Bai Use in Forest Elephants (*Loxodonta africana cyclotis*): Ecology, Sociality & Risk

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Declaration

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

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Abstract

Forest elephant (*Loxodonta africana cyclotis*) sociality is relatively little-studied due to the difficulties of making direct observations in rainforests. In Central Africa elephants aggregate at large natural forest clearings known as *bais*, which have been postulated to offer social benefits in addition to nutritional resources. This thesis explores the role of these clearings as social arenas by examining bai use within three main themes; ecology, sociality and risk factors. Seasonal changes in elephant use of the Maya Nord *bai* (Republic of Congo) are described, along with the demography of the visiting population. Elephant visit rate was highly variable; the number of elephants using Maya Nord in an observation day ranged from 0 to 117 animals. This variability was unrelated to local resource availability and productivity suggesting that bai use occurs year round. Elephants in Odzala-Kokoua do not show high fidelity to a single clearing; 454 elephants were individually identified and re-sighted an average of 1.76 times (range 1-10) during the twelve month study period.

Previous bai studies have yet to quantify how elephants associate with one another within the bai area. This study examines socio-spatial organisation and associate choice using two measures of association within the 0.23 km^2 bai area; aggregations (all elephants present in the clearing) and parties (elephants spatially co-ordinated in activity and movement) and distinguishes these from parties that range together (i.e. arrive and leave together). Social network analyses (SocProg) were used to describe inter- and intra-sexual multi-level organisation in the bai environment, and to illustrate the non-random nature of elephant aggregations and parties. Bais were shown to function as social arenas; female elephants showed active choice of certain associates and active avoidance of others when creating parties, whereas males were less discriminatory. Parties formed in the clearing (mean size= 3.93, SE= 0.186) were larger than ranging parties (mean size= 2.71, SE= 0.084) and elephants stayed for 50% longer in the clearing when they associated with individuals from outside their ranging party. Inter- and intra-sexual relationships were maintained within the clearing, and these are suggested to offer elephants essential opportunities for social learning. The patterning and nature of the relationships observed at the Maya Nord clearing indicates that forest elephants use a fission-fusion social structure similar to that of savannah elephants (*Loxodonta africana africana*); relationships are significantly structured by age- and sex- and underpinned by individual identity. Old experienced females hold key roles for forest elephants, and male relationships are superimposed on the network of female associations. Odzala-Kokoua elephants use bais to maintain their social relationships despite being highly sensitive to the anthropogenic risks involved in using these open areas.

The results of this study suggest that forest and savannah elephants lie on the same social continuum, balancing social “pulls” to aggregate against the ecological “pushes” that force groups to fission. Previous models of savannah elephant sociality construct levels of association and social complexity upwards from the basic mother-calf unit (e.g. Wittemyer & Getz 2007). My results suggest that it may be more appropriate to consider elephant sociality and associations as in dynamic equilibrium between social and ecological

influences acting at all levels of grouping, and to explicitly test how these underlie the opportunity costs that elephants are willing to pay in order to maintain social groupings.

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For the dubious honour of dedicating this thesis, I follow Rich Parnell’s example: like his gorillas, my study subjects have little need of such a thing, though they have given me much pleasure (and occasionally scared me witless) and I am incredibly privileged to have spent time with them. Instead, this thesis is for all those who know Africa’s “heart of darkness” is a place of vivid life, light and beauty, and who work so hard to keep it that way in a harsh timber- and ivory-hungry world.

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Chapter One

Introduction

Chapter 1 Introduction

1.1 Sociality: Ecological and Evolutionary Considerations

In an evolutionary context, animals that live in groups must gain benefits from doing so that outweigh the inherent costs of such groupings (Alexander 1974; Hamilton 1964; Trivers 1972). Benefits include enhanced predator detection, increased foraging efficiency, or the ability to acquire important information from group members, either about resources or conspecifics (e.g. Creel & Creel 1995; Isbell & Young 2002; Macdonald 1983; Pacala et al. 1996; van Schaik & van Noordwijk 1986), or benefits can be related to communal defence of resources or offspring (Creel & Creel 1995; Grinnell et al. 1995; Lee 1987; McComb et al. 1994; Packer et al. 1990). Costs include increased conspicuousness to predators, within-group competition or increased energy demands for movement between feeding sites, time demands placed on the maintenance of within-group bonds, and the potential for disease transmission (e.g. Boesch 1991; Clutton-Brock & Harvey 1977; Henzi et al. 1997; Isbell & Young 2002). Food availability and predation risks are considered to be the principal environmental influences that underlie why animals live in groups, and the costs and benefits of living in groups may thus vary over space and time according to local ecological conditions (Alexander 1974). These drivers lead to testable hypotheses regarding optimal group size, and models of socio-ecology have differed in their emphasis on different types of competition, predation risk, habitat saturation and the costs of dispersal and infanticide (e.g. Alberts & Altmann 1995; Isbell 2004; Isbell & Young 2002; Sterck et al. 1997; van Schaik et al. 1983; Wrangham 1980).

For many animals, including fish, bats and ungulates, grouping trade-offs result in social and sexual segregation, and a number of hypotheses currently compete to explain this segregation (e.g. Ruckstuhl & Neuhaus 2000; Ruckstuhl & Kokko 2002). The predation risk (or reproductive strategy) hypothesis suggests that females choose to rear offspring in habitats that minimise the risk from predators despite incurring foraging costs (Corti & Shackleton 2002), while males favour nutrient-rich habitats that increase their energetically costly competitive advantage in male-male competition (Clutton-Brock et al. 1982). The forage selection (or sexual dimorphism) hypothesis posits that allometric scaling effects on body size produce divergence in foraging efficiencies between the sexes, altering habitat preferences (Barboza & Bowyer 2000). Thirdly, the social factors hypothesis states that males and females differ ontogenetically in behaviour, leading to differences in interaction patterns and activity levels which give rise to social segregation by sex- and age-class (Bon & Campan 1996). Finally the activity budget hypothesis suggests that the main force driving sexual segregation is the difference in activity budget between individuals of different body mass, based on differences in digestive efficiency (Conradt 1998), which may become sufficiently large as to make synchrony of behaviour between the sexes difficult and possibly costly. These competing hypotheses have generated intense research interest (e.g. Ciuti & Apollonio 2008; Hay et al. 2008; Li & Jiang 2007; Macfarlane & Coulson 2007; Yearsley & Pérez-Barbería 2005), as none completely explain the observed patterns of sexual segregation. Dunbar & Shi (2008) propose that these explanations may be best interpreted as “factors in a multivariate model” where the likelihood of segregation is altered by habitat- and species-specific factors. Furthermore, the drivers for grouping (aggregation and patterns of shared use of resources and strata) need to be contrasted with the costs and benefits of permanent, knowledge-based associations between individuals in social groups over time (Lee, 1994).

Different strategies for social group living impact on individual resource acquisition with associated fitness consequences, and socially structured societies thus impose costs at an individual level at least some of which influence population dynamics through birth and death rates (Dunbar 1985). Grouping decisions are particularly important for female mammals because of their costly energy and time investment in reproductive effort. Therefore the ecological factors which enable or structure female group living strategies have been explored in depth on the assumption that female grouping decisions will ultimately determine social systems (Bradbury & Vehrencamp 1977; Jarman 1974; Wrangham 1980; Wrangham & Rubenstein 1986).

A variety of types of complex social groupings can emerge as specific solutions to ecological problems, where complexity is a function of the number of individuals and their structured relationships and networks of relationship. This social complexity is thought to select for an increase in brain size – the so-called "social brain hypothesis". This states that an individual's ability to manage the complex relational information involved in intricate social landscapes is dependent on cognitive capacity and by default on some aspect of brain size (Dunbar 1998). Since brain tissue is metabolically costly (Aiello & Wheeler 1995) these costs add an additional component to the costs and benefits of living in groups. In addition, body size, basal metabolic rate and life history parameters act as constraints on brain evolution (Dunbar & Shultz 2007). Highly encephalised animals are characterised by slow maturation (requiring increased parental investment) and relatively late reproduction, which in turn selects for longevity and low early mortality (Promislow & Harvey 1990). The reduced rate of early mortality associated with high parental investment and slow maturation generates what are classically termed K-selected species (Stearns 1976).

High social complexity is not a simple function of group size, but rather of the quality and nature of individual relationships: large aggregations of animals such as birds or migratory wildebeest (*Connochaetes* sp.) are relatively unstable and individuals do not necessarily have repeated interactions or stable bonds with all other members (Lee 1994). In an exploration of African ungulate brain size Shultz & Dunbar (2007) showed that relative brain size was independently associated with sociality and social complexity – here taken as the ability to recognise and discriminate among individuals in iterated interactions over time – as well as with habitat use, while relative neocortex size was associated with social but not ecological factors. Brain size and social complexity can therefore form a positive evolutionary feedback loop which may function to dissociate group size from simple ecological predictors in some species, although sociality and relative brain size may themselves become decoupled in certain species (Pérez-Barbería et al. 2007). Thus social complexity can interact with ecological dynamics and alter the costs and benefits associated with different modes of social grouping.

1.2 The Challenge of Fission-Fusion Sociality

Intense competition between group members may be reduced when group members temporarily disperse into smaller sub-groups (e.g. Chapman 1990; Kummer 1971). Animals that do this regularly are said to exhibit fission-fusion sociality, and sub-units may move independently of one another and rarely aggregate into the larger social group (Robinson & Janson 1987). A variety of taxa do this, including hamadrayas baboons (*Papio hamadryas*: Kummer 1968), some bats (e.g. *Myotis bechsteinii*: Kerth & König 1999), chimpanzees (*Pan troglodytes* e.g. Goodall 1986), spotted hyaenas (*Crocuta crocuta*, Holekamp et al. 1997) and a number of cetacean species (e.g. sperm whales *Physter macrocephalus*: Christal & Whitehead 2001; Whitehead 2003; bottlenose dolphins, *Tursiops sp.* Smolker et al. 1992). Fission-fusion tendencies are particularly well-studied amongst chimpanzees where a variety of ecological factors have been proposed to affect fission-fusion including food availability (Anderson et al. 2002; Chapman et al. 1994; Wrangham & Rubenstein 1986), predation pressure (Boesch 1991), reproductive parameters (Goodall 1986; Mitani et al. 2002) and demographic factors (Goodall 1986; Lehmann & Boesch 2004; Newton-Fisher 2000). A recent analysis by Lehmann et al. (2007) however suggests that travel costs are limiting for chimpanzees, who may dramatically reduce these costs through fission-fusion sociality and thereby occupy habitats they would otherwise be unable to exploit. Fission-fusion sociality may therefore fundamentally underpin species biogeography.

