	Other woodland	*Terminalia* woodland
Low open bare woodland in meso delta channels with tall *C. mopane*	Mopane woodland	Mopane woodland
Low open bare woodland in meso delta with tall *C. mopane*	Mopane woodland	Mopane woodland
Low open bare woodland in meso delta with *C. mopane*	Mopane woodland	Mopane woodland

Low bare scrubland in meso delta with shrub *C. mopane*	Mopane woodland	Mopane woodland
Low open bare grassland with *Pechuel-loeschea leubnitziae*	Grassland/floodplain	Grassland/floodplain
Open mixed *C. mopane* in meso delta channels with *C. mopane*	Mopane woodland	Mopane woodland
Low open grassland with *Baikiaea* spp. trees and mixed shrubs	Grassland/floodplain	Grassland/floodplain
Low open grassland with *Burkea* spp. trees and mixed shrubs	Grassland/floodplain	Grassland/floodplain
Low open grassland with *Baikiae* spp./ *C. mopane* trees and mixed shrubs	Grassland/floodplain	Grassland/floodplain
Low open grassed/treed scrubland with *Terminalia* spp. and *Acacia* spp.	Grassland/floodplain	*Terminalia* woodland
Low open shrubby grassland with mixed shrubs	Grassland/floodplain	Grassland/floodplain
Low open shrubby woodland of *Terminalia* spp. tree islands	Other woodland	*Terminalia* woodland
Low open treed scrubland with *Acacia* spp.	Other woodland	Other woodland
Tall open treed grassland with *Acacia* spp.	Grassland/floodplain	Grassland/floodplain
Low open/dense shrubby grassland on former floodplain	Grassland/floodplain	Grassland/floodplain
Grassland on dry floodplain and island interiors	Grassland/floodplain	Grassland/floodplain
Tall open shrubby woodland dry riparian zones and adjacent *Acacia* spp. thickets	Other woodland	Other woodland
Open shrubby woodlands on islands	Island vegetation	Island vegetation
Low open shrubby grassland with *Acacia* spp.	Grassland/floodplain	Grassland/floodplain
Low open grassed/treed scrubland with *Terminalia* spp. and *Acacia* spp.	Other woodland	*Terminalia* woodland
Low open shrubby woodland on former floodplain with *Acacia* spp.	Other woodland	Other woodland
Low open shrubby grassland on former floodplain	Grassland/floodplain	Grassland/floodplain
Low open grasslands on former floodplain with burned peat	Grassland/floodplain	Grassland/floodplain
Low open *Combretum* spp. woodlands of former riparian zone	Other woodland	Other woodland
Tall dense grassland on inundated higher floodplain	Grassland/floodplain	Grassland/floodplain
Dense grassland on inundated lower floodplain	Grassland/floodplain	Grassland/floodplain
Tall open shrubby woodland island riparian zone and adjacent *Acacia* spp. thickets	Island vegetation	Island vegetation
Tall channel fringing emergents and mats of reeds and Cyperaceae	Grassland/floodplain	Grassland/floodplain
Channels and recently inundated floodplains	Grassland/floodplain	Grassland/floodplain
Seasonal swamp and floodplain edges with reeds, Cyperaceous and grasses	Grassland/floodplain	Grassland/floodplain
Permanent back swamp areas with reeds and sedges	Grassland/floodplain	Grassland/floodplain

2.3.   Study animals

2.3.1. Collaring of wild adolescent males

For the purpose of this study, adolescence was defined as the period between 10 and 20 years of age. This includes the majority of male elephants that have reached puberty or sexual maturity and are going through the process of independence. This was further subdivided into early adolescence (10-15 years), when the majority of individuals are still in their herds, and late adolescence (16-20 years), when most have left their natal herd and are independent. These age groups were selected to correspond to previous and current studies of the African elephant (Poole 1982; Moss 1996; Lee & Moss 1999).

Five adolescent male elephants were randomly selected from female herds (Table 2.2) within a radius of 10km of the research camp on the 16th or 17th of February 2002. They were located from a helicopter and immobilised using gun-propelled syringes containing 12mg of the anaesthetic drug etorphine hydrochloride (M99) with 5000 international units of the enzyme hilaze to increase absorption rates. Once anaesthetised, the elephant was measured and fitted with a DM 200 Imarsat Unite satellite radio collar (Africa Wildlife Tracking cc. Pretoria, South Africa). These collars were programmed to collect and transmit geographical coordinates (10m spatial accuracy), the date and time every 12 hours for 12 months. Each collar was also fitted with a VHF transmitter that was set to an individual frequency to enable tracking from the ground and air with a Telonics TR4 receiver (Telonics Inc., Mesa, Arizona, USA). Throughout the thesis, these individuals will be referred to as Abu2, Abu3, Abu4, Abu5 and Abu6.

All individuals were subsequently re-collared on the 13th or 14th March 2003 with an AWTSM2000E satellite radio collar (Africa Wildlife Tracking cc. Pretoria, South Africa) programmed to download every eight hours and last for two years. Due to further problems with the collars, Abu2 was re-collared on the 28th June 2004, Abu5 on the 6th October 2003 and Abu6 on the 1st April 2004. Abu3 and Abu4's collars were removed on the 9th November 2004. An observation during two of the re-collaring exercises, the darted elephant put his trunk to the dart in his rump and then immediately to his collar.

Table 2.2: Grouping codes

Code	Social status
1	Alone, no other elephant within 500m
2	Small group of bulls, 1-5 males within 500m of each other
3	Large group of bulls, > 5 within 500m of each other
4	Female herd (no male $\geq$ 21 years of age present) within 500m of each other
5	Mixed herd (male over $\geq$ 21 years of age present) within 500m of each other
6	Within 500m of Elephant Back Safaris herd

2.3.2. Release of captive elephants

Three adolescent males and one young female were released from Elephant Back Safaris (EBS) during the course of the three-year study. All these individuals were orphans of culling operations in the Kruger National Park (NP), South Africa, in 1989 and 1995. They were estimated to have been one or two years of age on arrival in Botswana. A 14-year-old male (Mafunyane) was the first to be released on the 1st February 2002. Prior to the release he spent all his time with the EBS herd. He was fitted with a DM 200 Imarsat Unite satellite radio collar, which was programmed to record his position every 12 hours (Africa Wildlife Tracking cc.). However, following a low download rate, he was re-collared on 17th November 2002 with a Globaltrack AWTSM2000E satellite radio collar (Africa Wildlife Tracking cc) programmed to download every eight hours. Due to faulty collars, he was re-collared on the 4th February 2004 and the 9th November 2004. After his first re-collaring, which was undertaken without the use of anaesthetic drugs, all released elephants were immobilised using gun-propelled syringes containing 7-12mg of etorphine hydrochloride (M99) with 5000 international units of the enzyme hilaze to increase absorption rates. After collaring, individuals were given 25mg of the antagonist diprenorphine (M50/50) to reverse the effects of the anaesthetic.

In 2003, permission was granted by the Department of Wildlife and National Parks (DWNP) to release the two remaining adolescent males of the EBS herd (Thando and Seba). One month prior to the release date of February 10th, these males were separated from the herd and moved to the research camp. Whilst they were able to

communicate vocally with the herd (the electric fenced boma where the EBS herd were housed was 2.7 km away), they had no physical contact with the other elephants during this time. Their daily routine remained the same with mahouts (elephant handlers) taking them out to feed during the day and then returning to the research camp one hour before dusk. At night they were provided with *Colophospermum mopane* branches for food supplemented with horse nuts, which was their training reward throughout captivity. Both males were fitted with Globaltrack AWTSM2000E satellite radio collars two days prior to their release. Thando was re-collared on 28th June 2004 and Seba on 1st April 2004 and 10th November 2004. On the day of their release, they were walked five kilometres south of their boma to feed for the day. At dusk, instead of returning to camp, their chains were removed and the mahouts departed; the research team then monitored them until it was dark.

The female (Nandipa) was released on 13th September 2003. She was estimated to have been one year old when she was brought to Botswana in 1989. Two days prior to her release she was fitted with a Globaltrack AWTSM2000E satellite radio collar. Before her release she spent all her time in captivity with the EBS herd. On the morning of her release, the EBS herd were moved 20 kilometres east of camp, and she was released directly from the boma.

Once released, contact with both humans and the EBS herd was discouraged and the 'reward' relationship that had been the basis of their training was terminated. They were discouraged by the camp staff from coming too close to the camp by shouting, clapping and, in extreme cases, by shooting over their heads. One exception to these rules was when Mafunyane injured his foot two weeks after his release, and it was decided that this wound should be treated with anti-inflammatory drugs. He was called, given horse nuts, chained and injected intramuscularly with Finadyne (1ml/50kg) every morning for four days.

Prior to each of the releases, all of the other camps in the Okavango Delta were notified and given an identification sheet and photographs of each of the elephants and asked to treat them like wild individuals should they come within their vicinity. During the study, released individuals were reported near tourist camps on two occasions; in both instances, they were reported acting like wild elephants.

Before being released all animals were tested for *Mycobacterium tuberculosis* by the DWNP. The DWNP was also concerned about the phylogeographic compatibility of the released elephants, as there was the potential for genetic maladaption to local environmental conditions (Tutin *et al*. 2001), as well as potential dilution effects on the resident population (Goossens *et al*. 2002). However, previous work has shown that the elephant populations of northern Botswana and Kruger NP are not genetically distinct (Georgiadis *et al*. 1994).

2.3.3. Radio tracking procedures

Wherever possible, all collared elephants were tracked bimonthly from the air using a Piper J-3 Cub plane (1946 Model, 100HP) with H-aerials attached to each wing (African Wildlife Tracking) fixed at 45 degrees to the ground. Aerials were linked to a single Telonics R-4 (Telonics, Inc. Arizona, USA) receiver through a switch box (African Wildlife Tracking cc. Pretoria, South Africa). Once located, the elephant(s) was circled a couple of times to collect all necessary data. Given that aircraft regularly fly over the Delta, this procedure did not seem to unduly disturb focal individuals, although they did display a tendency to move into thicker vegetation when alone. At each sighting, GPS (Global Positional System) location, habitat type at first sighting, social status (Table 2.2), number and sex of any other elephants present and distance from the nearest elephant(s) were recorded. Whenever any of the collared elephants were within 10km of the research camp, they were then located from the ground. These data were used to analyze social interactions, habitat selection and individual movement patterns.

2.3.4. Ground data collection

Data were collected on a population of free-ranging African elephants from 1st February 2002 until 10th February 2005. Five routes set along established roads were used to locate individuals for focal observations and which incorporated all the main habitats in the study area (Figure 2.3). However, annual floods made driving difficult at certain times of the year. Whilst most of the roads were usable during 2002 and 2004, the

floods in 2003 were the highest recorded in 20 years and cut off the majority of roads, thereby limiting the area that I could access. Furthermore, driving off-road was severely restricted during all flood seasons. The rainy season did not affect access to roads, but going off-road in certain habitats was avoided. Monthly road transects were carried out along a transect incorporating all the five routes, covering 58.7km.

The behaviour of released and wild elephants was quantified using 30-minute focal observation periods. Wild individuals were aged using a combination of established methodologies such as the measurement of tusks (Hanks 1972), measurement of footprints (Tables A.1, A.2. & A.3. in Appendix: Western, Moss & Georgiadis 1983; Lee & Moss 1995), estimation of shoulder-height (Appendix: Croze 1972; Douglas-Hamilton 1973; Douglas-Hamilton, Hillman & Moss 1981; Lark 1984; Jachmann 1991; Lee & Moss 1995) and additional physical characteristics such as tusk girth and head shape (Appendix, Poole 1982). For the purposes of this study, male elephants were classified into five age classes (Moss 1996): Class 1, 10-15 years (n = 65); Class 2, 16-20 years (n = 73); Class 3, 21-25 years (n = 78); Class 4, 26-36 years (n = 103); Class 5, >36 years (n = 98) (Appendix.). Animals were assumed to increase in age on January 1st.

2.4.   Statistical analyses

Throughout this thesis a combination of parametric and non-parametric statistics have been used where appropriate. The underlying assumptions were met for all tests (Zar 1984) and analyses were conducted using MINITAB (version 14, 2004), SPSS (version 12.0, 2003) and S-PLUS (version 6.1, 2002 Insightful Corporation). Results were considered significant where $\alpha = 0.05$.
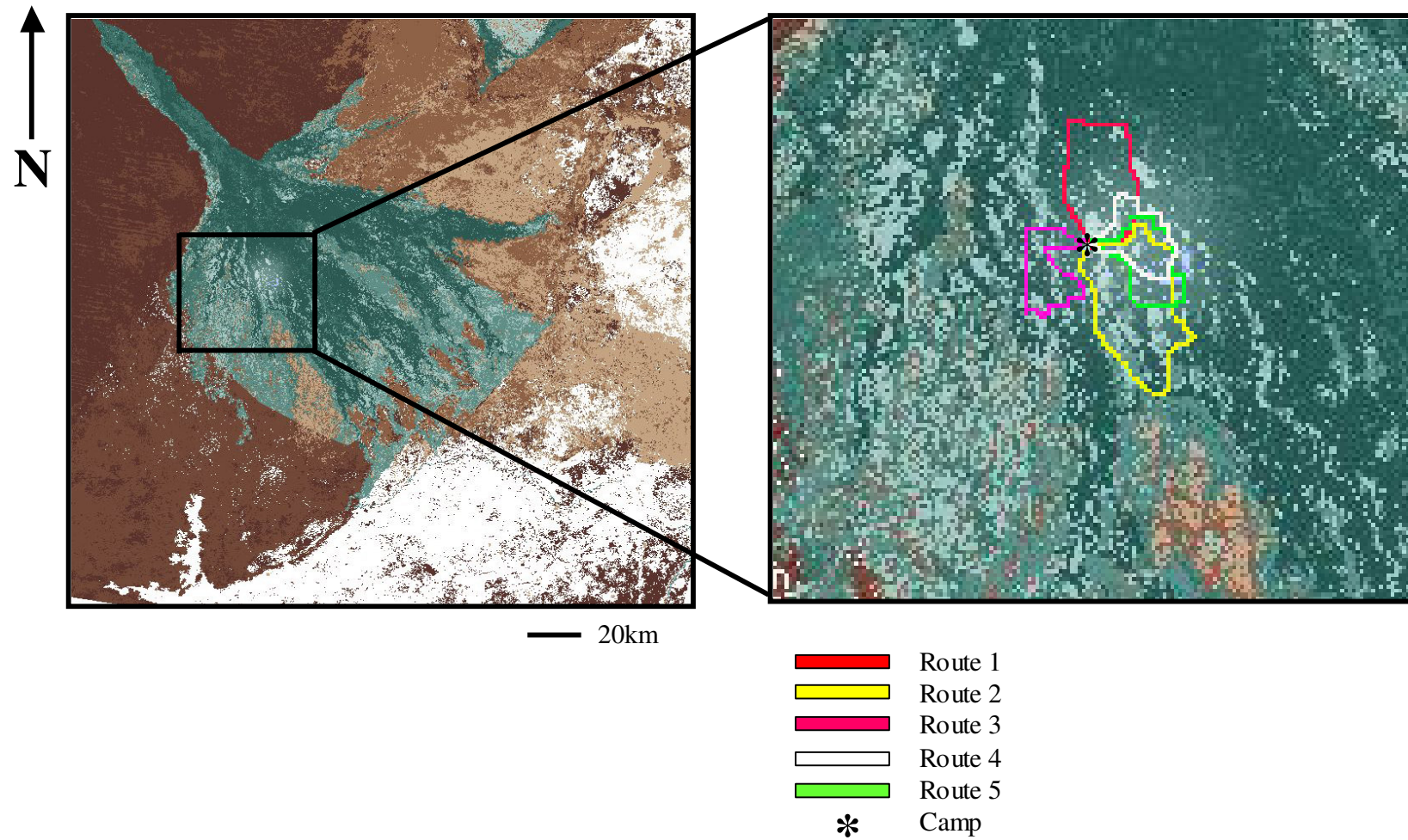
Figure 2.3: Map of routes driven in the study area

Chapter 3

The demography of elephants utilizing the Wildlife Management Area, NG26, in the Okavango Delta

Summary

A survey of elephants in NG26, was carried out between 2003 and 2005 to assess population structure and density of elephants utilizing the area and to confirm if this is a bull area. Fifteen monthly road transects carried out along a transect representative of the habitats available were completed during this period. Incidental data and reports of legal hunting of elephants between February 2002 and February 2005 were used to assess mortality. Densities, cluster size and population estimates were calculated for the rainy, flood and dry seasons in the habitats grassland/floodplain and woodlands, using the program DISTANCE for distance sampling.

Single males were sighted more frequently than herds. There was a tendency for larger groups of elephants to be sighted in the flood and dry season. It was found that the lowest densities (0.79 per km^2) occurred during the rainy season and the highest during the dry season (7.33 per km^2). The density did not exceed the theoretical maximum of 8.03 per km^2, although in the dry season the estimated density was higher than the recommended density of 2.59 per km^2.

Birth rate was 0.13 per adult. There was no obvious calving period. All of the elephants that were known to have died in the study area over the study period were males, of these 76% were mature bulls hunted for trophies.

3.1. Introduction

Understanding the spatial distribution, abundance, structure, age and sex-specifc movements of a species are major objectives of ecology (Andrewartha & Birch 1954; MacArthur 1972; Brown 1995) and have practical implications for wildlife conservation and management (Norton-Griffiths 1978). This information must be available in order to set and implement clear management objectives.

The Okavango Delta has an estimated 30, 971 elephants (Department of Wildlife and National Parks 1999). The Delta is a dynamic environment, constantly changing in shape and extent to small and large degrees. Annually, the areas available and therefore inhabited by large mammals are affected by the extent of the floods (Mendelsohn & el Obeid 2004). Local topographic features (e.g. islands) and channel flanking vegetation exert a strong influence on water distribution across the Delta (Gumbricht, McCarthy & Merry 2001).

Currently the elephant range in Botswana is growing, which is increasing levels of conflict with farmers on the leading western edge of the expansion (Gibson, Craig & Mosogo 1998; Wheelwright *et al.* 1996; Blanc *et al.* 2003). This expansion in range is possibly due to changes in the flow of floodwaters into this area and increases in population. Also high densities in specific areas are causing considerable structural damage to the vegetation (Mosugelo *et al.* 2002).

Elephants are spatially segregated by sex, with certain areas being utilized by bulls or female herds. Although these areas are not exclusive, predominantly 'bull areas' have been noted in the African elephant range (Laws, Parker & Johnstone 1975; Moss & Poole 1983; Moss 1988; Poole 1996b; Whitehead & Wielgart 2000). Spatial segregation occurs in northern Botswana, and it is likely that females are restricted to areas near permanent water whilst males are able to utilize areas further away (Gibson, Craig & Masogo 1998; Stokke & du Toit 2000). Therefore the western Delta is thought to be a bull area as permanent water sources are limited. The annual flooding of the Delta may open up areas for females and therefore seasonality is likely to affect spatial segregation of elephants.

In this Chapter I analyze data collected from monthly road transects to assess if the density of elephants in the study area is at a sustainable level and if the population is increasing. Specifically, I address the following questions:

- Do male elephants utilize the WMA NG26 more than females?
- Is the occurrence of musth bulls affected by season?
- Does season affect the group size of elephants?
- Is the density of elephants utilizing the study area affected by season?

3.2. Methodology

3.2.1. Incidental data

As the Okavango Delta is an open system, mortality could not be assessed through identification of known individuals and their re-sightings. Therefore, mortality was based on the number of dead elephants found, and those reported shot for trophies in the study area. The age of dead elephants was assessed by criteria outlined in section 2.3.4. Elephants hunted in the area were aged, in accordance with Botswana hunting requirements, through assessment of their lower jaw and tusk measurements by D. Peake and C. Craig (Mochaba Developments, Maun).

Musth in males was assessed through established criteria (Poole 1982) and any males sighted in this state throughout the study period were noted to see if a peak in the occurrence of musth was linked to season and an increase in herd size during the monthly transects.

3.2.2. Monthly transects

Ideally, line transects for DISTANCE sampling should be randomly positioned and of known length, or a grid of systematically spaced lines randomly superimposed on the study area (Buckland *et al.* 2001). Due to the restraints of seasonal conditions and vegetation in the Okavango Delta, as well as the limitation on the number of roads

allowed in the study area, transects were carried out along the roads already present, which led to an over representation of woodland habitat surveyed (Table 3.1). Due to a low number of sightings, habitat was limited to two types, grassland/floodplains and woodlands to ensure a large enough sample size for calculations and in which detect ability of elephants is likely to differ.

To control for bias in coverage towards woodland habitat, densities were made for each of the habitat types and extrapolated to represent the proportion of habitat types available in NG26 as determined by satellite mapping (Table 3.1; Jellema, Ringrose & Matheson 2002).

Due to the distribution and potential danger of the study animals, the seasonal floods and the distances to be covered, observations were carried out from a 4x4 vehicle. Transects were driven monthly from March 2003 until January 2005. However, due to exceptionally large floods in 2004, road transects could not be completed from April through to September 2004.

Once an elephant or group of elephant was sighted, the perpendicular distance from the road to the animals was measured using a Bushnell Yardage Pro 500 range finder (Bushnell Corp. USA) following the protocol outlined in Buckland *et al*. (2001) for sampling objects in clusters. Group size was estimated by counting individual animals within groups. The habitat type, age and sex of elephants sighted were noted (Table A.1., A.2., A.3., Appendix). Estimated age classifications used in analysis were; newborn (<1 year), calves (1-4 years), juvenile (5-9 years), adolescent (10-20 years) and adult (>21 years old).

Table 3.1: The percentage of each habitat type measured from 100% Minimum Convex Polygon (MCP) of Wildlife Management Area NG26 and the habitat survey.

Habitat type used in DISTANCE analysis	Proportion of habitats NG26	Habitat survey
Grassland/floodplain	0.59	0.34
Woodland	0.41	0.66

3.2.3. Data analysis

Kruskal-Wallis was used to test the effects of groupings, males or herds (both female and mixed herds) on the number of sightings and the affect of season on number of calves. Birth rate was calculated as the ratio of adults to calves less than one year sighted during the road transects. Students *t*-test was used to test if herd size were significantly larger in the months that musth males were sighted.

The underlying assumptions of normality were met for all tests (Zar 1984). Analyses were conducted using MINITAB (version 14, 2004) Results were considered significant where $\alpha = 0.05$.

3.2.4. DISTANCE analysis

Densities, expected group sizes, and total abundance in the three seasons in the two habitats were estimated using distance-sampling methodology and the program DISTANCE 5.0 Beta 5 (Thomas *et al.* 2005). Distance-sampling models the fall off in det`ectability with distance from the survey line to estimate the proportion of individuals not detected by the observer and hence an estimate of total individuals present. Specifically this uses information on the total transect length, number of elephants observed and the perpendicular distance of each elephant sighting from the transect line. Density per km^2 and population estimates were estimated for NG26 (Figure 2.1).

Data preparation and analysis followed the general guidelines for clustered data of Buckland *et al.* (2001). The detection function was modelled using the half-normal, uniform, hazard rate and negative exponential key functions and hermite polynomial, cosine, and simple polynomial series adjustments following guidelines in Buckland *et al.* (2001). Covariates used were grouping, classified as sightings of male(s) only or herds (including both female herds and mixed herds) and habitat. Models were fitted and the following statistics computed (i) Akaikes Information Criterion (*AIC*) (Buckland *et al.* 2001) when sample size was greater than 20, (ii) *AIC*$_c$, the small sample *AIC* when sample size was less than 20 (Burnham & Anderson 2002), (ii) ΔAIC, the difference in AIC between a fitted model and the lowest *AIC* of any model fitted and (iii) AICw or

AIC$_c$W, the AIC weight. From the set of *M* competing models, the AIC weight for model *M$_i$* was

$$AIC\mathrm{w_i} = \frac{\exp(-0.5\Delta AIC\ \mathrm{I}Mi)}{\displaystyle\sum_{i=1}^{M}\exp(-0.5\Delta AIC)}$$

The best model in DISTANCE was selected with the best relative fit assessed as the minimum *AIC* or *AIC*$_c$. Estimates of the variances of the probability density functions evaluated on the line were computed by maximum likelihood χ^2 goodness-of-fit Kolmogorov-Smirnov tests. These are reported routinely by DISTANCE, and were used to gauge the fit of estimated detection functions to the empirical histograms of distance data. The Kolmogorov-Smirnov tests were non significant for all models, thus providing no evidence for lack of fit of the detection function models.

Histograms were created from in gxhisto.exe application for Microsoft Excel (http://www.ruwpa.st-and.ac.uk/distance).

3.3.   Results

3.3.1. Population structure

Monthly road transects were carried out for 15 months, between March 2003 and January 2005. In total 263 elephants were seen in 73 sightings (Table 3.2.). The mean group size for female and mixed herds was 9.65 with a median of 8.50, ranging from 4 - 40 individuals. Mean group size for male only sightings was 1.71 with a median of 1.00.

Sightings were affected by the grouping of elephants (Kruskal-Wallis *H$_2$*=6.91, *P*<0.001), with male only groups being sighted more often than mixed herds (Figure 3.1).

Table 3.2: Summary of elephants sighted in the monthly transects. M = males, F = Female, UK = Unknown

	Sex /age/ grouping	Rainy season	Flood season	Dry season	Total
Number of transects		8	6	1	15
Number of sightings	Male (s) only	15	28	2	45
	Herds	8	12	8	28
	Subtotal	*23*	*40*	*10*	*73*
Number of elephants sighted	Newborn - M	1	0	0	1
	Newborn – F	0	0	0	0
	Newborn - UK	4	8	5	17
	Calves -M	2	0	0	2
	Calves –F	0	0	0	0
	Calves -UK	4	14	18	36
	Juveniles - M	1	3	1	5
	Juveniles – F	0	0	1	1
	Juveniles - UK	4	9	9	22
	Adolescents – M	14	18	4	36
	Adolescents – F	4	9	3	16
	Adolescents - UK	2	14	2	18
	Adults – M	22	32	2	56
	Adults – F	14	20	17	51
	Adults – UK	0	0	2	2
	Subtotal	*72*	*127*	*64*	*263*
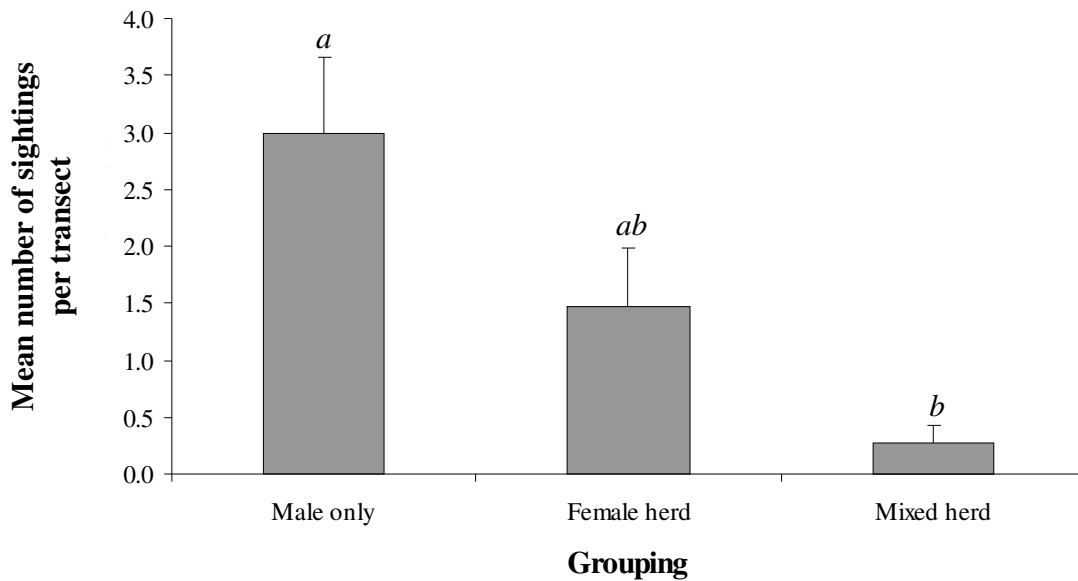
Figure 3.1: Mean (+SE) number of sightings of males, herds and mixed herds during monthly road transects.   Different italicised letters indicate significant differences identified by *post hoc* comparisons.   Sample sizes for sightings are outlined in Table 3.2.

There was a tendency for sightings of males in musth to be more frequent in the flood season, when larger herds were present, than the rainy season (ratio 1:0.6; Figure 3.2).   However, the size of female and mixed herds was not significantly larger when musth males were present than when they were not (t_{10}=-0.66, *P*=0.525).

Of the elephants sighted during the road transects, the majority were adults (Figure 3.3) and 34% were less than 10 years old. Sexing individuals less than 10 years of age is difficult, although males tended to be easier to identify and so bias is likely to occur in the sexes identified between 0-10 years of age. The birth rate was 0.13, with a ratio of 7.78:1 adults to newborn calves. Season did not affect the number of newborns sighted (Kruskal-Wallis H_2=0.705, *P*=0.703).

During the study period seventeen dead elephants were found or reported hunted, of which 76% were males hunted legally for trophies (Table 3.3).
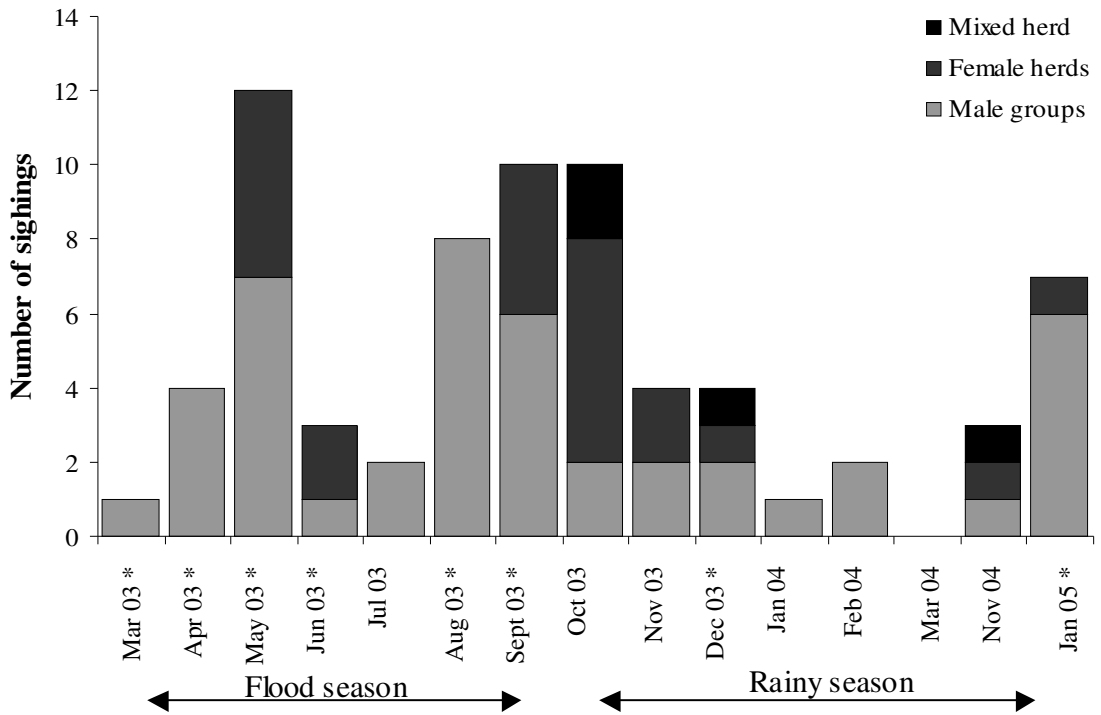
Figure 3.2: Number of sightings of males, herds and mixed herds during monthly road transects. * = month when musth bull was seen in study area.
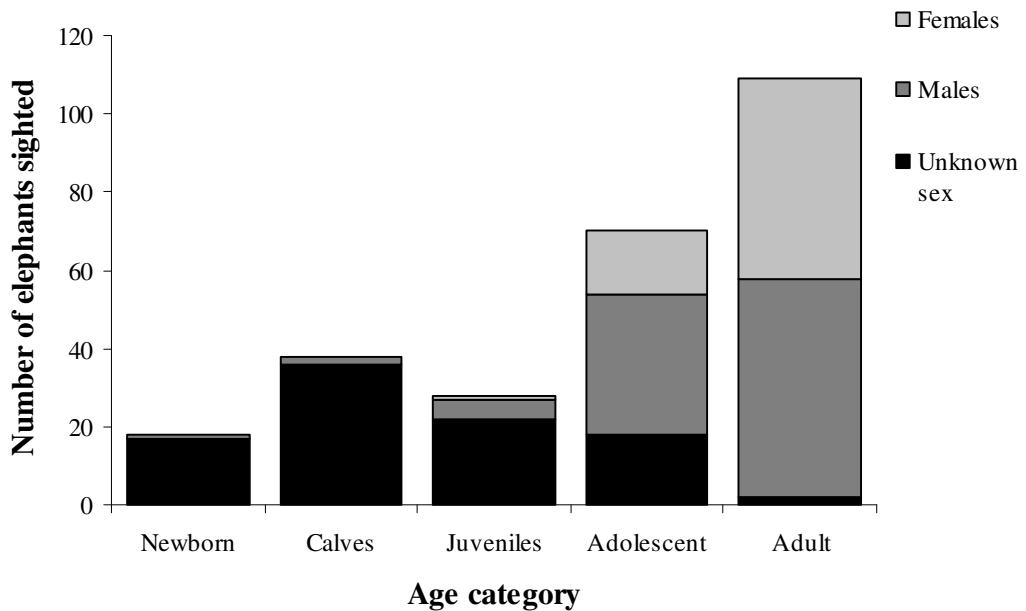
Figure 3.3: Age structure of elephants sighted during monthly transects in the study area. Sample sizes for sighting data are outlined in Table 3.2

Table 3.3: Sex, age and cause of death of elephants found in the study area.

Date	Age	Sex	Cause of death
13th Sept 2002	21-25 years	Male	Thought to be anthrax
April-Sept 2002	>36 years	Male	Hunted
18th June 2002	39 years	Male	Hunted
24th June 2003	47 years	Male	Hunted
7th July 2003	32 years	Male	Hunted
13th July 2003	36 years	Male	Hunted
13th July 2003	36+ years	Male	Hunted
15th July 2003	36+ years	Male	Hunted
21st Sept 2003	2 years	Male	Unknown
27th Sept 2003	< 1 week	Male	Unknown
April-Sept 2004	Unknown	Male	Hunted
April-Sept 2004	Unknown	Male	Hunted
April-Sept 2004	Unknown	Male	Hunted
April-Sept 2004	Unknown	Male	Hunted
April-Sept 2004	Unknown	Male	Hunted
April-Sept 2004	Unknown	Male	Hunted
11 Nov 2004	36+ years	Male	Poached/hunted. Skull and tusks missing

3.3.2. Density and population estimates

Preliminary exploratory analysis indicated no major problems with the data as assessed visually through fit of the line, although there was slight avoidance of roads (Figure 3.4). Maximum detection distance was 900m but since the graph showed a long tail of larger distances, data were truncated at 5% of data set to increase fit (Table 3.4). This excluded sightings > 450m away (Figure 3.4.).

Table 3.4: Summary of detection-function model fits with *AIC*, Δ *AIC*, *AIC*w (see section 3.2.4. for Akaike statistic definitions) *h:* habitat*; s:* season; *g:* grouping; (.) no covariates. Model type varies as all were modelled using the half-normal, uniform, hazard rate and negative exponential key functions and the model with the lowest *AIC* value was selected. All models were 5% truncated except were indicated.