Many of the best-known taxa that employ fission-fusion are also known for their advanced cognitive skills, although fission-fusion is not necessarily causally related to cognition (Aureli et al. 2008; Barrett et al. 2003). In fact, fission-fusion may be employed by animals in a single taxon that exhibit otherwise marked differences in the degree of behavioural plasticity (e.g. lions and wolves, Holekamp et al. 2000). Nevertheless, there are particular cognitive demands (and therefore costs) associated with a fission-fusion system that is based on social knowledge (i.e. high complexity):

individuals must monitor changes in social relationships that occur in other sub-groupings, and must cope with patchy social information, such as who was present (and equally importantly who was absent) at key interactions. Individuals also have limited and irregular opportunities to observe conspecifics, and must remember the outcomes of previous interactions in order to maintain relationships whilst avoiding potentially costly repetitious interactions in order to (re)establish potentially valuable relationships (Barrett et al. 2003; Kummer 1978). The overall value of individual relationships depends on individual components of worth based on the partner's availability, qualities (such as social status, reproductive condition, knowledge or skills: Cords & Aureli 2000; Kummer 1978) and behavioural tendencies. These behavioural tendencies may include the tendency to tolerate others near resources, to support others in aggressive encounters with third parties, to provide protection from external threats, to facilitate access to nutritional and social resources, or to participate in reproduction (Cords & Aureli 2000; van Schaik & Aureli 2000). The cognitive costs associated with fission-fusion are especially demanding in species showing multilevel organisation e.g. relationships in dolphin coalitions may alter on the basis of inter-coalitionary interactions (Connor & Krützen 2003). Cognitive skills are expected to "peak" in fission-fusion species whose groupings are large and variable, where there are many more partner combinations to monitor (Aureli et al. 2008; Barrett et al. 2003). The ability to monitor conspecifics at a distance through olfactory or auditory cues might release animals from the need to maintain proximity without compromising the quality or complexity of relationships (Aureli et al. 2008).

1.3 Elephants as a Study Species

Elephants epitomise a charismatic mega-fauna, presenting a complex model system for researchers, a flagship for conservation, and some of the most extreme challenges for the management and mitigation of human-wildlife interaction. Modern elephants survive as just two genera, *Loxodonta* in Africa and *Elephas* in Asia, but these are the remnants of a much wider radiation of proboscidean taxa that peaked in the middle Miocene, 15 million years ago (Haynes 1991). African elephants have been the subjects of much taxonomic debate, as they exhibit marked genetic differentiation between populations potentially representing speciation (e.g. Debruyne 2005; Eggert et al. 2002; Roca et al. 2001) but are also genetically linked to all other clusters (Johnson et al. 2007; Johnson 2008). They are currently classified as a single species, with savannah elephants (*Loxodonta africana africana)* ranging across East and Southern Africa and forest elephants (*Loxodonta africana cyclotis)* occupying the Congo Basin (Blanc 2010). The remnant populations of West African elephants may form a third taxonomic unit, but their status is currently uncertain (Eggert et al. 2002, but see also Johnson et al. 2007). In addition to their genetic diversity, elephants show a high degree of behavioural plasticity, which may partially explain their ability to adapt to a wide range of ecological conditions.

African elephants have been best-studied in the relatively accessible savannah ecosystems of East and Southern Africa. Here, their behaviour is known from longitudinal studies, some of which span several decades (e.g. Addo: Whitehouse & Hall-Martin 2000; Amboseli: Moss et al. in press a; Manyara: Douglas-Hamilton 1972; Samburu: Wittemyer et al. 2009). Long-term studies have shown savannah elephants live in a complex fission-fusion society with stable multi-female groups and gregarious but independent males (e.g. Moss 1988, 2001; Moss & Poole 1983; Moss et al. in press a; Whitehouse & Hall-Martin 2000; Wittemyer et al. 2005). Stable dominance hierarchies exist for both males and females which are size-dependent and thereby age-graded. Within family units dominance relationships are transitive but not nepotistic so that older, larger females consistently dominate smaller younger females, regardless of the closeness of kin relationships (Archie et al. 2006a; Wittemyer & Getz 2007). The complex nature of elephant society has been described as a series of "social circles" (Moss 1981), with a female and her dependent offspring at the centre, encompassed by a series of progressively larger circles, representing family units, bond groups, clans and ultimately including the entire population. Each individual's relationships incorporate other individuals beyond the family group (McComb et al. 2001; Moss & Poole 1983).

Wittemyer & Getz (2007) present a slightly different model of elephant sociality (Figure 1.1), where animals may be viewed as kin "molecules", rather than independent "atoms", and the structure is based on a foundation of associations between mother-calf units (Wittemyer et al. 2005). Family units are consistent in individual associations over time, but individuals are by no means always found together with all family members, and the degree of cohesiveness at each level is highly variable between families (Moss & Lee in press b).

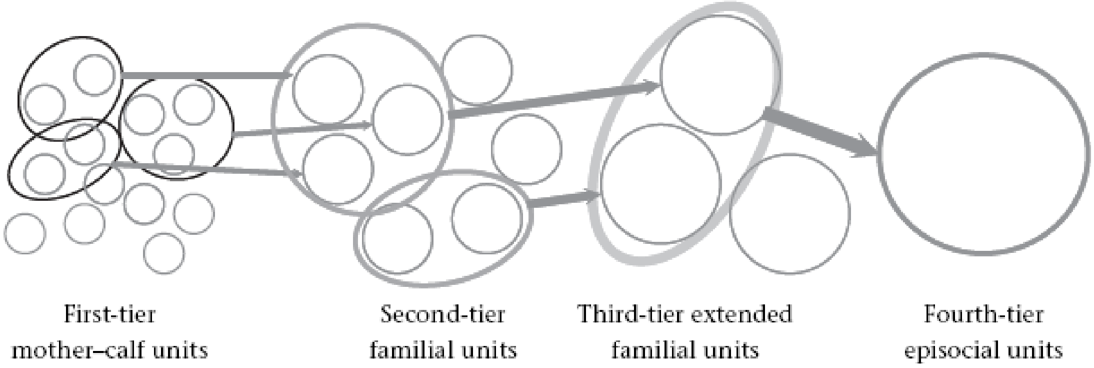

Figure 1.1. The hierarchical social structure of savannah elephants (from Wittemyer & Getz 2007). Two or more regularly associating mother-calf units (tier 1) coalesce into "familial" units (tier 2, also termed "core social groups"), which in turn, combine with other familial units into "extended familial units" (tier 3, or bond groups). The final tier of "episocial units" (clans) consist of individuals that overlap dry season home ranges (Charif et al. 2005; Douglas-Hamilton 1972; Moss 1988; Moss & Poole 1983).

The social levels described in these models represent gradients of familiarity and association, and may correlate with matrilineal kinship: Relatedness has been shown to predict both fission and fusion patterns among savannah females. Adult females were more likely to remain with first-order maternal relatives when core groups (also termed "familial units", Figure 1.2) temporarily fissioned, and core groups were more likely to fuse when their matriarchs (the oldest, largest and most dominant females) were genetic relatives (Archie et al. 2006b, in press). Charif et al. (2005) showed that within clans ("episocial units", Figure 1.2) there was no relationship between home range overlap and the proportion of maternal haplotypes that elephants shared. Wittemyer et al. (2009) found that while the majority of core familial units were significantly related, this was not always the case, and that in higher social tiers bonds tended to be stronger between relatives but again this was not universal. These groupings and levels of social organisation thus provide elephants with direct benefits in addition to inclusive fitness gains, and it is these direct benefits that form and maintain higher-level bonds (Wittemyer et al. 2009).

Sex differences in elephants are apparent from birth; behaviourally males are more persistent and frequent in their suckling demands and move further from their mothers, actively seeking social novelty (Lee & Moss 1986, 1999, in press). Elephants are sexually dimorphic and males continue to grow in height until they are 30-45 years of age when their long bones fuse (compared to 15-25 years for females (Lee & Moss 1995). Male disperse from their natal group in a prolonged process during or after puberty; this is highly variable between individuals and may occur at any point between 8 and 20 years of age, although most disperse by the age of 14 (Douglas-Hamilton 1972; Evans 2006; Evans & Harris 2008; Lee 1987; Lee & Moss 1986, 1999; Poole 1996). Males are sexually mature from around 17 years of age (Laws 1966; Poole 1994) but not sexually competitive until they are 30-35 years old, and not in their sexual prime until around the age of 45 (Poole 1982). The process of independence may take from one to four years (Lee & Moss 1986) and is variable between individuals; males may leave the natal group abruptly or slowly, and they may join directly with other males, join other families for a period, or move between several families (Poole 1996). Since male and female elephants are spatially and socially segregated (Laws et al. 1975; Moss & Poole 1983; Shannon et al. 2006a, 2006b) the process of leaving the natal group involves both social and locational dispersal (Isbell 2004).

By their early twenties males are fully independent of female groups, and have entered male society which is governed by rank and sexual state and which also contains associations and friendships (Evans 2006; Fishlock et al. 2008; Hall-Martin 1987; Lee et al. in press b; Poole 1989a, 1989b, 1996). Adolescent males in particular are highly social, and older males are important role models during this period (Evans 2006). Males cannot monopolise females when inter-birth intervals are 4-5 years (Douglas-Hamilton 1972; Moss 2001; Moss & Lee in press) and males may minimise intersexual competition by moving into “bull areas” in order to invest in increasing their body mass to enhance their competitive ability (a similar strategy to that observed in sperm whales Whitehead & Weilgart 2000). Older, larger males are the most dominant individuals but male social relationships as also affected by the phenomenon of musth, an annual period of elevated sexual and hormonal activity among mature males (Ganswindt et al. 2005; Poole 1987, 1989a; Poole & Moss 1981). During these times males signal their sexually active status via a series of visual (Kahl & Armstrong 2002; Poole & Granli in press) and auditory cues (“musth rumbles” Poole 1987, 1999; Poole et al. 1988) and chemical signals associated with highly elevated circulating testosterone, delivered via urine dribbling and secretion from swollen temporal glands (Ganswindt et al. 2005; Hall-Martin & van der Walt 1984; Poole 1987; Poole & Moss 1981; Poole et al. 1984). Musth periods are asynchronous between males and males generally fix their annual pattern by 30 years of age, although the duration of individual periods increases with age (Poole 1987).