Model	*AIC*	Δ *AIC*	*AIC*w
Half-normal (*s,g,h*)	717.55	0.53	0.38
Hazard (*s,g*)	732.89	15.87	2.2×10^4
Half-normal (*g*)	732.96	15.94	2.17×10^4
Half-normal (*s,h*)	733.46	16.44	1.17×10^4
Negative exponential (5% truncation)	734.42	17.40	1.05×10^4
Half-normal (*h*)	734.60	17.58	9.3×10^5
Hazard (s)	744.52	7.5	6.8×10^7
Negative exponential (.) –(no truncation)	803.63	86.61	9.68×10^{20}

From the models, habitat and grouping are the most influential factors affecting detection probability; with season also being important (Table 3.4 and Figure 3.5). Because the proportion of habitats surveyed were not representative of the proportion available in WMA NG26, and as there was not enough data to divide by grouping sightings to get cluster size and density estimates, the data were reanalyzed by habitat and season to get estimates of density from these, from which an unbiased total population estimate for the area could be produced
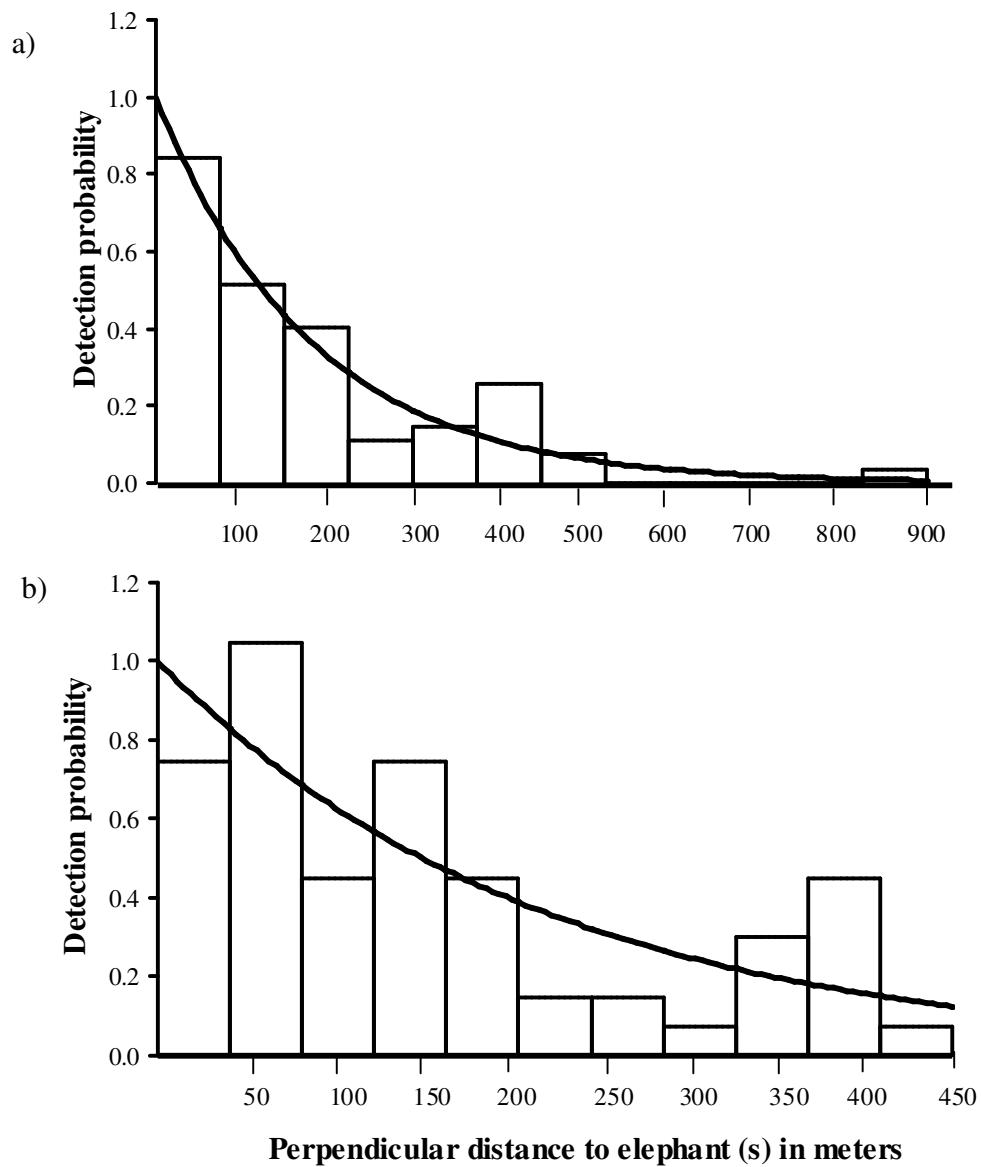
Figure 3.4: Detection probability of elephants with distance from transect line. A fitted negative-exponential key with one cosine adjustment term is shown as model of best fit. a) no truncation of data and b) 5% truncation of data.

a)

b)
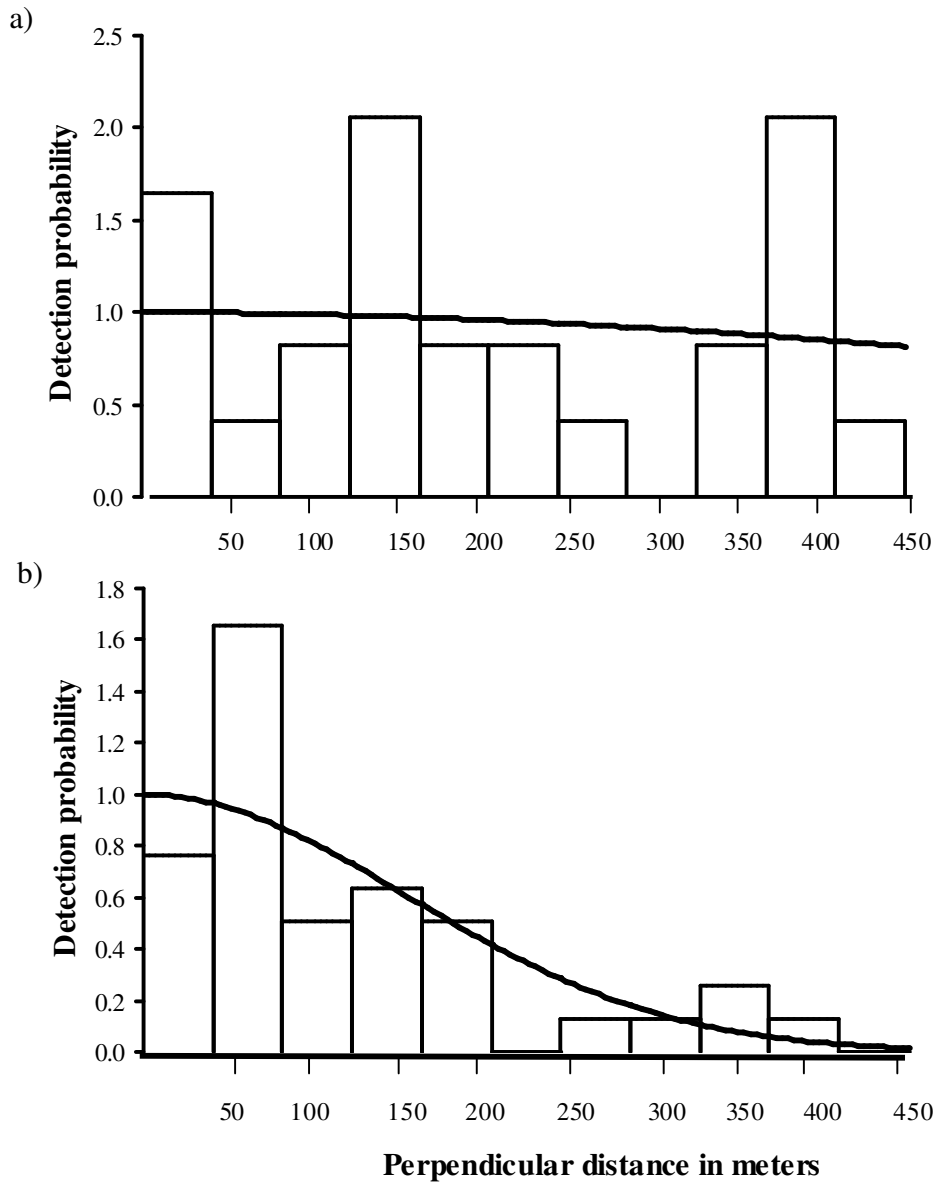
Figure 3.5: Detection probability of elephants with distance from transect line. A fitted half-normal key with one hermite adjustment term is shown as model of best fit. a) floodplain/grassland habitats b) woodland habitats.

Based on AIC_c and likelihood ratio tests, the best-approximating models for the detection function were selected for the two habitat types in the three seasons (Table 3.5). The density of the elephant utilizing the study area was dependent on season, with the highest density (7.33/km^2) occurring in the dry season and the lowest in the rainy season (0.79/km^2) (Table 3.5 and Figure 3.6). The density in the woodland habitat was higher than in the grassland/floodplain habitat throughout the seasons (Table 3.5 and Figure 3.6). Group size was also affected by habitat and season, with the largest occurring in the grassland/floodplain habitat during the rainy and flood seasons and in the woodland habitat during the dry season (Figure 3.7). It should be noted that the sample size for the dry season was small and so variances large.

Table 3.5: Estimated density of elephant per km^2 and population of WMA NG26 ($\pm$ confidence intervals)

Season	Habitat	Model	Density estimate per km^2	Population estimate for WMA NG26
Rainy	Grassland/ floodplain	Uniform	0.28 (0.10-0.79)	820 (290-2318)
	Woodland	Uniform	0.51 (0.19-1.34)	1055 (405-2749)
	Total		*0.79 (0.39-1.61)*	*2338 (1148-4763)*
Flood	Grassland/ floodplain	Uniform	0.81 (0.34-1.80)	2390 (1028-5557)
	Woodland	Half-normal	1.07 (0.50-2.32)	2208 (1023-4765)
	Total		*1.89 (1.08-3.30)*	*5568 (3180-9749)*
Dry	Grassland/ floodplain	Half-normal	0.44 (<0.01-1628)	1287 (0-4801500)
	Woodland	Uniform	6.90 (1.13-41.90)	14137 (2327-85884)
	Total		*7.33 (1.31-40.98)*	*21631 (3871-120880)*
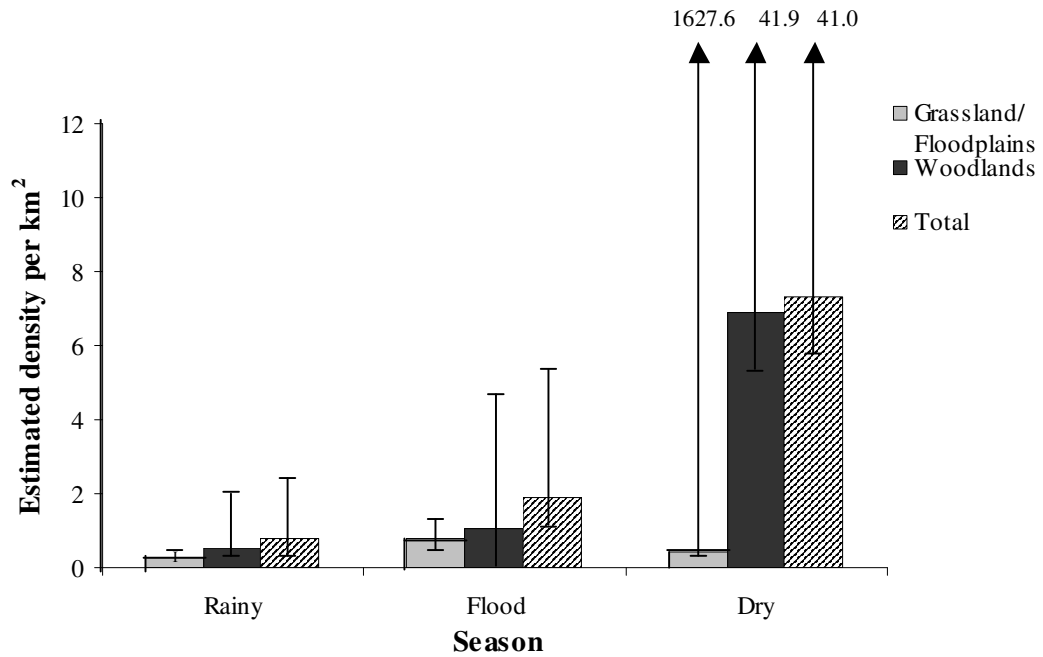
Figure 3.6: Estimated densities (+confidence intervals) for the habitat types in the three seasons
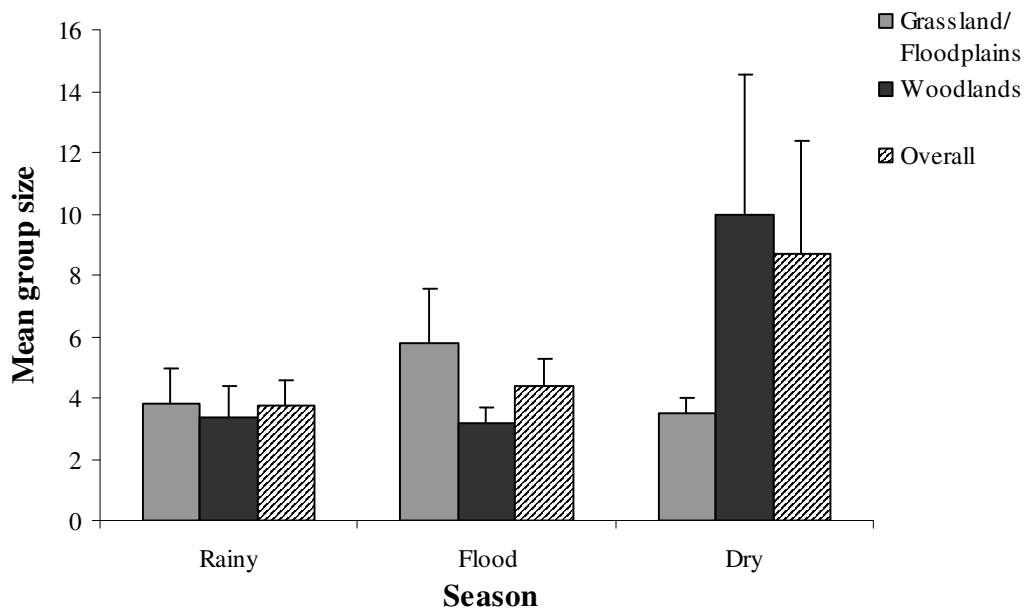
Figure 3.7: The mean (+SE) size of elephant groups sighted in the three seasons. Sample sizes for sighting data are outlined in Table 3.3

3.4.   Discussion

Bulls dominated the sightings of elephants in both the rainy and flood season, indicating that the study area is a bull area. Whilst more herds were sighted during the dry season, only one transect was driven during this season and so any conclusions drawn from this transect have limitations. Musth bulls were sighted most regularly during the floods when there was a tendency for more herds to be sighted. However, mixed herds (i.e. female herd with a male over 21 years of age present) were only sighted during the dry and rainy seasons, indicating that the musth males were not linking up with these female herds. Therefore, it seems likely that mating occurred infrequently in the study area and that the musth males were moving out in search of female herds and receptive females, which is also characteristic of a bull area.

The birth rate for the elephant in the study area is estimated at 0.13 per adult. Unusually, all elephants known to have died in the study area during the study period were male. Whilst two were young calves the remainder were mature bulls, most of which were shot legally for trophies, and as these have to be reported there will be an overrepresentation of this information in the data set. In addition most of the elephants sighted in the area were bulls and therefore any found dead are more likely to be males.

The effect that hunting, both legal and illegal, in the Okavango Delta is having on elephant numbers in the area is unlikely to be significant in view of the numbers taken. However, it could be affecting their behavioural ecology. As males continue to grow, both in height and weaponry, old male elephants are the primary target for the legal and illegal ivory trade (Laws 1969; Lewis 1984; Poole & Thomsen 1989). One or two males, that have the longest musth periods during a period when most of the females are receptive, dominate male elephants hierarchal system (Poole & Moss 1981). If these are taken out the effects on both the males and females can be significant, with males increasing their fighting to gain the top places and immature less experienced males trying to mate with females; which can be a dangerous and stressful for the females (Moss 1983; Poole 1989). In addition old males have an important part to play in the social and ecological development of adolescent males (Chapter 4; Slotow *et al.* 2000; Slotow & Van Dyk 2001) and the full effects of their loss on population dynamics and social stability have not been fully investigated.

The elephants formed larger groups in the flood and dry season, which is contrary to other parts of Africa where the largest groups are located in the rainy season (Poole 1994; Dublin 1996; Charif *et al.* 2005). The floods may be affecting group size by forcing the elephants into restricted areas, indicated by their higher densities, and larger groups are formed as a consequence. Mean group size of elephants and other mammals are known to decrease in poor quality habitat (Olivier 1978; in Katugaha, de Silva & Santiapillai 1999; Loe *et al.* 2006), since smaller groups are better able to exploit a patchily available resource (White, Tutin & Fernandez 1993). The densities of elephant in the study area throughout the seasons were comparable to other African elephant ranges and areas in Botswana (Table A.4, Appendix). The highest density of elephants was found during the dry season, corresponding to densities found along main water courses, such as the Linyanti river (Gibson, Craig and Masogo 1998). These unusual findings can again be attributed to water, but more to the limitation in water availability than its over-abundance and consequent restriction of elephants into smaller areas (Gibson, Craig and Masogo 1998). Habitat also affected the densities of elephants, with higher densities being found in woodland habitat. The elephants appeared to be more dependent on this habitat during the dry season estimated densities were much higher and this could be linked to times of stress and an increase in food diversity utilization (Chapter 5)

During the rainy and flood seasons the density of elephant in the study area is low at 0.79 and 1.89 per km^2 respectively. These densities could increase if the population is expanding westward into historic ranges as has been postulated (Melton 1985; Gibson, Craig & Masogo 1998). This theory can also be supported by the dominance of males that utilize the area, as males are more exploratory and found in new areas before females (Clout & Efford 1984; Spinage 1994). The birth rate for elephants in the study area is estimated at 0.13 per adult, therefore it seems unlikely that the habitat is of a low quality. However, the herds utilizing the area are migratory and are only found in the study area for short periods. Repeated surveys over the next five years will give more indication as to whether female herds are moving into the area, or whether the area is a bull area.

The Okavango Delta is a very heterogeneous terrain and therefore the distribution of elephants is likely to be random, with clustering of elephants in certain areas. Therefore, the density for elephants calculated for this area will not be applicable to other areas of the Delta. Aerial surveys covering a larger area may be better suited for this. However, counting the number of individuals present in a population at a particular time from an airplane cannot provide sufficient detailed demographic data to identify critical life history stages and the causes of variation in population growth rate, predict population trends of responses to changes and disturbances accurately, or enable effective management (Wheelwright *et al.* 1996). Therefore a combination of both aerial distance-sampling alongside detailed ground surveys, throughout the Delta in the different seasons, will give a clearer indication of actual population and size, demography and some of the factors limiting population size and/or growth.

3.5. Conclusions

At present the study area is a bull area, indicated by: the dominance of male sightings; resident males; visiting female herds; and the musth males moving out of the area and not joining up with herds in the area. In this Chapter I have shown that:

- The study area was a bull area, with female herds being sighted infrequently.
- Larger groups were sighted in the flood season.
- There was a tendency for more musth males to be sighted in the flood season
- Season affected density, with higher density of elephants utilizing the study area during the dry season and the lowest density in the rainy season.

Chapter 4

Adolescent male African elephant behaviour

Summary

Adolescence in male elephants is a very influential period during which they leave the herd and assert themselves in the male hierarchy. This in turn can affect their future mating success. Focal and observational data were collected on male elephants in the Okavango Delta, Botswana, to assess how behaviour and social interactions differed between age groups (10-15 years, 16-20 years, 21-25 years, 26-36 years, >36 years), with particular reference to the period of adolescence and independence. Adolescent males (10-20 year olds) showed a preference for larger social groupings and being in closer proximity to other elephants, of which the majority were males older than 36 years. Males in the 16-20 year age group spent significantly more time socialising (greeting and sparring) than older or younger males. Males >36 years of age vocalized more frequently than males in younger age groups. The tendency of adolescent males to associate with other elephants, in particular older males, may provide them with the opportunities to establish themselves within the social hierarchy and to learn appropriate patterns of social behaviour from older individuals.

4.1. Introduction

Knowledge about adolescence and the attainment of independence in male African elephants is limited, as studies have tended to concentrate on the behaviour of females and mature bulls (Buss 1961; Douglas-Hamilton 1973; Croze 1974; Poole 1982; Moss 1983, 1988; Moss & Poole 1983; McComb *et al.* 2001). In many mammals, puberty is a key prompt for one of the sexes to disperse (Dobson 1982; Alberts & Altmann 1995), but in the African elephant there appears to be additional triggers for males to leave the

natal herd e.g. although some males initiate their own departure (Lee 1986), others are forcibly expelled from the group by the matriarch (Sikes 1971; Douglas-Hamilton 1972; Moss 1988). Most males leave their herd at 14 years of age during the period of adolescence (10-20 years), although there is great variation with some leaving as early as eight years old while others delay leaving until 20 years of age (Douglas-Hamilton 1972; Poole 1994, 1996b; Lee & Moss 1999). Puberty, the period of becoming physically capable of reproducing, occurs between the ages of nine and fifteen (Short, Mann & Hay 1967; Hanks & McIntosh 1973; Lee 1986). Yet, whilst they are sexually mature at 17 years (Laws 1969; Poole 1994), few rarely get the opportunity to mate until their thirties (Poole 1994). The process of becoming independent takes between one and four years (Lee & Moss 1986), and newly independent males follow one of several different courses to social maturity: some leave their herd and join up with another family for a couple of years; others go off to a bull area and join up with groups of bulls; and others stay in the natal herd home range moving from family to family (Poole 1996b), or vary in a shifting pattern.

However, despite the potential importance of adolescence and independence in affecting an individual's social standing and future reproductive success, these periods have not been studied in detail. In this Chapter, I analyze focal behavioural data to determine whether adolescent males behave and interact differently to males in other age groups. Specifically, I address the following questions:

- Do adolescent male elephants exhibit a higher frequency of social interactions, such as greeting and sparring?
- Do adolescent male elephants have a higher rate of vocalization?
- Do adolescent male elephants show a group size preference?
- Do adolescent male elephants prefer to be in closer proximity to other elephants?

4.2. Methodology

4.2.1. Data collection

Data on associations, behaviour were collected during 30-minute focal observations, which were collected by myself or under my direct supervision thereby ensuring consistency of the data. Data on the focal individual's social grouping (Table 2.2) and, where applicable, the identity of other individuals present, were collected at the start of the focal period. The activity (Table 4.1), habitat (Table 2.1), location (measured with Garmin GPS III plus, Garmin International Inc, USA), identification of and distance to (Table 4.2) the nearest neighbour from the focal individual were recorded every five minutes. For analysis, activities were quantified as the rate per 30-minutes; nearest neighbour distance was averaged across the 30-minute period.

Focal observations were undertaken on males from the five age groups throughout the study period and throughout the study area. Males were located by driving set (Figure 2.3) and random routes during the morning (05.30-11.59) and afternoon (12.00–19.00). The identity and ages of the elephants present was then assessed, and a focal animal was selected by choosing one individual that had not knowingly been sampled previously. Identification of the individual was later verified upon return to the camp using digital photographs and identification files. This approach was not ideal as replicate samples were obtained for some individuals e.g. 286 focal periods were replicates from known animals. Yet, given the numbers of elephants identified (417 males, 34 females, 15 calves) this was the most sensible way to collect field data. To avoid pseudoreplication, where repeat data had been collected from the same individual during the study period and where more than one elephant was sampled within one social grouping at a given time, a single focal period was selected at random for analysis. Overall, 283 independent focal samples were collected from known individuals, of which 222 were of elephants in a social situation.

During observation periods, the length and rate of audible vocalizations were noted and the identity of the caller was documented wherever possible. Callers were determined by audible (e.g. direction and intensity) and visual clues such as ear flapping

(McComb 1996), listening, forehead vibrations (Poole 1988) and the opening of the mouth (McComb 1996).

Table 4.1: Activity codes used during the collection of focal data.

Code	Activity	Description
1	Sleeping	Standing in one place with eyes closed not feeding for longer than one minute
2	Feeding	Chewing or the manipulation of food items by the trunk
3	Drinking	Intake of water
4	Social behaviours	Focal elephant interacting with at least one other elephant
4.1	Greeting	Raises trunk to mouth of another elephant
4.1.1		Another elephant greets focal elephant
4.2/4.3	Sparring/playing	Head to head contact and pushing between two or more elephants
4.4	Pushes from behind	Either with trunk resting over back of the other and pushing or using their tusks.
4.4.1		Focal elephant is pushed from behind
4.5	Display	Destruction of vegetation without eating, crashing through vegetation, headshaking
4.5.1		Another elephant is displaying
4.6	Head over back	Standing or walking with head and and/or trunk resting on the back of another.
4.6.1		Another elephant has his head and or trunk on back of the focal elephant
5	Mud bathing/ dusting	Collection of dust or mud with trunk and then using trunk to throw dust over themselves.
6	Walking	To move at a steady pace in a general direction
7	Walking whilst feeding	To move at a steady pace while chewing or manipulating food items
8	Standing	Standing in one place with eyes open not feeding for longer than one minute
9	Vocalization	
9.1		Vocalization by focal individual
9.2		Vocalization by known other
10	Running	Moving at pace, generally when alarmed
11	Other	Focal elephant does another activity e.g. pushes over tree to eat
11.1		Another elephant does another activity

Table 4.2: Distance codes used during the collection of focal data.

Code	Distance (m) to nearest neighbour
0	0m, elephants are touching
1	0 – 4m
2	5 – 9m
3	10 – 24m
4	25 – 49m
5	50 – 99m
6	100 – 199m
7	200 – 299m
8	300 – 399m
9	400 - 500m

Habitat was classified on the basis of the satellite vegetation-mapping project by the HOORC (Jellema, Ringrose & Matheson 2002). The main ecotypes within the study area were floodplains, island vegetation, *Terminalia sericea* woodland, *Colophospermum mopane* woodland and *Hyphaene ventricosa* palm woodland (Table 2.1).

4.2.2. Statistical analyses

4.2.2.1. Social behaviours

As the data were not normally distributed, and could not be transformed, the effect of season and age on the frequency of social behaviours (Code 4: Table 4.1), greeting (Code 4.1), sparring/playing (Codes 4.2 and 4.3), vocalization (Code 9) and distance to nearest neighbour were analyzed separately using nonparametric statistics. As the dry season only lasted one month each year, the volume of data collected during this period was limited. Consequently, only data from the rainy and flood seasons were compared using a Mann-Whitney U test. Differences between age classes were compared using a series of Kruskal-Wallis tests; statistically different groups were then identified using the *post hoc* procedures outlined by Siegel and Castellan (1988). For the analysis of the

vocalization and non-social activity data all the independent focals, not just social focals, were included.

4.2.2.2. Social groupings

Patterns of association of individual male elephants in different age classes were quantified using all observations (i.e. focal and non-focal) of animals seen during the study. Each time a male elephant was observed, the number of male and female animals within 500m was recorded; animals were aged according to the criteria outlined in Chapter 2. Assuming that the presence of >1 animal together represents a 'choice' of all individuals to associate with one another, data were recorded separately for every animal in each social grouping observed i.e. a group of five individuals would generate five data points; every animal in the cluster would be categorised as having been in a group of five individuals. Differences in the mean observed group size between age classes was analyzed using a Kruskal Wallis test. To determine whether any observed differences in mean group size between age classes were an artefact of associations with females, the data were also analyzed considering only sightings of all male groupings. Trophy hunting of elephant occurred between April and September from 2002 onwards. To see if this had an effect, a Mann-Whitney test was used to compare group size in non-hunted versus hunted periods.

Patterns of association between males of different age classes were examined using simple association indices (Ginsberg & Young 1992). The association ratio between two particular age classes was defined as: R=X/(N-D), where X is the number of viewing periods where animals of age class A and age class B were seen together, N is the total number of viewing periods across all age classes and D is the number of viewing periods in which neither animals of age class A and age class B were sighted. The frequency with which animals of a given age class were sighted with males in each age class were analyzed using chi square tests, assuming an expected equal distribution.

Preferences for nearest neighbour were analyzed using χ^2. Firstly a test was carried out to see if their choice of nearest neighbour was non-random. If it was then the highest partial value was removed and χ^2. recalculated. This was repeated until χ^2. was non-significant.

4.3. Results

4.3.1. Social behaviours

The distribution of focal samples by age class and season is summarised in Table 4.3. Season did not affect the frequency of social behaviours per half hour focal (Mann-Whitney test: $W_{88, 124}$=9800, P=0.145) or sparring/playing ($W_{88, 124}$=9349, P=0.908) exhibited by focal individuals. However, it did affect the rate of greeting ($W_{88, 124}$=9863, P=0.046), with a higher level during the rainy season.   The frequency of social behaviours did not vary significantly with age (Kruskal-Wallis test: H_4=9.11, P=0.058) nor did sparring/playing (H_4=1.82, P=0.769). The rate of greeting did vary significantly with age (H_4=13.31, P=0.010).   In all instances, 16-20 year old males exhibited the highest rate of these behaviours (Figures 4.1-4.3), but there were no significant subgroups identified in the *post hoc* testing procedures for either the frequency of social behaviours (Figure 4.1); the rate of greeting was lowest in males >36 years old (Figure 4.2).   Conversely, age did not affect the frequency that focal males were greeted by other individuals (H_4=3.38, P=0.496).

Table 4.3: Summary of the data collected in the different seasons of the study. Total sightings data used to analyze patterns of social grouping; social focal data used to analyze patterns of social behaviour within groups (see Code 4, Table 4.1) and nearest-neighbour distances; focal data used to analyze patterns of activity and vocalization.

Data set	Age class	Rainy	Flood	Dry	Total
Total sightings of male elephants		1484	2288	300	4072
Total sightings of male groups		661	1014	99	1774
Total sightings of male elephants in male only groups	10-15 yr	96	168	28	292
	16-20 yr	146	321	33	500
	21-25 yr	166	273	27	466
	26-36 yr	300	527	48	875
	>36 yr	387	437	23	847
	Sub-total	*1095*	*1726*	*159*	*2980*
Social focal data	10-15 yr	19	28	3	50
	16-20 yr	21	19	2	42
	21-25 yr	15	27	0	42
	26-36 yr	13	26	4	43
	>36 yr	20	24	1	45
	Sub-total	*88*	*124*	*10*	*222*
Focal data	10-15 yr	19	30	3	52
	16-20 yr	21	22	2	45
	21-25 yr	20	30	1	51
	26-36 yr	24	48	4	76
	>36 yr	26	32	1	59
	Sub-total	*110*	*162*	*11*	*283*
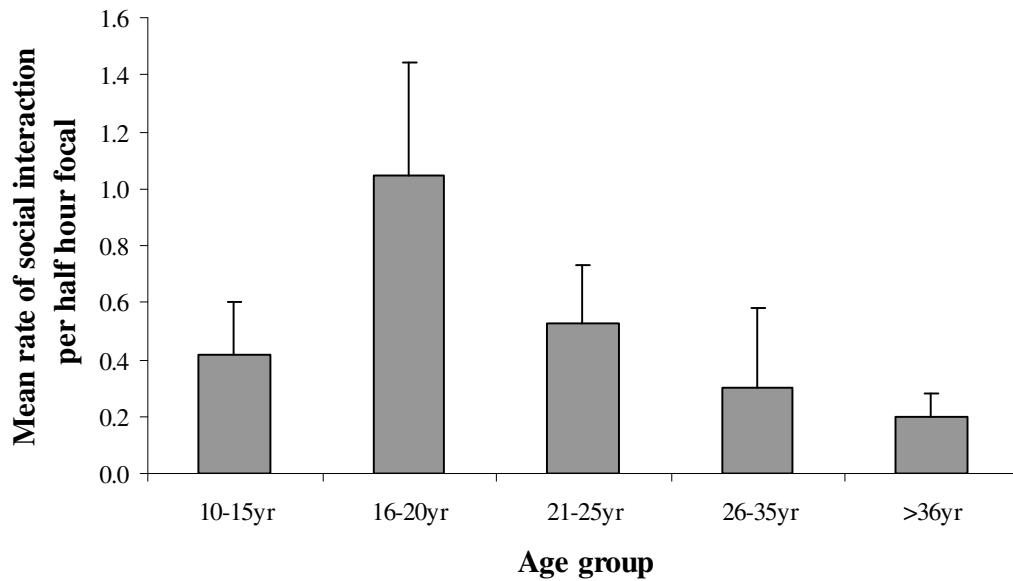
Figure 4.1: Mean (+SE) rate of social behaviours per half hour focal within the different age groups. Sample sizes for social focal data are outlined in Table 4.3.
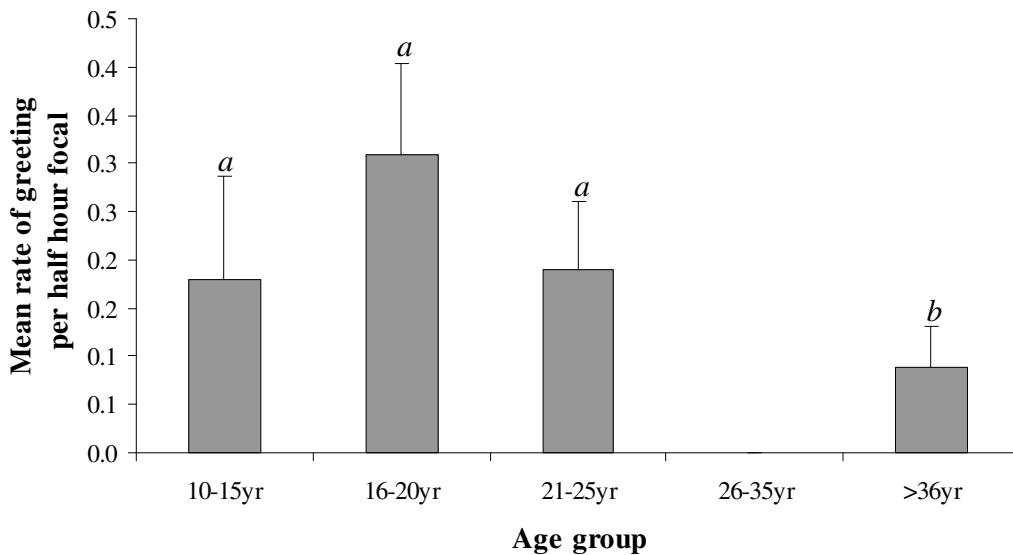
Figure 4.2: Mean (+SE) rate of greeting per half hour focal within the different age groups. Sample sizes for social focal data are outlined in Table 4.3. Letters denote significantly different groups as identified by *post hoc* comparisons.
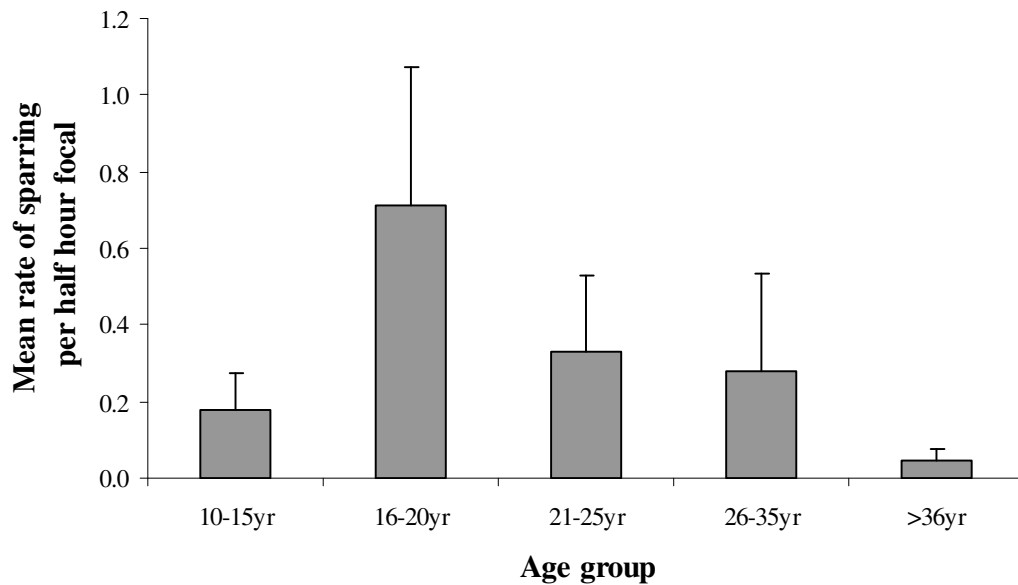
Figure 4.3: Mean (+SE) rate of sparring per half hour focal within the different age groups. Sample sizes for social focal data are outlined in Table 4.3.

The rate of vocalization per half hour focal was not affected by season ($W_{110, 162}=14540$, $P=0.144$) or age ($H_4=8.83$, $P=0.066$), although this latter result is close to significance with males >36yr vocalizing most often (Figure 4.4). Focal data collected from musth males were excluded, as it is known that this significantly affects their tendency to vocalize (Poole 1987b).

The only non-social activity significantly affected by season was the amount of time that male elephants spent dusting and/or mudbathing, with the highest level recorded in the rainy season (Figure 4.5; $W_{110, 162}=16640$, $P=0.012$). Male elephants spent the majority of their time feeding (57%), walking (16%) or resting/sleeping (12%).
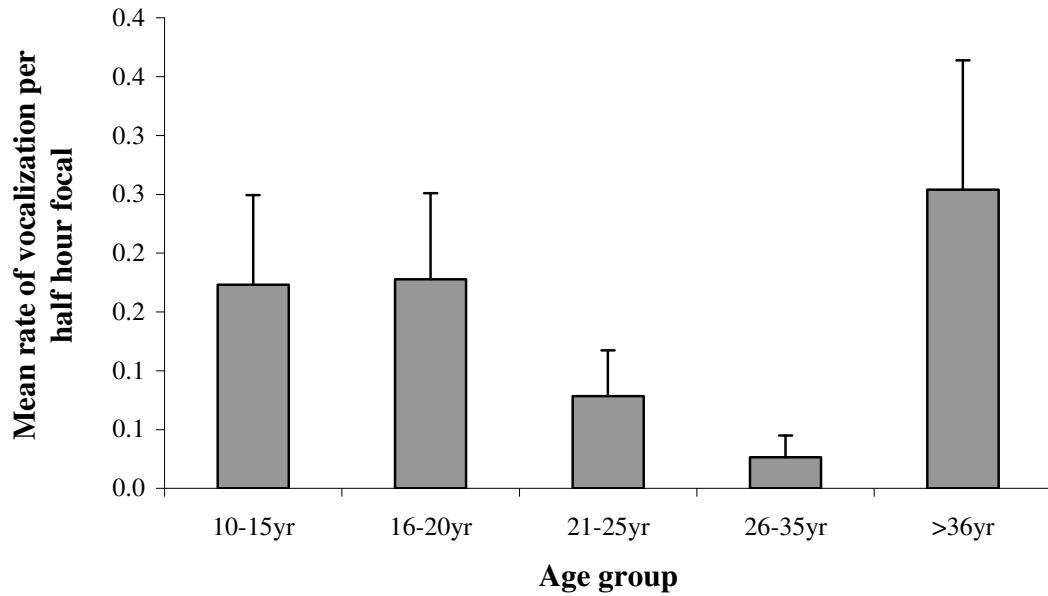
Figure 4.4: Mean (+SE) rate of vocalization per half hour focal within the different age groups. Sample sizes for focal data are outlined in Table 4.3.
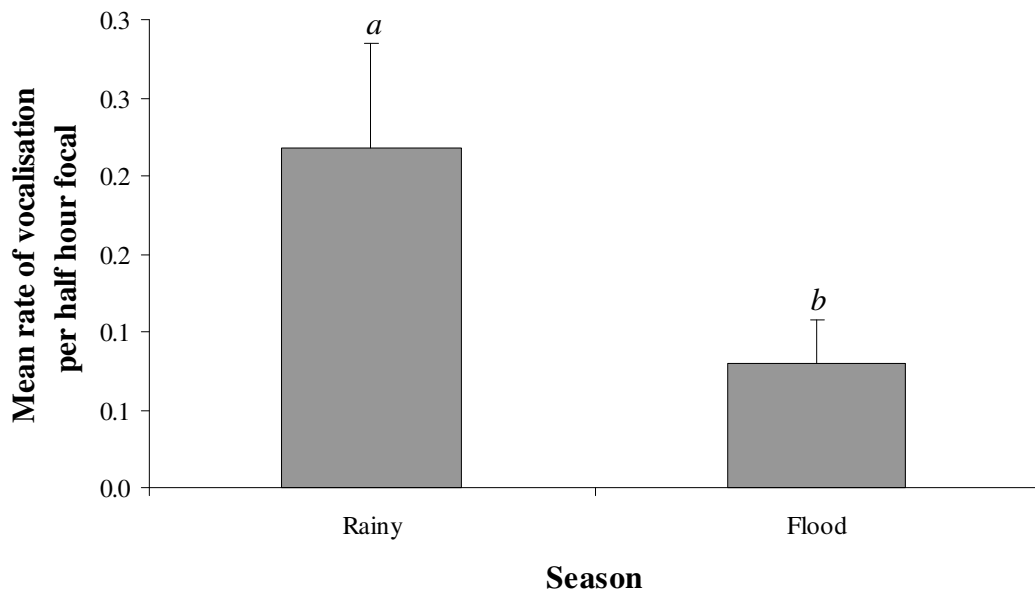
Figure 4.5: Seasonal variation in the frequency of dusting and mudbathing by male elephants. Sample sizes for focal data are outlined in Table 4.3.

4.3.2. Social groupings

Age significantly affected the number of male and female elephants individual males were sighted with (Kruskal Wallis test: H_4=431.53, P<0.001; N=4072 sightings of male elephants). Mean group size declined significantly with increasing age class, with the exception of 26-36 and >36 year old males, which were not significantly different (Figure 4.6). The trophy hunting of elephants in the area did not affect the size of male groups ($W_{675, 1099}$=601903, P=0.762).
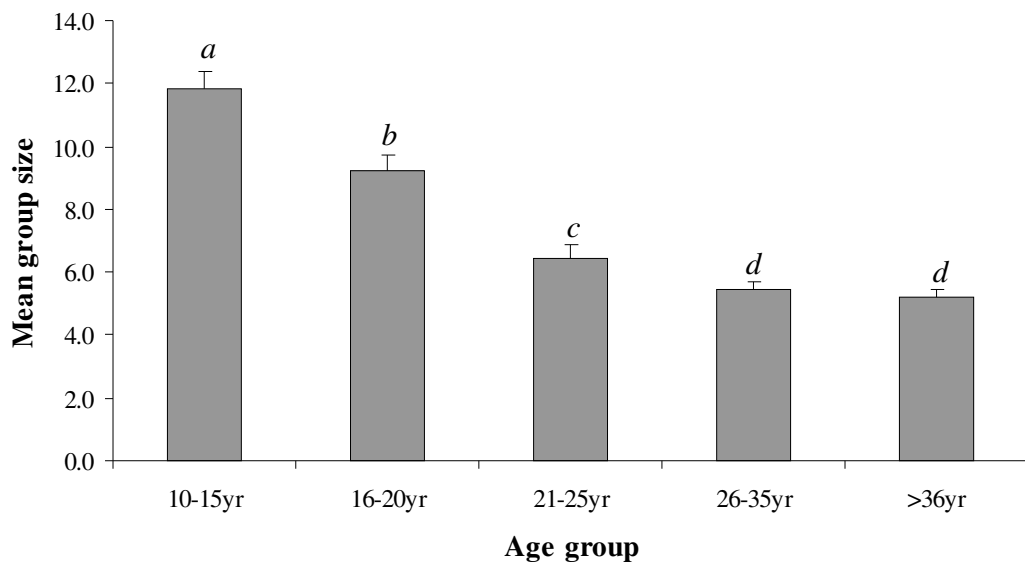
Figure 4.6: Mean (+SE) number of male and female elephants in social groups of males of different age classes. Letters denote significantly different groups as identified by *post hoc* comparisons. Sample sizes for focal data are outlined in Table 4.3.

All-male groupings (N=1774) varied in size from 1 to 17 individuals, with a mean of two, median of one and a mode of one. The size of all-male groupings was not affected by season (H_2=1.90, P=0.386), but was significantly affected by age (H_4=94.90, P<0.001), with younger males being sighted in larger groups (Figure 4.7).
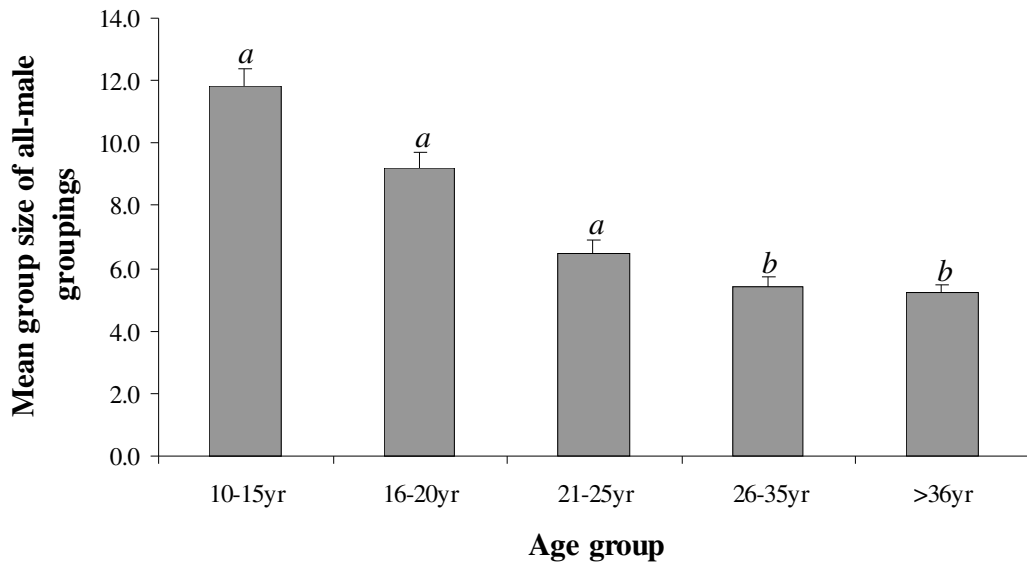
Figure 4.7: Mean (+SE) number of elephants in all-male social groups of males of different age classes. Letters denote significantly different groups as identified by *post hoc* comparisons. Sample sizes for focal data are outlined in Table 4.3.

Males of all age classes did not associate equally with males of other age classes (10-15yr: χ^2_4=119.63, P<0.001; 16-20yr: χ^2_4=99.81, P<0.001; 21-25yr: χ^2_4=10.26, P=0.036; 26-36yr: χ^2_4=30.53, P<0.001; >36yr: χ^2_4=15.09, P=0.004). All age groups spent a higher proportion of time in groups with males of a similar age (Figure 4.8).
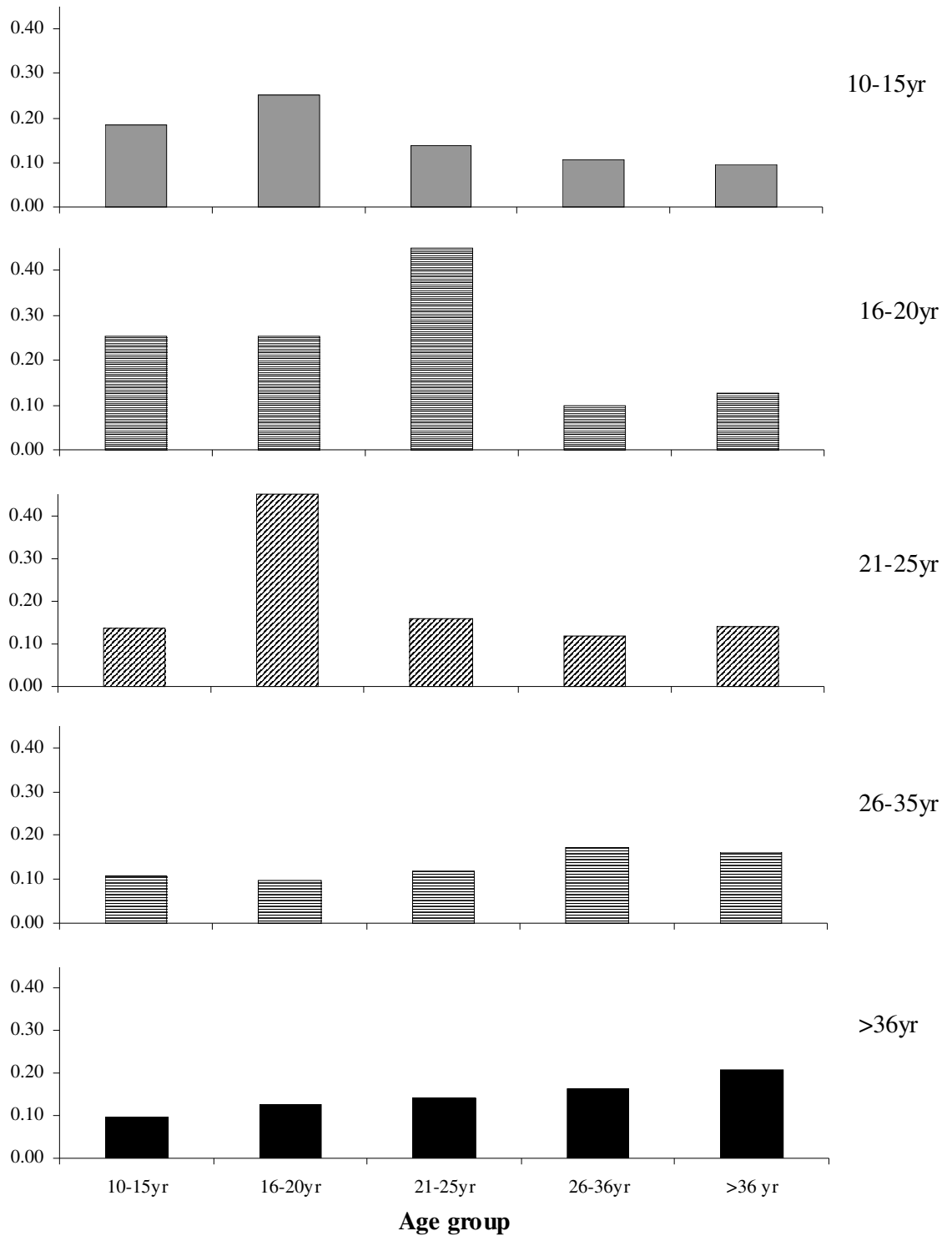
Figure 4.8: Association indices of males within different age classes. Age group of focal age class is indicated on right hand side of figure. Sample sizes for social focal data are outlined in Table 4.4.

Season did not affect the distance to nearest neighbour (Kruskal-Wallis test: H_2=3.82, P=0.148), but age did (H_4=17.68, P=0.001), with median distance increasing with increasing age (Figure 4.9). Male elephants preferred to be closer to older elephants (Figure 4.10; Table 4.4). 10-15yr were least likely to be closest to other 10-15yr olds (χ_4^2=70.94, P<0.001) and males of all age groups preferred to be closest to males >36yr (10-15, χ_3^2=8.65, P=0.03; 16-20yr, χ_4^2=70.94, P<0.001; 21-25yr, χ_4^2=122.46, P<0.001; 26-35yr, χ_4^2=146.98, P<0.001; >36yr, χ_4^2=317.83, P<0.001).
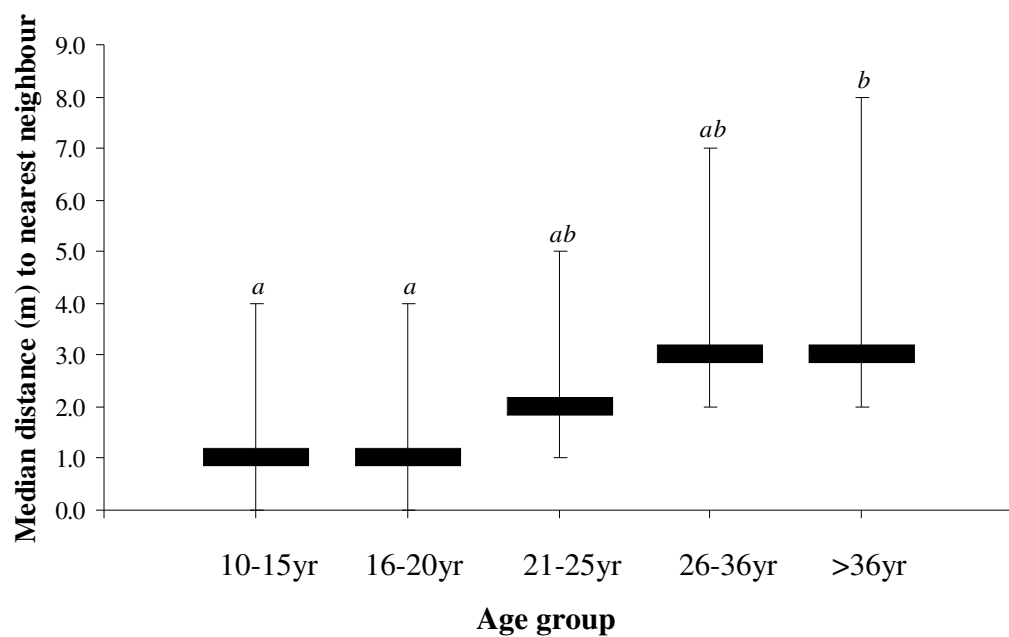
Figure 4.9: Median (± interquartile range) distance (m) between focal males and their nearest neighbour during half hour focal observations. Letters denote significantly different groups as identified by *post hoc* comparisons. Sample sizes for focal data are outlined in Table 4.3.

Age of focal individual
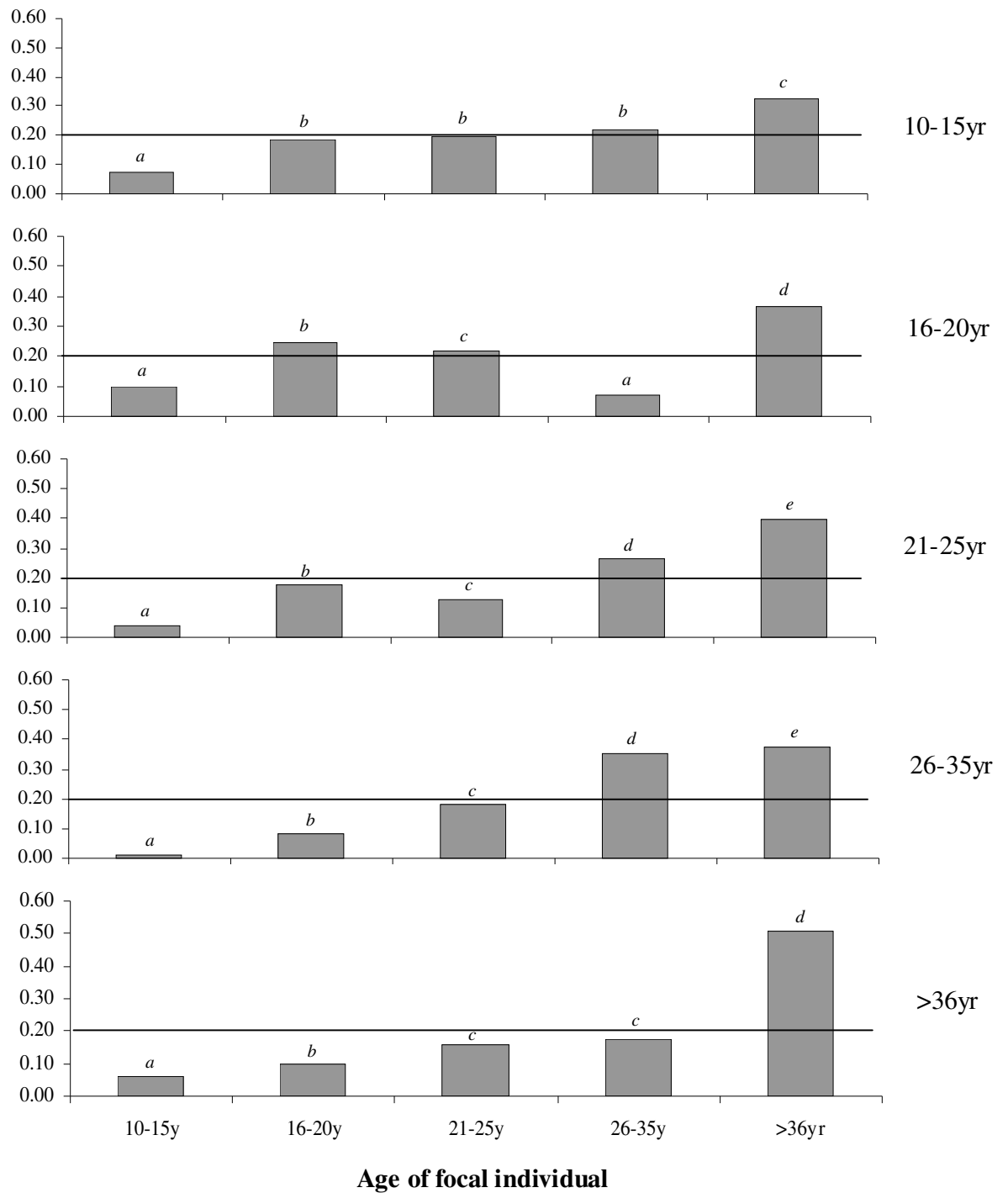
Figure 4.10: Percentage time males in different age categories were recorded as the nearest neighbour to focal males during half hour observations. Letters denote significantly different groups as identified by *post hoc* comparisons. Horizontal lines equals expected values. Sample sizes for focal data outlined in Table 4.4.

Table 4.4: Number of observations focal individual of certain age group had nearest neighbour of different age groups.

Age group of nearest neighbour	Age group of focal individual				
	10-15yr	16-20yr	21-25yr	26-35yr	>36yr
10-15yr	12	31	33	36	54
16-20yr	26	63	57	19	94
21-25yr	13	57	41	86	130
26-35yr	3	24	51	101	106
>36yr	31	50	81	90	257

4.4. Discussion

The relative size and morphology of an elephant's brain suggests that memory, communication and coordination are all highly developed (Shoshani 1991; Lee & Moss 1999). It has long been accepted that young elephants are taught by females within the herd (Lee & Moss 1986; 1999), and observations from captive elephants indicate that elephants are quick to learn from older individuals (Moore & Munnion 1989; de Alwis 1991; McKnight 1992; Daim 1995; Lee & Moss 1999; Moore 2000; Bhaumik 2005). In females this extends beyond sexual maturity, with matriarchs passing on knowledge of the local area, including where to go during times of difficulty such as drought (Viljoen 1989a; McComb *et al*. 2001), and older females assisting in the birth and raising of calves (Moss 1988).

In contrast, independent males change their social environment, from the highly social herd to the much more fluid social system exhibited by adult males. Correspondingly, newly independent males must learn to traverse and forage within new areas as well as learning the rules of social etiquette when interacting with other males. In primates, a physically independent but naïve individual learning how to deal with the social and physical environment is facilitated by proximity to experienced individuals (Pereiva & Altmann 1985; Box 1999). This agrees closely with what was observed in this study. Adolescent males (10-20 yr) were the most social age-class; they were recorded in the largest groups (Figure 4.6) and with the lowest nearest-neighbour distances (Figure 4.9). In addition, they often had older bulls as their nearest neighbour within social groupings (Figure 4.10). This may, therefore, provide an opportunity for

young males to learn from older individuals. Furthermore, this pattern of association was not limited to adolescent individuals, as males of most age-classes typically had older bulls as their nearest neighbour (Figure 4.10).

The significance of older males in regulating the behaviour of younger individuals has been demonstrated in recent re-population and translocation programs in South Africa, where, in the absence of older bulls, young males have caused a number of management problems through inappropriate behaviour, such as killing white rhino (*Ceratotherium simum*) in the Pilansberg NP, South Africa (Slotow, Balfour & Howison 2001; Slotow & van Dyk 2001). These problems are thought to arise through young males coming into musth prematurely (Slotow *et al.* 2000), which would be suppressed in normal situations by older bulls (Rasmussen, & Krishnamurthy 2000; Slotow *et al.* 2000). Furthermore, males over 36 years of age were the most vocal age group in this study, which is contrary to previous perceptions, which suggest that rates of communication would decrease as male elephants age (J. Poole, *pers. comm.*). Consequently, these calls may serve to assert the male's dominance amongst other males of similar status and/or to serve as a tool for teaching and disciplining younger bulls during their social development. The older males may be the ones choosing to be closer to the younger males, to suppress musth and therefore eliminate mating competition. In addition we cannot rule out the possibility of kin recognition and old bulls are providing protection and lesion to related males (Petrie, Krupa & Burke 1999).

An alternative explanation for the close proximity of adolescent males to older elephants could be that of predator avoidance. Although as tall as, if not taller, than most female elephants when they leave their natal herd, a lone adolescent male is still vulnerable and susceptible to predation (Joubert 2006). Therefore, being closer to older males could offer them protection, and personal observations suggest that, within male groups, older elephants will form a ring around younger individuals as has been observed in female herds. Apart from providing physical protection, time spent by juveniles in proximity to adult individuals also provides a context in which they may readily react to, and learn about, the alarm or cautious behaviour of adults in dangerous situations (Box 1999).

However, it is unlikely that predator avoidance is a function of the tendency for older males to associate with one another except, perhaps, where poaching and hunting occur; in these circumstances, larger groups may be more able to spot human threats, although, conversely, larger groupings may be more visible to hunters. Yet, there was no evidence from this study that the trophy hunting affected social group sizes. Instead, group size appeared to be related to seasonal conditions affecting the availability of resources, such as fresh grasses and fruit (Chapter 3 & 5).

Adolescent males were observed within significantly larger groups than males >21 years old (Figure 4.6), generally because they tended to be sighted more often with female and mixed herds. This could be because: (i) they may not yet have left their natal herd; (ii) they had left their natal herd but joined up with another herd; or (iii) they had joined up temporarily with a herd to spar with the young males present in that herd. The tendency of adolescent males to be in groups with males of a similar age (Figure 4.8) could be attributed to the hypothesis that they leave their natal herd with a male of a similar age (J. Poole, *pers comm*), as in some primates (Mitchell 1994; Strier 2000). Associating with similarly aged males will enable an individual to establish its position in the hierarchy that dominates the bull social system (Poole 1989a). In particular, sparring with young males within their own and other herds, and greeting males generally, may play a role in the establishment of social position and familiarisation with social etiquette. In this study, mean greeting and sparring rates were highest in 16-20yr old adolescents and lowest in the oldest males, although differences in sparring rates between age-classes were not significant because of the large variation within age-classes.

The decline in the sparring rate with age is consistent with the establishment of a social hierarchy and the ritualization of male-male competition. In many mammalian species, male rank or fighting ability is a good indicator of mating success e.g. red deer *Cervus elaphus* (Clutton-Brock, Guinness & Albon 1982), fallow deer *Dama dama* (Moore *et al.* 1995), chimpanzee *Pan troglodytes* (Constable *et al.* 2001) and domestic cat *Felis catus* (Say, Pontier & Natoli 2001). This is especially so when mate guarding is the principal means by which males gain access to sexually receptive females e.g. elephant seal *Mirouga angustirostris* (Haley, Deutsch & Le Boeuf 1994), African

elephant (Poole 1989b), Soay sheep *Ovis aries* (Preston *et al.* 2001). However, as fighting can impose significant fitness costs, it tends to decrease in frequency once a hierarchy has been established i.e. with age (Parker 1978), and also tends to become more ritualised. In elephants this reduction in physical confrontation is assisted by the signalling of musth periods, which are accompanied by temporal gland secretions, urine marking and vocalizations (Poole 1981b, 1982, 1987b, 1989a); despite being in this highly aggressive state, contests are rare, suggesting that opponents are able to indirectly assess the dominance of each other with relative accuracy (Poole 1989a). The period of adolescence could, therefore, be considered the most important stage in their development if sparring during this period acts to determine their social rank and future mating opportunities.

4.5. Conclusions

Male elephant society is a complex hierarchy, which changes with regard to rank, sexual state, age and presence or absence of males in certain areas. Adolescence in males is perhaps the most changeable and influential period as they go through puberty, become sexually mature, become independent and ascertain their rank in the male hierarchy. In this Chapter, I have shown that:

- Adolescent males exhibited higher levels of social behaviour than males of other age-classes.
- The highest rate of vocalization was seen in >36yr males.
- Adolescent males (10-20 years) were seen in larger social groups than males of older age-classes.
- Within social groups, adolescent males were closer to other elephants.
- When in social groupings of just males, adolescent males were more often closer to males older than themselves.

In the next Chapter, I consider the habitat preferences of adolescent male elephants in comparison with female herds and older bulls.

Chapter 5

Habitat utilization of the African elephant
in the Okavango Delta

Summary

Data were collected to assess movements of adolescent male elephants and the effect of age and sex on habitat selection and utilization in the Okavango Delta. The Okavango Delta is a unique environment that supports a large elephant population, but it is unknown which resources are important to them. Data were collected through observations on male and female elephants, satellite radio collar data on adolescent males and focal data on male elephants. Feeding preferences were also investigated by analyzing focal data collected on male elephants. Observational, satellite and focal data were collected throughout the three-year study.

The satellite collared adolescent males utilized an average area of 4823 km^2. They did not select habitat randomly; there was positive selection for island vegetation and the grassland/floodplain habitat in relation to availability and negative selection for Terminalia *and mopane woodlands.*

The male and female elephants observed from the ground positively selected island vegetation and mopane woodlands and negatively selected grassland/floodplain and Terminalia *woodland habitats. The bulk of male elephant's food was made up of grasses and sedges and the trees* Colophospermum mopane, Croton megalobotrys *and* Hyphaene petersiania*. Both male and females were selective in their choice of habitat. However, they utilized the habitat in proportion to availability during the dry season. Sex affected selectivity in the flood season, with females being more selective. Age had no affect on habitat utilization or selection in male elephants.*

5.1.   Introduction

An animal's home range is defined as 'the entire area over which an animal normally moves', this being very distinct from the total area over which it moves (White and Garrott 1990). Fundamentally, the home range is the area that meets the energy requirements of the individual or group that occupies it (Jewell 1966), and its size and shape is determined by many different factors (Sanderson 1966). However, the area covered by an animal is just one means by which to measure the interaction between the environment and the individual. Movement within the home range is similarly affected by a diversity of factors including the spatio-temporal distribution of resources (Leuthold & Sale 1973; Sukumar 1989; Viljoen & Bothma 1990), intra-specific interactions (Isbell, Cheney & Seyfarth 1990), inter-specific interactions and human disturbance (Osborn 2004; Douglas-Hamilton, Krink & Vollrath 2005). The home range of an individual is also likely to change significantly during its development. For example, the home range of a juvenile male elephant will match that of the matriarch when in its natal herd, but change in size and location when he leaves the natal herd and joins bull society. It may then change again once he is established in the hierarchy and has knowledge of available resources, including receptive females.

However, with human population growth, the loss and fragmentation of natural habitats has led to increased conflict between wildlife and humans (Parker & Graham 1989; O'Connell-Rodwell *et al.* 2000). Due to their large size and their ability to destroy a farmer's crop in a single night (Sukumar 1989), conflict between humans and elephants is often high on the agenda of local wildlife departments. The resolution of such conflicts is, in part, reliant on identifying the basic requirements of elephants in terms of e.g. resources and social interactions. Yet, identifying these requirements in areas where habitats have already been seriously impacted can be problematic. Consequently, data are required from undisturbed environments where elephants do not come into contact with humans on a regular basis, such as the Okavango Delta. Furthermore, the elephant population within Botswana is of particular conservation importance because it is part of a larger population that traverses the borders of Namibia, Angola, Zimbabwe and Zambia. Lastly, because the Delta lacks distinct wet and dry seasons due to the occurrence of the annual flood, it also provides an

opportunity to test generally accepted theories on elephant ecology, but which were developed in other habitats.

With a poor digestive system and large body size, elephants require six to eight percent of their body weight in food each day (Sukumar 1991). Consequently, elephants are an important component of their ecological communities and can seriously degrade habitats at certain densities where resource availability is limited (Ben-Shahar 1993; Herremans 1995; Nelleman, Moe & Rutina 2002), which can in turn lead to reduced fertility and growth rates (Laws & Parker 1968). Previous studies have shown that their diet consists of up to 500 different plant species (Sukumar 1991), although the bulk of this consists of only a few species (Sukumar 1990, 1991; Tchamba & Seme 1993; Babaasa 2000; De Boer *et al.* 2000; Smallie & O'Connor 2000). Diet composition varies with region, vegetation cover, water availability, soil nutrient composition, rainfall and season (Owen-Smith 1988; Codron *et al.* 2006), in certain areas they are mainly browsers (Jachmann & Bell 1985; Dublin 1995) and elsewhere grazers (Field 1971; Western & Lindsay 1984).

As the bulk of an elephant's diet consists of a relatively small number of different plant species, it is not surprising that, across species, individuals have been shown to be selective in the habitats they utilize and that their pattern of utilization changes in relation to variation in resource availability (Laws, Parker & Johnstone 1975; Eltringham 1977; du Toit & Owen-Smith 1989; Sukumar 1989; Tchamba & Seme 1993; Dublin 1996; Stokke 1999; Babaasa 2000; De Boer *et al*. 2000; Stokke & du Toit 2000, 2002; Blake, Douglas-Hamilton & Karesh 2001; Blake *et al.* 2003). Such patterns of habitat selection also have important implications for social behaviour and for management.

Among large herbivores, males and females differ in their nutritional requirements and in their need to obtain high quality resources (Stokke & du Toit 2002). Therefore, the forage selection hypothesis suggests that such differences may lead to segregation of the sexes by virtue of their size dimorphism (Berteaux 1993; Mysterud 2000; Hellstedt & Henttonen 2006). For example, female elephants are smaller than males but have higher energy requirements due to gestation and lactation and, as a consequence, are more selective over the resources they utilize. In contrast, adult males

can tolerate a wider range of forage quality and be less selective. Furthermore, females also need to be closer to water due to their smaller size and the presence of young (Stokke & du Toit 2002). Although, in the Delta, the availability of water in both the rainy and flood seasons may enable them to roam further from permanent water sources thereby giving them access to more habitats. In contrast, the indirect-competition hypothesis proposes that differences in the pattern of habitat use between males and females may arise because one sex is a superior competitor thereby forcing the other into utilizing suboptimal habitats (Conradt, Clutton-Brock & Thomson 1999; Perez-Barberia & Gordon 1999; Mysterud 2000; Conradt *et al.* 2001; Pelletier & Festa-Bianchet 2004). Although both these hypotheses emphasise the size dimorphism between males and females, such physical differences may also be evident between old and young animals of the larger sex. For example, adolescent male elephants are comparable in size to adult females. Consequently, patterns of spatial segregation may be evident between both males and females and between mature and adolescent males.

The patterns of habitat utilization by male elephants are of particular management concern because males tend to be the main crop raiders (Sukumar & Gadgil 1988; Sukumar 1990; Hoare 1999; Osborn 1998; 2003; Smith & Kasiki 2000; Chiyo & Cochrane 2005; Ogola & Omondi 2005). Furthermore, males have a propensity for exploration, which is important in terms of the invasion of depopulated areas and in response to a lack of resources (Stickel 1954; Osborn 2004), but as the Delta is surrounded by agricultural land, this tendency also increases the likelihood of conflict with humans. However, patterns of habitat utilization by male elephants have rarely been considered, in particular the patterns of habitat utilization by adolescent male elephants. Therefore, in this Chapter I address the following questions:

- What is the area ranged by adolescent males, and is this affected by rainfall and/or season?
- How far do adolescent male elephants move in a 24hr period, and how does this vary between seasons?
- Do adolescent male elephants exhibit preferences for particular habitat types, and are these preferences consistent across seasons?

- Do patterns of habitat selection vary between males and females and/or between males of different ages?

- Are the elephants of the Okavango Delta mainly grazers during the rainy season?

- Are the food preferences of elephants affected by the annual floods of the Delta?

5.2. Methodology

5.2.1. *Home range and core area size*

Five adolescent males were fitted with satellite collars as outlined in Chapter 2 (Section 2.3.1). Based on tooth wear (Laws 1966), tusk measurements (Hanks 1972), height (Croze 1972; Douglas-Hamilton 1973; Douglas-Hamilton, Hillman & Moss 1981; Lark 1984; Jachmann 1991; Lee & Moss 1995) and foot dimensions (Western, Moss & Georgiadis 1983) these individuals were estimated to be between 12 and 17 years old. The data collected from these five adolescent males provided information at a greater spatial scale (up to 10,000km^2) than from the ground observational data (604km^2). Initially, collars were programmed to record the animal's location once every 12hr; following the replacement of the original collars, however, the frequency of recording was increased to one location every 8hr (Chapter 2).

Prior to analyses, errors (e.g. locations >100km from the previous download) and duplicates were removed. Data on home range size and utilization were analyzed using the Animal Movement SA 2.0 extension (Hooge & Eichenlaib 2000) in Arcview GIS 3.2 (ESRI 1996). The following parameters were calculated for each collared elephant in the rainy and flood seasons: (i) 100% minimum convex polygon (100% MCP); (ii) 95% MCP; (iii) 95% kernel density isopleth; and (iv) 70% kernel density isopleth (Galanti *et al*. 2006). The inflection point in the slope of the utilization distribution indicated that the 70% core area best described the animal's core centre of activity. Insufficient data were collected in the dry season for analysis of home range size, so data are presented only for the rainy and flood seasons.

5.2.2. Distance moved

Minimum daily distance travelled was estimated from locations of satellite-collared individuals; distances were estimated from the first reading after 0500 on consecutive days. As collars were accurate to 10m, zero values were converted to a half measure of 0.005km, as it is unlikely that an elephant had not moved at all in the intervening 24hrs. For analyses, values were log transformed and a two-way ANOVA was used to determine the effect of season and individual, with Bonferroni *post hoc* tests where appropriate.

5.2.3. Habitat selection and utilization

Patterns of habitat selection and utilization were quantified using locational data collected from satellite collared individuals and from ground observations of elephants sighted within the intensive study area in the vicinity of the research camp (see Section 2.1). The pattern of data collection for collared individuals is outlined above. Ground observations of elephants sighted within the study area were collected from February 2002 to February 2005. Sampling was restricted to daylight hours (0600-1900) and carried out on a daily basis. Observations were recorded when elephants were encountered whilst driving set and random transect routes (Stokke & du Toit 2002); the five set routes, totalling 145km, were selected because they were accessible throughout the seasons. The transect driven on a given day was selected pseudo-randomly e.g. to avoid local safari activities. In total, >18,000 km were covered (~57% and ~43% on set and random routes respectively). Sightings of groups of males containing one or more of the released elephants were excluded from analyses, as it was not known if the habitat choice of these groups was influenced by the presence of the released elephants.

At each sighting, the location, habitat (Table 2.1) and size and composition of the group were recorded. A group was defined as any aggregation of individuals within 500m of one another; where possible, the identification and sex of each individual was recorded. Individuals and groups were categorised as outlined in Table 2.2. The GPS location of all observations was plotted in Arcview and linked to the satellite vegetation map to ensure that habitats were identified correctly.

One inherent problem with quantifying patterns of habitat utilization from observational data is that animals are not equally visible in all habitats. Therefore, in this study, analyses were restricted to those observations collected within the maximum distance that elephants could be reliably observed in the most visually congested habitat: dense woodland (Table 2.1). This critical distance was 60m (Figure A.1. Appendix).

5.2.3.1. Compositional analysis of satellite data

Patterns of habitat selection and utilization were quantified at two levels using compositional analysis based on log ratio transformed proportions (Aebischer & Robertson 1992) in the Excel program (Smith 2003): (i) the composition of individual home ranges versus the composition of the total available habitat, and (ii) the proportional use of habitats (i.e. the proportion of fixes within each habitat) versus the composition of the home range. In both analyses, a lambda test (λ) was initially conducted to determine whether habitat use/selection deviated significantly from random. Where habitat use/selection was significantly different from random, habitats were ranked according to the degree of preference. Ideally, for compositional analysis, data from a minimum of six animals should be utilized. However, financial and logistical constraints meant that only five individuals could be fitted with satellite collars.