Musth males leave bull areas actively searching for receptive females, and spending more time associating with females (Poole 1989b). Musth has dramatic impacts on male ranks; generally larger males are dominant but in nearly all cases musth males outrank non-musth males regardless of body size (Lee et al. in press b; Poole 1989a). Since musth is metabolically costly, males lose body condition over the course of their musth period, and a larger male towards the end of his musth episode may therefore be challenged by a smaller (younger) male just entering peak musth (Poole 1982; Poole 1989a). The majority of escalated competitions between males involve at least one musth male and are generally between males closely matched in size (Hall-Martin 1987; Poole 1989b; Poole et al. in press). Musth is therefore an honest signal of a male's willingness to contest access to oestrous females, and a mechanism to increase reproductive competitiveness, although musth males do not entirely monopolise reproduction (Ganswindt et al. 2005; Hollister-Smith et al. 2007; Poole et al. in press; Rasmussen 2005). Musth bulls are reproductively competitive and males thus delay such competition until they have attained large body size, relatively late in life (Whitehead 1994). Younger, non-musth bulls also engage in sexually active periods characterised by increased travel and association with females; these periods are longer and less costly than the energetic demands associated with the metabolic changes of musth (Rasmussen 2005) but females prefer to mate with older musth males (Moss 1983).

Individual elephants therefore live in an intricate social landscape in which relationships persist over decades and social experience has long-term consequences for survival and reproductive success. Individual elephants may live for more than 60 years (Laws 1966; Moss et al in press b). Cognitive abilities are associated with the need to learn, navigate and monitor this social world (Lee & Moss 1999) and elephants exhibit excellent long-term spatial-temporal and social memory. Elephants communicate with the use of a complex system of acoustic calls, many of which are below the range of human hearing, and which serve to individually identify callers (McComb et al. 2000, 2003), signal social information in mate searching, male-male competition and the maintenance of social bonds (Poole 1999; Poole et al. 1988) and convey information about the emotional state of callers (Soltis et al. 2005). Elephants use these calls to co-ordinate movements with associates who may be up to 2.5km away (McComb et al. 2003) and they show strong responses to the calls of unfamiliar conspecifics and expectations about the location of out-of-sight family members (Bates et al. 2008b). Elephants' ability to discriminate individuals extends to humans; both in distinguishing between threatening and non-threatening groups of humans (Bates et al. 2007) and in greeting familiar human observers (P.C. Lee pers. comm.). Individual experience plays a key role in elephant families; families with older matriarchs benefit from enhanced social discriminatory abilities (McComb et al. 2001) and matriarchs also provide repositories of ecological knowledge that can prove crucial for family survival in times of ecological stress (Foley et al. 2008; Mutinda et al. in press). Thus individual knowledge and experience accumulated over decades affects reproductive success and families with older matriarchs have a higher reproductive output and calf survival than families with younger matriarchs (Moss & Lee in press a).

Discussions of empathy among elephants have been prompted by their consistent responses to the carcasses and bones of conspecifics. Elephants show great interest in both carcasses and bones, and will attempt to raise prone individuals who are ill or dying, stand guard over those individuals after death and continue to handle the bones of conspecifics months after death has occurred (Douglas-Hamilton et al. 2006; McComb et al. 2005; Moss 1988). Individuals have also been observed to remove tranquilliser darts and spears from the bodies of conspecifics, and to actively prevent calves from eating plastic bags (Bates et al. 2008a). Elephants therefore show sophisticated social intelligence and social flexibility within a dynamic social environment.

In contrast, relatively little is known of social dynamics in the forest elephants inhabiting the Congo basin (but see Payne 2003; Turkalo 1996) and no model of sociality has been empirically demonstrated. Sociality affects how animals move across and use resources in their landscape, and this knowledge gap therefore limits our understanding of important drivers in the evolution of elephant social systems, and of the environmental requirements for forest elephants. Fission-fusion systems in elephants are proposed to have evolved as a mechanism for minimising the costs of group-living. These costs are habitat- rather than species-specific, although their evaluation is complicated by behavioural strategies which may have developed to minimise costs (Lehmann et al. 2007; van Schaik & van Hooff 1983). Savannah elephant groups thus fission to minimise competition and use fusion to maintain social relationships and access older individuals who function as repositories of social and ecological knowledge (*sensu* McComb et al. 2001).

For savannah elephants cycles of resource deprivation followed by periods of proliferation have the effect of bringing females into a degree of reproductive synchrony which has cascading effects on male-male competition and reproductive tactics (e.g. Moss 1988; Rasmussen 2005; Wittemyer et al. 2006). The ecological pressures experienced by elephants in the lush equatorial rainforests are radically different to those on the arid plains of East Africa; water and food are not limited, although the availability of fruit crops makes high quality resources patchy in both time and space (Blake 2002; Powell 1997). Our ability to relate resource base to sociality in forest elephants requires that we have a description of and insight into their social systems.

1.3.1 The Forest as an Elephant Environment

The rainforests of Central Africa are some of the most contiguous elephant habitat left on Earth. The forest block of the Congo basin spans around 200 million hectares (CBFP 2007), from costal Gabon to eastern Democratic Republic of Congo. Population estimates suggested that upwards of 50,000 elephants remained in these habitats (Blanc et al. 2007) down from 1.2 million in 1980; however huge population losses have occurred in the past three years and are ongoing (Blake et al. 2007; Bouché et al. 2009; Wasser et al. 2008, 2009). Even the most remote populations are under threat as poaching across Africa continues to rise alarmingly (Blake & Hedges 2004; Wasser et al. 2004, 2010). The distribution of roads and people negatively correlate with elephant density (Barnes et al. 1991; Buij et al. 2007), and encroaching road infrastructure can profoundly alter elephant ranging decisions, even where forest structure remains intact, both by facilitating access for poachers and through risk perception by elephants themselves (Blake et al. 2008).

The ivory crisis in the late 1980s focused world attention on Africa’s elephants, and since that time research has concentrated principally on estimates of elephant density and distribution in the forest region (e.g. Barnes 2001; Barnes & Jensen 1987; Blake 2002; Blake et al. 2001; Stokes et al. 2010). Large mammal work in Central Africa has typically been based on tracks, feeding trails and other “sign”, rather than direct observations of animals, as these are both difficult and potentially dangerous in the dense rainforest environment. Telemetry data indicate that individual elephant home ranges may be up to 2,000km^2 and, similar to savannah elephants, are individually highly variable and subject to seasonal changes (Blake 2002; Momont 2007). Elephant ranging is affected by the availability of high-quality fruit resources (Blake 2002; Morgan & Lee 2007; Short 1983; White 1994). Although forest elephant diet is largely dominated by leaves and browse, they devote special effort to locating fruit resources, and consume it whenever it is available (Blake 2002; Short 1983). Elephant activity constructs conspicuous elephant trails that link important resources in the landscape; namely water, forest clearings, and important fruit trees (Blake 2002; Blake & Inkamba-Nkulu 2004; Vanleeuwe & Gautier-Hion 1998).

Opportunistic observations and indirect sign (tracks and trail) suggest forest elephants range in small groups, where the basic unit is a mother and her dependent offspring (Morgan & Lee 2007; Theuerkauf et al. 2000; White et al. 1993). Thus among forest elephants, there is dispersal from the natal family by both males and females; a sharp contrast to savannah elephants. The age at which the dispersal occurs also appears to be younger than the 10-16 of male savannah elephants (Turkalo & Fay 1995). The average group size of elephants seen in the forest is 2 (Powell 1997; White et al. 1993). Large multi-female groups have not been observed within the forest, however, the infrasonic communication abilities of forest elephants are similar to those described for savannah elephants (Payne 2003; Payne et al. 2003; Thompson 2009) and may serve to maintain a higher level of co-ordination than is inferred from relatively low rates of associations or interaction (Aureli et al. 2008). In addition, large natural forest clearings, known locally as *bais,* or *salines* provide animals with food and mineral resources, provide excellent observation conditions and are known to attract large aggregations of elephants, sometimes numbering hundreds of animals (Querouil et al. 1999; Turkalo & Fay 2001; Turkalo in progress). Forest elephants also regularly congregate at other kinds of open areas (rocky outcrops, Powell 1997; beaches, Morgan & Lee 2007 and riverbanks VF pers. obs.). In such open areas, average group size is between 2 and 4, (reviewed in Morgan & Lee 2007; Theuerkauf et al. 2000; Powell 1997).

Conventional theory has thus held that forest elephant group sizes are constrained by the patchy nature of high quality fruit resources and that bais may function as social arenas, allowing animals to aggregate and exchange social information. These "social hubs" would thereby be fundamental in supporting a fission-fusion social system (Fishlock et al. 2008; White et al. 1993).

1.4 Studying Social Systems

Sociality reflects the dynamic outcome of interactions between an individual, its conspecifics and its environment. Thus, social systems can be viewed as the product of interactions between competing and co-operating individuals, seeking to maximise reproductive success when the environment provides opportunities or imposes constraints on individual resource acquisition (van Schaik & van Hooff 1983; Wrangham 1980). Social structure and dynamics influence how and when individuals use habitats and social behaviour interacts with population demography and dynamics (Dunbar 1985; Lehmann et al. 2007; Tuyttens & Macdonald 2000; Wrangham 1980).

Many researchers interested in describing and modelling social systems have adhered to Hinde's classical (1976) framework. Data are collected on associations and interactions between individuals and used to construct matrices describing the relationships between individuals. The patterning of these relationships builds into a social structure, which may be visualised through the use of dendrograms or sociograms. For savannah elephants, these techniques work well, as survey effort can be allocated to locating target individuals as and when required. However, such individually-based approaches are simply inapplicable in the field conditions presented by Central African rainforests, where direct observations of elephants and elephant behaviours are restricted to forest clearings or other open areas. Generally, the matrices of associations or interactions obtained from clearing studies are simply too sparse to be informative; many missing dyads reflect the fact a large proportion of the population is not observed to associate in the clearing due to individual ranging decisions. In addition to individual differences in patterns of clearing use, individuals may suddenly shift their ranging in response to life history stages, reproductive status (e.g. Momont 2007) or for no discernable reason. Studies at both Mbeli and Dzanga clearings (in northern Congo and southern CAR) document sudden range shifts in prime-age adult males (35-49 years old). Males are often regularly sighted during a particular period over the course of several years and may then disappear. For example, at Dzanga, one prime male did not visit the clearing for seven years and was presumed dead, before returning during his "normal" annual visiting period (A. Turkalo pers. comm.). Such "disappearances" by males from habitual ranges are known in savannah elephants (K. Evans pers. comm.; P.C. Lee pers. comm.). But among forest elephants, even well-known females may "vanish" only to reappear several months later (Mbeli Bai, long-term records), although this is rarer than for males.

1.4.1 Social Networks

Network analyses developed from graph theory and have been applied to a range of research questions, including the web of human sexual contacts (Liljeros et al. 2001) and the connections of the World Wide Web (Yook et al. 2002). Network descriptions have focused on information transfer between constituent elements (nodes) and have provided new insights into the structure and function of biological systems at levels ranging from genes to ecosystems (Proulx et al. 2005). The application of social networks to the study of animal behaviour has been slower than in some other fields despite the fact it provides quantitative measures that allow for modelling of relationships and structures (Krause et al. 2009; Wey et al. 2008). Network analyses allow researchers to define groups based on interactions rather than just spatial measures such as proximity; for example Lusseau et al. (2006) used this technique to distinguish between spatial and active social associations in bottlenose dolphins. Network theory provides additional benefits for animal behaviour studies, including the identification of the fitness consequences of sociality, defining important or valuable individuals and distinguishing their structural social roles, and distinguishing the key characteristics of stable groups (Lusseau & Newman 2004; Wey et al. 2008; Williams & Lusseau 2006). It therefore provides an analytical framework for linking individual behaviours, such as associations, with higher-level phenomena (Patriquin et al. 2010).

Networks can be visualised as sociograms, but they have the additional advantage of generating specific mathematical properties which describe the network. One of the problems with network analyses has been the difficulty in drawing biological inferences from observed network statistics (Croft et al. 2005; Lusseau et al. 2006). Advances in the incorporation of uncertainty into networks, and improved computational power in the modelling of weighted (rather than simple binary) networks has much improved the capacity to meaningfully capture social organisation (Lusseau et al. 2008). Networks can be subject to highly advanced modelling to predict network behaviour (Newman 2003), but their main advantage for the purposes of this thesis lies in the ability to compare various measures of aggregation between groups or classes of individuals, and to test these observed values against randomly generated datasets. Their development in behavioural ecology has been primarily driven by researchers investigating cetacean social structures, where severe observational constraints limit association matrices and measures in a similar manner to forest elephant studies (e.g. Lusseau & Newman 2004; Lusseau et al. 2008; Whitehead 1995, 1997, 2009; Whitehead 2008a, 2008b). They have also been adopted for use in primate social networks, where they have been applied to studies of stability and robustness to perturbation, and the prospect of "social niches" (Flack et al. 2005, 2006), and for other taxa such as northern long-eared bats (*Myotis septentrionalis*) to examine changes in social networks resulting from life history stages (Patriquin et al. 2010). Networks remain computationally intensive (especially for larger datasets) but the advent of new permutational techniques has significantly reduced these costs (Lusseau et al. 2008; Whitehead 2008b). Network analyses have been successfully applied to describe elements of the processes structuring savannah elephant sociality

(Wittemyer et al. 2005), although alternative models of exploring elephant socio-ecology also exist (Vance et al. 2009).

1.5 Thesis Aims and Objectives

The savannah elephant fission-fusion model of sociality has yet to be formally demonstrated in forest elephants, making the study of patterns of association and aggregation particularly important. This thesis focuses on appraising sociality and its consequences for forest elephants in the bai environment and in the wider context. Bais are hypothesised to function as social arenas, as the aggregations of elephants observed there do not occur elsewhere in the dense forest environment. This thesis aims to evaluate the social and nutritional resources available to elephants, and to examine alternative hypotheses for bai use as set out in Table 1.1.

Specifically, this thesis centres on two main questions;

1. Do bais function as social arenas?
2. What can observations at bais reveal about forest elephant social structure?

To overcome the problems inherent in fixed point studies (see Chapter 2), the observed data are tested against the expectations of a fission-fusion system, focusing on age-sex patterns of clearing use (Fishlock et al. 2008). Network analyses are used to generate random datasets in order to evaluate the observed association patterns. Throughout the thesis, results are discussed in the context of existing knowledge on savannah and Asian elephants (*Elephas maximus*) to consider larger questions regarding the expression and evolution of elephant social systems.

Proposed function	**Expectations to test the model**
Nutritional resource base, providing micro- and macronutrients, no important social component for forest elephants	Bai visiting patterns show a strongly seasonal component for the majority of the visiting population. Animals enter the bai and use the first available resource point, and do not engage in social behaviour
Bull area (Moss & Poole 1983; Evans 2006)	Disproportionate number (relative to population age-sex composition) of bulls using the bai. Few musth (reproductively active) bulls. Uncertain predictions *re.* group size, as a lack of sexual competition may increase group size.
Mating arena	Large number of musth bulls, and majority associating with females. Sexual behaviours seen (e.g. urine testing of females by musth bulls). Possible "harassment" of females by subordinate but sexually active young males.
Area for exchange of female social knowledge (McComb et al. 2001)	Large numbers of female aggregations: females associate at above chance levels in order to exchange information and refresh social knowledge.
Nutritional resource base that facilitates social behaviour	Some combination of the expectations above; seasonal changes in usage density (associated with resource availability outside the bai and nutritional requirements for reproduction), coupled with one/more of the social functions.

Table 1.1. Proposed functions of bai use.

1.6 Thesis Outline

This thesis is divided into two parts; the first of these presents descriptive data on the Maya Nord site and elephant population, and in the second themes of sociality and risk are explored to assess the hypothesis that bais function as social arenas for forest elephants. Chapter 3 broadly categorises ecological factors deemed to be relevant to clearing use, including definitions of seasonality, chemical analysis of soil from geophagy sites and gross changes in local forest productivity. Chapter 4 provides an account of visiting patterns to the clearing, describing daily, monthly and seasonal variation in visiting patterns and socio-spatial organisation. Chapter 5 describes the population structure as captured from elephant observations, provides a comparison to a previous study at this site, and then discusses reproductive parameters and elephant health. In Part Two, Chapter 6 evaluates elephant socio-spatial organisation by describing gregariousness, and then considers the dynamics of the observed association patterns. Chapter 7 details the nature of elephant interactions, and attempts to evaluate relationships according to the expectations of a fission-fusion model. Chapter 8 explores aspects of risk involved in clearing use, especially as regards human-mediated threats to the population. Chapter 9 synthesises the main findings, evaluates the function of the Maya Nord clearing, the role of clearings in forest elephant sociality, and summarises what bai studies can tell us about the nature of forest elephant society.

Chapter Two

Methods

Chapter 2 Methods

2.1 Overview of Methods

This study focuses on direct observations of elephant behaviour at the Maya Nord clearing to assess the use of bais as social arenas for forest elephants. Data were collected on the physical and floristic environment as well as the elephants in order to establish ecologically relevant seasons and place observed behaviour in a socio-ecological context given the resources that bais provide. As this elephant population is previously unstudied in any detail, a discussion of elephant health and population structure was also important for describing the contexts in which sociality and interactions occurred.

2.2 Study Site

Odzala-Kokoua National Park (hereafter PNOK) lies in the North-West Republic of Congo (Brazzaville) covering 13,545km^2 (Figure 2.1). It is the second largest forested national park in the Congo basin, and abuts the Gabonese-Congolese border on its Western edge. Odzala National Park (PNO) was created in 1935, and originally covered 2,800km^2. The extension creating PNOK was formalised in 2001 (Aveling & Fromont 2001). The southern sector of the Park is covered by a mosaic of savannah and gallery forest and the northern half contains dense stands of Marantaceae forest on base-poor soils (which have poor nutrient content and are generally acidic), with smaller areas of primary and seasonally inundated forest (Hecketsweiler et al. 1991; Lejoly

1996; Vanleeuwe & Gautier-Hion 1998). PNOK supports a large and geographically important population of forest elephants (Fay & Agnagna 1991; Turkalo & Kidjo 1996); the most recent surveys estimated 11,000 – 18,000 animals may be present in the Park (Blake 2006; Blanc et al. 2007).

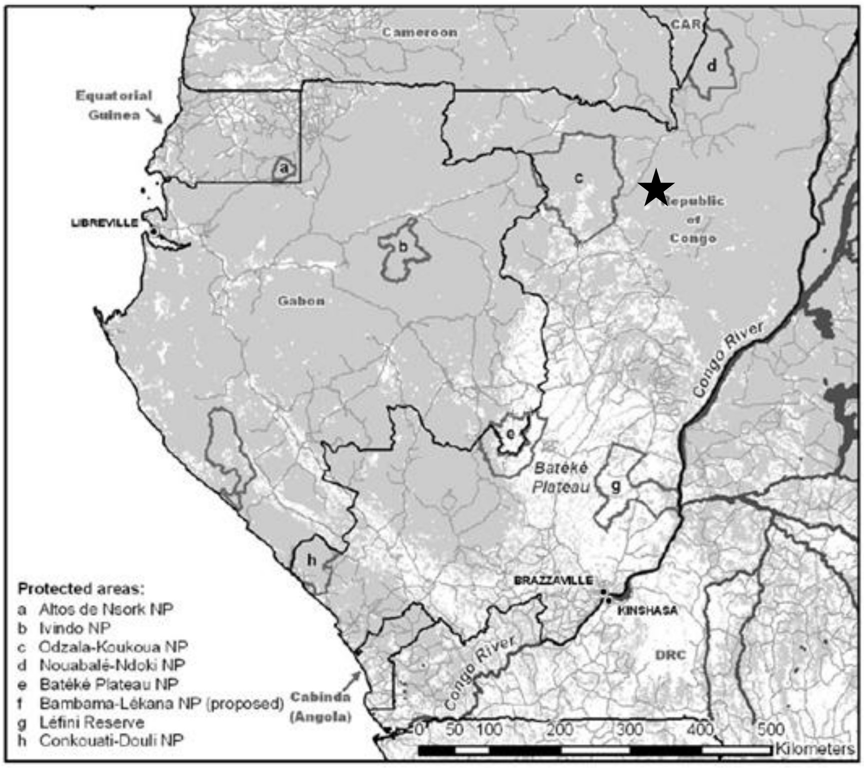

Figure 2.1. Location of Odzala-Kokoua National Park (from Henschel 2008). Star indicates location of Maya Nord.