As compositional analysis requires that the number of habitats analyzed can not exceed the number of individuals followed (Aebischer, Robertson & Kenward 1993), the 47 habitat types present in the Delta (Jellema, Ringrose & Matheson 2002; Table 2.1) were grouped into four major groupings for the analysis of the satellite data; grassland/floodplain; mopane (*Colophospermum mopane*) woodland; 'other' woodland (*Acacia* spp., *Combretum* spp., *Terminalia sericea*); and island vegetation (*Hyphaene petersiana* and/or *Phoenix reclinata*). In the area accessible from the ground, *Terminalia sericea* was such an abundant species that five habitat types were utilized in the analyses: grassland/floodplain, mopane woodland, other woodland, island vegetation and *Terminalia* woodland.

For the analysis of satellite locational data, the area of available habitat within the Delta and within individual MCPs were calculated using Arcview GIS 3.2 based on

the data collated by Jellema, Ringrose and Matheson (2002) (Figure 2.3). For the ground observation data, the proportion of available habitat was estimated by recording the habitat type and distance that could be seen on both sides of the vehicle every 400m along all routes from which data were collected. The habitat composition of the Delta and the area accessible from the ground is summarised in Table 5.1.

Table 5.1: Habitat composition of the Okavango Delta and the area accessible from the ground.

Habitat type	Delta	Habitat survey
Grassland/floodplain	61%	30%
Mopane woodland	19%	3%
Other woodland	18%	24%
Island vegetation	2%	11%
Terminalia woodland	-	33%

5.2.3.2. Analysis of ground observation data

To test whether elephants were randomly distributed in the available habitats, the total number of (i) male groups, (ii) female herds and (iii) males of different ages observed in each habitat was compared to an expected frequency distribution in each of the three seasons elephants using the Manly's standardized selection ratio (Manly, McDonald & Thomas 1993). Manly's standardized selection ratio for each habitat (*Bi*) was calculated as:

$$\beta i = \frac{Wi}{\sum_{i=1}^{n} Wi}$$

where $W_i = u_i/a_i$, u_i is the proportion of sightings of elephants of a given social grouping (e.g. male groups, female herds etc) in habitat i, a_i is the proportion of the total road distance surveyed in habitat i and n is the total number of habitat classes. This index represents the estimated probability that elephants will select habitat i within the area studied. The log-likelihood χ^2 statistic with Bonferroni-adjusted 95% confidence

intervals was then used to test the null hypothesis that habitat use was directly proportional to spatial availability (Manly, McDonald & Thomas 1993).

Differences in the diversity of habitat utilization between females and males, and between males of different ages were tested using the method described by Stokke and du Toit (2002). The proportion of sightings of each social grouping in the ith habitat when census effort is equalized across all habitats (P_{ui}) was calculated as:

$$Pui = \frac{ni/Pai}{\sum ni/Pai}$$

where n_i is the number of sightings of each social grouping in the ith habitat and P_{ai} is the proportion of total road distance surveyed in habitat i. The Shannon-Wiener diversity index (Shannon 1948) was then calculated as: $H' = \Sigma P_{ui}(\log(P_{ui}))$. H' varies in value from 0-1, where 1 indicates most diverse use of habitats and 0 the least diverse use. For each social grouping, the evenness of habitat use was calculated as: $J' = H'/\log k$, where k is the number of habitat categories; $J'=1$ indicates complete evenness of selection of habitats. A randomization test, set up in Microsoft Excel, with 10,000 repetitions was used to calculate significance probabilities (Manly, McDonald & Thomas 1993).

5.2.4. Feeding behaviour

The proportion of time spent feeding was recorded during focal observations (Code 2, Table 4.1); procedures for the collection of focal behavioural data are outlined in Section 4.2.1. Where possible, during feeding bouts animals were classified as (i) grazing, (ii) browsing, (iii) eating bark/roots or (iv) eating fruit. However, due to difficulties observing what animals were eating, data on the classification of feeding behaviour were limited. Therefore, all observations of feeding behaviour were pooled; however, as these data are not independent, they have not been analyzed statistically.

5.3. Results

The data collected from satellite collars and observations on elephants utilizing the study area are summarised in Table 5.2. There was no significant difference in the number of downloads obtained in the rainy and flood seasons from the five collared males (Paired-sample t test: $t_4 = -2.116$, $P = 0.102$), indicating that weather patterns did not affect the ability of the collars to upload to satellites.

Table 5.2: Summary of the (a) satellite and (b) observational data collected. Satellite data were used to analyze home range size and habitat utilization; consecutive 24hr locations were used to quantify distance travelled. Observational data were used to analyze the effect of age and sex on habitat utilization and selection. Feeding observations where used to assess the effect of habitat and season on feeding.

(a)

	Abu2	Abu3	Abu4	Abu5	Abu6	Total
Number of locations	1,825	1,617	2,160	2,678	2,521	10,801
No. consecutive 24hr locations	875	683	805	920	747	4,030

(b)

	Sex	Season			
		Rainy	Flood	Dry	Total
Sightings of elephants	Male only group	527	753	48	1,328
	Female herd and mixed herd	147	197	23	367
	Total	*674*	*950*	*71*	*1,695*
No. of elephants seen		3,998	5,040	1,505	10,543
No. of feeding observations from focal data	Male	955	1461	274	2690

5.3.1. Home range area

Mean ($\pm$ SE) 100% MCP home range area in the rainy and flood seasons combined was 4824 $\pm$ 1431 km^2 (Table 5.3), with the area used in the rainy season (3837 $\pm$ 2540 km^2) significantly larger than in the flood (2479 $\pm$ 689 km^2) season (Paired-sample t test: $t_4 =$ 2.876, $P = 0.045$ (Figure 5.1). Rainfall seemed to affect home range size, with increases

in cumulative rainfall reflected in increases in the area utilized by the collared males (Figure 5.2).

Table 5.3: Home range (100% MCP and 95% kernel) and core area (70% kernel) size (km^2) for each of the five collared adolescent male elephants.

Elephant ID	100% MCP	95% kernel	70% kernel
Abu2	4,551	1,657	391
Abu3	4,450	1,094	256
Abu4	3,228	2,440	807
Abu5	1,721	600	118
Abu6	10,168	3,183	820
Mean (±SE)	4,824 ± 1,431	1,795 ± 463	478 ± 143

a) Abu2   b) Abu3   c) Abu4

d) Abu5   e) Abu6
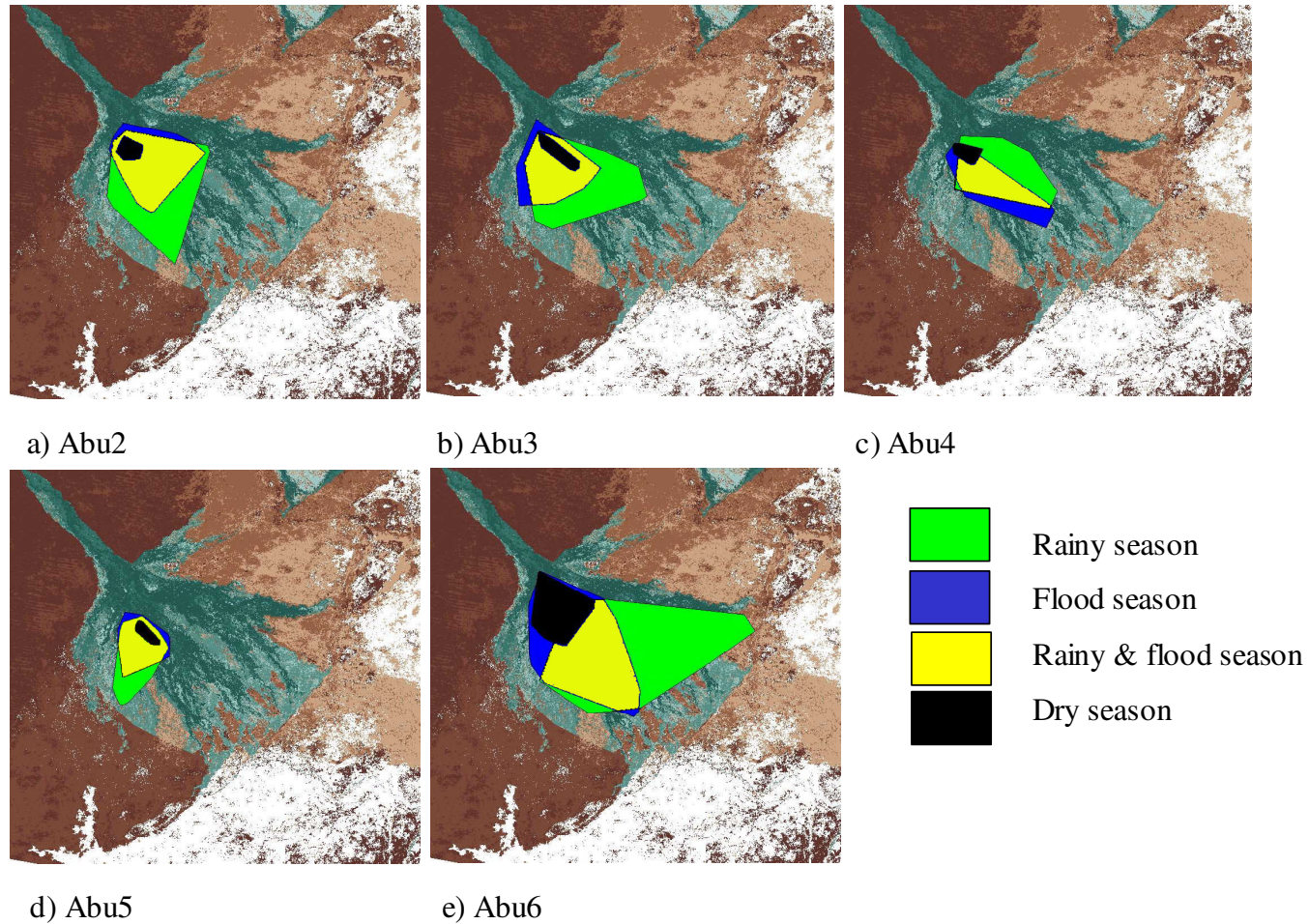
Figure 5.1: Map of the Okavango Delta with the 100% minimum convex polygon (MCP) for the rainy season, flood season, rainy, flood season and dry season of the five collared wild adolescent elephants.
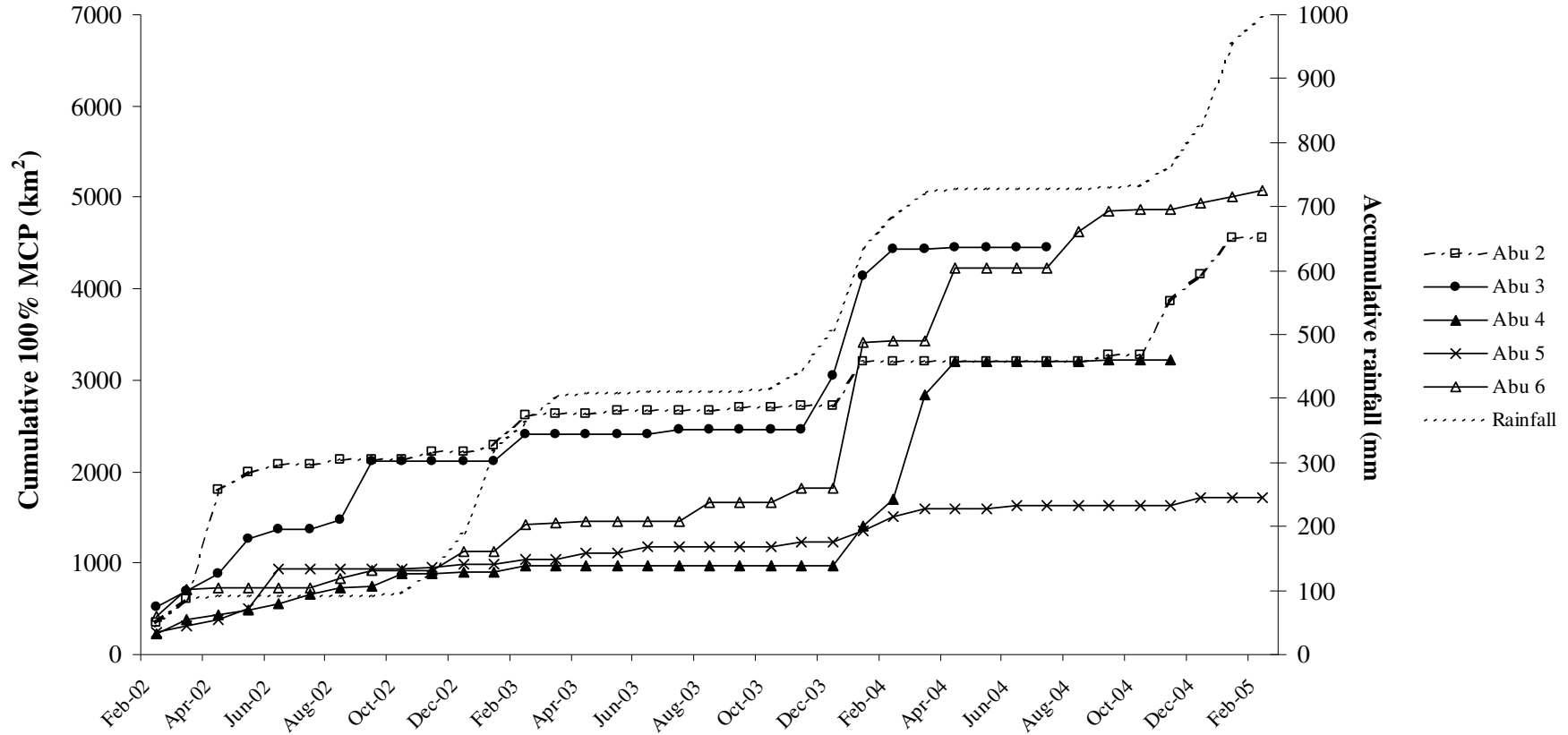
Figure 5.2: Cumulative 100% MCP area (km^2) for the collared wild elephants versus cumulative rainfall (mm) throughout the study period.

5.3.2. Distance travelled

Mean (±SE) straight-line distance travelled per day was 3.69 ± 0.06 km, with a maximum of 60km. Distance travelled was affected by both elephant ($F_{4, 4015}$=256.00, P<0.001) and season ($F_{2, 4015}$=36.38, P<0.001), with larger distances travelled during the rainy season (Figure 5.3).
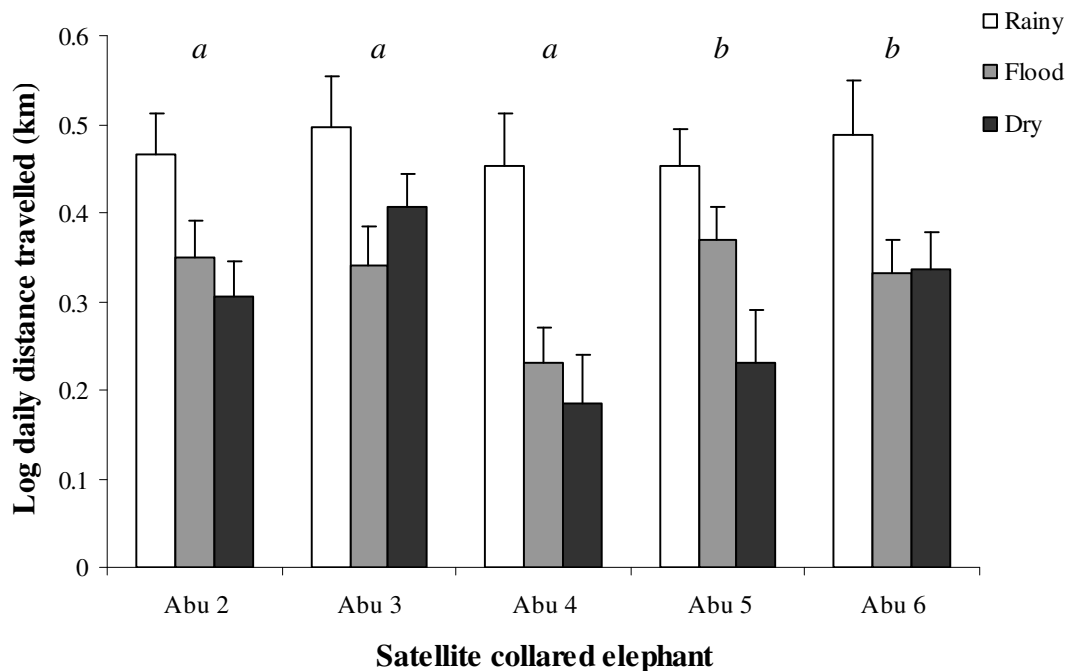
Figure 5.3: Log mean (+SE) distance (km) between locations at 24hr intervals for each of the wild adolescent male elephants in the rainy, flood and dry seasons. Letters indicate significant differences identified by *post hoc* comparisons. Sample sizes for social focal data are outlined in Table 5.2.

5.3.3. Habitat selection and utilization

5.3.3.1. Satellite collared elephants

The composition of the home ranges of the wild adolescent male elephants was significantly different from the composition of the study area as a whole (Λ=0.0008; χ^2_3=35.68, P<0.001), and was dominated by grassland/floodplain and island vegetation habitats (Tables 5.4 and 5.5).

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Table 5.4: Habitat composition of the 100% MCP home ranges of the individual wild adolescent male elephants. Figures are percentage of total area.

Habitat	Abu2	Abu3	Abu4	Abu5	Abu6
Grassland/ floodplains	69.52	71.65	76.62	66.18	64.11
Mopane woodland	7.74	4.02	1.23	5.20	13.08
Other woodland	10.48	11.42	6.87	15.06	10.37
Island vegetation	12.27	12.90	15.28	13.55	12.47

Table 5.5: Simplified ranking matrix for the home ranges relative to spatial availability. Preferred and avoided habitats are indicated by '+' and '-' signs respectively. +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$; -, $P < 0.05$; --, $P < 0.01$; ---, $P < 0.001$.

	Grassland/ floodplains	Mopane woodland	Other woodland	Island vegetation	Rank
Grassland/floodplain		+++	+++	---	2
Mopane woodland	---		-	---	0
Other woodland	---	+		---	1
Island vegetation	+++	+++	+++		3

Adolescent male elephants also utilized habitats within their home ranges significantly differently from their spatial availability ($\Lambda=0.027$, $\chi^2_3=18.05$, P<0.001) (Figure 5.4). In order of relative preference, habitats ranked as: island vegetation>grassland>other woodland>mopane woodland (Table 5.6).

Table 5.6: Simplified ranking matrix for the relative preference of habitats within home ranges relative to spatial availability. Preferred and avoided habitats are indicated by '+' and '-' signs respectively. +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$; -, $P < 0.05$; --, $P < 0.01$; ---, $P < 0.001$.

	Grassland/ floodplains	Mopane woodland	Other woodland	Island vegetation	Rank
Grassland/floodplain		+++	+++	---	2
Mopane woodland	---		-	---	0
Other woodland	---	+		---	1
Island vegetation	+++	+++	+++		3

Figure 5.4: Comparison of the availability of the four habitat types versus the mean (+SE) utilization for the five wild adolescent collared males across all seasons.

However, the pattern of habitat preference varied between seasons, with a preference for 'other' woodland during the rainy season (Λ=0.037, χ^2_3=27.96, P<0.0001), island vegetation during the flood season (Λ=0.009, χ^2_3 = 23.75, P<0.0001) and grassland during the dry season (Λ=0.061, χ^2_3=3.98, P<0.01) (Table 5.7).

5.3.3.2. Ground observation data

Both males (log likelihood χ^2: rainy, χ^2_4=1589, *P*<0.001; flood, χ^2_4=2244, *P*<0.001; dry χ^2_4=143, P<0.001) and females (rainy, χ^2_4=109.32, *P*<0.001; flood, χ^2_4=188.81, *P*<0.001; dry χ^2_4=87.63, P<0.001) exhibited distinct habitat preferences across seasons (Figure 5.5). During the rainy and flood seasons, both males and females favoured the mopane woodland; this was also the case for females during the dry season, whereas males favoured 'other' woodland (Figure 5.5).

Table 5.7: Simplified ranking matrix for the relative preference of habitats within home ranges relative to spatial availability during the (a) rainy, (b) flood and (c) dry seasons. Preferred and avoided habitats are indicated by '+' and '-' signs respectively. +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$; -, $P < 0.05$; --, $P < 0.01$; ---, $P < 0.001$.

(a) Rainy

	Grassland/ floodplains	Mopane woodland	Other woodland	Island vegetation	Rank
Grassland/floodplain		-	---	---	0
Mopane woodland	+		---	-	1
Other woodland	+++	+++		+	3
Island vegetation	+++	+	-		2

(b) Flood

	Grassland/ floodplains	Mopane woodland	Other woodland	Island vegetation	Rank
Grassland/floodplain		+++	+++	---	2
Mopane woodland	---			---	0
Other woodland	---	+		---	1
Island vegetation	+++	+++	+++		3

(c) Dry

	Grassland/ floodplains	Mopane woodland	Other woodland	Island vegetation	Rank
Grassland/floodplain		+++	+++	+	3
Mopane woodland	---		+	-	1
Other woodland	---	-		---	0
Island vegetation	-	+	+		2

For males, the evenness of habitat use ($J'_{FLOOD} = 0.88$, $J'_{RAINY} = 0.80$, $P=0.05$) and diversity of habitat use ($H'_{FLOOD}=1.42$, $H'_{RAINY}=1.28$, $P=0.05$) were significantly higher in the flood season than in the rainy season. This was also the case for females ($J'_{FLOOD}=0.95$, $J'_{RAINY}=0.72$, $P=0.005$; $H'_{FLOOD}=1.53$, $H'_{RAINY}=1.16$, $P=0.001$). Values for males were significantly lower than for females in the flood season ($J'_{MALES}=0.88$, $J'_{FEMALES}=0.95$, $P=0.005$; $H'_{MALES}=1.42$, $H'_{FEMALES}=1.53$, $P=0.027$). However, during the rainy season there was no significant difference between males and females rainy season ($J'_{MALES}=0.80$, $J'_{FEMALES}=0.72$, $P=0.243$; $H'_{MALES}=1.28$, $H'_{FEMALES}=1.16$, $P=0.243$).

Age did not affect the pattern of habitat utilization by male elephants, with all age classes negatively selecting grassland/floodplains and preferring island vegetation and mopane woodland (Figure 5.6), or the evenness or diversity of habitat use (Table 5.8).

Table 5.8: Comparison of (a) diversity (*H'*) and (b) evenness (*J'*) of habitat use between male age-classes.

(a)

Age group	*J'*	Age group	*J'*	*P*
Adolescent	1.17	21-25yr	1.09	0.130
		26-35yr	1.07	0.153
		>36yr	1.12	0.435
21-25y	1.09	26-35yr	1.07	0.864
		>36yr	1.12	0.457
26-35y	1.07	>36yr	1.12	0.864

(b)

Age group	*J'*	Age group	*J'*	*P*
Adolescent	0.73	21-25yr	0.68	0.130
		26-35yr	0.67	0.153
		>36yr	0.70	0.435
21-25y	0.67	26-35yr	0.67	0.864
		>36yr	0.66	0.457
26-35y	0.67	>36yr	0.70	0.864

a) Male groups
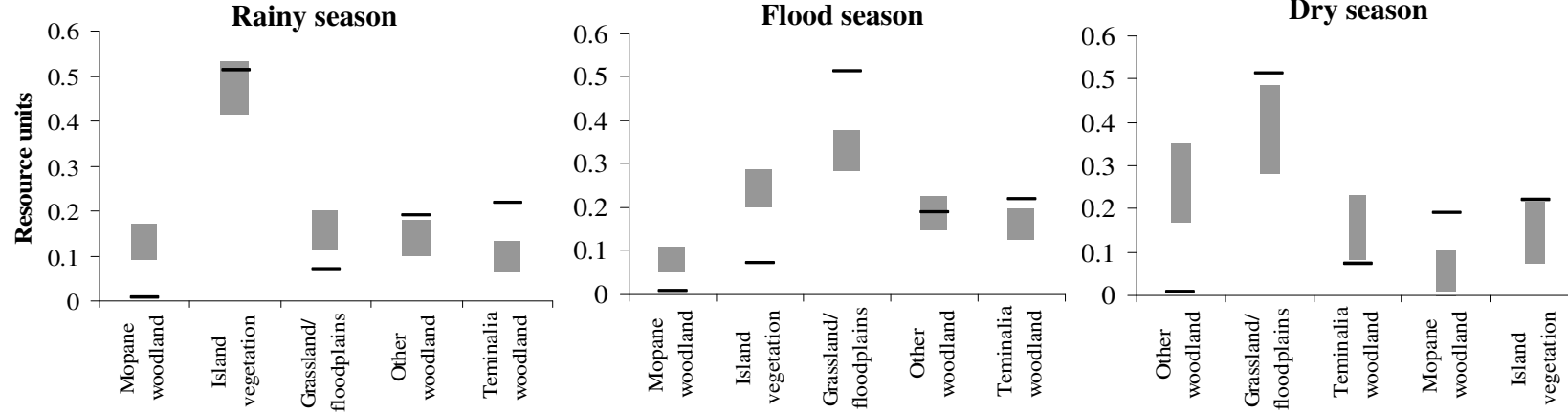
b) Female groups
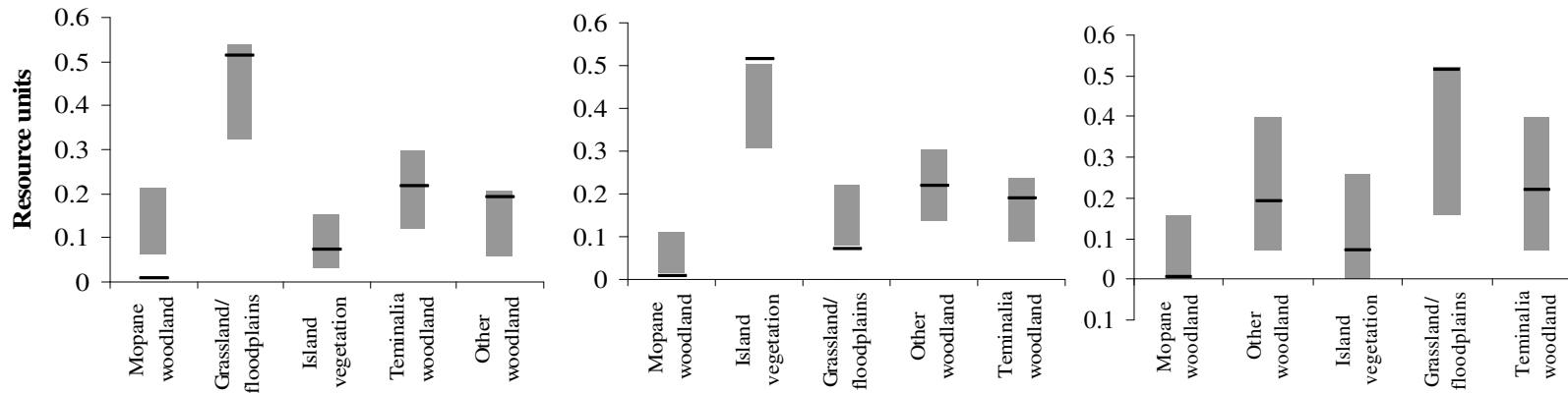
Figure 5.5: Bonferroni adjusted confidence limits for the proportions of habitat use compared to the observed proportions of available habitats across the seasons by male and female elephants sighted in the study area between February 2002 and February 2005. ▬ = habitat available. ▮ = upper and lower Bonferroni 95% confidence limits of habitat use.
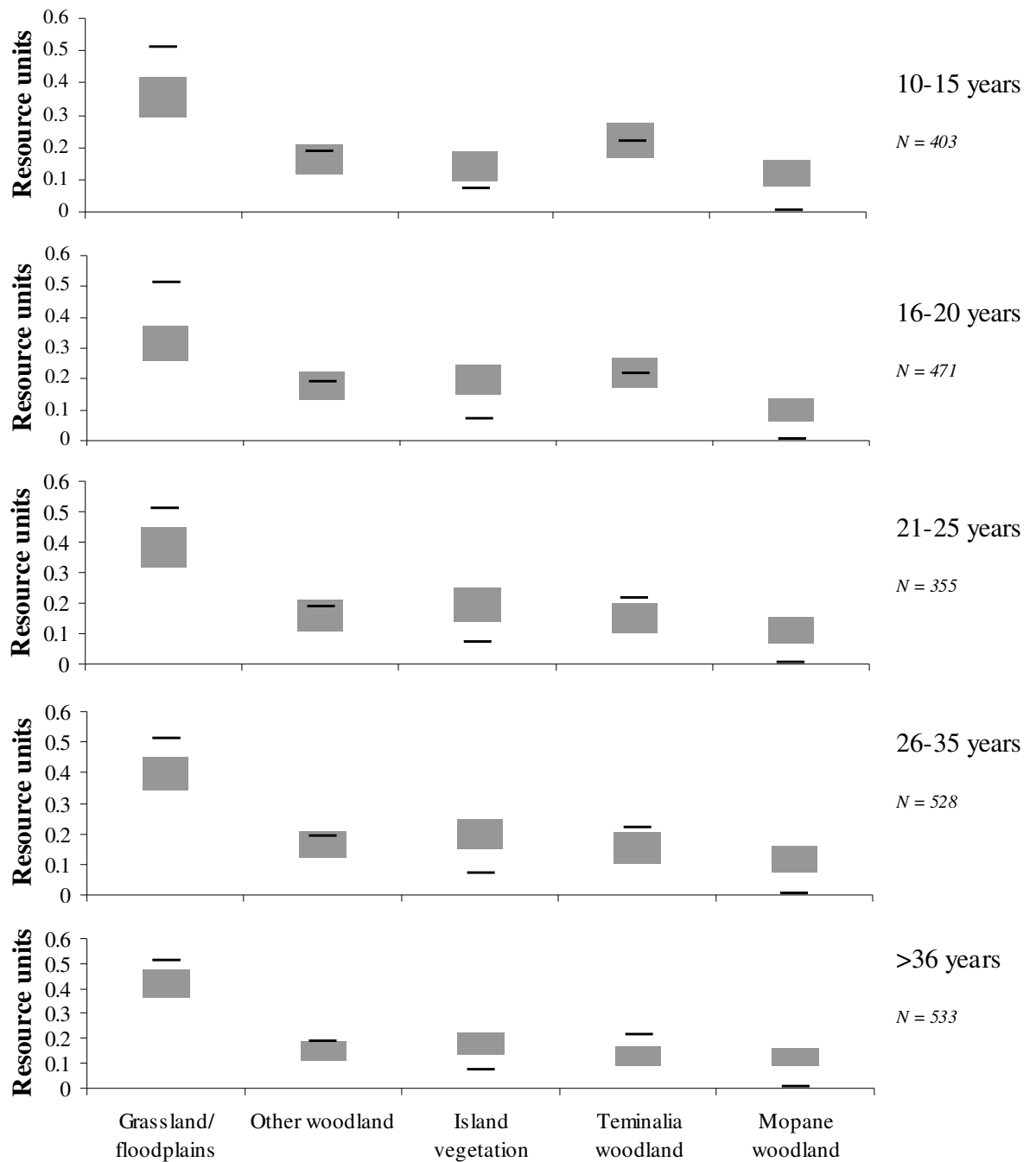
Figure 5.6: Bonferroni adjusted confidence limits for the proportions of habitat use compared to the observed proportions of available habitats for male elephants by age group. ━ = habitat available. ▓ = upper and lower Bonferroni 95% confidence limits of habitat use. *N* = sample size.

5.3.4. Feeding behaviour

There was no significant difference between seasons in the proportion of time males spent feeding (H_2=3.74, P=0.154). Elephants consumed a wide variety of foods, of which 15 species were eaten regularly (Table A.5, Appendix) with six making up the bulk of their diet (Table 5.9); grasses and sedges were grouped together, as these could not be distinguished when observed from a distance. Grazing was the most commonly recorded feeding behaviours during the rainy season, whilst and browsing was recorded more frequently during the flood and dry seasons (Figure 5.7). The consumption of bark and roots was more common during the dry season (14% of feeding time) than in other seasons.

Table 5.9: Mean (±SE) percentage of feeding time male elephants were recorded consuming the six commonest food plants.

Food item	Total	Rain	Flood	Dry
Acacia spp.	3.7 ± 1.0	2.9 ± 6.9	2.1 ± 11.5	4.3 ± 14.9
Colophospermum mopane	31.3 ± 4.0	35.6 ± 6.9	27.4 ± 4.5	-
Croton megalobotrys	20.2 ± 2.8	17.7 ± 2.4	18.7 ± 2.3	62.5 ± 37.5
Grasses and sedges	47.7 ± 2.5	39.8 ± 3.9	55.1 ± 3.4	33.7 ± 9.8
Hyphaene petersiania	44.0 ± 2.7	42.8 ± 3.1	39.5 ± 8.2	53.5 ± 7.2
Terminalia sericea	31.5 ± 3.6	32.1 ± 4.6	35.0 ± 8.1	20.4 ± 5.5
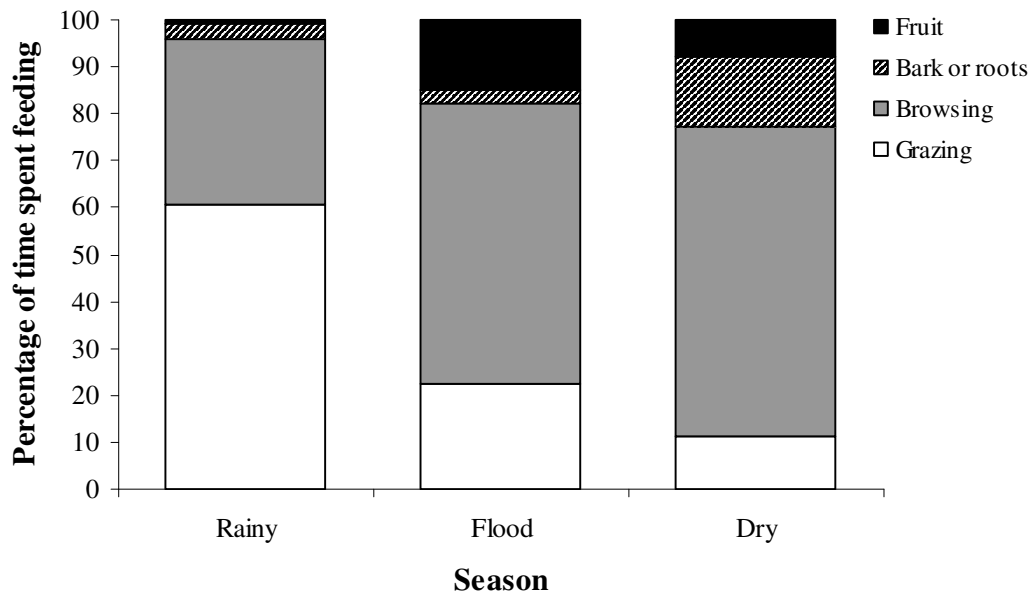
Figure 5.7: Proportion of feeding time elephants were recorded grazing, browsing, and eating bark/roots and fruit. Sample sizes for focal feeding data are outlined in Table 3.4.

5.4. Discussion

Previous studies have suggested that elephant bulls have clearly defined home ranges (Grainger, van Aarde & Whyte 2005). However, in this study, adolescent males continually increased the area that they ranged over during the three-year period, and the area that they utilized was larger than recorded in most other populations (Table A.6, Appendix). This pattern of ranging behaviour may be related to the availability of water and food after heavy rainfall. For example, elephants are able to distinguish conspecific infrasound calls from over four kilometres away (Langbauer 2000) and are probably able to detect storms, which also produce infrasound (Johnson, Lees & Yepes 2006), over considerable distances. The increase in range area following periods of rainfall observed in this study could, therefore, be related to individuals following storms to areas of rainfall that generate fresh grass growth. This willingness to venture into new areas is also likely to be partly linked to age, as adolescent bulls are generally the first age group to occupy new areas and are highly migratory (Spinage 1994). Long-term

monitoring of the same individuals would be required to determine whether these individuals established a spatially stable home range as they matured.

The spatial and temporal availability of water is the most important factor affecting the distribution of elephants (Laws 1970; Viljoen 1989a), although the Delta is unusual in that it has a very short dry season in comparison to the ranges of other elephant populations. Consequently, although the area ranged in the dry seasons was markedly smaller than in the other seasons (Figure 5.1), this period of potential resource limitation is very short-lived. During the flood season, males utilized a significantly smaller area than during the rainy season and travelled significantly less far during 24hr periods. These differences can be attributed to several factors. First, elephants are able to move into less heavily utilized areas to find seasonal ephemeral foods such as fresh grasses, forbs and climbers (Owen-Smith 1988). Second, the presence of standing floodwaters may physically restrict their movements and, therefore, influence optimal foraging strategies. Last, floodwaters decrease the need to move to sporadic watering holes.