2.2.1 The Maya Nord Clearing

Maya Nord is situated in the heart of present-day PNOK (Figure 2.1). Although human settlement of the region has changed profoundly at least twice in modern history, the Maya zone has never held permanent settlements in recent times (Hecketsweiler et al. 1991). In 1996 the Maya Nord clearing was (re)discovered during surveys of the clearings north of the PNO boundaries (Vanleeuwe et al. 1998), and was developed for research and tourism between 1996 and 1998. Filmmakers, researchers and tourists visited the clearing regularly during this period as the clearing became a key site for research and ecotourism for Western lowland gorillas (*Gorilla gorilla gorilla;* e.g. Magliocca & Gautier-Hion 2002, 2004). Ebola outbreaks in and around PNOK from 2001 onwards effectively ended gorilla research within PNOK until 2008 and were reported to have devastated ape populations (Bermejo et al. 2006; Caillaud et al. 2006; Gross 2005). Prior to my study, no Park staff or researchers had visiting the Maya zone since the construction of an observation platform at Maya Nord in 2004.

The North sector of PNOK contains over a hundred clearings of varying sizes (Vanleeuwe et al. 1998). Maya Nord is unique amongst these in that it was never targeted for large-scale ivory poaching. Ancient hunting and fishing camps along the Mambili river provided bases for ivory poachers from the 1960s onwards (R. Andembo pers. comm.), and heavy poaching occurred in the 1990s at other PNOK clearings (specifically Moadje bai; Vanleeuwe et al. 1997). Maya Nord's remote location 12km north of the Mambili River apparently conferred security and poachers were able to target elephants at more accessible sites (Vanleeuwe et al. 1998). These facts, along with historic reports of large aggregations of elephants (Querouil et al. 1999; Vanleeuwe et al. 1998), the lack of recent human presence in the research area and the almost unstudied elephant population made Maya Nord an ideal site for this study.

The Maya Nord clearing covers 22.9 ha (see Figure 2.2), and is dominated by herbs in the Cyperaceae and Poaceae families (Magliocca & Gautier-Hion 2002; Vanleeuwe et al. 1998). The clearing contains two elephant pools, connected by a series of permanent streams, and areas of bare earth around the forest edge, with a sharp delimitation between the forest edge and the clearing. The clearing is heart-shaped (Figure 2.2) but elephant activity is heavily concentrated around the pools; elephants were rarely observed in the two sections to the North, and when present in these zones elephants were generally travelling or feeding on herbaceous vegetation. The clearing floods during wet season months; maximal inundations are rare and occur perhaps twice per wet season, but cause the water level to rise by more than a metre. Elephants generally avoided using the clearing at these times.

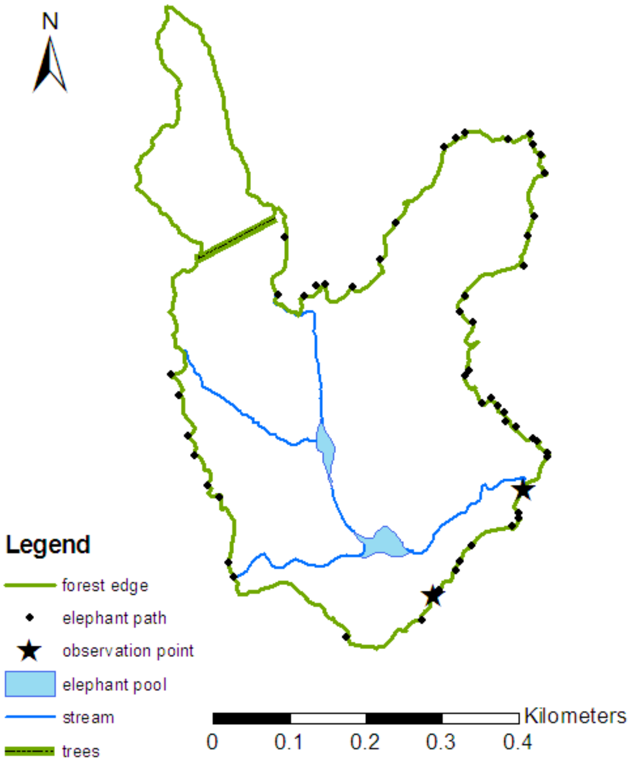

Figure 2.2. Map of the Maya Nord clearing.

2.2.2 Climate

Various classifications have been applied to the region's climate, but the preferred is Leroux's (1983), "Atlantic monsoon of the Congo Basin"[1] (Hecketsweiler et al. 1991). This is characterised by moderately high temperatures, with low annual temperature range (1-2^{0}C) and a low daily temperature range (<10^{0}C). High annual rainfall (>1500mm) falls bimodally, with peaks in October and March-May. PNOK straddles the equator and is influenced by the rainfall patterns of both hemispheres, and the "small" wet season which occurs early in the year is approximately a month later in the North compared to the south of the Park. Inter-annual variation in rainfall is high: the driest month of the year generally has >30mm of rainfall, but in some sites or years this figure may be as little as 3mm per month (Maisels 1996).

2.2.3 Study Period

Data were collected between July 2007 and June 2008. The remoteness of the study site made it impossible to maintain a continual research presence, so work was carried out in blocks (see Table 2.1). No data were collected in January 2008 as I travelled to Brazzaville for logistical and recuperation purposes. Observations were carried out on 187 days, totalling 1835 hours of observation, upon which this thesis is based.

---

[1] Approximate translation from the French; "domaine de la mousson atlantique permanente de la Cuvette Congolaise".

Work Block	Start Date	End Date	N observation Days
I	21 Jul 07	02 Sep 07	30
II	16 Sep 07	30 Oct 07	30
III	10 Nov 07	30 Dec 07	33
IV	8 Feb 08	29 Mar 08	37
V	14 Apr 08	04 Jul 08	57

Table 2.1. Fieldwork schedule for study period.

2.3 Elephant Observations

Observations were made from one of two platforms at the edge of the Maya Nord clearing, using spotting scopes and binoculars. A new platform was constructed at the end of November 2007, as it became apparent that the original platform (built for tourism purposes in 2004) was poorly situated, being downwind of the principal elephant paths leading into the clearing and causing elephants to flee as soon as they detected observers. The second observation platform was further to the East of the clearing, and was situated 200-250m from both elephant pools (Figure 2.2). Data were collected from this platform from the beginning of December 2007. Observation days generally ran from 05:30 to 17:30 once we had constructed the new observation platform and could be reasonably confident of our safety when walking to the bai in the dark.

The number of fresh dung piles recorded at the start of each observation day was used as an index of nocturnal activity. Dung piles in each of the pools were counted on arrival at the clearing when observation conditions permitted. Counts were not made after heavy rain or heavy activity by seed predators dispersing dung piles (mainly red river hogs, *Potamochoerous porcus* and sitatunga, *Tragelaphus spekei*). Dung counts were made from both observation platforms where possible, and were highly correlated (r=0.803, p<0.001) so data were analysed without reference to the observation point used, using a mean score where data from both points were available.

2.3.1 Individual Identifications

Elephants are individually distinct in their overall body morphology, and more specifically in the growth form of tusks, tail hair and patterns of tusk wear and breakage and of notches, holes and veins on the ear margins (Douglas-Hamilton 1972; Moss 1996). Using these features, sketches were made of individual characteristics (see Figure 2.3), and individual identities were assigned by name when observers were confident of being able to re-identify animals on subsequent visits. A library of individual cards was compiled, and grouped according to whether the left, right, or both ears were distinctive. To authenticate individual identities, a library of digital photographs was compiled for each animal, where possible including left and right body profiles and head-on shots.

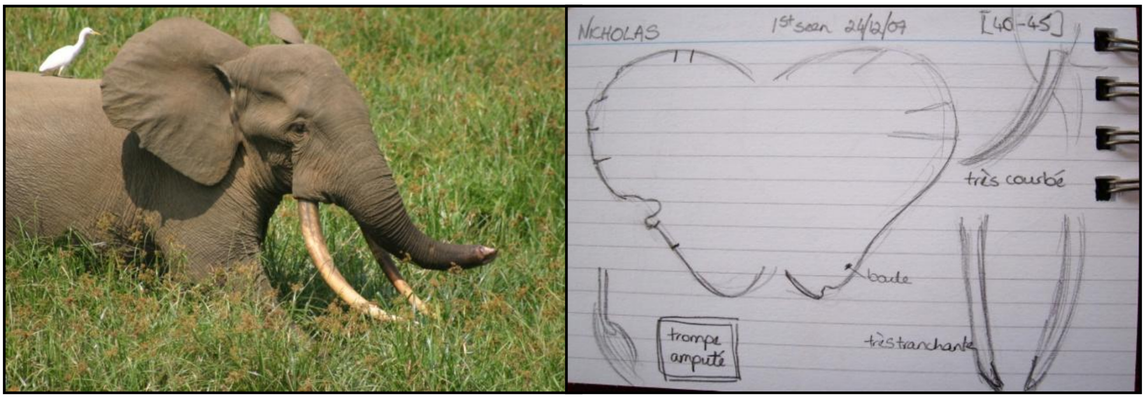

Figure 2.3. Adult male Nicholas and his ID card.

2.3.2 Age Validations

All elephants were assigned a life-history stage when first observed (see Table 2.2), based on shoulder height, body mass and tusk development cues (Laws 1966; Moss 1996). Where observations conditions permitted ages were estimated. To verify these subjective judgements, highly experienced elephant observers (P.C. Lee and A. Turkalo) were asked to judge the ages of individuals using photographs, and these ages were compared to VF's estimates. Known individuals were re-aged several times in the field, and also through the use of digital photographs to assess intra-observer consistency. Re-estimates in the field were only performed when VF could not recall the previous estimate assigned to an individual, and were separated by intervals of weeks or months. Re-estimates using photographs were done on two separate occasions in August 2008 and January 2009, with the order of individuals randomised each time. P.C. Lee's judgements were used to reconcile age estimates for "problem" animals and A. Turkalo's estimates were used to verify judgements, using 37 individuals chosen on the basis of the quality of the photographs, and who represented a full age range.

<table>
<tr><th>Age (years)</th><th>Males</th><th>Females</th></tr>
<tr><td>0-4</td><td colspan="2"><6mo = newborn
6-12mo = small infant
1-2years = infant
2-4years = young juvenile</td></tr>
<tr><td>5-9</td><td colspan="2">old juvenile</td></tr>
<tr><td>10-14</td><td colspan="2">sub-adult</td></tr>
<tr><td>15-19</td><td>old sub-adult</td><td>young adult</td></tr>
<tr><td>20-24</td><td>young adult</td><td rowspan="3">adult</td></tr>
<tr><td>25-34</td><td>adult</td></tr>
<tr><td>35-49</td><td>“prime"</td></tr>
<tr><td>50+</td><td colspan="2">old</td></tr>
</table>

dependent offspring = “calves”

Table 2.2. Age classes used in this thesis and associated life history descriptions.

Inter-observer agreement was evaluated by visually inspecting plots of age estimates, marking those which showed greater than 10 year disagreement in the estimate band and using these to calculate a percentage agreement score. This manipulation takes into account the degree of observer certainty and overlap in estimates, which is lost when converting scores to point estimates. Only 18.9% of animals (n=7) showed divergence of more than 10 years in estimates (Figure 2.4). This is a reasonably high inter-observer reliability score (81%) considering that judgements made via photographs are inherently more difficult than observing live animals, and that some of the photographs undeniably lacked cues for AT which VF had knowledge of.

The midpoints of age estimates were correlated for both inter- and intra-observer agreement. Intra-observer agreement was calculated through repeated judgements in the field (n=60) or through photographs (n=37; the same used for inter-observer reliability assessment). All scores were highly correlated (Table 2.3) although differences were apparent in ageing according to whether it was done via photographs or in the field. There were also clear gender differences; males were easier to age than females, primarily because their prolonged maturation shows a more distinct gradient of age-related cues. This was also the case for 60 animals aged in the field by VF, where scores for males were more consistent (males r_s=0.979, n=29, p<0.001; females r_s=0.841, n=31, p<0.001). Having demonstrated high levels of concordance, I then assigned individuals to age classes using "reconciled" ages, based on the mid-points of estimates.

		Females			**Males**		
		Photo2	Field	AT photo	Photo 2	Field	AT photo
Photo 1	r_s	$.906^{**}$	$.483^{*}$	$.526^{**}$	.994**	.895**	.886**
	p	.000	.012	.005	.000	.001	.001
	n	26	26	27	8	9	9
Photo 2	r_s		$.520^{**}$	$.642^{**}$		.898**	.868**
	p		.008	.000		.002	.005
	n		25	26		8	8
Field	r_s			$.420^{*}$			.963**
	p			.033			.000
	n			26			10

Table 2.3. Correlations (Spearman's rho) for the midpoints of age-estimates assigned to 37 animals judged by AT and the estimates assigned by VF on the same animals in three rounds (where photo 1 and photo 2 indicate separate judgements on the same set of photographs).

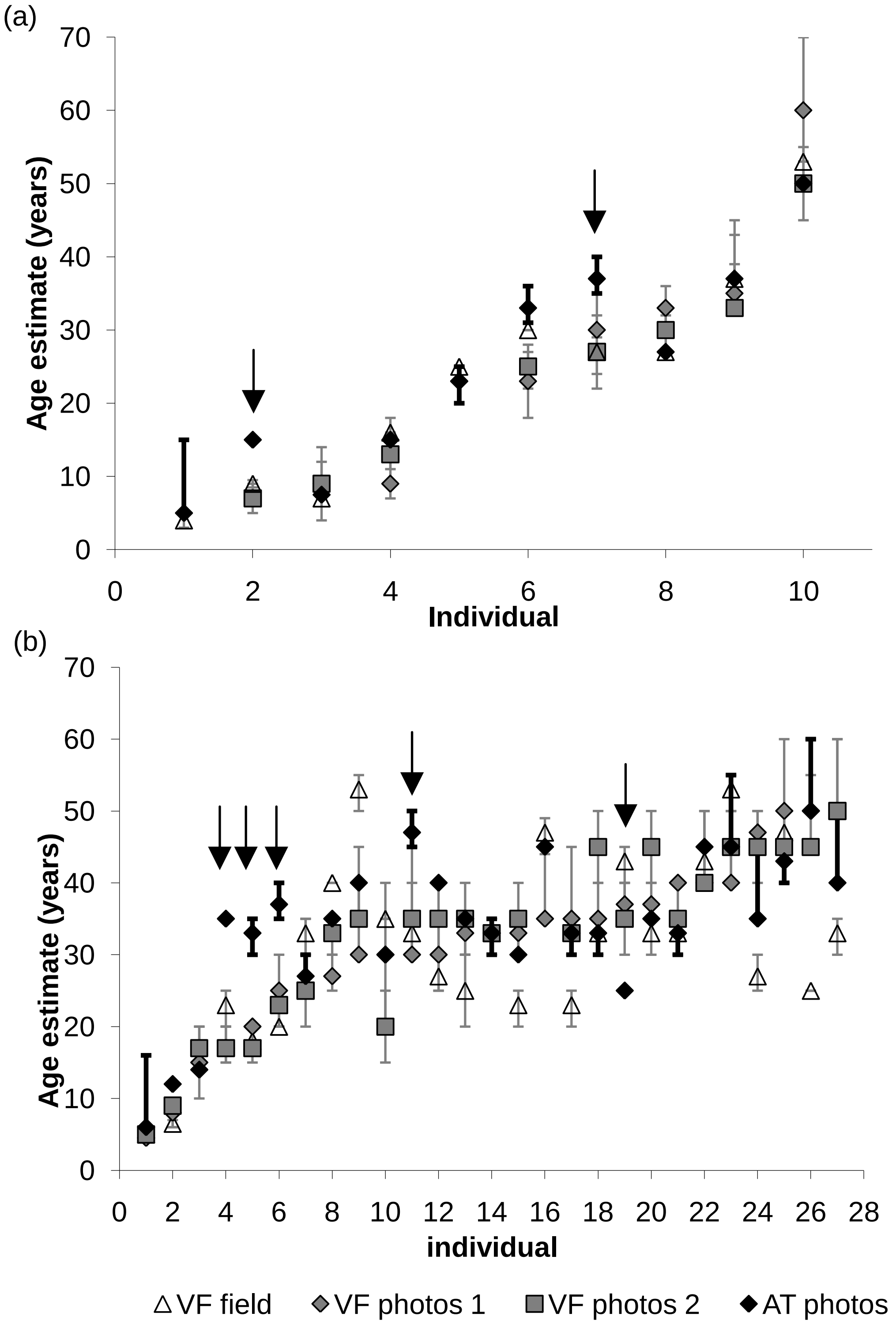

Figure 2.4. Age estimates for (a) 10 males and (b) 27 females aged by two observers using field estimates (VF) and photo estimates (VF and AT). Error bars show estimates of precision. Asymmetric error bars indicate where observers scored an animal as "x years or older" rather than providing an upper age estimate. Arrows disagreement of >10 years between observers' estimates.

2.3.3 Levels of Organisation

Two levels of organisation were described for animals present in the clearing; parties, and aggregations (see Table 2.4). Elephant parties were defined using an adaptation of the group definition used at Amboseli (Moss 1983; Moss et al in press b). The use of term “party” is adopted throughout this thesis, rather than “group”, consistent with the language used in the chimpanzee fission-fusion literature. The methodology thus makes no implicit assumptions regarding the long-term associations, kinship or familiarity of individuals within the party. Rather, it is a statement reflecting the cognitive choices of individuals to group at a given moment. The flexibility of this definition allows for systematic examination of the nature of party changes, from which inferences of association and familiarity can be determined, along with behavioural data. Aggregation level organisation is used as a description of a second tier of associations, as elephants could observe conspecifics and “eavesdrop” on other parties and their interactions within the clearing (Bonnie & Earley 2007). Information regarding the cohesiveness and affiliation between individuals were made where appropriate by assigning individuals to putative family units or bond groups (Table 2.4).

Term	Definition
Party	A body of elephants co-ordinated fashion in activity, with no individual from the main body of the party than the maximal width of the main body of the party[1].
Aggregation	All elephants present in the clearing at any one time.
Family Unit	Putative assignment of individuals to family units was based on proximity, co-ordination, affiliation and tolerance between group members. This term makes no assumptions regarding genetic relatedness between unit members[2].
Bond group	Members associated with known family units, but either not present on all visits, were deferential to or less tolerated by family members or were of an age that they could not be the offspring of family unit females.

Table 2.4. Terms used to describe elephant social organisation in this thesis.[1]after Moss 1983; Moss et al. in press. [2]Studies of savannah elephant genetics have shown that association is usually, but not always, correlated with kinship e.g. Archie et al. 2006b, Charif et al. 2005; Wittemyer et al. 2009.

On arrival at the clearing, the number of elephants present in the aggregation was noted, along with party locations, sizes and compositions. Party composition was classified as “unknown” where the age-sex of members could not be determined; “cow-calf”- one adult female, alone or with immature animals; “multi-female” - 2 or more adult females, with or without immature elephants; “male”=adult males only; “mixed” - both adult males and females present; or “immature”- no adults present in the party. Aggregation size and composition were noted every 30 minutes throughout the observation day. Behaviour-dependent sampling began immediately (see Section 2.6.5) and party changes were recorded, whilst systematically attempting to identify the individuals present. All elephant entrances and exits from the clearing were recorded with the time, party composition and location. Animals were almost always assigned age-sex classes (based on life history stage, see Table 2.2) and when observation conditions permitted ages were estimated within age classes. These age-classes are used throughout this thesis rather than age-descriptions, as males and females mature at different rates (Lee & Moss 1995; Moss 1996; Poole 1982).