The preferred habitat of the satellite-collared males was island vegetation and, contrary to other studies (Lewis 1991; Smallie & O'Connor 2000; Styles & Skinner 2000; Ben-Shahar 2002), they utilized 'other' woodland and mopane woodland less than expected given their availability. However, one potential problem with using satellite collars to quantify patterns of habitat utilization is the loss of signals from marked individuals in particular congested habitats, which can generate biased estimates of habitat selectivity. For example, mopane comes in two physiognomic forms, shrubs (1-3 metres) and trees (>3 metres), the latter being more likely to cause interference with collar signals. But, as elephants prefer the shrubs and actively coppice them to encourage higher biomass, productivity and earlier budding (Smallie & O'Connor 2000; Ben-Shahar 2002), it is unlikely that this led to a sampling bias in this study. Similarly, there was no significant difference in the number of downloads recorded in the rainy or flood seasons.

Collared males increased their use of 'other' woodland habitat during the rainy season, whereas in the observational data male and female elephants increased their use of this habitat during the dry season. This apparent disparity, however, is probably

attributable to the phenology of the resident plants. For example, rainfall triggers the trees to sprout new leaves, which increases levels of protein (Dublin 1996), and many trees (e.g. *A. nigrescens* and *T. sericea*) also flower prior to the onset of the rains, whilst others (e.g. *Ficus sycomorus* and *Garcinia livingstonei*) fruit during the rains. These factors would increase the attractiveness of these habitats to the elephants at these times. However, the large variation in the arrival and duration of the rains throughout the Delta (Mendelsohn & el Obeid 2004) creates temporal and spatial differences in the availability of flowering and leafing trees, which in turn causes elephants to utilize different areas at different times.

Male elephants actively selected island vegetation throughout the year. During the flood season these islands provide dry access to sedges (Cyperaceae) and to the palm *H. petersiania*, which fruits at this time. When available, fruits and seedpods are actively sought by savannah elephants (Buss 1961; Laws & Parker 1968; Field 1971; Field & Ross 1976; Barnes 1982), and older males in the present study walked purposefully and directly between clumps of these trees to shake them for fruit, although adolescent males and females were not observed doing this. However, it is unclear specifically what this fruit provides in nutritional terms, but they must be highly profitable due to the high handling costs involved in securing them. The method used during this study to assess feeding is limited, especially due to variance in the distances the elephants can be observed from in the different seasons and therefore what species of plants can be identified. Future work on the importance of these trees and others of the island vegetation habitat could explain the elephant's positive selection for this habitat.

Based on ground observation data, mopane woodland was favoured throughout the year by both males and females on a local scale, with the exception of males during the dry season. *C. mopane* was eaten most by males during the rainy season, when twigs are most palatable (Styles & Skinner 2000), although this difference was not marked. Unlike males, females still favoured mopane woodland during the dry season, and this resource may be particularly important for them, as the major leaf flush occurs before the spring rains occur i.e. in the dry season, and protein levels are substantially higher at this time (Styles & Skinner 2000).

Sexual segregation of habitat utilization was only evident during the flood season, when the females were less selective. This may, in part, reflect the ability of males to specialise in certain habitats e.g. island vegetation, where they can manipulate food types due to their size and strength. However, age did not affect patterns of habitat selection, so sexual differences in habitat utilization cannot be due to size alone, and might be more associated with different social and nutritional requirements. This may be due to the affiliation of younger, and therefore smaller males, have with older bulls (Chapter 4). Furthermore, this pattern of habitat use is markedly different to that exhibited by male elephants in Chobe NP in northern Botswana, where bulls frequented all habitat types in proportion to their relative occurrence (Stokke & du Toit 2000). Adolescent males utilizing the *Terminalia* woodland to an expected degree was the only difference amongst males of different ages. This could be a result of habitat imprinting, due to them having only recently left their herd.

The male elephants were primarily grazers during the rainy season and shifted to being browsers during the flood and dry season, corresponding to a shift in habitat utilization during these seasons to dry land habitats, such as 'other' woodland. Whilst the dry season in a good year only lasts a month or two, it is the harshest time of the year for the elephants as the floods have dried and they await the arrival of the rains. As competition for resources increase during these harsh times they expand browse species niche (Makhabu 2005), resulting in an expansion in habitats utilized. They utilized habitats to the expected degree and the elephants included different food types in their diet such as the roots of *Grewia* spp. and various barks during this period. Chemical analysis of the kinds of barks that the elephants eat indicate that these may be a significant source of minerals such as calcium, manganese, iron, boron and copper (Laws, Parker & Johnstone 1975). Other theories are that elephants eat bark because of its high fibrous content, or certain essential fatty acids that the bark provides (McCullagh 1973; Sukumar 1991). As debarking mainly occurred between September and December (*pers. obs)*, it seems an important resource during this stressful time. These foods may also appear more attractive to the elephants during this period as this is when the phloem tissue in the plants is transporting sugars prior to flowering (Owen-Smith 1988).

Human activity and disturbances are exceptionally low for elephants within the protected areas of the Okavango Delta. Therefore the large areas that the collared elephants roamed are indicative of the low availability of essential resources of an environment reliant on the nutrient poor Kalahari sands and the arrival of the annual floods from Angola (Mendelssohn & el Obeid 2004). The mopane woodland grassland/floodplains and island vegetation are the most important habitats for both male and female elephants in the vicinity of the research camp. The grassland/floodplains is a highly available resource and only utilized to an expected degree by the females during the rainy and dry season and the males used it less than the expected throughout the year. In spite of its limited availability, mopane woodland was positively selected for by male and female elephants and the island vegetation by males throughout the year. This finding is similar to other studies in Africa, indicating that mopane is a locally important resource and along with the island vegetation is of vital importance to the population of elephants that utilize the Okavango Delta.

5.5.   Conclusions

The Okavango Delta provides important resources for elephants. However, the preferred resources are not widely available and so the elephants must roam over vast areas. The adolescent males do not have a distinct home range as they are continually exploring new areas. In this Chapter I have shown that:

- Adolescent male elephants in the Okavango Delta do not have a distinct home range.
- Adolescent male elephants in the Okavango Delta utilize an area bigger than most other elephant populations (Table A.6.).
- The flood season of the Okavango Delta affected the area utilized, habitat utilization and daily distances travelled.
- Adolescent males were non random in their selection of habitat and their preference was affected by season.

- Females were more selective than males in their habitat utilization during the flood season but not in the rainy or dry season.

- Adolescent males do not differ from adult male elephants in the habitats that they utilize or select.

- The male elephants were predominantly grazers during the rainy season, browsers during the flood season and relied on a more diverse diet during the dry season.

- *C. mopane* was positively selected by male and female elephants observed from the ground, indicating that it is an important local resource. However the collared elephants negatively selected for this resource, preferring island vegetation.

In this Chapter I have shown that the unique conditions of the Okavango Delta affects home range, habitat utilization, distance travelled and diet of the elephants utilizing the area. I have also shown that whilst sexual segregation in habitat utilization does occur it is limited to the flood season and is not attributed to sexual size dimorphism.

In the next Chapter I will investigate the viability of releasing captive habituated adolescent male elephants into the wild.

Chapter 6

The release of captive raised adolescent male
elephants into the Okavango Delta

Summary

The care and management of bull elephants in captivity currently lacks consideration of their social and physical requirements. At puberty many are removed from their mothers and other group members and housed separately. In the management of wild populations, growing public support for humane practices has led to an increase in the use of translocation. Translocation is used in both Africa and Asia to deal with problem animals, over-population and genetic bottlenecks. However the effects on the individual or the population to which they are being introduced have not been fully considered. The release of three captive raised adolescent male elephants in the Okavango Delta, Botswana provided an opportunity to investigate these issues.

The biological, social and political context of the release site, and the health and genetic status of the candidates for release were considered during the planning and implementation of the releases. A 14-year-old male was released in 2002 and a nine-year-old and 16-year-old in 2003. All three were collared with satellite radio collars and monitored from the ground and air throughout the three-year study. There was no significant difference between wild and released adolescent male elephants in home rang size, habitat selection and social interactions. However, released elephants sparred and vocalized more often, as well as showed premature social aging by spending more time alone and in smaller social groupings.

The release of these individuals showed that captive raised elephants can integrate back into a wild population and highlighted some of the issues elephants face when translocated to new populations.

6.1.   Introduction

Reintroduction is the attempt to establish captive-raised organisms in an appropriate wild environment (Stanley-Price 1991; Stuart 1991), and has been used as a management tool for over 200 years, for example in 1837 capercaillie (*Tetrao urogallus)* were reintroduced to Scotland (Stuart 1991). Sarrazin and Barbault (1996) concluded that most reintroduction efforts concern charismatic megafauna; e.g. Californian condor (*Gymnogyps californianus),* white-tailed sea eagle *(Haliaeetus albicilla),* griffon vulture *(Gyps fulvus),* Przewalski's horse *(Equus caballus przewalskii),* white rhinoceros *(Ceratotherium simum)* and orang-utan *(Pongo pygmaeus).* Yet these species often display the most extreme life history traits among the pool of endangered species, such as low reproductive rate, late age at maturation, long generation times and low density, which mean that they cannot be studied in the laboratory and cannot easily be manipulated in the wild. Consequently, reintroduction programmes represent an opportunity to study elements of their behaviour, and ecology.

Reintroduction is also commonly described as 'an attempt to establish a species in an area which was once part of its historical range' (Wilson & Stanley-Price 1994), which can include the translocation of wild individuals from one area to another. Translocation is increasingly being used as a management tool for the removal of problem animals (Fritts, Paul & Mech 1984; O'Bryan & McCullough 1985; Blanchard & Knight 1995; Mosillo, Heske & Thompson 1999; Angelici *et al.* 2000; Sullivan, Kwiakowski & Schuett 2004), the alleviation of overpopulated areas and the restocking of areas (Griffith *et al.* 1989; Woodroffe & Ginsberg 1999; Dublin & Niskanen 2003; Garai *et al*. 2004; Anon 2005). With nearly 700 translocation programmes conducted annually in the USA alone (Griffith *et al.* 1989; Wolf *et al.* 1996), it is increasingly used as a conservation tool but requires monitoring to ensure success rates increase. However the translocation of animals can generate conflict (Yeager 1997; Woodroffe & Ginsberg 1999) and in particular the translocation of elephants without regard for their social structure has led to the creation of problem animals in both Africa and Asia (McKnight 1992; Lahiri-Choudhury 1993; Slotow & van Dyk 2001; Slotow, Balfour & Howison 2001; Garia *et al.* 2004).

The benefits of rehabilitation and the importance of avoiding extinction are clear and it is generally accepted that animals living in natural habitats enjoy better welfare (Veasey, Waran & Young 1996), but are such 'welfare' arguments sufficient to justify attempts to return captive individuals to the wild and translocate wild animals when the costs are so high (Cade 1988; Griffith *et al.* 1989; Kleiman *et al.* 1991; Daim 1995) and success rates so low (Griffith *et al.* 1989; Beck *et al.* 1994; Reeve 1998; Struhsaker & Siex 1998; Krűger, Lawes & Maddock 1999; Woodroffe & Ginsberg 1999)? Several authors have argued that money invested in such programmes would be better spent on conserving wildlife areas where the species already exists (e.g. Struhsaker & Siex 1998; Woodroffe & Ginsberg 1999).

There have been many successful reintroductions involving the use of both captive (American bison *Bison bison*, alpine ibex *Capra ibex,* bald eagle *Haliaeetus leucocephalus,* peregine falcon *Falco peregrinus*, bean goose *Anser fabalis*, orang-utan*,* Arabian oryx *Oryx leucoryx*) and wild caught individuals; (wild turkey *Meleagris gallopavo*, bighorn sheep *Ovis canadensis,* elk *Cervus elephus,* pronghorn *Antilocapra americana,* black-faced impala *Aepyceros melampus petersi* and red colobus monkeys *Procolobus kirkii;* Griffith *et al.* 1989; Beck *et al.* 1994; Wolf *et al.* 1996; Yeager 1997; Struhsaker & Siex 1998; Spalton, Lawrence & Brend 1999). Whilst the release of wild caught individuals are more successful (Griffith *et al.* 1989*),* the translocation of both captive and wild individuals has proved to be an effective tool for conserving, at least some, wild populations (Wolf *et al.* 1996). However, one important element to consider in translocation programmes is the welfare of the animals involved, particularly as these programmes can attract significant media coverage and may, therefore, in turn affect future conservation efforts.   The welfare standards associated with the success of reintroduction programmes can depend, in part, upon the individuals to be released (Kleiman *et al.* 1991; Woodroffe & Ginsberg 1999), including the age of the animals to be released.

In many reintroduction and translocation programmes it has been found that adolescence is the ideal time to release captive raised individuals as they have greater behavioural flexibility and adaptability (Kawai 1965; Suzuki 1965; Box 1984; Kleiman *et al.* 1991; Custance, Whiten & Fredman 2002) and consequently have better survival

rates (Borner 1985; Harcourt 1987; Custance, Whiten & Fredman 2002; Moehrenschlager & Macdonald 2003). However, problems associated with releasing captive-raised animals include disorientation in a new environment, lack of adaptive capabilities and seeking the company of humans (Yeager 1997; Woodroffe & Ginsberg 1999).

In captive situations, male elephants are difficult to manage and handle (Spinage 1994) as they naturally spend more time sparring (Lee 1986), which can become aggressive. This aggression may become a problem at adolescence, as it is a male elephant's natural instinct to leave the natal herd and assert themselves in the male hierarchy. This aggression can be heightened by premature musth, especially when older males are not present (Poole 1987b, 1989; Ramussen, Hall-Martin & Hess 1996; Slotow *et al.* 2000). Which was the case when Mafunyane experienced his first musth period at the age of 14. He immediately fell out of musth when an older wild bull came to the boma where he was being kept. As a consequence, young bulls are often separated prematurely from their mothers and housed separately in zoos (Taylor & Poole 1998; Schulte 2000; Clubb & Mason 2002). Male elephants also appear to die earlier in captivity (Clubb & Mason 2002).

Documented releases of captive raised elephants have occurred since 1954, when the David Sheldrick Wildlife Trust started to capture, raise and release orphan elephants in Tsavo East National Park (NP) Kenya (McKnight 2002). Other examples include two wild-born females raised in American zoos and released into the Pilanesberg NP, South Africa (Anderson 1986; Moore & Munnion 1989; Moore 2000), and a 25-year-old African female released in Tanzania (Clunes 1997). However, the monitoring of these releases was limited and mainly involved the collection of incidental data.

The long-term management of the adolescent males in a captive group utilized in the safari industry at Elephant Back Safaris (EBS) in the Okavango Delta, Botswana, was always seen as a potential problem and releasing them into the wild was considered a viable management plan (Moore 2000). This group consisted of seven males and four females aged 2-46 years used to take clients out on safari. The utilization of elephants in a commercial capacity in the safari industry is increasing in Africa, particularly southern Africa, and the long-term management of young males is already an issue

(SAPA 2005; Pretorius 2006). The adolescent males chosen for release from EBS were unlikely to suffer disorientation or lack adaptive capabilities as they had lived in the vicinity of the release site for five years. Instead the main concern was their affiliation to humans.

The success of translocations and reintroductions are ultimately based on whether released individuals establish self-sustaining populations (Griffith *et al.* 1989). However, given the short timescale of the present study, other indicators of success were utilized including levels of interaction with wild conspecifics (Goossens *et al.* 2005), patterns of range utilization and foraging behaviour.

In this Chapter I analyze the behavioural, observation and satellite collar data collected on three released male elephants and compare to data collected on wild male elephants. The overall aim is to determine whether captive raised adolescent male elephants behave and interact significantly different to wild males. Specifically, I address the following questions:

- Do captive raised released adolescent male elephants spend more time alone and in smaller social groupings than wild conspecifics?
- Do captive raised released adolescent male elephants have a lower frequency of social interactions such as greeting and sparring than wild conspecifics?
- Do captive raised released adolescent male elephants spend time further away from their nearest neighbour than wild conspecifics?
- Do captive raised released adolescent male elephants use significantly smaller areas than wild conspecifics?
- Do captive raised released adolescent male elephants utilize the different habitats of the Okavango Delta to a similar degree as wild conspecifics?

6.2. Methodology

6.2.1. The releases

Three adolescent male elephants were released from EBS as outlined in section 2.3.2.

6.2.2. Data collection

Data collected on the released males consisted of satellite downloads, aerial and ground observations and focal observation data collected over a 30 minute period as outlined in section 3.2.1. Focal data were also collected on wild adolescent males (10-20 years old) for comparison and five wild adolescent males were fitted with satellite collars to compare habitat utilization and social interactions. Social groupings were classified as for the wild males (Table 2.2), with the additional grouping Code 7 for when sighting with the released female (Chapter 7) in a otherwise all male group.

6.2.3. Data analysis

6.2.3.1. Focal and observational data

Comparisons were made between the released adolescent male elephants and their wild collared counterparts to see if released male elephants differed significantly in social groupings, social interactions and certain social behaviours.

To see if the released males differed in their social groupings to their wild counterparts a GLM (Generalized Linear Model) was used, where Code 4, 5 and 6 (Table 2.2) were treated as one and Code 7 was not used. χ^2 was used to see if the individual released elephants differed from the wild collared adolescent males in their social groupings. Mann-Whitney test were used to compare the social groupings of Seba and Thando, one and two years post-release. Whilst Kruskal-Wallis was used to compare the social groupings of Mafunyane, one, two and three years post-release. Seba was nine-years-old when he was released. However for statistical analysis all released elephants were treated as adolescent and compared to 10-20 year old males.

The differences between the distance to nearest neighbour of wild and released males was analyzed carrying out a Mann-Whitney test to compare the median distance

of the three released males from all their focal samples to the medians for each of the independent focals on wild adolescent male elephants. When analyzing their social interactions, number of greeting (when focal elephant greeted another elephant) and sparring events only the focal samples when they were with one or more other elephant were considered. When analyzing their number of vocalizations per half hour vocal, focal data when they were alone were also included. When the released males were sighted three times or more during a day a sample was randomly selected from the morning and one from the afternoon for use in analyses. Nested GLM with Poisson distribution were used to analyze the differences in the rate of social interaction, sparring, greeting and vocalization between the wild and released elephants, and between released individuals with individual status (released or wild) as a factor. Data were analyzed using S-PLUS 6.1 (Insightful Corporation). Where data were over dispersed, results are presented as F values; where data are not over dispersed, χ^2 are presented (Crawley 2002).

Two sample t-tests and Mann-Whitney tests were used as appropriate. Proportional data were logratio transformed (Aebischer & Roberston 1992) and compared using 1 or 2 sample t-tests, paired t-tests or one-way ANOVA.

6.2.3.2. Satellite collar data

The satellite collar data were sorted as outlined in Section 5.2.3.1.

In order to test the null hypothesis that the released elephants were randomly distributed across the different habitat types of the Okavango Delta, i.e. habitat use is directly proportional to habitat availability, the log-likelihood statistic χ^2 was applied and Bonferroni-adjusted 95% confidence intervals calculated (Manly, Macdonald & Thomas 1993). To compare the habitat utilization between the collared wild and released males the data were logratio transformed (Aebischer & Robertson 1992) and the logratios were compared using a GLM.

The underlying assumptions were met for all tests (Zar 1984). Analysis were conducted using MINITAB (version 14, 2004) and results were considered significant where $\alpha = 0.05$.

6.3. Results

A summary of the data collected on the released elephants is presented in Table 6.1. A total of 920 independent sightings of the released elephants were noted during the study period, of which 60% were when they were with one or more of the other released elephants. Seven hundred and twenty focal samples were collected from the released adolescent male elephants and 102 from wild adolescent male elephants (Chapter 4).

6.3.1. Social groupings

The released adolescent male elephants tended to spend more time alone and in smaller social groupings than the collared wild males who spent more of their time within female and mixed herds (Figure 6.1 & Table 6.2). The time spent in different social groupings did not differ significantly from the collared wild males ($F_{1, 27}$=0.01, P=0.938). The released males, like the collared wild males were non-random in the selection of age groups of male elephants (Figure 6.2: χ^2_4= 623.40, P<0.001), and were spotted more frequently in groups of 1-4 other male elephants than groups containing >5 males. The number of males the released males were sighted with did not differ significantly from the collared wild males (Figure 6.3: Mann-Whitney: $W_{3, 5}$=8.0, P=0.136).
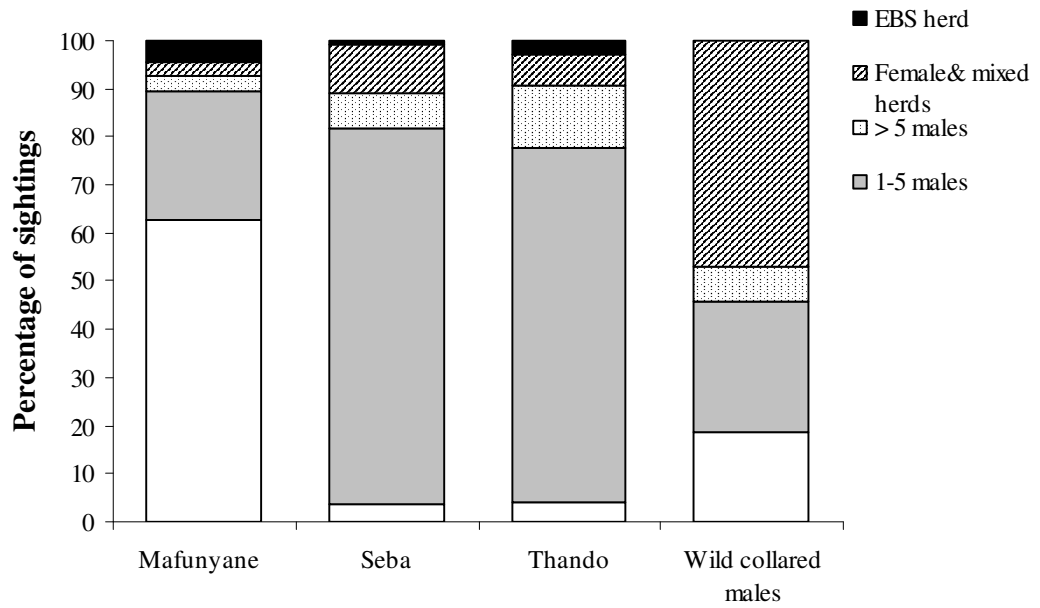
Figure 6.1: Percentage time released and wild collared adolescent male elephants were sighted in different social groupings (Table 4.1).

Table 6.1. Summary of the data collected in the different seasons of the study. Total sightings data used to analyze patterns of social grouping; social focal data used to analyze patterns of social behaviour within groups (see Code 4, Table 4.1); nearest-neighbour distances; focal data used to analyze patterns of activity and vocalization; satellite downloads to analysis home range and habitat utilized: consecutive 24 hour downloads to analyze daily distance travelled.

Data set	Elephant	Rainy	Flood	Dry	Total
Sightings of released elephants	Mafunyane	193	391	34	618
	Thando	44	90	11	145
	Seba	53	88	14	155
	Sub-total	*285*	*576*	*59*	*920*
Sightings of released males with other released elephant	Mafunyane	84	153	26	263
	Thando	49	81	9	139
	Seba	42	93	14	149
	Sub-total	*175*	*327*	*49*	*551*
Sightings of wild collared males	Abu2	36	49	9	94
	Abu3	24	44	9	77
	Abu4	25	46	10	81
	Abu5	42	56	9	107
	Abu6	18	50	7	75
	Sub-total	*144*	*245*	*44*	*434*
Social focal data	Mafunyane	49	144	10	203
	Thando	18	37	6	61
	Seba	19	41	6	66
	Wild adolescent males	43	53	6	102
	Sub-total	*129*	*275*	*28*	*432*
Focal data	Mafunyane	137	317	34	488
	Thando	19	39	6	64
	Seba	21	39	6	66
	Wild adolescent males	43	53	6	102
	Sub-total	*220*	*448*	*52*	*720*
Satellite downloads	Mafunyane	750	955	108	1813
	Thando	716	774	184	1674
	Seba	546	969	163	1678
	Sub-total	*2012*	*2698*	*455*	*5165*
Consecutive 24 hour downloads	Mafunyane	249	322	39	610
	Thando	207	263	52	522
	Seba	214	312	53	579
	Sub-total	*670*	*897*	*144*	*1711*

Mafunyane spent the majority of his time alone and was different from wild adolescent males in the time that he spent in different social groupings (Figure 6.3 and Table 6.2; χ^2_3=696, P<0.001). As years post release increased, the time he spent with other males and herds increased (Kruskal-Wallis H_2=7.31, P=0.026). Thando's social groupings was significantly different to wild males (χ^2_3=95, P<0.001) as he spent the majority of his time with Seba, making the sightings of him in a group size of one to five males the dominant social sighting (Figure 6.1 & Table 6.2). There was no significant difference in the number of sightings in particular social groupings from the first and second year post release ($W_{89, 56}$=6259.5, P=0.250). Seba spent the least time alone, and spent the majority of his time with Thando, making the sightings of him in a group size of one to five males the dominant social sighting (Figure 6.1 & Table 6.2), thus differing from wild males (χ^2_3=152, P<0.001) There was a significant difference in the number of sightings in particular social groupings from the first and second year post release ($W_{102, 53}$=4848.5, P=0.023), as he spent more time with the released female during the second year.

Table 6.2: Type of group the released males and wild males of difference age classes were most often sighted in.

Individual/ Age group	The most frequent social grouping	Median number of elephants in group
Mafunyane	Alone	1
Thando	1-5 males	3
Seba	1-5 males	3
10-15yr	With female herd	7
16-20 yr	With 1-5 males	6.5
21-25yr	With 1-5 males	4
26-35yr	Alone	3
>36+	Alone	3

b)
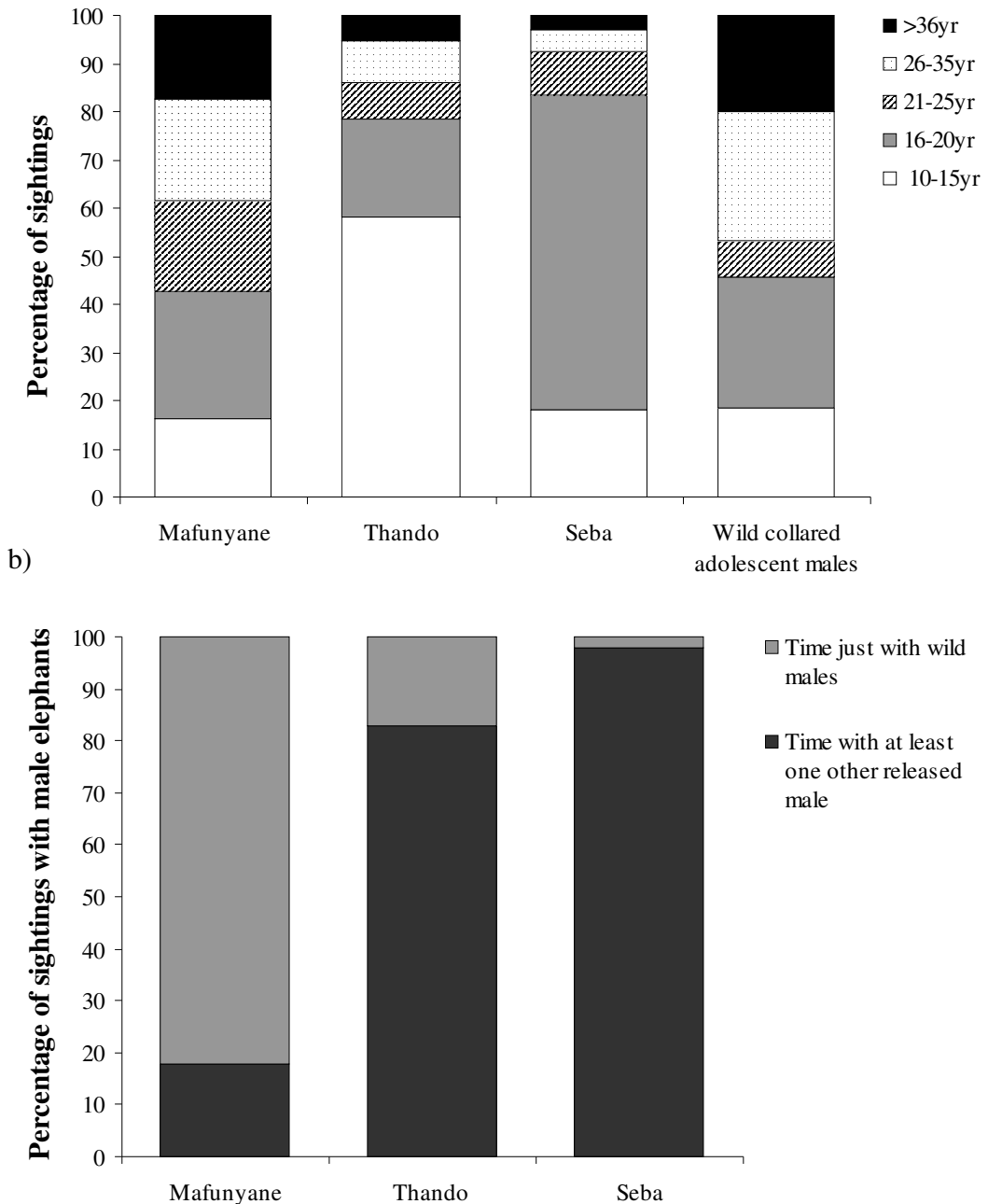
Figure 6.2: Percentage of sightings of the released and wild collared adolescent male elephants with males of different age groups. Sample sizes for social focal data are outlined in Table 6.1. a) all data b) time released males spent with at least one other released male elephant and just wild males.

The released male elephants were non-uniform in which age group of male elephants they were sighted with (Mafunyane: χ^2_4=49.87, P<0.001; Thando: χ^2_4=108.84, P<0.001; Seba: χ^2_4=455.63 P<0.001; all released male elephants: χ^2_4=43.78, P<0.001), being seen more frequently with adolescent males than males of other age groups (Figure 6.5). There was no significant difference between wild and released adolescent males and the age groups they spent time with. ($F_{1,\ 37}$=0.00, P=1.000). The number of males that the released males and collared wild males were sighted with did not differ significantly ($W_{113,\ 388}$ = 28813.5, P=0.722).

6.3.1.1. *Distance to nearest neighbour*

Distance to nearest neighbour did not differ significantly between the released and wild adolescent males (Figure 6.3: $W_{3,\ 101}$=5249, P=0.303). The released elephants spent more time closer to males of a similar age (Figure 6.4), which differs from the wild adolescent males who where significantly closer to older males (Chapter 4).
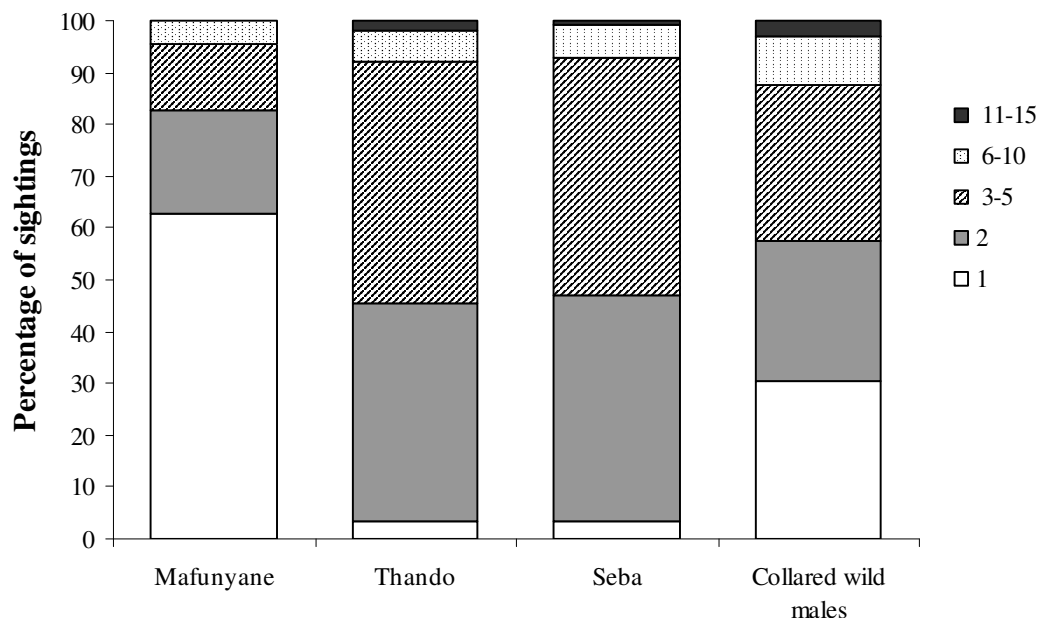
Figure 6.3: Percentage of time released and wild collared adolescent male elephants were sighted in male groups of different sizes.
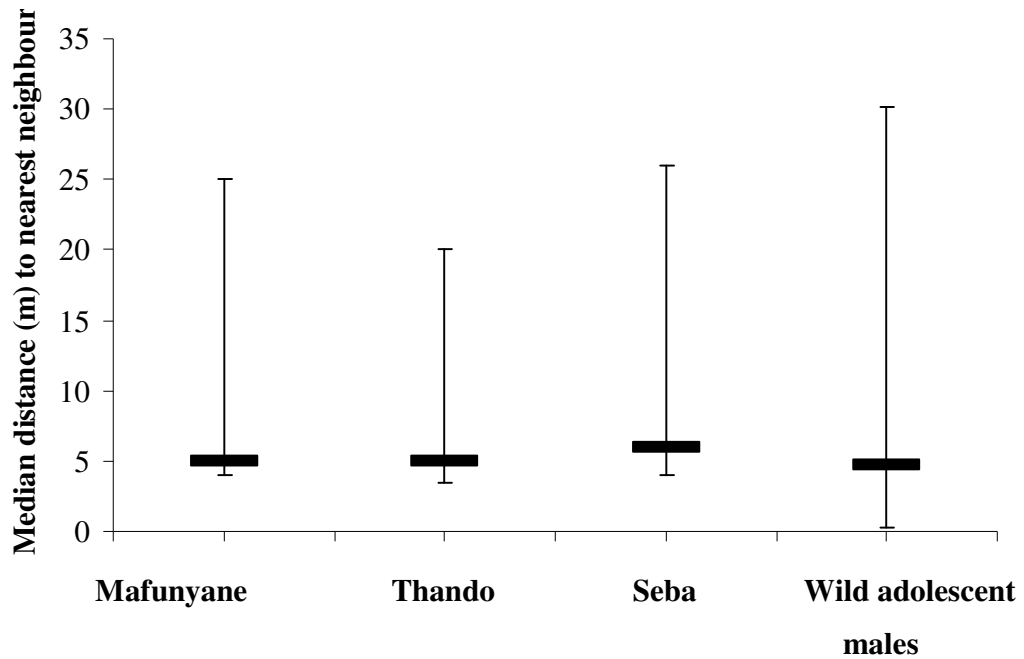
Figure 6.4: Median (±95% confidence limits) distance (m) from focal elephants to nearest neighbour during half hour focal data. Sample sizes are outlined in Table 6.1
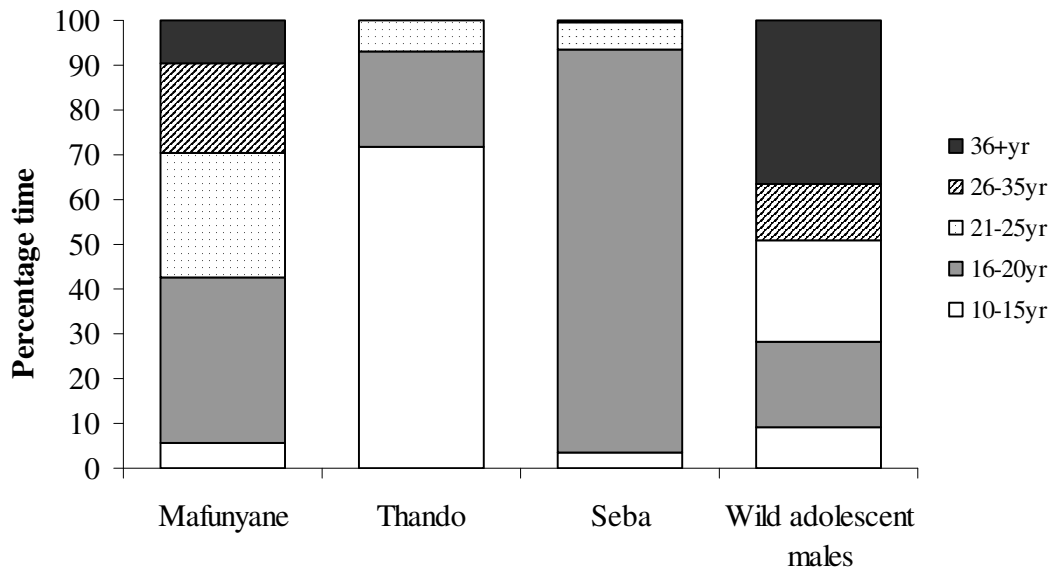
Figure 6.5: Proportion of time the released and wild adolescent male elephants had male nearest neighbours of certain age groups. Sample sizes are outlined in Table 6.1

6.3.2. Social behaviours

There was no significant difference between the level of social interactions of the released and wild adolescent male elephants (Figure 6.6; $F_{1, 430}$=0.02, P=0.899). Nor was there difference between the released individuals ($F_{2, 327}$=1.77, P=0.171).