Parties and aggregations are described in this thesis in terms of size and composition. Parties are also described in terms of their duration: party changes were noted when individuals joined or left existing parties. New parties were only created by the instigators of change i.e. elephants joining or leaving conspecifics, so that elephants who were left in these “residual” parties did not change their party unless they joined, or were joined by, other elephants. Elephant presence is also described in terms of “visit duration”, which is the total time that animals spent in the clearing. Multiple visits to the clearing on the same observation day were rare, but were separated according to the time between observations (see Section 2.7).

2.3.4 Behaviour

Behaviour dependent sampling was used to record all instances of social interactions, vigilance, inter-species interactions and responses to observers. Altmann (1974) refers to this as “sequence sampling”, where the observation focus is the sequence of behaviours rather than particular individuals. Sampling begins once an interaction sequence starts and all behaviours are recorded in order of occurrence until the sequence is terminated or interrupted. This enables detailed data collection on social behaviours (e.g. Lee 1987) and is used to record complete interaction bouts without constraining observations to a focal animal (Newton-Fisher 1997). Sampling bias was avoided by recording all instances of social interactions, rather than selecting particular sequences to record (Altmann 1974). Interactions were described using functional descriptions (see Ethogram Appendix A) which were used to create behaviour categories for analysis (see Chapter 7). Elephant interactions were recorded noting the initiator and recipient (identity or age-sex class for unidentified animals), along with the dyadic context in which they occurred; within- or between-parties, within- or between-families or between individuals who entered the clearing together. Responses to third party interactions were also recorded, and when interactions involved families or multi-female units these were classified according to matriarch identity. Audible vocalisations and vocalisation postures were recorded along with the context in which they occurred, although inevitably the rate of vocalisations was underestimated since so much of elephant communication is beyond the range of human hearing (e.g. Poole et al. 1988). Elephants vocalisations from the forest edge were also recorded along with any elephant responses to these. When elephants fled the clearing the time of the flight event was noted, as well as the time at which animals exited the clearing, the direction of flight and the cause if it could be determined.

2.3.5 Nocturnal Observations

The size of the clearing, and distance to the elephant pools that were the foci of elephant activity made night observations impossible except on fully moonlit, clear nights, which may have biased the activity levels observed. Night observations were attempted whenever observation conditions looked promising, but were often abandoned due to rain, fog or cloud cover. Since it was impossible to track individual animals (except for very distinctive individuals e.g. one-tuskers), night observations were restricted to 15 minute counts of party sizes and estimated compositions. Animals were assigned to broad life history stage classes; adult males, adult females, immatures, old sub-adult/young adult males (distinguishable from adult females mainly by tusk development) or non-identifiable. Immature animals were the most difficult category to count with certainty, and were almost certainly underestimated.

2.4 Statistical Analyses

Data were manipulated and analysed using Excel, PASW v.17, Minitab v.15 and SocProg v.2.4 (for MATLAB 7.7.0.471, release 2008b; Whitehead 2009) and details of the specific statistical tests applied are provided in relevant chapters. All data were tested for normality using the ratio skew: SE skew <3 (Sokal & Rohlf 1995). Data were transformed if normality assumptions were not met to remove the majority of the skew ($\log_{10}$, square root, reciprocal square, reciprocal root transformations), or non-parametric tests were applied where transformations were not possible (Spearman's correlation, chi-square, Kruskal-Wallis, Mann-Whitney U, Kolmogorov-Smirnov 2-sample). All tests were performed as 2-tailed and the critical significance value was set at 5%. Adjusted R^2 values (or equivalents) are reported throughout as indications of model fit. Error bars on graphs represent 95% confidence intervals (95% CI) unless otherwise stated.

Tests of autocorrelation relating to sampling intervals were conducted and are discussed in Chapter 4 in relation to aggregation size, time of maximum aggregation, party size and visit duration. To minimise pseudoreplication and autocorrelation within observation days, visit duration data were examined using log survivorship analysis to determine visit bout length and ascertain appropriate units of analysis (Martin & Bateson 1993). The first major change in slope occurred around 1 hr 40 minutes (Figure 2.5), so to examine time of day effects observation days were split into 90 minute blocks (see Table 2.6) where visits occurring in one time block were considered independent of those occurring in other blocks through the day. Visits were assigned to the first time block in which individuals were recorded and considered unique events. Aggregation sizes were thus assessed on the basis of 30-minute counts and in order to use the same time blocks for continuously recorded data (i.e. visit durations) 2 additional blocks were included, covering the earliest and latest part of the day. The same 90-minute criterion was applied when analysing association data to define aggregations (see below and Chapter 6).

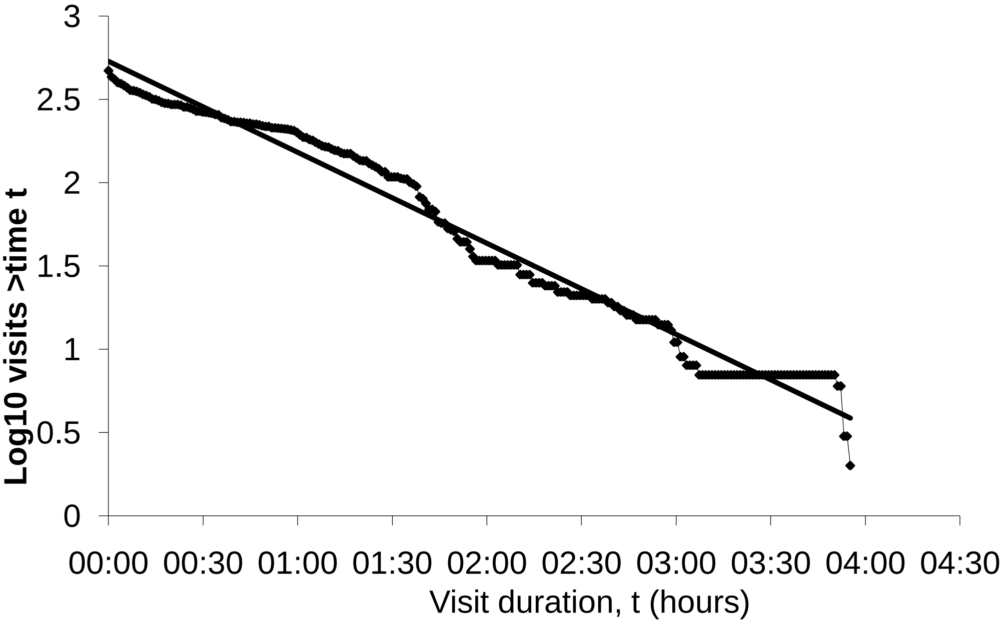

Figure 2.5. Log survivorship plot of visit duration (n=470 undisturbed elephant visits).

Time block	Start	End
0	05:00	05:59
1	06:00	07:29
2	07:30	08:59
3	09:00	10:29
4	10:30	11:59
5	12:00	13:29
6	13:30	14:59
7	15:00	16:29
8	16:30	17:59
9	18:00	-

Table 2.5. Time block classifications applied to elephant observations.

Where ANOVA models were applied Type I Sums of Squares were used to examine hierarchically the variable of interest whilst controlling for other factors. Type I models were particularly important where field conditions inherently affected the variable under examination e.g. where strong time of day effects may have obscured monthly or seasonal changes in visit durations. These are tabulated throughout, reporting mean squares in order to show the relative contribution of factors to the overall model. Adjusted R^2 values are reported as estimate of model fit. Post-hoc tests were applied to determine the direction of significant differences between groups using Games-Howell or Hochberg tests according to whether or not equal variances could be assumed (ascertained through Levene's Tests).

2.5 Limitations of This Study

Studies of elephant sociality are fundamentally constrained in statistical analyses because there is no way to confirm independence in individual choices of associates. The problems of analysing elephant grouping dynamics are three-fold: firstly, recognition of conspecifics extends over an individual's lifetime, which may be over sixty years. Secondly, individual recognition may extend to as many as 1,000 individuals and thirdly, acoustic and olfactory communication systems mean that individual recognition may operate over scales of tens of kilometres. Thus no associations – whether parties or aggregations as defined in this thesis – can be considered truly independent and a degree of autocorrelation is unavoidable when studying elephants. Filtering datasets in an attempt to achieve statistical independence is costly in terms of information loss and is unlikely to completely remove bias (e.g. Cushman et al. 2005) since relationships among associates, as explored here, are patterned over time and space. For some datasets it is difficult to remove autocorrelation, for example when the variable of interest is not based on individuals but on grouping attributes such as party size or composition and removing dependent samples removes the capacity to analyse the "independent" samples. As noted above seeking statistical independence can result in loss of significant proportions of data. As with any behavioural study on a long-lived, cognitive species, where long and short term interactions and events can be remembered and influence behaviour, true statistical independence is a problematic assumption. In this thesis, I have attempted to minimise the immediate autocorrelation between contiguous events, but make no claims to complete statistical independence.

This thesis assumes that elephant parties represent choices about immediate close proximity, and that these can be analysed as such. I have excluded extreme autocorrelation (Chapter 4), assisted by the low repeated sightings of individuals, and wherever possible selected analyses that do not require statistical independence, such as logistic regressions and social networks. Where ANOVA models have been used, I have used a log survivorship analysis to ensure independence between data points within sampling periods by separating temporal data into appropriate units of analysis. The use of sequence sampling when recording interactions also minimises pseudoreplication, as the entire sequence (interaction) is considered as one unit, regardless of the number of individual components e.g. an aggressive interaction is scored only once, regardless of the number of tusk pokes, charges or supplants it may contain.