There was no significant difference between the level of greeting per half hour focal of the released male elephants and wild adolescent male elephants (Figure 6.7; Poisson χ^2_{430}, P=0.254). However, there was a difference between the released individuals (Poisson χ^2_{327}, P=0.029). Whilst Seba had the highest mean value (Figure 6.8), Mafunyane greeted more frequently during a half hour focal (Figure 6.8). Wild and released male elephants differed significantly in the amount of sparring per half hour focal with the wild elephants sparring more (Figure 6.9; $F_{1, 430}$=7.075, P=0.008). There was also a significant difference between the released males ($F_{2, 327}$=3.399, P=0.035), with Mafunyane having the highest mean frequency per half hour focal (Figure 6.10).
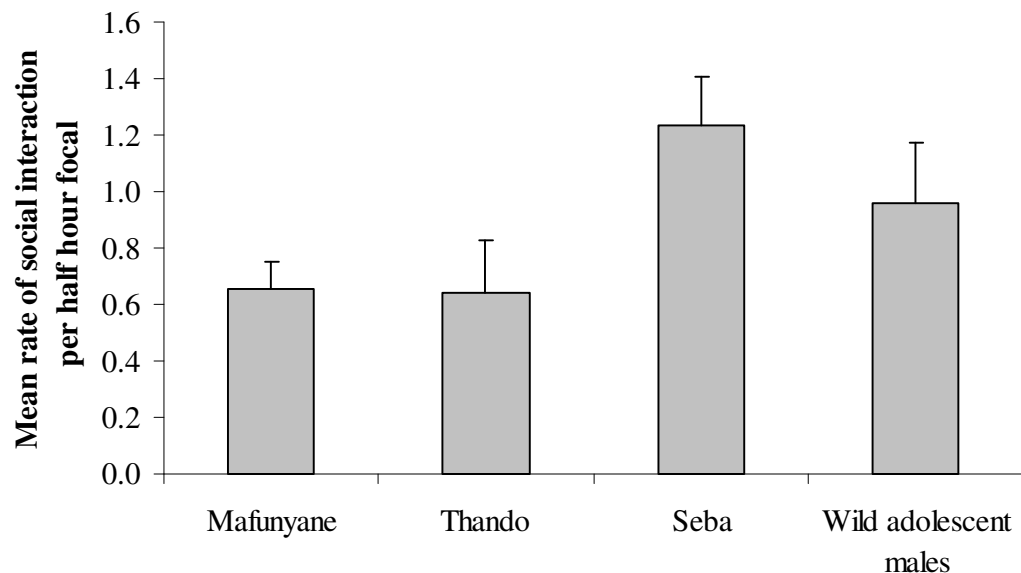
Figure 6.6: Mean (+SE) number of social interactions per half hour focal of the released and wild adolescent male elephants. Sample sizes for social focal data are outlined in Table 6.1
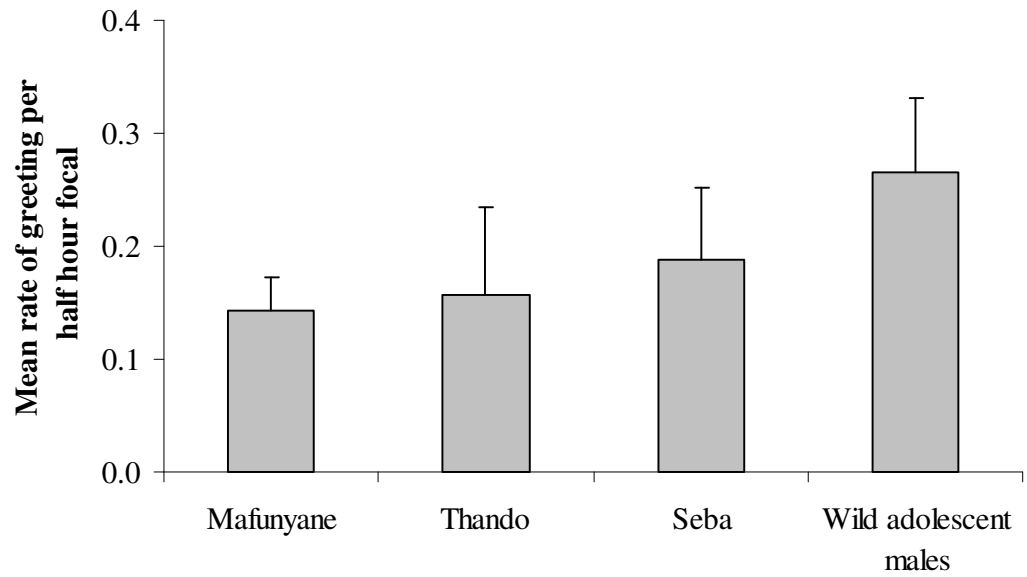
Figure 6.7: Mean (+SE) number of greeting events per half hour focal by the released and wild adolescent male elephants. Sample sizes for social focal data are outlined in Table 6.1
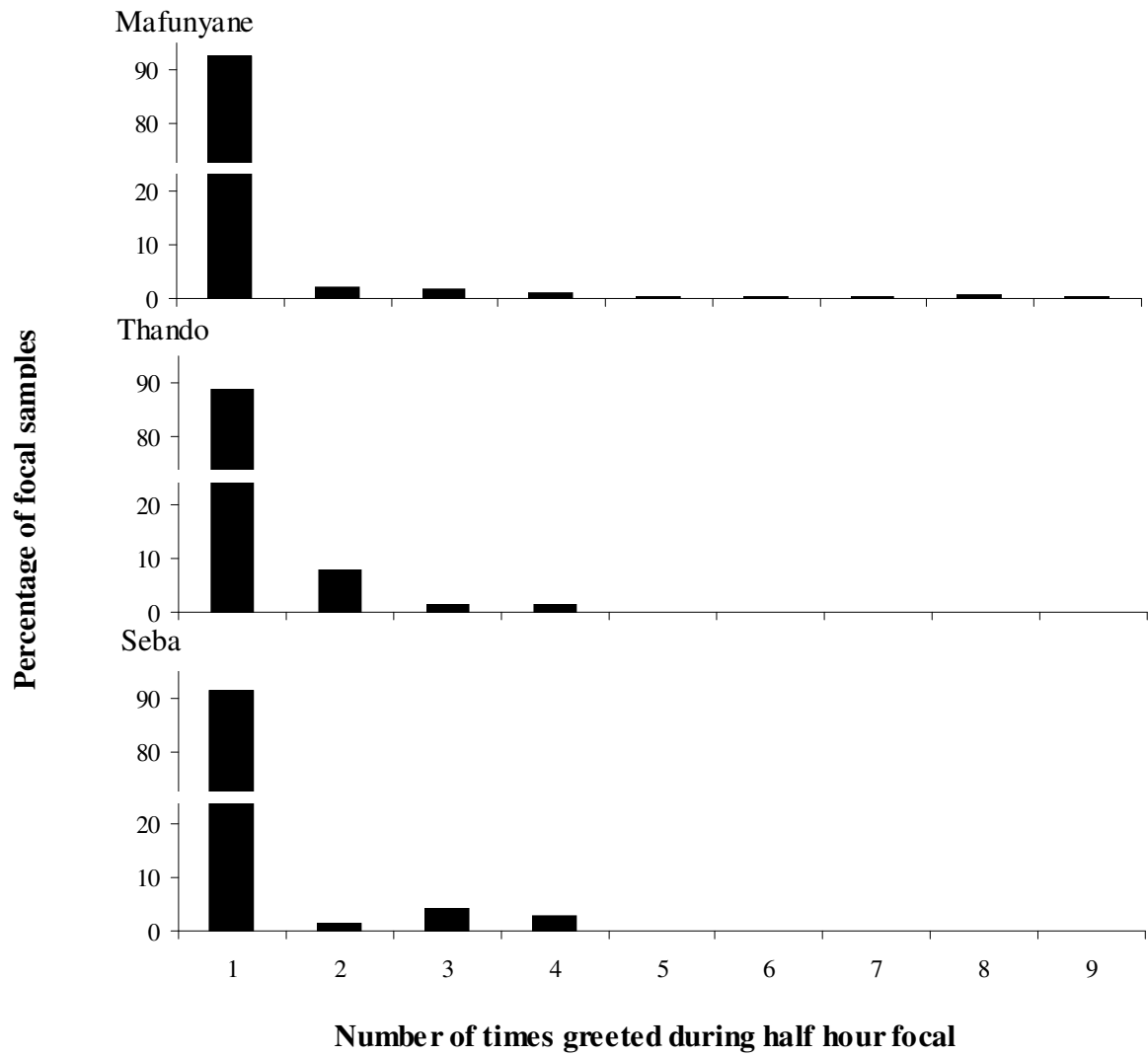
Figure 6.8: Mean number of greeting events per half hour focal by the released adolescent male elephants. Sample sizes for social focal data are outlined in Table 6.1
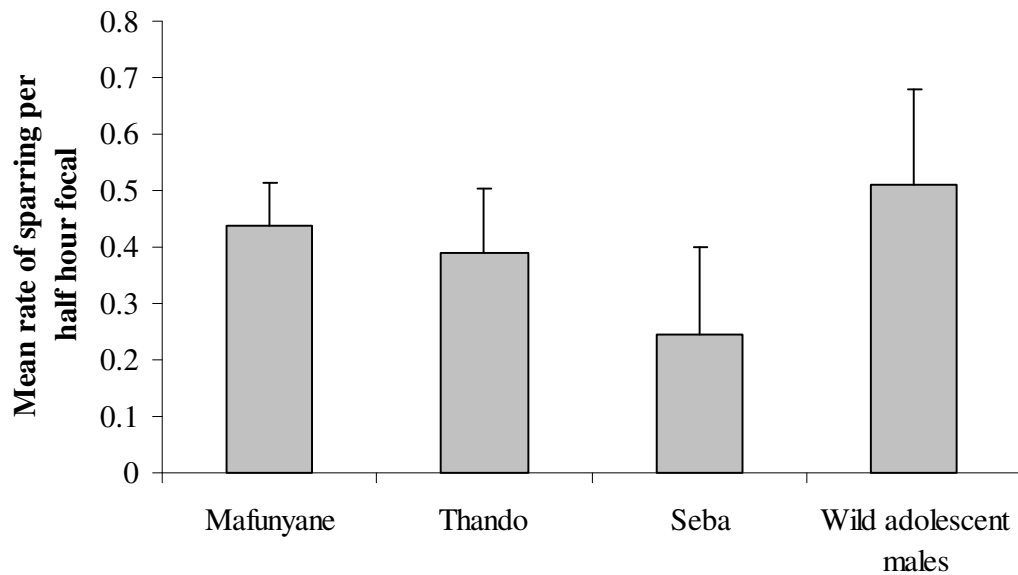
Figure 6.9: Mean (+SE) number of sparring events per half hour focal of the released and wild adolescent males. Sample sizes for social focal data are outlined in Table 6.1

Wild and released males also differed significantly in the level of vocalization per half hour focal (Figure 6.11; $F_{1, 718}$=14.425, P<0.001), with the released elephants vocalizing more often. There was also a significant difference amongst the released male elephants (Figure 6.12; $F_{2, 615}$=4.66, P=0.010), with Thando being more likely to vocalize per half hour. However Mafunyane, when he vocalized, vocalized more often during a per half hour.
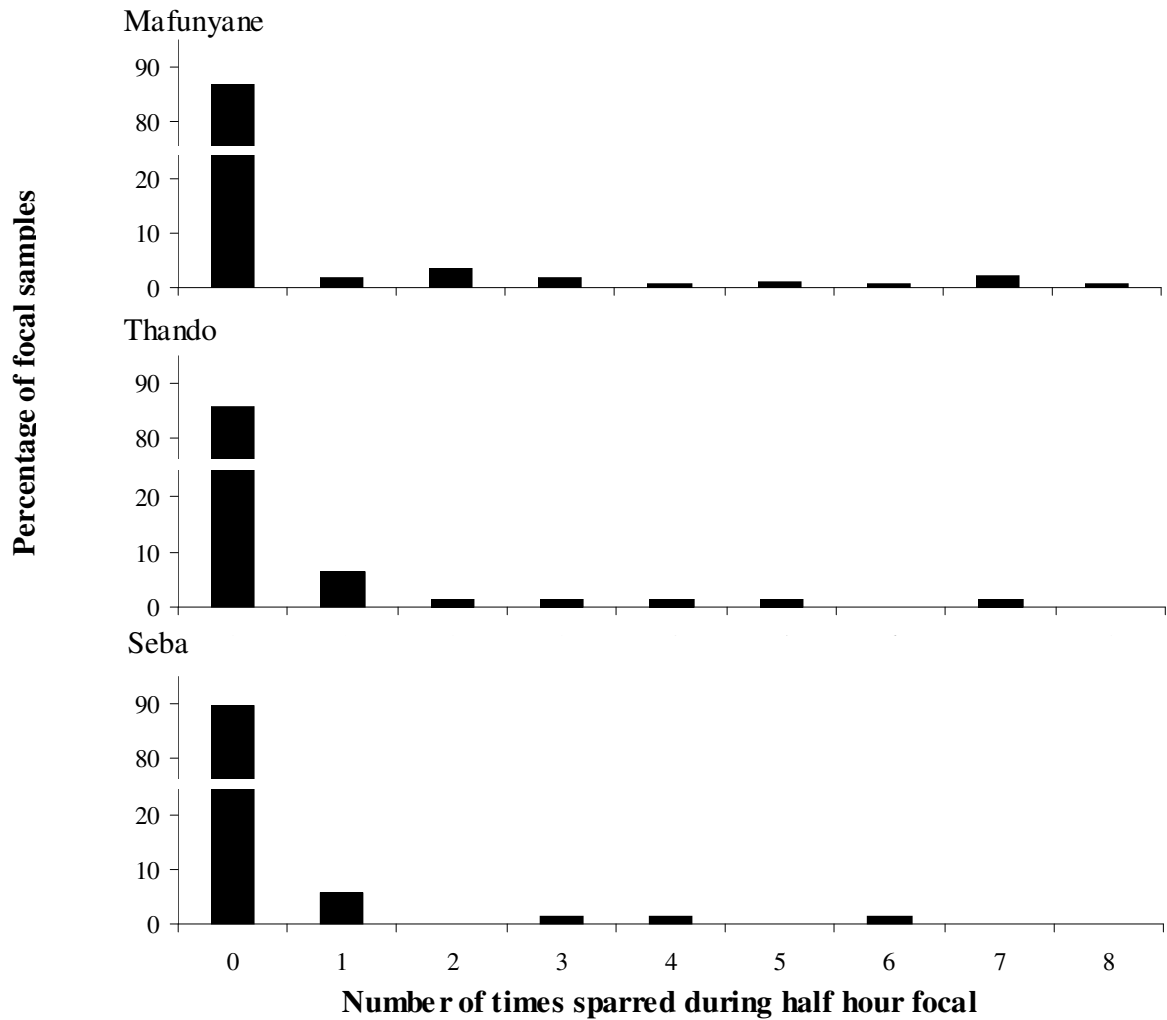
Figure 6.10: Frequency of sparing events per half hour focal by the released adolescent male elephants: Sample sizes for social focal data are outlined in Table 6.1

Figure 6.11: Mean (+SE) number of vocalizations per half hour focal of the released and wild adolescent male elephants Sample sizes for focal data are outlined in Table 6.1

6.3.3. Area utilized

Mean $\pm$ SE home range estimated using the MCP (Table 6.3 and Figure 6.13) was 2269 $\pm$ 372 km^2 for the released elephants, which was not significantly different from the wild collared males (Table 5.3) (t_4=-1.51, P=0.206). In the rainy season it was 2035 $\pm$ 382 km^2, which is not significant from the wild counterparts (t_4=-0.01, P=0.996), and in the flood season it was smaller at 1322 $\pm$ 47.9 km^2, which is not significant from the wild collared males ($t_{4=}$-2.25, P=0.088). However, when the size of the core areas (70% kernels) utilized by the released males and the wild collared males were compared the released males utilized a significantly smaller area during the rainy season (t_4=-3.15, P=0.034).

Table 6.3: Home range size in km^2 (estimated by MCP and 95% kernel) and core area (estimated by 70% kernel) of the released male elephants.

Elephant	100% MCP	95% kernel	70% kernel
Mafunyane	2003	653	282
Thando	2924	1317	285
Seba	1679	992	285
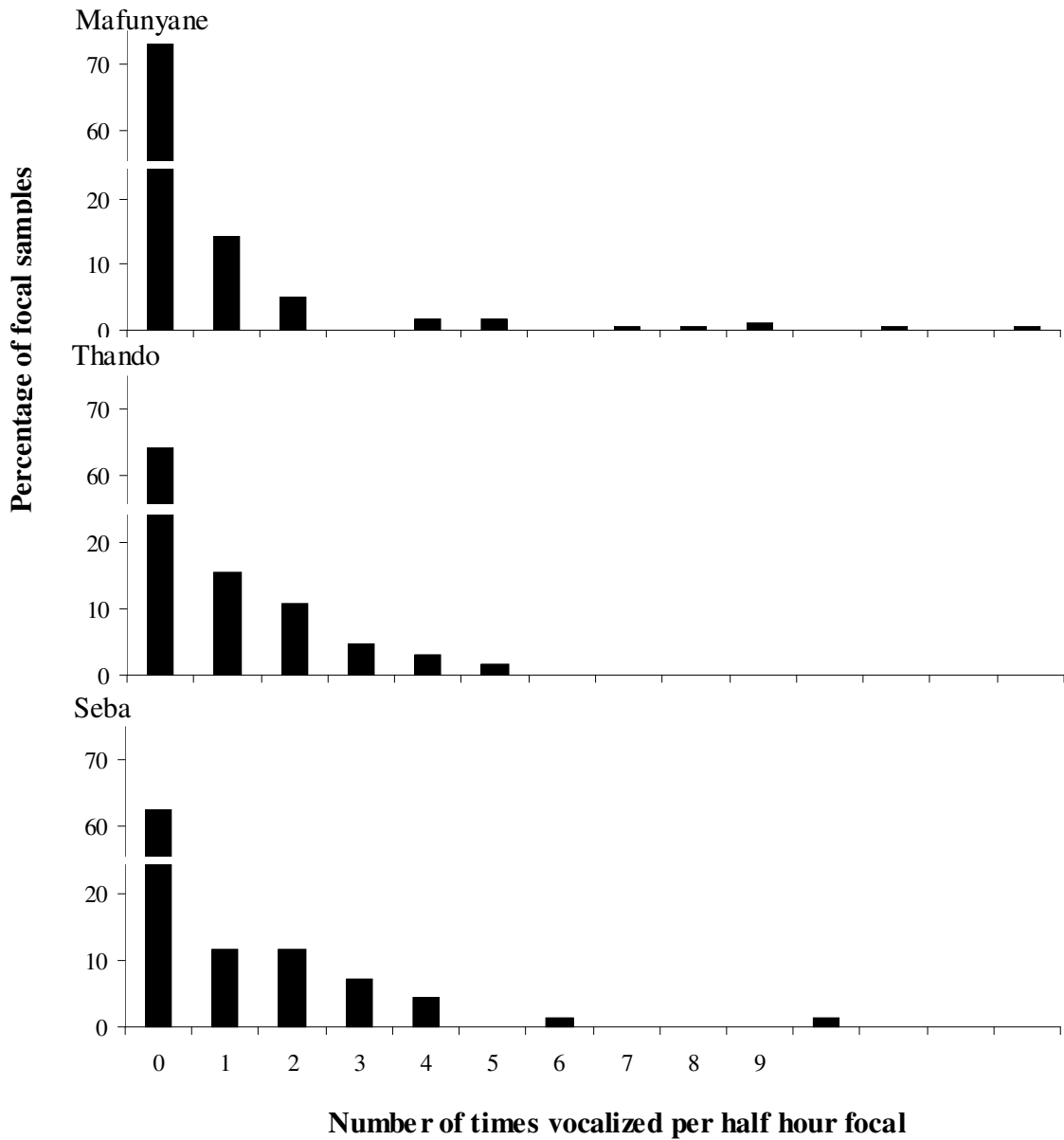
Figure 6.12: Rate of vocalization per half hour focal by the released adolescent male elephants. a) Mafunyane b) Seba and c) Thando.

Mafunyane   Thando   Seba

- 🟩 Rainy season
- 🟦 Flood season
- 🟨 Rainy & flood season
- ⬛ Dry season
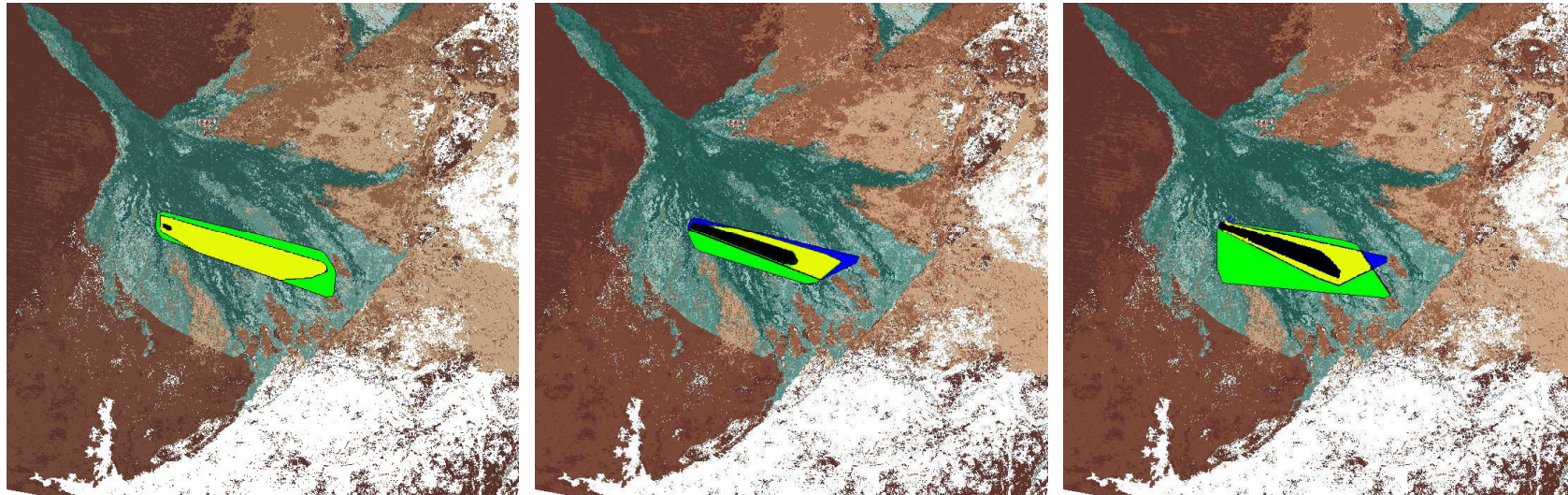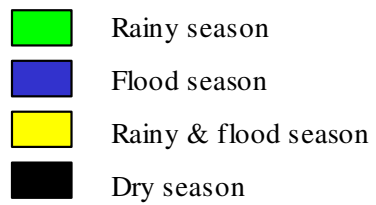
Figure 6.13: Map of the Okavango Delta with the 100% minimum convex polygon (MCP) for the rainy season, flood season and dry season of the three released male adolescent elephants.

The distance travelled by the released elephants between daily satellite downloads ranged from 0.005km, up to 18.56 km. Season affected distance travelled (Figure 6.14), with both the released and wild collared elephants travelling smaller distances during the dry season ($F_{2, 14}$=29.93, P<0.001).
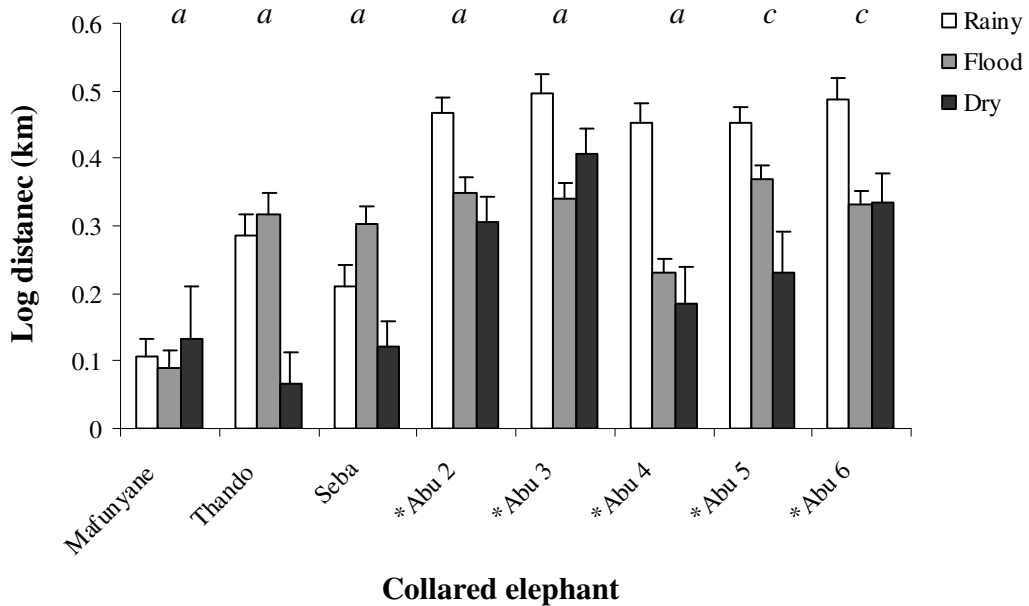
Figure 6.14: Log mean (+SE) distance travelled per season in km between satellite downloads at 24-hour intervals for each of the released and wild collared males. Different italicised letters indicate significant differences identified by *post hoc* comparisons. Sample sizes for consecutive 24 hour downloads are outlined in Table 6.1 and 5.2a. * = wild collared elephant.

6.3.4. Habitat utilization

The released elephants were non-random in their habitat utilization (log likelihood χ^2: χ^2_3=6109, P<0.001). Whilst they utilized the grassland/floodplains habitat to the expected degree, positively selected for island vegetation and negatively selected for mopane woodland and other woodlands (Figure 6.15). The only difference with the collared wild males was that the released males utilized the grassland/floodplains more than expected (Figure 6.15). Statistically there was no difference between the released

males and the wild collared males both when their MCP was compared to the total available habitat ($F_{1, 23}$=0.31, P=0.587) and when the habit used was compared to their MCP home range ($F_{1, 23}$=1.56, P=0.226).
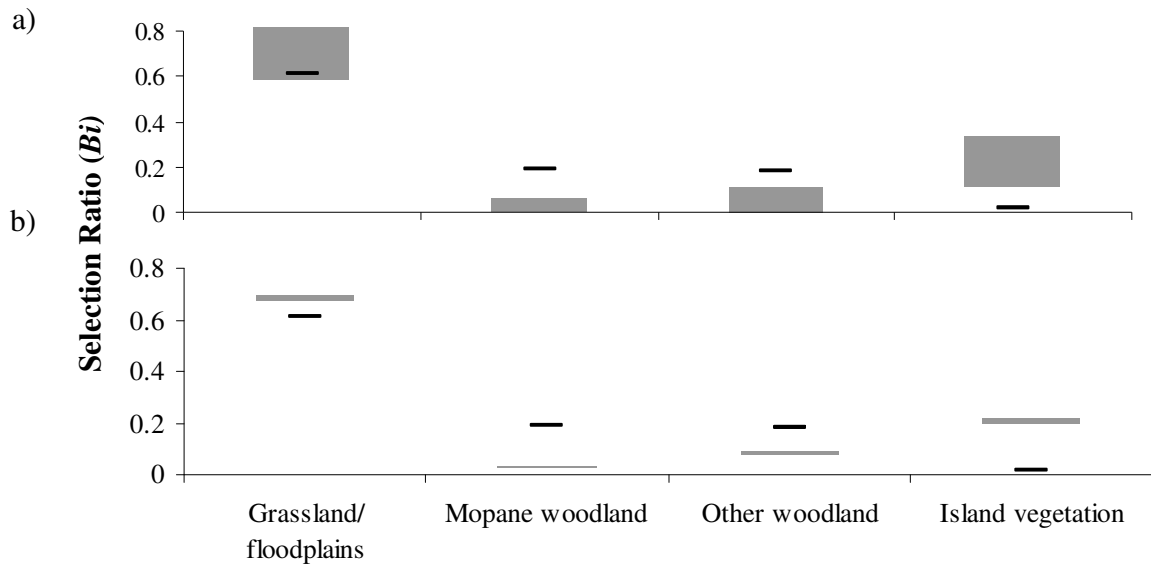
Figure 6.15: Bonferroni adjusted confidence limits for the proportions of habitat use compared to the observed proportions of available habitats ▬ = Habitat available ▇ = Upper and lower Bonferroni 95% confidence limits of habitat use. a) released elephants b) wild adolescent males.

6.3.4.1. Feeding type

Browsing was the dominant feeding type of the released elephants throughout the seasons and grazing was highest during the rainy season (Figure 6.16). There was insufficient data to compare between individuals. Feeding was not affected by season ($F_{2, 30}$=1.71, P=0.199) but was affected by type ($F_{3, 30}$=2.89, P=0.05), where browsing was most probably significantly more common than eating fruit or bark however *post hoc* comparisons was unable to distinguish.
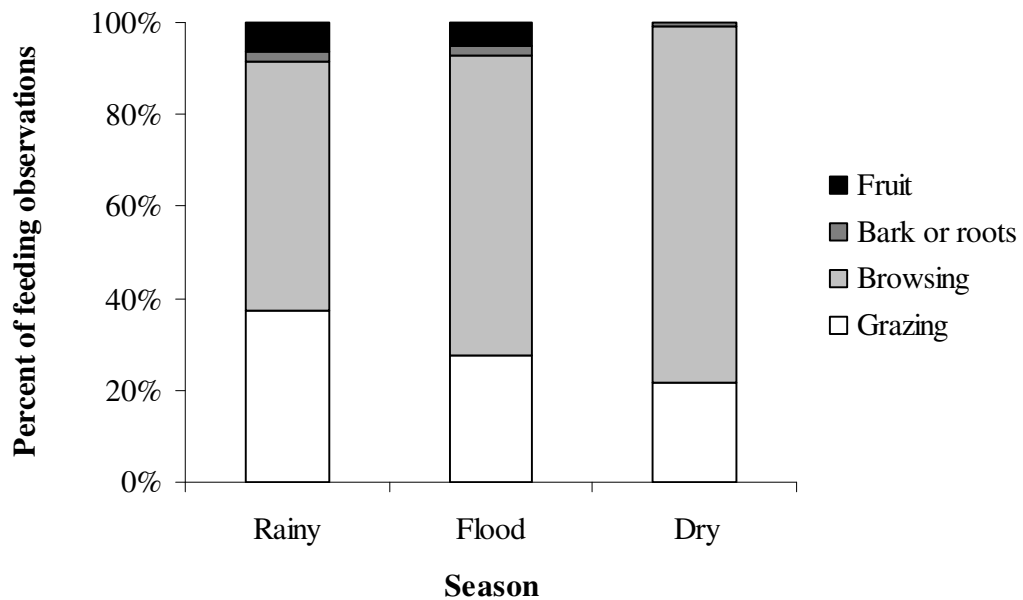
Figure 6.16: Effect of season on the percentage time the released elephants spent grazing, browsing, eating bark and eating fruit.

6.3.4.2. Seasonal use of food plants

The released male elephants fed on a variety of food plants, which included 28 identifiable plant species (Table A.5., Appendix). Grasses and sedges made up the bulk of their diet, followed by *C. mopane* and *H . petersiania* (Table 6.4)

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Table 6.4: The six most frequently eaten food items for the released elephants and the percentage of time spent feeding on them of the total time feeding. R = rainy season, F = flood season, D = dry season. There was not a large sample size for the wild adolescent males in the dry season so these data have not been included.

Food item	Proportion of feeding time										
	Mafunyane			Thando			Seba			Wild adolescent males	
	R	F	D	R	F	D	R	F	D	R	F
Acacia spp.	3.18	3.54	5.03	2.38	0	0	0	0	0	2.70	1.29
Colophospermum mopane	19.25	5.37	0	19.05	7.92	0	0	5.79	0	9.91	14.84
Croton megalobotrys	1.31	6.64	9.55	4.76	11.88	9.09	2.70	7.25	8.33	4.50	3.23
Grasses and sedges	38.32	27.12	22.11	26.19	31.68	18.18	32.43	26.09	0	54.05	15.48
Hyphaene petersiania	11.40	23.38	16.08	2.38	28.71	9.09	10.81	21.74	0	1.80	25.16
Terminalia sericea	8.60	13.28	27.64	5.41	13.04	58.33	35.71	0	0	9.01	16.77
Other	17.01	20.47	19.60	48.65	26.09	33.33	9.52	19.81	63.64	18.02	23.33

6.4.   Discussion

The capacity of captive animals to integrate into the wild is an important measure of a releases success (Krűger, Lawes & Maddock 1999; Goossens *et al.* 2005) and may be attributed to the species chosen for reintroduction, adaptability, age of release, amount of contact with humans, process of release and the release site characteristics. Success rates can be increased by correct management decisions, such as choosing the right individuals for release (Goossens *et al.* 2005) and acclimatisation to the release site (Moehrenschlager & Macdonald 2003). Adolescence is a period of social change for many mammals and, therefore, is often the best time for reintroduction and translocation (Moehrenschlager & Macdonald 2003; Goossens *et al.* 2005). A measure of successful reintroduction is often said to be whether the subjects survive long enough to breed (Sarrazin & Barbault 1996). Given that male elephants only start coming into musth in their late twenties to early thirties (Poole 1982) and the low likelihood of knowing who had fathered the calves, this measure of success could not be used within the context of this research.

After eight, fourteen and fifteen years in captivity the released adolescent elephants integrated into the fission-fusion society of the wild elephants to a degree, and interactions between the released and wild animals were non-aggressive. Whilst there was no difference between wild and released adolescent males in their levels of total social interactions or greeting, the released males sparred significantly less than the wild males and they spent more time with adolescent male elephants. This is in agreement with captive raised elephants released between the ages of 1-5 years (McKnight 1992). This could be attributed to the released males being new to the male social system and not knowing individuals. The wild males will have been doing this whilst in their natal herds and prior to becoming independent. The released males vocalized at a higher rate than their wild conspecifics. This was largely due to Thando, who vocalized nearly four times as much as the other released males. Other individual differences amongst the released males include Mafunyane sparring and greeting significantly more than the others. This may be an artefact of the number of focals gathered on each, as three times more focals were collected on Mafunyane than Seba or Thando.

In spite of there being no statistical differences in the total social interactions of the released males as compared to their wild counterparts. They did not appear to be fully integrated into the wild hierarchy. Although Mafunyane was apparently very social, with high levels of greeting and sparring, he showed premature social aging as he spent the majority of his time alone. He was also unusual in that he spent the majority of his time in a very small area of the home range he had explored. Whilst Seba and Thando were much more exploratory, they were located together 80% of the time. It has been postulated that male elephants leave their natal herd together and socialize with each other more then other males (Moss & Poole 1983), as do many mammals (Boelkins & Wilson 1972; Cheney & Seyfarth 1986; Pusey & Packer 1987; Mitchell 1994; Strier 2000; Sharpe 2005). In Amboseli NP, several pairs of males were observed in association with other males for more than 30% of the time (Moss & Poole 1983), whilst in Samburu it was 20% (Rasmussen 2005). Seba spent nearly all his time with released elephants, perhaps indicating that he was too young, and therefore not ready for independence, at the time of his release. The released elephants spent more time closer to adolescent males whilst wild males spent more time closer to older males. This may be due to the released males not knowing many of the wild adolescent males and having to establish themselves in the hierarchy. The wild males already knew a proportion of the adolescent males in the population, having associated with them whilst they were younger and, therefore, can invest more time getting to know the older bulls.

Habitat utilization or plant species utilized did not differ between the wild or released males. Whilst the areas the released males used were similar in size to the wild males, they utilized a significantly smaller core area during the rainy season and travelled significantly shorter distances daily. Adolescent males spend most of their time with female and mixed herds and other males and their movements are likely to be influenced by the movements of these groups. The released males had a tendency to be alone or, in the case of Thando and Seba, together, and this may explain the difference in movement patterns. It is likely that the wild males had prior knowledge of some of the area that they utilize, through movements with their natal herd. The released males were very restricted in their movements whilst captive and, therefore, still have a lot to learn. Many mammals learn to identify food socially, e.g. orang-utan, chimpanzees

(*Pan troglodytes*) and other primates, resulting in many released primates being naïve about foods (Yeager 1997; Box 1999; Russon 2002). The released male elephants consumed the same food items as their wild counterpart, and in similar quantities, throughout the year and this is probably a result of innate knowledge as well as the freedom to choose what they ate and learning from the older group members whilst in captivity.

All the released elephants had limited experience in the wild, as they were very young when captured. However, they were raised amongst and able to interact freely with male and female African elephants whilst in captivity. Low success rates following the release of captive-reared birds and mammals into natural habitats have suggested the hypothesis that these animals acquire a variety of perceptual and motor skills in their natal habitat that affect their success in the wild (Beck *et al.* 1994; Sheperdson 1994; Stamps 2001). Early social interaction has already been shown to be of benefit with the orphans of the David Sheldrick Wildlife Trust. Releasing adolescent individuals from a captive environment is the best criterion for successful release (Goossens *et al.* 2005), particularly for elephants as it is a natural period to leave their natal herd and become independent (Douglas-Hamilton 1972, 1973; Poole 1987, 1994, 1996b; Lee & Moss 1999) and older bulls are harder to contain within reserves (Garai & Carr 2001; Dublin & Niskanen 2003). Releasing individuals in groups may have a positive affect on their integration into the wild as well as increasing the likelihood of them exploring new areas and decreasing their likelihood of trying to return to their place of origin (Dublin & Niskanen 2003). This appeared to be the case with Thando and Seba, who explored the area more and spent more time away from the area familiar to them

Translocation of elephants, in particular males, currently ignores the social ecology of the individuals (Stanley-Price 1986; Garai *et al.* 2004). Allowing the elephants time to get to know each other prior to release into the new area, or choosing elephants that know each other before capture, could decrease the likelihood of them trying to return from where they came and encourage them to explore the new area. For releasing adolescent males into a new area the presence of older bulls is a prerequisite.

If repopulating an area, translocating the right sex ratio of both males and females is important (Moehrenschlager & Macdonald 2003).

The number of reintroductions and therefore translocations needed in the future is expected to increase considerably as wild populations become segregated and/or endangered. The technology and expertise being currently developed will be increasingly important in facilitating gene flow between isolated populations (Stuart 1991) and social integration.

For some species, captive breeding and subsequent reintroduction is the only means of survival (Krűger, Lawes & Maddock 1999; Spalton, Lawrence & Brend 1999). The high cost of losing individuals of an endangered species inadequately prepared for release, or through releasing them into inappropriate areas, are not acceptable. Therefore learning from other release programmes (Letty *et al.* 2000) will help minimise these risks and ensure increased success rates.

6.5.   Conclusions

Whilst, the release of captive bred and raised individuals into the wild is still controversial, it is widely supported publicly as a means of management and conservation (which evokes high emotion and media coverage for the species and habitat) (Clunes 1997; Allen 2004; Anon 2005). In this Chapter I have shown that:

- Released adolescent male elephants spent more time alone and in smaller social groupings.
- Released adolescent male elephants do not differ significantly from their wild counterparts in their rate of social interactions.
- Released adolescent male elephants sparred more often.
- Released adolescent male elephants vocalized more often.
- There were individual differences amongst the released elephants in the time spent sparring and the rate of vocalization.
- Released adolescent male elephants do not differ significantly from their wild counterparts in habitat utilization.

- Wild-born captive elephants can be rehabilitated and released into the wild.

In this Chapter I have investigated the viability of releasing captive raised adolescent male elephants into the wild environment. The next Chapter expands on this by looking at the release of a single female elephant.

Chapter 7

Observations on the release of a captive raised female African elephant into the Okavango Delta

Summary

A female elephant that was wild born in the Kruger National Park, South Africa but captive raised by Elephant Back Safaris in Botswana, was released on the 13th September 2003. She was fitted with a satellite radio collar and monitored from the ground and air. Focal, satellite and observational data were collected over this period to see if and how she integrated into the wild population.

She spent the majority of her time with three released males, who were also released from Elephant Back Safaris, and therefore elephants she knew. She spent a quarter of her time with wild female herds for extended periods. Whilst with wild female herds there was a tendency for her to be more social and to spend more time closer to other elephants. There was no observed aggression towards her by any of the wild elephants with which she was sociable.

She utilized an area comparable to wild female elephants in other parts of Africa. However the area she utilized continued to increase, indicating that she was constantly exploring new areas whereas wild females tend to have a distinct home range.

7.1.   Introduction

Female elephants form close long lasting social bonds (Wrangham 1980) and a female typically spends her entire time in the female herd into which she was born (Moss 1988). On rare occasions unrelated family groups have been known to fuse (Moss 1988), raising the possibility that unrelated females may associate with each other regularly (Charif *et al.* 2005). Lone female elephants are rare, but have been observed (Mubalama 2000). This close-knit social system posed particular problems for the

release of a captive female elephant, as unlike males, they do not typically exhibit any phase of solitariness during their life. Furthermore, females are easier to handle in captivity, such that there are very few instances where they have been released into the wild and their subsequent patterns of social interaction observed or quantified. For example, in 1982, two females, formerly housed in zoos in America, were released into the Pilanesberg NP, South Africa, where they have since 'adopted' orphaned calves introduced from the Kruger NP and have also had their own calves (Anderson 1986; Moore & Munnion 1989; Moore 2000). Similarly, in 1997, a 25-year-old female was released into the Mkomazi Reserve in Kenya, where she was observed briefly to join up with existing female herds (Clunes 1997).

In this Chapter, I analyze behavioural and movement data from a single female (Nandipa) released by Elephant Back Safaris (EBS) in Botswana because she was never fully accepted by the matriarch of the captive group. This provided an important opportunity to assess whether a captive raised female could be successfully released into the wild and accepted by a wild population. In particular I address the following questions

- Is a lone released female able to socialize, move and integrate with a wild herd?
- Does she spend the majority of her time alone, with wild herds or with the released males whom she knew whilst captive?
- Does the area that she utilizes reflect that of the area she knew prior to release or will she explore novel areas?
- Is the size of the area she utilized comparable to female areas elsewhere in the African elephant range?

7.2. Methodology

On the 12th September 2003, Nandipa was fitted with an AWTSM2000E satellite radio collar (Africa Wildlife Tracking cc. Pretoria, South Africa) and released the next day from the boma where she was housed, whilst the rest of the EBS herd were out. She was

monitored from the ground and air until the 10th February 2004. Otherwise the release protocols and methods for the collection and analysis of focal behavioural data and movement data were identical to those for the released male elephants in Chapter 6.

7.2.1. Data analysis

7.2.1.1. Focal data

As there were no comparative data collected on wild females in the area where possible comparisons have been made with other studies on females elsewhere in Africa. As the activity data were not normally distributed, and could not be transformed, the effect of season and social grouping (between when she was with a wild herd or with one or more released males) on the frequency of social behaviours (Code 4: Table 4.1), greeting (Code 4.1), sparring/playing (Codes 4.2 and 4.3), vocalization (Code 9) and distance to nearest neighbour were analyzed separately using nonparametric statistics. For the analysis of time budgets an additional social grouping, alone, was included and therefore Kruskal-Wallis tests were used.

7.2.1.2. Satellite collar data

The satellite collar data were analyzed as outlined in Chapter 5.

7.3.   Results

The total sightings and focal data collected on the female is summarised in Table 7.1.

Table 7.1: Summary of the data collected in different seasons on Nandipa. Total sightings data used to analyze patterns of social grouping; social focal data used to analyze patterns of social behaviour within groups (see Code 4, Table 4.1) and nearest-neighbour distances; focal data used to analyze patterns of activity and the rate of vocalization; satellite downloads used to analyze home range and habitat utilized: consecutive 24hr downloads to analyze daily distance travelled.

Data set	Rainy	Flood	Dry	Total
Total sightings of Nandipa	59	72	29	160
Social focal data	17	21	5	43
Focal data	18	22	5	45
Satellite downloads	910	753	218	1881
Consecutive 24hr downloads	268	195	60	523

7.3.1. Social behaviours

Whilst there was an apparent tendency for the released female to be more social and more vocal when she was with one or more of the released males (Figure 7.1), these differences were not significant (Mann-Whitney $U:$ social, $W_{10, \, 33}=203$, $P=0.535$; greeted, $W_{10, \, 33}=221$, $P=0.977$; sparring, $W_{10, \, 33}=231$, $P=0.408$; vocalization, Kruskal-Wallis: $H_2=2.45$, $P=0.294$).
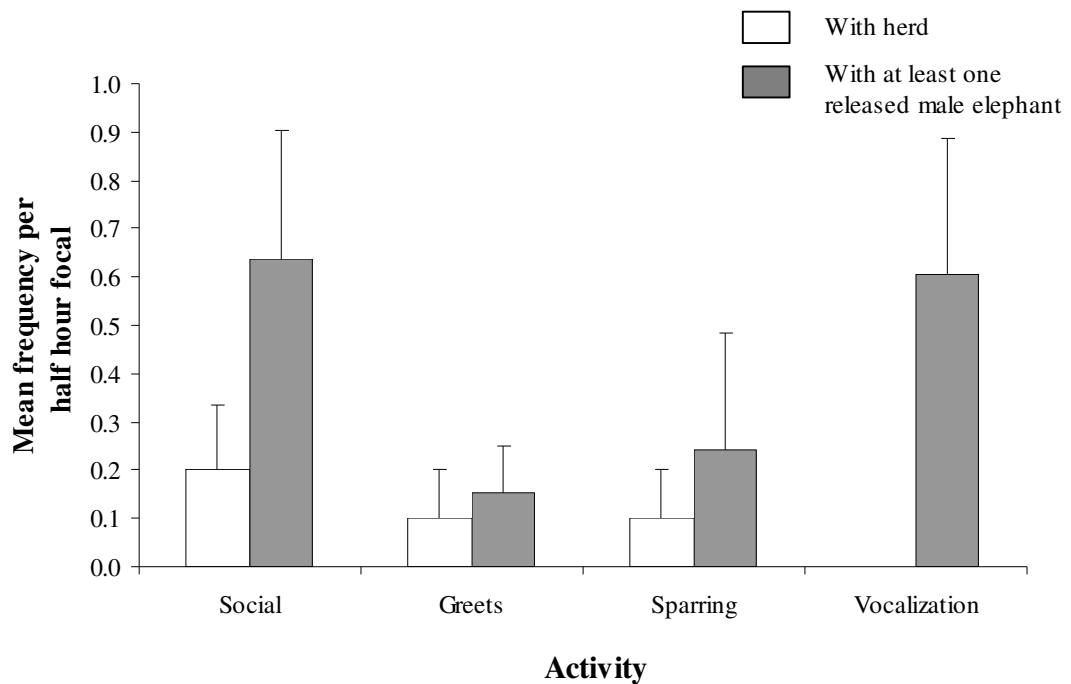
Figure 7.1: Mean (+SE) rate of social behaviours and vocalization per half hour focal of Nandipa when she associated with female and mixed herds and when she was with one or more of the released male elephants. Sample sizes for social focal data are outlined in Table 7.1.

7.3.2. Social grouping

Over the 17 months she was monitored, Nandipa spent 55% of her time with the released males and the males they associated with and only 28% of her time with wild female and mixed herds. Twelve per cent of her time was spent alone, whilst the remaining 5% was spent with the EBS group (Figure 7.2).

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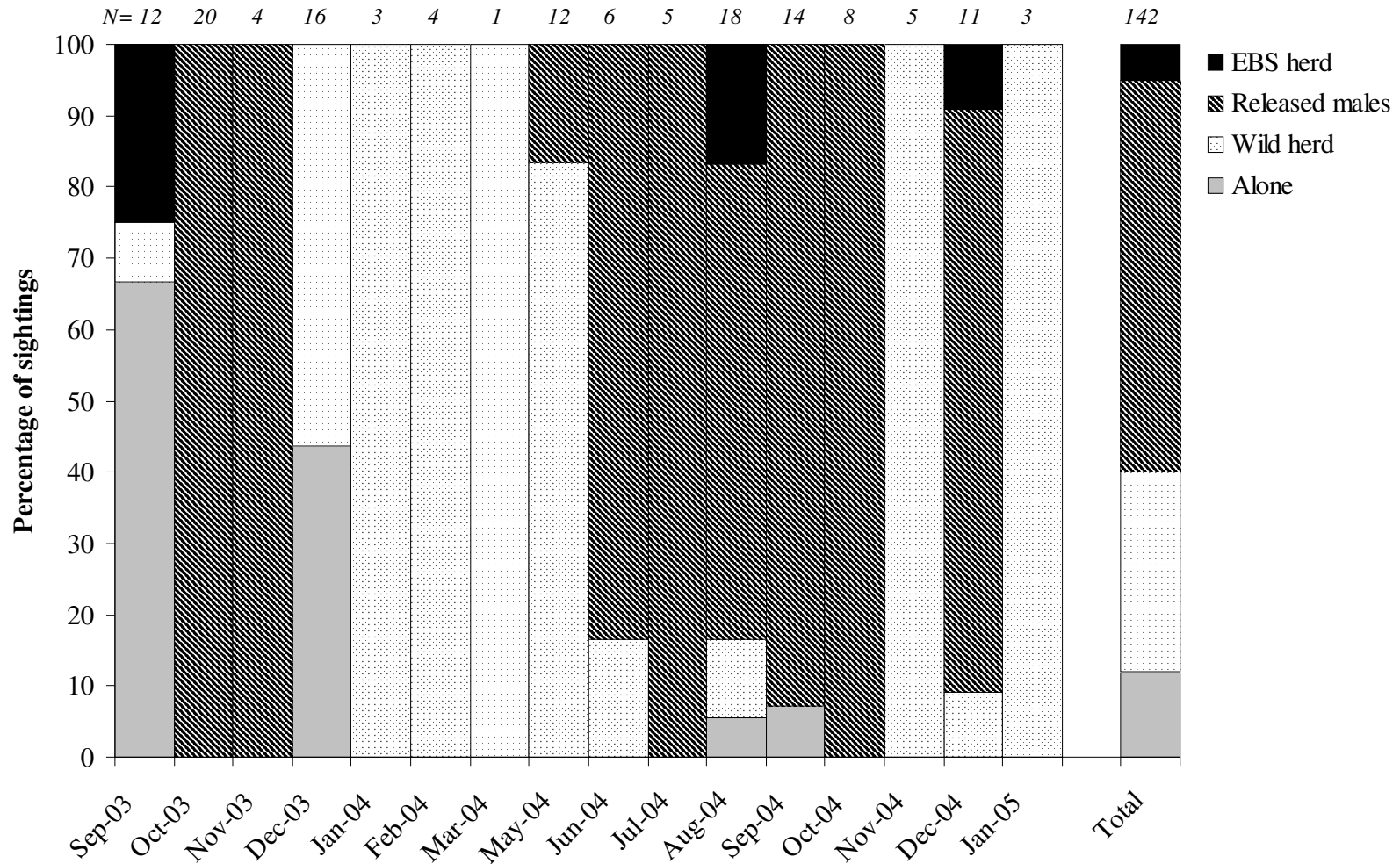
Figure 7.2: Proportion of sightings of Nandipa within different social groupings months post release. *N* = sample size.

In December 2003, the three released male elephants left the vicinity of the research camp and moved east; Nandipa did not go with them. Instead she joined a wild female herd and when this herd left the vicinity of camp at the end of December, she went with them and spent five months with herds (Figure 7.2), 20 kilometres southwest of the camp (Figure 2.3).

7.3.2.1. Distance to nearest neighbour

Distance to nearest neighbour was not affected by season ($F_{2, 43}$=1.100, P=0.343), nor time post release ($F_{15, 43}$=1.610, P=0.139). However, it was affected by social grouping (t=-3.56, P=0.004), being significantly smaller when Nandipa was with a wild female and mixed herds than when she was with the released males (Figure 7.3).
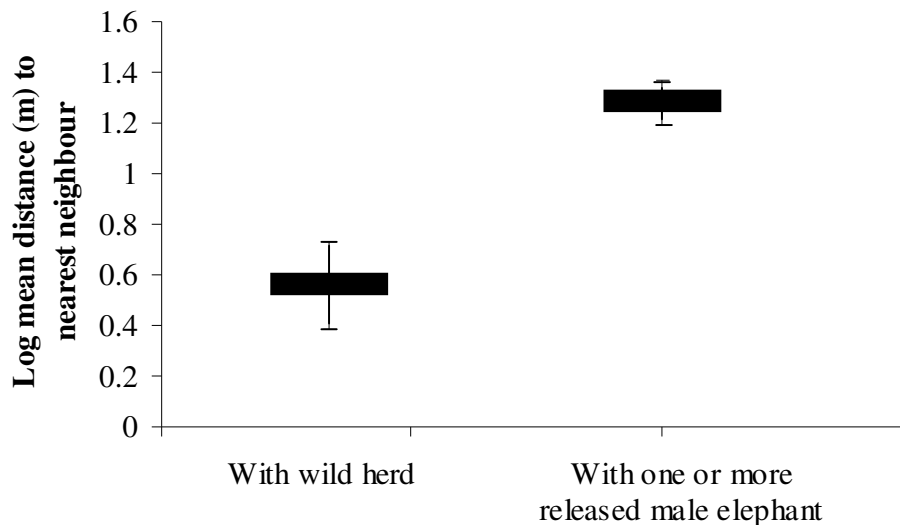
Figure 7.3: Mean ($\pm$95% confidence limits) distance (m) Nandipa was to nearest neighbour during half hour focal data whilst she was with wild female and mixed herds and when she was with the released male elephants.

7.3.3. Time budgets

Season did not significantly affect the proportion of time Nandipa spent feeding (H_2=1.09, P=0.579), walking (H_2=2.11, P=0.347), dusting/mudbathing (H_2=0.39,

$P=0.822$), sleeping/resting ($H_3=4.33$, $P=0.115$), or engaged in other activities ($H_2=1.37$, $P=0.504$).

Her social grouping (Figure 7.4) did not significantly affect the proportion of time Nandipa spent feeding ($H_2=1.89$, $P=0.376$), walking ($H_2=2.35$, $P=0.308$), dusting/mudbathing ($H_2=0.45$, $P=0.799$), sleeping/resting ($H_2=0.41$, $P=0.815$) or engaged in other activities ($H_2=2.14$, $P=0.342$).
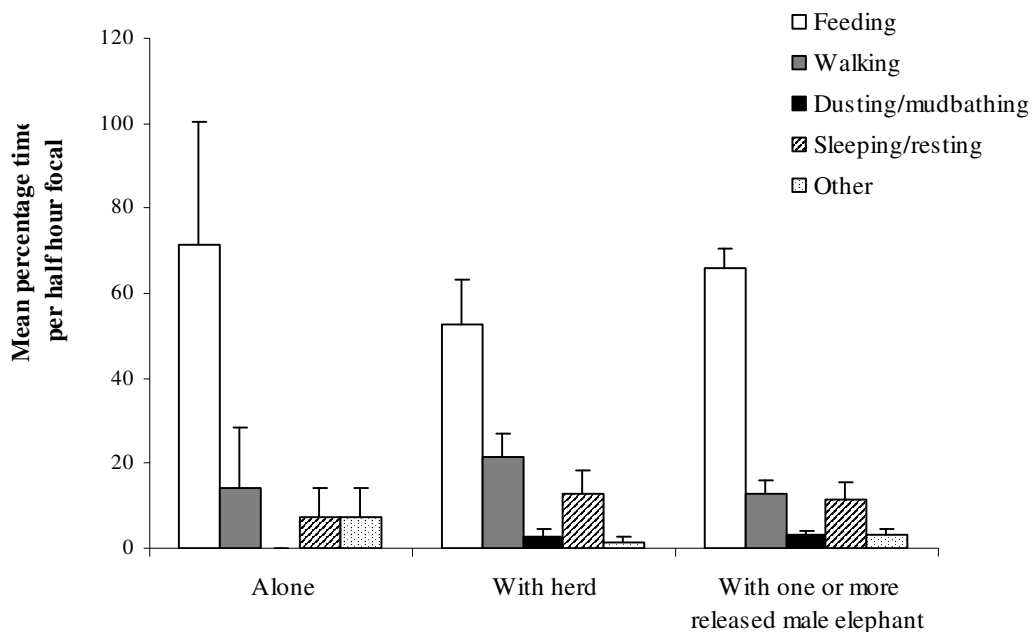
Figure 7.4: Mean (+SE) percentage time for different behaviours per half hour focal by Nandipa when she associated with female and mixed herds and when she was with one or more of the released male elephants. Sample sizes for focal data are outlined in Table 7.1.

7.3.4. Home range size

Nandipa utilized a total (100% MCP) of 2017km^2 between September 2003 and February 2005. Season did not affect the area utilized (Figure 7.5 and 7.6). However, the total area utilized (100% MCP) increased with time post-release (Figure 7.7), although her core area of activity remained fairly constant averaging 37.5 km^2 (SE$\pm$11.2). The daily distance travelled was affected by season ($F_{2, 520}=8.885$;

$P<0.001$), with the distance travelled significantly lower in the dry then in the rainy or flood seasons (Figure 7.8).
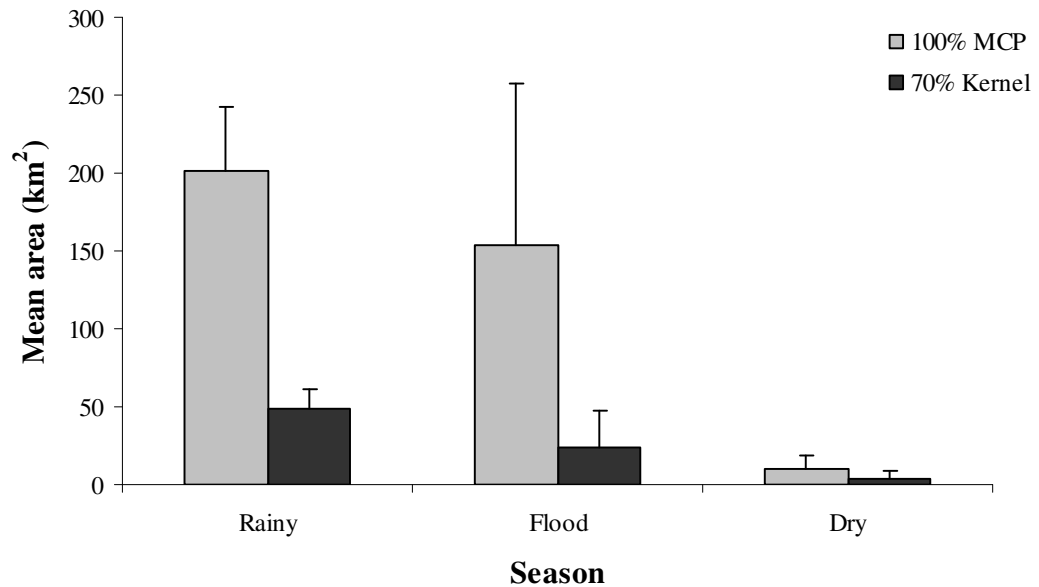
Figure 7.5: Total mean area (km^2) utilized (100% MCP) and mean core area utilized (70% Kernel) Nandipa from September 2003 until February 2005.
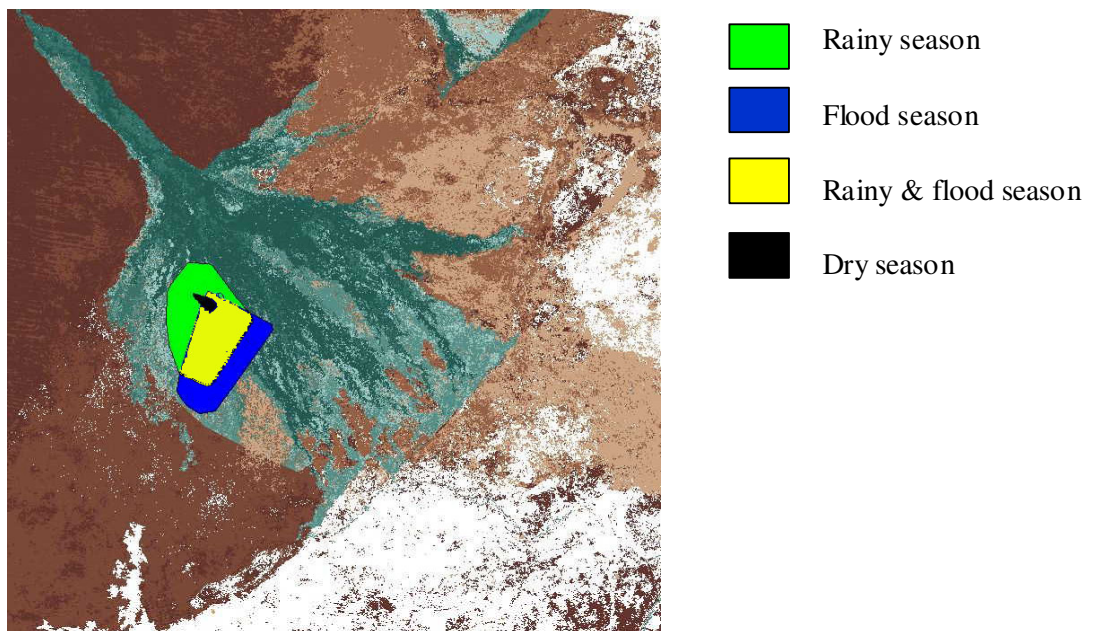
Figure 7.6.Map of the Okavango Delta with the 100% minimum convex polygon (MCP) for the seasonal utilization of Nandipa.
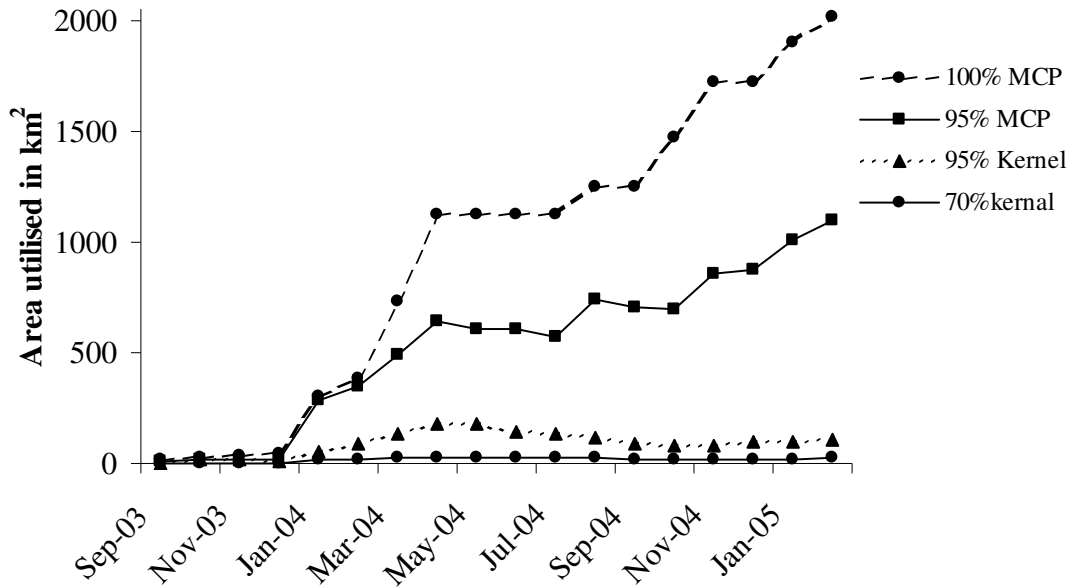
Figure 7.7: Accumulative 100% and 95% MCP, 95% and 70% Kernel of the areas utilized by Nandipa in the months post release.
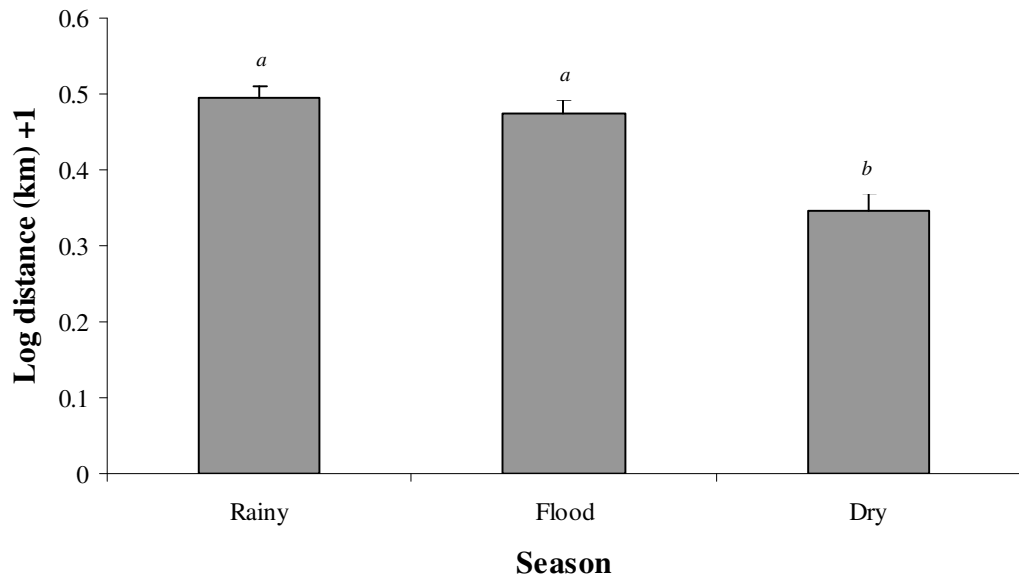
Figure 7.8: Log mean (+SE) distance travelled in kilometres between satellite downloads at 24hr intervals for Nandipa in the rainy, flood and dry seasons. Sample sizes for focal data are outlined in Table 7.1. Italised letters signify statistical differences.
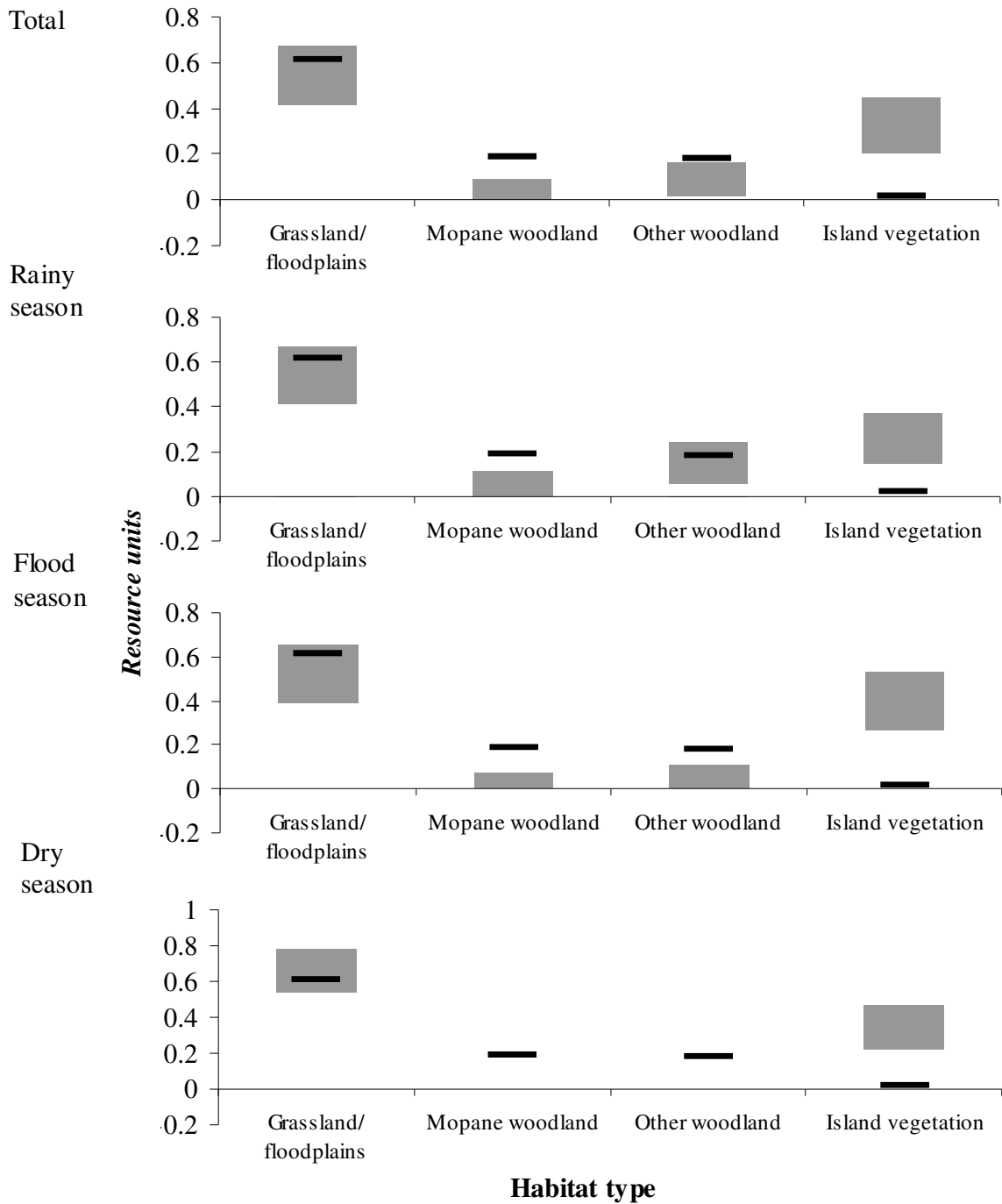
Figure 7.9: Bonferroni adjusted confidence limits for the proportions of habitat use compared to the observed proportions of available habitats for Nandipa. ▬ = Habitat available ▬ = Upper and lower Bonferroni 95% confidence limits of habitat use.

7.3.5. Habitat utilization

The released female did not utilize the habitats randomly (χ^2_3=10252, P<0.001). Whilst she utilized grassland/floodplain habitat to the expected degree throughout the seasons (Figure 7.9), Mopane woodland was negatively selected for and island vegetation was positively selected for throughout the year. Other woodland was negatively selected for during the flood and dry season but utilized to the expected degree during the rainy season.

7.4. Discussion

Examples of lone females leaving a matrilineal society are rare. However, in *Macaca mulatto* fission of groups does take place, with peripheral females being the most likely to form a new group (Chepko-Sade & Sade 1979). Released chimpanzees integrated into wild groups for extended periods but were never fully accepted (Goossens *et al.* 2005). A released hand reared female meerkat (*Suricata suricatta)* was not socially accepted into a group of wild meerkats, although she did mate and start her own group (*pers. obs*.) and elephants from culled or introduced populations form new and stable 'families' made up of unrelated youngsters (Shoshani 1991; Moore 2000; Slotow *et al.* 2005). In India escaped tame female elephants have been reported to join up with wild female herds (Sanderson 1963). However, these may be related as captive elephants at that time were wild caught when young. Therefore the released females social interactions were the main concern and area of interest upon her release.

Whilst Nandipa was not fully accepted and integrated into a wild herd, she spent over a quarter of her time with them. Similar behaviour was seen in a female released after 25 years in captivity in Tanzania, who would socialize with female herds for a while and then be alone (Clunes 1997). When Nandipa was with the wild herds she was significantly closer to other elephants when she was with one or more of the released male elephants. There was also a tendency for Nandipa to greet more when in wild herds. This indicates that she was socializing with wild herds. Also there were no signs of aggression towards her by members of the wild herds and the only time she sparred,

an activity unusual for adult female elephants, was when she was with one or more of the released male elephants.

Immediately after her release, Nandipa spent a week alone in thick woodland vegetation, before starting to explore the area and spend time with wild herds. After 17 days she joined up with all three of the released males. In spite of being accepted by wild herds, she 'chose' to spend the majority of her time with one or more of the released males. It is not natural for a female to associate with adolescent and mature males, unless they are herd members prior to independence or mating, so her social interactions highlight the importance of 'knowing' individuals in elephant society. The majority of time Nandipa was with wild herds was during the rainy season when resources are not limited and therefore elephants are able to spend more time socializing and playing (Moss 1988; B. Schulte, *pers. comms*.). In other populations of elephants the rainy season is when large aggregations of elephants are sighted where families have joined up into bond groups and clans (Moss 1988; Wittemyer, Douglas-Hamilton & Getz 2005) and thus the herds may have been more willing to accept her during these times as competition for resources were low.

The area Nandipa utilized was comparable to populations of wild elephants and larger than most (Table A.6, Appendix). She continually explored new areas, whilst her core area remained fairly constant. This is unusual for a female elephant, which generally have a set wet and dry season range (Grainger, van Aarde & Whyte 2005). Only continued monitoring will reveal if she adopts a distinct range. Whilst the area she utilized was not significantly affected by season, she used a smaller area during the dry season; this may be due to her returning to an area she was familiar with and in which she was able to locate resources, or it may be an artefact of the small sample size for this period. She also travelled less distance daily than female elephants elsewhere in Africa (Blake *et al.* 2003).

Her habitat utilization differed to that of wild female elephants in that she negatively selected for mopane woodland whereas wild female elephants utilized this habitat more than expected (Figure 5.5). Island vegetation was positively selected whilst grassland/floodplain was utilized to the expected degree. However these data sets are not directly comparable as satellite collar data from the released female elephant was

compared to observational data taken whilst driving around the study area. To really investigate whether Nandipa was selecting habitats differently to wild females, data on wild satellite collared females in the same area should be collected.

A standard measure of the success of reintroduction is whether the subjects survive long enough to breed (Sarrazin & Barbault 1996), and so perhaps the best measure of the success of this release is the fact that Nandipa gave birth to a male in July 2006.

7.5.   Conclusions

In spite of being released alone and not having met or socialized with any of the female herds in the study area, Nandipa was partly integrated into the wild elephant population, spending considerable amounts of time with wild herds and visiting new areas with them within the 17 months she was monitored. This is unusual, as it is generally accepted that females will not socialize with unknown elephants.

Only further monitoring will show if a wild female herd accepts her permanently, or whether the birth of her calf will be the beginning of her own herd. In this Chapter I have shown:

- Released female elephants can be accepted, integrate and move with wild female and mixed herds.
- Socializing with known individuals is important to elephants, as indicated by the time Nandipa spent socializing with the released male elephants.
- A released female will explore novel areas and expand her known range to an area comparable in size to wild female elephants.

In this Chapter I have investigated the viability of releasing captive raised female elephants into the wild environment.

Chapter 8

General discussion

8.1.   Foreword

In this final Chapter I have drawn together the findings of the previous chapters and related them to my primary objectives. First, I assess the importance of the Okavango Delta as a habitat for the elephant population in Botswana and the notion that the elephant population is re-inhabiting historical ranges. Secondly, I discuss adolescence and the period of independence in the male African elephant and polygynous mammals in general. I discuss how this work is applicable to the conservation and management of the African elephant. Finally I give some suggestions for possible future research.

The physical environment of the Okavango Delta made the collection of data throughout the year challenging. Tried and tested methods were applied wherever possible and in spite of difficulties the quantity and quality of data were good. A larger sample size for the released elephants would have been ideal, however this was beyond the capacity of the project. Undertaking aerial surveys in conjunction with demographic studies from the ground would have given a better estimation of population and density of elephants utilizing the study area. The recordings of vocalizations of the male elephants may have helped explain the variances between the age classes, however delicate equipment could not stand up to the conditions.

8.2.   The Okavango Delta as a resource for elephants

Adequate quantities of usable resources are necessary to sustain animal populations; this is especially critical for endangered species and exploited populations. Determining which resources are selected for is of particular interest because it provides fundamental information about how animals meet their requirements for survival.

Environments are continually changing with season and time and therefore must be considered when implementing management and conservation decisions in a

dynamic ecosystem. The Delta is spatially and temporally variable, particularly in respect to the extent and duration of the annual floodwaters. These water movements affect the areas accessible to animals and in recent years there has been a westward spreading of water. The higher density of males than females in the study area could be indicative of the shifting ecology of the Delta and the exploratory nature of male elephants. Only continued monitoring will show if the western Delta is in fact a bull area or on the margins of an expanding elephant range.

The elephants of the Delta utilized the habitats available non-randomly and were dependent on different resources at different times of the year. Season affected both home range size and the habitats they were selecting, the daily distance travelled by the collared elephants, the diet of the local male population and the density of elephants in the area. The adolescent males utilized larger areas during the rainy season, as is found in other elephant populations (Table A.6, Appendix). The habitats important to the elephants also varied spatially with local and regional differences in habitat utilization. The dry season range is perhaps the most important to the elephants, as it is the most stressful time in terms of resource availability. Knowledge about local plant phenology and water availability will be invaluable at this time (Waser & Jones 1983; Stamps 2001). Variation between the location of the wild and adolescent male's dry season range perhaps highlight the importance of familiarity. Whilst the released males dry season range centred on the area that they knew well prior to release, the wild adolescent males were located further north near more permanent and reliable waterways. Prolonged dry periods in the Delta is likely to increase utilization of certain habitats as high densities of elephants are restricted to small areas.

8.3. Adolescence in the male African elephant

Behavioural development continues throughout a mammal's life, and involves the continual adjustment of individuals to the diversity of social and ecological features of their environments. Competence in dealing successfully with these demands involves acquiring knowledge that includes developing relationships with other group members (Box 1999). In male elephants, the period of adolescence is a time of huge social

change as they leave their natal herd and join the much more fluid social system of bull society. Not only does their social system change, they are likely to change their physical environment as they disperse from their natal herd area. Box (1999) concludes that for a physically independent but naïve animal, learning how to deal with the social and physical environment is facilitated by proximity to experienced individuals. Therefore, during the transfer and settlement phase of dispersal, newcomers will spend time investigating the features of the new area and establishing social relationships with conspecifics in the area (Stamps 1995, 2001). The adolescent males trend of being more social than males of other age groups, their preference for being in larger social groupings, being closer to other elephants and in particular to older elephants, suggests that they are somehow gaining information from conspecifics. It has long been accepted that matriarchs are the repositories of knowledge within the female elephant social system (Moss 1988; McComb *et al.* 2001). My work suggests that mature bulls have the same role in male society.

Whilst later adolescent males had a tendency to spar the most, it was still an important social activity in males between the ages of 21-35yrs. Sparring in both the wild and released males occurred most often between males of a similar age (*pers. obs*) and thus similar skill. Therefore, this activity is most likely to serve as a tool to establish and reinforce the hierarchy of male society (Miller & Byers 1998). Also, season is known to affect rates of social interactions in many mammals (Barrett, Robin & Dunbar 1992; Sommer & Mendoza-Granados 1995). Whilst the social behaviour, greeting, was affected by season, sparring was not, which highlights the importance of this activity and the price males are prepared to pay to assert their dominance at every opportunity. Male mating success is dependent on large body size and dominance within the hierarchy; by establishing themselves in the hierarchy early on, i.e. when adolescent, they can devote more time to eating and building up bulk and avoid dangerous conflict and reap the rewards when mature (Poirier & Smith 1974; Hall 1998).

Adolescent 'home ranges' continuously expanded during the three-year study, which is indicative of a transfer period (Andreassen, Stenseth & Ims 2002), as was the tendency for adolescent males to have a higher rate of social interactions than older

males (Whitehead & Weilgart 2000). Research in other areas shows that mature bulls have a stable home range (van Aarde 2005), and so this behaviour may be a consequence of adolescence. It is during this period, when they may still be rejoining their herd, that male elephants may be gathering information about potential dispersal sites (Boelkins & Wilson 1972; Sharpe 2005). Many animals value familiarity when it comes to the environment they inhabit and the fact that they are willing to incur costs to remain in a familiar area implies that experience with space enhances fitness in that space (Stamps 1995). Therefore, the more information and social relationships a male is able to gather during the period of adolescence prior to independence, when he still has some protection from the herd, could stand him in good stead when he becomes independent and will be reliant on his own or conspecifics, ability to locate food and water in times of stress.

The areas utilized by the collared elephants were large in comparison to studies elsewhere, which is against the trend that elephants in wet areas have smaller home ranges (Osborn 2004). The vast areas utilized by elephants in Namibia have been attributed to low habitat quality (Table A.6, Appendix; Lindeque & Lindeque 1991). Whilst the Okavango Delta appears to be lush, it is based on the sands of the Kalahari Desert and highly dependent on the nutrient-rich sediment brought down by the Okavango river from the Angolan highlands (Mendelsohn & el Obeid 2004). Therefore, the large home ranges exhibited by adolescent male elephants could be the result of a combination of explorative behaviour and low quality habitat. Another consideration is that whilst water and food availability are the major influences on elephant home range size, increasing habitat fragmentation also affects the size of area that they can utilize. Home range size of many African elephant populations is under anthropogenic affect and the large sizes utilized in the Delta could be representative of an undisturbed population, rather then a nutrient-poor area.

In elephants there is no one mechanism to explain the social and spatial segregation of the sexes that begins at adolescence. Spatial segregation due to forage selection was not due to sexual size dimorphism, as shown by the non-segregation of the males of different ages. Social preferences are an important factor, as from a young age the sexes show preferences for being with same sexed peers. In many mammals this

extends to same aged peers (Villaret & Bon 1995; Ruckstuhl 1999). In elephants this is not the case, with young females socializing with females of all ages, and showing great interest in younger elephants (Moss 1988; Lee & Moss 1999). Whilst, males spar with same aged peers (*pers. obs)*, they prefer to be closer to older males when in a male social group. This again provides evidence against the forage selection and activity budget hypotheses. Therefore social and spatial segregation in elephants is due to differing social and nutritional requirements of the sexes, most of which become apparent at adolescence.

The lack of an adolescent growth spurt in height in elephants (Lee & Moss 1995; Bogin 1999), which is characteristic of adolescence in humans, does not eliminate the potential for a spurt in weight gain during this time (Lee & Moss 1995). Also, the distinct differences in head shape between the sexes start to appear during this period, becoming pronounced by 26-30years. Both these changes may slow height gain in bulls during this time.

During independence adolescent, males will be weighing up the costs and benefits of socializing with other young to spar, and old elephants to gain information from, whilst foraging and exploring potential dispersal areas. Their primary objectives are to grow as fast as possible and to establish and maintain their position in the hierarchy. Once independent they do not have the limitations of the requirements of others to consider, reflected in their fission-fusion social system, and can concentrate on these primary objectives.

8.4.   Adolescence in mammals

The life history of elephants has many similarities to primates and whales. Perhaps the most comparable is that of the sperm whale. In both species the females live in highly social family units, displaying communal care of youngsters and allosuckling, that rely on well-developed communication. The much larger males live separate, more solitary lives, dispersing when young, becoming less social, forming loose-knit 'bachelor groups' or spending time alone, utilizing male areas, roving between female groups during the breeding season whilst avoiding each other and delaying breeding until they

are large and dominant (Weilgart, Whitehead & Payne 1996). No other male mammal share the life history of leaving their family unit, delay competitive breeding for many years and then rove between cooperative groups of related females (Weilgart, Whitehead & Payne 1996). Whilst they do share so many characteristics, their environments make studying the terrestrial elephant much simpler than the aquatic whale and therefore more detailed behavioural and social interaction data can be collected. My work is therefore not only transferable to the study of elephants but to other large social polygynous mammals, especially whales.

A cost of the intense mating access that occurs among males of polygynous species is that successful breeding is commonly delayed until males have reached full adult size, although sexual maturity may be attained several years earlier (Clutton-Brock 1994; Poole 1994; Whitehead & Weilgart 2000; Setchell 2003). Therefore a male must invest in growing and asserting dominance if he is to be reproductively successful.

The nutritional requirements of males mean that they have to spend more time feeding and may seek areas where food is more abundant, but of lower nutritional quality than in areas used heavily by females. Therefore the cost to a male of synchronising its behaviour for group cohesion, in a group led by a matriarch and the requirements of her young, would be detrimental to his growth and hence future mating success, leading to spatial segregation of the sexes.

The prolonged period of adolescence seen in elephants, primates and whales (Poole 1996b; Whitehead & Weilgart 2000; Setchell 2003), could reflect the amount of information they need to collect about an area and/or conspecifics prior to dispersal. Therefore it would be of benefit to the males to stay as long as possible with their group to collect the most information. However this strategy could be of cost to the females due to the potential for inbreeding and the increased risk taking behaviour of adolescent males (Berndt 1979; Laviola & Adriani 1998; Spear 2000) exposing females and their young. So the time and length of dispersal in polygynous mammals will be a balance between the benefits to the males and the costs to the rest of the group.

Animals that require large home ranges to survive must rely on their ability to retrieve and respond to memories, to enable them to exploit a large and diverse home range (Weilgart, Whitehead & Payne 1996). Stable groups, such as female herds in

elephants, depend on the older group members and information is passed down through learning. An independent male has to rely on himself and the elders in his new social network. The prolonged period of development shown in primates, whales and elephants parallels the importance of learned behaviours, compared with inflexible innately programmed behaviours (Savin-Williams & Weisfeld 1989). The very long delay in both elephants and whales from the onset of fertility to the appearance of physical maturity, i.e. large body and weapon size, may reflect selection pressures for delayed growth pending the accumulation of sufficient experience for successful competition with other males. A longer maturation time allows additional opportunities for learning, during which the individual is exempt from potentially dangerous encounters with mature males. Delaying, then extending maturation may extend the period for the cerebral cortex to mature (Tanner 1962) and for opportunities to learn various skills, primarily through play interactions with peers and adults (Savin-Williams & Weisfeld 1989). Long juvenile and adolescent periods will allow males to learn to adapt efficiently and effectively to environmental conditions while not being perceived as a serious competitor by more powerful adults.

The period of adolescence has been over looked in the past as a period of play and freedom from the energetic costs of reproduction (Walters 1987). However, it is becoming increasingly clear that the transition to adulthood is the time for individuals to develop relationships and acquire skills and knowledge that may be of both immediate and long-term benefit, at considerable costs.

8.5.   Application to elephant conservation and management

Over the past 35 years the context within which conservation biologists' work has changed considerably; scientifically a far more rigorous approach has developed, based on the theory of population dynamics, and incorporating evolutionary and behavioural ecological principles (Pettifor, Norris & Rowcliffe 2000).

Elephants pose two contrasting problems for conservationists, local overabundance and dwindling numbers. These problems have been caused by human-socioeconomic influences, such as habitat loss, fragmentation, over-harvesting,

introduction of diseases and pollution. All of these are affecting wildlife physiological and sociological requirements. Studies of behaviour can offer new insights into conservation problems, and the evolutionary understanding of the behaviour of individuals in populations allows us to predict responses under changed conditions with greater confidence (Sutherland & Gosling 2000; Woodroffe & Ginsberg 2000).

The areas available to wildlife over much of the world are often surrounded by agricultural land, leading to increased human-wildlife conflict when wildlife traverses from designated areas. Crop raiding by elephants is a huge economical and social issue (Osborn 1998), and more innovative methods to dissuade elephants from crop raiding are needed because elephants learn to short electric fences and ignore traditional methods employed by farmers (Osborn 1998; Vollrath & Douglas-Hamilton 2002).

Although detrimental in terms of crop raiding, the exploratory nature of bulls, in particular during adolescence (Sukumar 1990; Daim 1995; Osborn 1998; Smith & Kasiki 2000; Knickerbocker & Waithaka 2005; Rice 2005), is important in the invasion of depopulated areas and the extension of a species' range (Stickel 1954). Bulls precede female herds when re-colonising areas of traditional elephant ranges following the dispersion of humans due to war or the designation of wildlife areas (Lindeque 1995; Osborn 2004). The transfer phase of adolescent male elephants will play an important role in the repopulation of areas being converted back to wildlife areas through the establishment of Peace Parks in Africa (Mayoral-Philips 2002) and the increasing trend to develop private game reserves from old agricultural land. In fact the only prospect for reversing local extinction is the arrival of such dispersers (Brown & Kodric-Brown 1977; Hanski 1999). However, natural dispersal into new areas and the maintenance of genetic diversity of patchy populations is often inhibited by fragmentation of available habitats (Griffith *et al.* 1989; van Dyk *et al.* 1997; Slotow *et al.* 2000). Metapopulation management in the form of translocation is increasingly being used in southern Africa. Such interventive management mimicking dispersal may increasingly be necessary as a last resort to conserve species in landscapes dominated by humans (Woodroffe & Ginsberg 2000) and alleviate human-elephant conflict (Knickerbocker & Waithaka 2005; Daim 1995; Rice 2005).

In the past, many translocations have taken place without considering the behavioural ecology of the individuals being introduced or the receptive population (Slotow *et al.* 2000; Slotow, Balfour & Howison 2001; Slotow & van Dyk 2001). The exploratory nature of adolescent males makes them ideal candidates for translocation, as they are unlikely to upset an established social system as they are natural intruders and pose no competition to the large bulls. However, it is important that they are released into an established bull society or where older males are present. Translocation of herds involves the movement of the whole family unit, which is important for the maintenance of herd stability. Translocating bulls in pairs, or more, of known individuals will improve the transition for the individuals and increase success rate, making them more likely to explore the new territory, and may decrease the likelihood of them moving back to their established home range, which is the tendency for mature males (Dublin & Niskanen 2003). This latter behaviour can increase conflict with humans as it generally takes them through agricultural lands. Translocating elephants into habitats similar to their natal area could also enhance reintroduction attempts; due to prior habitat imprinting that may occur and an increased foraging efficiency in familiar areas (Stephens & Krebs 1986; Stamps 2001).

The tendency for animals to select areas already occupied by conspecifics slows down the re-colonisation of areas, so whilst habitat may seem appropriate we cannot expect animals to return and settle fast once the cause of their local extinction has been removed. Therefore the management and conservation of elephants must look at the long-term picture, both local and at the metapopulation scale, incorporating population dynamics, behavioural and ecological principles.

8.6.   Future work

The future of the African elephant is far from certain, yet our basic understanding of male behavioural ecology is limited, particularly during the period of adolescence.

Chapter 3 showed that the study area was a bull area but also discussed the possibility that this may change over time as the Delta waters shift. Further studies on what factors make male and females areas in spatial segregated species are necessary to

ensure that long term conservation and management needs of mammalian populations are met for both sexes.

Chapter 4 highlighted the importance of sociality in male elephants and in particular the importance of older bulls to adolescent males. Further research on males and whether they have stronger social bonds with certain individuals whom they may have known and interacted with when young and possibly related to could alleviate some of the problems associated with translocation seen in males. There is evidence for affiliation between male elephants and within the study the relationship between the released elephants highlights the importance of knowing individuals. In addition sporadic behavioural observations, such as when an old bull from the EBS herd died in 2002, Mafunyane spent three nights chasing off spotted hyaena from the carcass, are providing evidence of strong bonds between male elephants. This Chapter also showed the importance of sparring to male elephants. The distinction between play and fighting in males needs to be made clearer, to see when one becomes more important. Do they play post adolescence or is their play when young as important as fighting when older?

African elephants have a large vocal range: rumbles, trumpets, roars, screams, snorts and bellows (Poole 1994). The most frequently used calls are the rumbles, which mostly contain components below the range of human hearing; some are totally infrasonic. In many mammals, the vocalizations of males and females differ (Clutton-Brock, Guinness & Albon 1982; Fischer *et al*. 2002). Female elephants use different calls to communicate within and between family groups, whilst males use fewer vocalizations (Poole 1994). The majority of calls used by females are related to group coordination, infant care and social excitement, whilst the male calls are related to male-male dominance, interactions and reproduction (Poole 1994). At adolescence, not only does the social context of calls change in many male mammals, they also begin to learn new vocalizations (Fischer *et al.* 2002; Rendall, Kollias & Ney 2005). The variations in the rate of vocalization can only be confirmed by recording them to ensure there were no bias in the age of elephant I could hear, or identification of caller, and that all infrasound calls are counted. As the sociality in male elephants change with age, vocalizations may change too with younger males learning sex specific calls through copying (Poole *et al.* 2005) needed in older life, such as musth calls (Poole 1987b).

Female herds coordinate their movements over large distances (Payne 1988), older, larger elephants need to be able to communicate over vast distances as well, especially when in musth, to avoid other musth males and to attract oestrus females. The increase in infrasonic noise pollution due to terrestrial and aerial vehicles over much of Africa could be having an affect on the ability of elephants and other mammals to communicate over large distance and their behaviour, as is the case of boat noise on cetaceans and traffic on birds (Reijnen, Foppen & Meeuwsen 1999; Erbe 2002; Brumm 2004).

Chapter 5 suggests that adolescent male elephants undergo an exploratory phase of dispersal. Research into the factors that promote variation in the timing of dispersal, such as optimal size of disperser, the time of year or amount of information needed about the area for dispersal to take place and also to see if dispersal in large mammals shows delayed dispersion in times of drought, as seen in smaller mammals (Pocock, Hauffe & Searle 2005). Does the size of range or homogeneity of habitat and availability of water enable dispersers to leave sooner because there is less information to gather about dispersal sites? The simultaneous collaring of mature and adolescent males may shed more light on the period of adolescence and the exploration of new areas, or if mature males continue to explore more areas, or stick to certain ranges. Using isotopes analysis of the elephants tail hair could shed more light on the feeding habits of the Okavango Delta elephants (Cerling *et al.* 2006).

Chapters 6 and 7 showed the capacity of elephants to modify their behaviour to deal with new situations and in particular for captive elephants to be released successfully without posing a threat to humans or other elephants. These chapters highlighted the importance for these individuals to spend time with 'known' individuals. Further work on the social bonds of male elephants will shed light on the importance of knowing individual elephants.

As with so many mammalian studies this research has shown the significance of taking into account the affect of ecological factors on the ecology of a species, and so whilst, much of the work on mammals is transferable to populations in different areas, there is no substitute for in situ research.

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APPENDIX

Table A.1: Age classification of male elephants (Lee & Moss 1986; Moss 1996; Western, Moss & Georgiadis 1983).

Class	Foot length (cm)	Height (cm)	Age (yrs)	Description
Class 1	36.00 - ?	204-228	10-15	Male head shape more noticeable; tusk circumference and shoulder height greater than females of the same age.
Class 2	? – 41.9	229 - 243	16-20	At about 17yrs males reach same height as largest adult female over 40yrs.
Class 3	42.0 - 45.9	244 - 275	21-25	Taller than most females; but most still slender and narrow in the head compared to older males.
Class 4	46.0 - 49.9	276 - 296	26-35	Head shape has changed to an hour-glass shape. The head gets broader as they move through the age group, height increases steadily.
Class 5	50.0 – 53.9	>297	36+	Very big, tower over largest female by three feet or more at shoulder, neck thick, tusk circumference at lip strikingly greater than younger males and all females

Table A.2. Age classification of zero to 10 years old (males and females) elephants (Moss 1996). Calf sizes are relative to an adult female between 25 and 45 years old with a should height of about 250cm.

Age	Shoulder height	Development
Newborn	Top of shoulders reach lower wrinkles below mother's 'elbow'; can easily walk beneath her.	Thin, stiff-legged; sometimes part of umbilical cord attached; whites of eyes often red; backs of ears bright pink; often hairy on head and back.
2-3 weeks	Same as above.	Walking well; more filled out in body; backs of ears non longer pink; trunk is short and slender but exploring, picking up sticks.
3-4 months	Reaches to below point of mother's elbow.	More rounded, fatter; begins trying to feed on grass; spends time away from mother; plays with other calves.
8-9 months	Reaches elbow; can still pass under mother but probably scraping.	Feeding adeptly and continuously for long stretches; capable of drinking with trunk.
1 year	Shoulder taller than breast level of mother, reaching to wrinkles above elbow.	Head and ears look in proportion to each other and body.
1-2 years	Top of shoulder midway between elbow and junction of leg with torso, the 'armpit' of mother.	Trunk looks more in proportion; tusks of males calves may show beyond lip from 18 months on.
2-3 years	Reaches mother's armpit.	Tusks of most claves and many female calves will show; mother may show signs of trying to wean calf.
3-4 years	Top of shoulder above mother's armpit; back almost level with anal flap and reach lower quarter of mother's ear.	Almost all calves will show at least 5-7cm of tusks; most calves still suckling, but some may be weaned.
4-5 years	Reaches mothers' anal flap or above.	Tusks are 15-18cm long; has probably stopped suckling and may have a younger sibling.
5-6 years	Appears to be about one-quarter the size of an adult female; back almost level with middle of mother's ear.	Tusks are about 15-18cm long; differences in male and female behaviour become more pronounced: female calves allomother younger calves; male claves seek out other males for sparring.
6-7 years	Shoulder and back height above base of mother's tail and above middle of ear.	Tusks begin to splay out in both males and females; sexual differences discernable: males have thicker tusks and heavier bodies..
7-8 years	Back level with adult female's eye and well	Tusks are usually splayed by now; no longer looks calf-like, but more like a small adult.

	above base of tail.	
8-9 years	Overall size in height and length over half an adult female.	Tusks are about 25-30cm.
9-10 years	Overall size almost three quarters of an adult female.	Male are larger than females of same age and spend more time on periphery of family; females are more integrated in family.

Table A.3. Ten years and above age classification for female elephants (Moss 1996).

| Age	Description
10-15 years	Thin tusks, probably still splayed rather then convergent; more square in body shape than older females who are rectangular
15-20 years	Tusks begin to take on their adult configuration that is convergent, straight, or asymmetrical with one higher than the other.
20-35 years	Circumference of tusks at base distinctly bigger than teenaged females
35-50 years	Tusks marginally thicker; back has lengthened so that animal appears long in body
50+ years	Hollow above the eyes, ears held lower, longer back length, sometimes long tusks
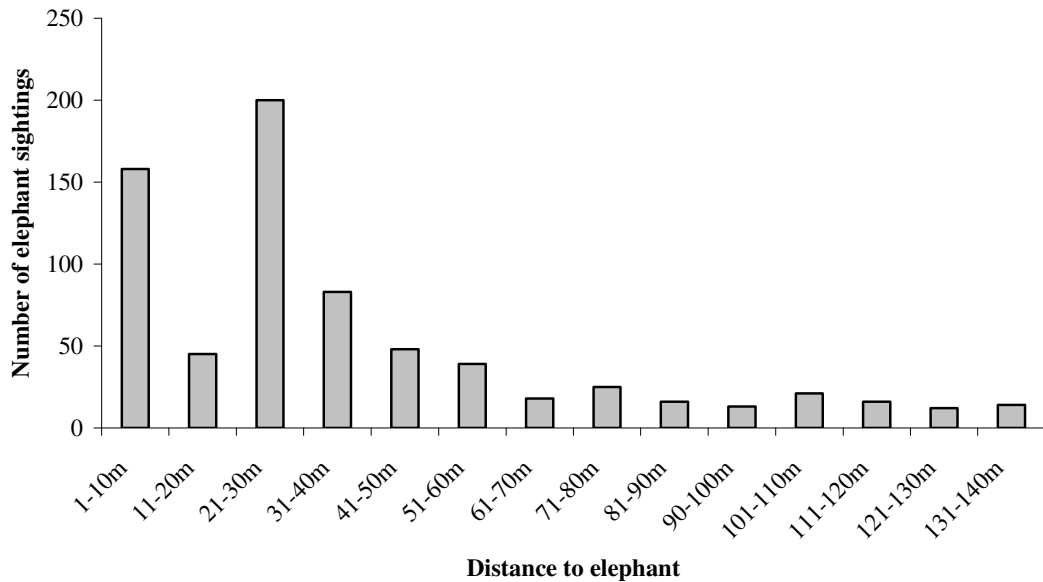
Figure A.1: The number of sightings of elephants in forest against distance (m) to elephants (measured with a range finder) from the road.

Table A.4: African elephant population density in areas of their range. NP = National Park. * = present study, ♦Theortical equilibrium (Armbruster & Lande 1993).

Location	Density (km²)	Extent (km²)	Period	Reference
Gourma region, Mali	0.01	30 000	2002	Blake *et al.* 2003
Kafue National Park, Zambia	0.07	22 480	2004	Guldemond *et al.* 2005
Sernegeti region, Tanzania	0.10	25 000	1972	Croze 1974
Kasungu NP, Malawi	0.15	2 300	2003	Bhima, Howard & Nyanyale 2003
Etosha NP, Namibia	0.15	17 000	1978	Berry 1980 (in Owen-Smith 1988)
Kafue National Park, Zambia	0.17	22 480	2001	Guldemond *et al.* 2005
Amboseli region, Kenya	0.20	3 000	1980	Moss 1983
Ithala, South Africa	0.20	300	2000-2001	Slotow *et al.* 2005
Welgevonden, South Africa	0.20	300	2000-2001	Slotow *et al.* 2005
Masai Mara, Kenya	0.21	6000	1984-94	Ottichilo 1999
Tai NP, Ivory Coast	0.23	3 400	1983	Merz 1986
Kafue NP, Zambia	0.25	20 000	1980	Bell 1982
Pilansberg, South Africa	0.29	490	2000-2001	Slotow *et al.* 2005
Mago NP, Ethiopia	0.30	1 564	1997-1998	Demeke & Bekele 2000
Virunga NP, Democratic Republic of Congo	0.30	2 400	1998	Mubalama 2000
Kibale NP, Uganda	0.34	766	2000	Plumptre in Chiyo & Cochrane 2005)
Hluhluwe-Umfolozi, South Africa	0.34	900	2000-2001	Slotow *et al.* 2005
Pongola, South Africa	0.37	90	2000-2001	Slotow *et al.* 2005
Kruger NP, South Africa	0.40	19 000	1981	Hall-Martin 1984 (in Owen-Smith 1988)
Makalali, South Africa	0.42	140	2000-2001	Slotow *et al.* 2005
Tembe, South Africa	0.47	300	2000-2001	Slotow *et al.* 2005
Nazinga ranch, Bukino Faso(dry season)	0.49	806	1988	Jachmann 1988
Northern Botswana	0.49	80 000	1980	Spinage 1990
Kasungu NP, Malawi	0.50	2 450	1978	Jachmann 1980

Madikwe, South Africa	0.51	620	2000-2001	Slotow *et al*. 2005
Kasungu NP, Malawi	0.52	2 300	1984	Bhima, Howard & Nyanyale 2003
Nazinga ranch, Bukino Faso (rainy season)	0.52	806	1988	Jachmann 1988
Kibale NP, Uganda	0.58	766	1960	Wing & Buss 1970 (in Chiyo & Cochrane 2005)
Munyawana, South Africa	0.59	145	2000-2001	Slotow *et al*. 2005
Ruaha-Rungwa, Tanzania	0.77		1977	Barnes & Douglas-Hamilton 1982
*Okavango Delta, Botswana (rainy season)	0.79	5 000	2003-2005	Present study
Sengwa Research Area, Zimbabwe	0.90	353	1984	Cumming 1983 (in Owen-Smith 1988)
South Luangwa NP	1.10		1985-86	Lewis 1991
Tsavo NP, Kenya	1.20	20 000	1967	Laws 1969 (in Owen-Smith 1988)
Hwange NP, Zimbabwe	1.33	14 620	1980	Cumming 1983 (in Owen-Smith 1988)
Ruaha region, Tanzania	1.39	31 500	1977	Barnes & Douglas-Hamilton 1982
Queen Elizabeth NP, Uganda	1.40	1 559	1972	Eltringham 1977
*Okavango Delta, Botswana (flood season)	1.89	5 000	2003-2005	Present study
Luangwa Valley, Zambia	2.17	40 000	1973	Caughley & Goddard 1975
Ruaha NP, Tanzania	2.41	10 300	1977	Barnes & Douglas-Hamilton 1982
Ruaha NP, Tanzania	2.41	31 500	1977	Barnes & Douglas-Hamilton 1982
Addo NP, South Africa	2.59	130	2000-2001	Slotow *et al*. 2005
♦*Maximum density to achieve biodiversity*	*2.59*			*Whyte 2006*
South Luangwa NP	3.35	12 500	1973	Caughley & Goddard 1975
North Bunyoro, Uganda	3.43	2 727	1969	Laws 1970
Addo NP, South Africa	4.10	23	1979	Hall-Martin 1980
Msembe area, Ruaha River, Tanzania	4.11	130	1977	Barnes & Douglas-Hamilton 1982
Msembe study area, Tanzania	4.11	130	1977	Barnes & Douglas-Hamilton 1982
Manyara NP, Tanzania	>5.00	82	1970	Douglas-Hamilton 1973
*Okavango Delta, Botswana (dry season)	7.33	5 000	2003-2005	Present study
Luangwa River alluvium	7.40	4 170	1973	Caughley & Goddard 1975
♦*Theortical equilibrium*	*8.03*			*Armbruster & Lande 1992*

Botswana data	Density (km²)	Extent (km²)	Period	Reference
Chobe region, Botswana (rainy season)	0.30	450	1974	Sommerlatte 1976
Chobe region, Botswana (rainy season)	0.60	450	1981	Melton 1985
Chobe NP, Botswana (rainy season)	0.50	-	-	Skarpe *et al.* 2004
Chobe, Botswana (rainy season)	0.50		1987-1996	Garai, Craig & Mosogo 1998
Chobe NP, Botswana	0.51	11 000	1973-75	Sommerlatte 1976
Tuli Block, Botswana	0.60	300	1990	Spinage 1990
Chobe region, Botswana (rainy season)	0.60	450	1973	Sommerlatte 1976
Northern Botswana	0.75	80 000	1989	Spinage 1990
*Okavango Delta, Botswana (rainy season)	0.79	55 000	2002-05	Present study
Chobe region, Botswana	1.10	16 000	1985	Work 1986 (in Owen-Smith 1988)
Chobe region, Botswana (dry season)	1.10	450	1963	Hepburn, in Child (1968)
Chobe NP, Botswana	1.11	11 000	1987	Spinage 1990
Chobe region, Botswana (dry season)	1.38	450	1966	Child 1968
Chobe region, Botswana (dry season)	1.42	450	1969	Simpson (in Sommerlatte 1976)
Chobe region, Botswana (dry season)	1.60	450	1974	Sommerlatte 1976
Chobe region, Botswana (dry season)	1.62	450	1965	Child 1968
Chobe region, Botswana (dry season)	1.70	450	1981	Melton 1985
*Okavango Delta, Botswana (flood season)	1.89	5 000	2003-05	Present study
Linyanti, Botswana (rainy season)	2.00		1987-1996	Garai, Craig & Mosogo 1998
Chobe region, Botswana (dry season)	2.16	450	1970	Simpson, in Sommerlatte 1976
♦*Maximum density to achieve biodiversity*	2.59			*Whyte 2006*
Chobe NP, Botswana (dry season)	4.00	450	1973	Sommerlatte 1976
Chobe, Botswana (dry season)	4.00		1987-1996	Garai, Craig & Mosogo 1998
Chobe NP, Botswana (dry season)	4.60	450	1982	Melton1985
Linyanti, Botswana (dry season)	7.00		1987-1996	Garai, Craig & Mosogo 1998
♦*Theoretical equilibrium*	*8.03*			*Armbruster & Lande 1992*
*Okavango Delta, Botswana (dry season)	8.70	5 000	2003-05	Present study

Table A.5: Food items eaten regularly by male elephants in the study area.

Scientific name	Common name	Wild	Released elephants
Acacia karoo	Sweet thorn	√	√
Acacia nigrecens	Knobthorn	√	√
Achyranthes aspera	Chaff flower	√	√
Colophospermum mopane	Mopane	√	√
Combretum hereorense	Russet bushwillow	√	√
Combretum imberde	Leadwood	√	√
Crotalaria sphaerocarpa	Wild Lucerne	√	√
Crotom megalobotrys	Large fever berry	√	√
Dichrostachys cinerea	Sickle bush	√	√
Diospyros mespiliformis	Jackal-Berry	√	√
Euclea divinorum	Magic Guarri	√	√
Ficus sycomorus	Sycamore Fig	√	√
Garcinia livingstonei	African mangosteen	√	√
Grewia bicolour	White raisin	√	√
Grewia flavescens	Sandpaper raisin	√	X
Grewia hexamita	Giant raisin bush	X	√
Gymnosporia buxifolia	Common spike thorn	√	√
Gymnosporia senegalensis	Confetti tree	√	√
Phoenix reclinata	Wild Date Palm	√	√
Rhus tenuinervis	Kalahari currant	√	√
Sclerocarya birrea	Marula	√	√
Terminalia sericea	Silver cluster-leaf	√	√
Ipomoea spp.	Tiger foot	√	X
Citrullus lanatus	Tsama melon	√	X

Table A.6: Home range size of African elephants in various locations. NP = national park; M = male; F = female;* = this study
Δ = released elephants from study.

Study site	Home range in km^2	Home range measurement	Time span in months	Sex of elephant	Reference
Lake Manyara, Tanzania	14-52		54	M&F	Douglas-Hamilton 1973
Maputo Elephant Reserve, Mozambique	129	MCP	4	1 F	De Boer *et al.* 2000
Luangwa, Zambia	219	95%MCP	3	8 F	van Aarde 2005
Zambezi Valley, Zimbabwe	94-263			11 F	Dunham 1986
Maputuland, South Africa	52-314	95%MCP	24	5 F	van Aarde 2005
Sengwa, Zimbabwe	322			9 M	Osborn 1998 (in Osborn 2004)
Private nature reserves, South Africa	157-342	MCP		21 M	De Villiers & Kok 1997
Zambezi Valley, Zimbabwe	353	95%MCP	4	6 F	van Aarde 2005
Private nature reserves, South Africa	115-465	MCP		11 F	De Villiers & Kok 1997
Queen Elizabeth NP, Uganda	363/500			6 F, 6 M	Abe 1994 (in Osborn 2004)
Kafue, Zambia	534	95%MCP	24	5 F	van Aarde 2005
Tsavo-West NP, Kenya	756			2 F	Leuthold 1977 (in Voljoen 1987)
Limpopo, South Africa	300-773	95%MCP	12	4 F	Van Aarde 2005
Laikipia	600-800			14 F	Thouless 1996
Kafue, Zambia	884	95%MCP	24	5 M	van Aarde 2005
Maputuland, South Africa	89-948	95%MCP	24	4 M	van Aarde 2005
Kruger NP, South Africa	126-987			F	Hall-Martin1987
Kruger NP, South Africa	129-1255	MCP		20 F	Whyte 1993
Mago NP, Ethiopia	1597				Demeke & Bekele 2000
Tsavo-East NP, Kenya	1620			8 F, 2M	Leutold 1977 (in Voljoen 1987)

Limpopo, South Africa	1442 & 1659	95%MCP	12	2 M	van Aarde 2005
KNP, South Africa	200-1707			M	Hall-Martin1987
Kruger NP, South Africa	45-1805				Whyte 2001
Chobe, Botswana	148-1960	95%MCP	12	4 F	van Aarde 2005
Ndoki Forest, Republic of Congo	677-1977	100 MCP	24	2 F, 2M	Blake *et al.* 2001
Maputuland, South Africa	1239 & 2022	95%MCP	12	2 M	van Aarde 2005
ΔOkavango Delta, Botswana	*2017*	*100% MCP*	*28*	*1 F*	*This study*
ΔOkavango Delta, Botswana	*2202± 373*	*100% MCP*	*36*	*3 M*	*This study*
Etosha, Namibia	2280	95%MCP	24	6 F	Van Aarde 2005
Hwange NP, Zimbabwe	1038-2544			11 F, 7 M	Conybeare 1991 (in Osborn 2004)
Amboseli NP, Kenya	2756			6 F	Western & Lindsay 1984
Hwange NP, Zimbabwe	1300-2981			7 M	Conybeare 1991 (in Osborn 2004)
Kaokoveld, Namibia	1763-2944	95% MCP	27	M & F	Viljoen 1989b
Waza NP	2484,3066	MCP	21	2 F	Tchamba, Bauer & De Iongh 1995
Kruger NP, South Africa	72-4451	95% MCP		50F, 37M	Grainger, van Aarde & Whyte 2005
Okavango Delta, Botswana	*4824 ± 1431*	*100%MCP*	*35*	*5 M*	*This study*
Tarangire-Manyara, Tanzania	477-5060	100%MCP	48	7 F	Galanti *et al.* 2006
Namibia	2136-10738		7	7 F	Lindeque & Lindeque 1991

Appendix A