In addition to general difficulties of studying elephant sociality, the research questions outlined in thesis have been framed in order to incorporate and address the limitations of studying elephants at bais. These include the “fixed point” nature of bai studies, where observations are constrained to the animals that visit the clearing during observation periods (i.e. during daylight hours): most bais have peak elephant activity during the hours of darkness, when it is impossible to track individuals and record interactions in the same level of detail as during diurnal observations. The largest elephant aggregations may thus occur during the night, and the implications of this are discussed in relevant chapters. In addition bais form a minority habitat in the landscape of Central African forests and the activities that occur there are not representative of overall activity budgets for elephants. Bais can also vary considerably in their size and topology (e.g. Blake 2002) so that not all clearings are equal. Maya Nord was selected as the study site because it was a known focus of elephant activity, but there are many such clearings in the north of PNOK and it is possible that they serve different functions. These issues are discussed when interpreting the results of this thesis. The study originally aimed to conduct observations at another important elephant bai but this proved impossible due to logistical complexities. Finally, of course, this study period is very short when considering the longevity of elephants, who may live to 60 years or more. Even the longest-running field site has yet to see an entire cohort of individuals be born, mature, reproduce and die from natural mortality (Moss et al. in press a). It should be noted however that short-term studies can yield rich and informative data sets as long as their limitations are borne in mind when interpreting results and considering their wider implications.

Chapter Three

Seasonality & Resource Use

Chapter 3 Seasonality & Resource Use

3.1 Abstract

Meteorological data collected during the study period showed marked seasonality in rainfall and little variation in temperature at Maya Nord, consistent with previous descriptions for PNOK (Hecketsweiler et al. 1991). Comparison with longitudinal data from a neighbouring research site indicated that rainfall during the study period followed a normal pattern for the region. The study period contained two wet seasons, which fell in October-December 2007 and March-May 2008. Forest production was seasonal, with unripe fruit present after the rains and ripe fruit during the drier months. Thus there were always some fruit foods present for elephants in the region around the bai, but at low densities. Fruit was consistently found in dung in all survey months: the percentage fruit content of dung varied between months, but the total number of species in each dung-pile was similar in all months. There was no evidence of large-scale fruiting events that might attract elephants to the Maya zone. Geochemical analyses of bai soils suggested that elephants may have selected geophagy sites based on the availability of sodium relative to other minerals, but elephants largely ignored aquatic vegetation, despite this vegetation containing higher mineral concentrations than the dominant Marantaceae species (Magliocca & Gautier-Hion 2002). Clay content of soils did not explain elephant selection of geophagy sites. The bai obviously attracted elephants for nutritional resources but the underlying causality of this attraction remains unclear.

3.2 Introduction

How animals move around and interact with one another is constrained by their physical environment and how resources are distributed within it, and socio-ecological studies must therefore address relevant aspects of this environment. Although water is not a limiting factor for elephants in the Central African forests, local and regional rainfall patterns do influence elephant ranging as a result of changes in browse quality, as well as through more complicated species-dependent effects on patterns of fruit and leaf production (Blake 2002). In some Central African sites, mast fruiting of certain locally abundant species such as *Sacoglottis gabonensis* has been shown to profoundly affect elephant density as elephants move to exploit abundant high quality fruit crops (Morgan 2009; White 1994). Elephants eat fruit in direct proportion to its availability and without restraint, so any local mast fruiting events would appear as high fruit content in the majority of dung-piles sampled (e.g. Morgan 2009). However, the large single-species stands of Marantaceae forest that surround Maya Nord make it unlikely that changes in local fruit availability or browse quality could attract large numbers of elephants to the area at particular times of year, as fruit tree density is extremely low in this forest type (e.g. Hecketsweiler et al. 1991; Maisels 1996; Vanleeuwe & Gautier-Hion 1998).

Elephants consume soil throughout their range, and mineral appetite has commonly been accepted as the most obvious explanation for the geophagy behaviour observed at Central African forest clearings, although elephants do not restrict their soil consumption to bais and may in fact dig in river beds, or in open understorey forest

(VF pers. obs.). Studies of mineral lick use by large mammals have generally found increased mineral concentrations in geophagical soils and almost all have found elevated sodium levels in licks across North America and African savannahs (Klaus & Schmid 1998). Sodium is the most common limiting mineral nutrient for generalist herbivores and they may develop a highly specific appetite for it (see Freeland et al. 1985 and references therein). Sodium has therefore been commonly considered to be the driving force for bai use in forest mammals; tropical forest soils are generally sodium poor and few plants require (and therefore accumulate) sodium (Klaus & Schmid 1998). Sodium appetite has been proposed as one motivation for coastal habitat use by elephants in Gabon (Morgan & Lee 2007), for the consumption of termitarium soils by elephants in northern Central African Republic (Ruggiero & Fay 1994) and for bai use by elephants in Northern Congo (Blake 2002).

In the most detailed Central African study to date, Klaus et al. (1998) studied geophagy pits at Dzanga bai, Central African Republic and found elevated levels of a number of minerals (sodium, potassium, calcium, magnesium, phosphorus, manganese and clay) in the geophagy pits compared to forest topsoil. However, researchers at other sites have failed to demonstrate elevated mineral levels in bai soils (for Congo: Maisels 1995; for Gabon: P. Wrege pers. comm.) and bais can vary considerably in their topology (Blake 2002) and underlying geology (Klaus et al. 1998). It is also important to note that elevated concentrations of minerals in geophagical soils are not necessarily beneficial for the animals consuming them. Soil consumption can elevate mineral intake to the point of mineral imbalance; for example, elevated potassium levels may compromise sodium and magnesium budgets (Kreulen 1985).

Previous researchers at Maya Nord have shown that the mineral content of the herbaceous vegetation forms the basis of food selection by gorillas. Magliocca & Gautier-Hion (2002) found that bai vegetation contained elevated levels of sodium and calcium in comparison to the dominant Marantaceae species in the surrounding forest. If elephants are indeed visiting the clearing in order to address dietary mineral deficiencies, it might be expected that they too would consume the relatively mineral-rich plants that grow there.

Lick soils tend to have a high clay fraction across their distribution and clay content has been suggested to be an important stimulus for geophagy (Kreulen 1985; Mahaney et al. 1996), although clay content may not be correlated with available sodium (e.g. Powell et al. 2009). Clay has been suggested to be more important for forest rather than savannah elephants, as secondary toxins may be more prevalent in their diet (e.g. Houston et al. 2001). Clays may absorb secondary toxic compounds found in plant material, especially tannins that can actively deplete mammalian mineral stores (Freeland et al. 1985; Houston et al. 2001). Clearings in Central African Republic are based on dolerite intrusions which weather to clay-rich soils, and may therefore be “predestined as geophagical soils” (Klaus et al. 1998). Similar intrusions occur in northern Congo (underlying the bais studied by Blake 2002), as well as Gabon and south-eastern Cameroon (Vicat et al. 1996) and have been suggested to underlie the large bai complexes in these areas (Klaus et al. 1998).

3.3 Chapter Aims

3.3.1 Distinguish seasons at the site and broadly categorise local forest productivity.

This chapter broadly describes the ecological features that may affect elephant ranging and thereby influence how animals use the Maya Nord clearing, as a preface to the variability in visiting described in Chapter 4. Firstly, site rainfall and temperature are described and compared with a long-term dataset from another Central African site, in order to establish seasonality during the study period. Whilst elephant ranging varies in response to regional changes in fruit availability and browse quality, it was beyond the scope of this study to undertake detailed phenological work on a spatial scale relevant to elephant movements. Rather, the paths were used to assess gross changes in seasonality that might correlate with changes in elephant visiting levels to the Maya Nord clearing. Forest productivity was assessed by a combination of fruit fall paths and elephant dung samples, as elephants are excellent at locating fruit resources and examination of dung-piles is thus an efficient way of monitoring the temporal changes in fruit crop availability.

3.3.2 Assess elephant appetite for mineral-rich bai vegetation and mineral resources in bai soils.

The number of instances elephants fed on mineral-rich bai vegetation is descried. The mineral resources available in bai soils were assessed by analysing soil samples for basic mineral content and clay fraction (hydrated aluminosilicates of varying composition).

3.4 Methods

3.4.1 Indicators of Seasonality

3.4.1.1 Meteorological Data

Rainfall and temperature data for the site were non-continuous, as it was only possible to collect these when observers were present at the site. Rainfall was measured daily using a rainfall gauge established at camp mounted 1m from the ground. Readings were taken at 18:00 on each day we were present in the forest. Temperature and humidity were measured with a digital thermometer mounted on the observation platform, and readings were taken at the end of each observation day. On days following a non-observation day, the previous day's maximum was noted at the start of observations.

Due to the high inter-annual variation in rainfall reported for PNOK (Hecketsweiler et al. 1991; Maisels 1996) and the paucity of recent rainfall data for the area, a comparison was made with long-term data available from the Mbeli Bai Study site in Nouabalé-Ndoki National Park, approximately 180km NE of Maya Nord. Months were classified as wet if total rainfall exceeded 100mm (Edwards & White 2000) and these classifications used to construct wet and dry seasons.

3.4.1.2 Forest Productivity

Two paths were established to monitor local forest productivity. Each path was 2.5km long, the first of which ran north to south from the Maya Nord clearing, and the second of which ran east-west from the Maya Centre clearing (4km south of Maya Nord). Paths were monitored on alternating weeks, applying a simple 4-point scale (“absent” /”rare”/”common”/”abundant”) to classify resource abundance (see White & Edwards 2000). Every 50m along the path, a score was assigned for the amount of ripe and unripe fallen fruit and the amount of new leaf production, at heights judged to be accessible by elephants. This “leaf score” excluded Marantaceae, as the quality and availability of this as a foodstuff was not considered to change on a seasonal basis (Vanleeuwe & Gautier-Hion 1998; White 1994). Visibility was also judged on a 3-point scale (<5m; 5-10m; 10-15m) to exclude the possibility that changes in leaf cover affected detection of fallen fruits.

In addition to forest productivity data, elephant dung-piles were counted on the Maya Centre path, and aged according to the methods as outlined by White & Edwards (2000). A total count was made for all dung-piles classified as “fresh” (odour and fatty acid sheen still present) or “recent” (odour present when boli broken but no fatty acid sheen) These counts were used as an indicator of widespread elephant presence or absence in the Maya zone and matched the activity levels around Maya Nord.

3.4.1.3 Dung Samples

Dung piles were used as a secondary measure to monitor changes in forest productivity, as elephants are excellent at locating fruit resources and consume preferred species whenever they are available (Blake 2002; Blake & Inkamba-Nkulu 2004; Short 1983). Every month we collected intact elephant dung-piles (all boli) which had not been dispersed by seed predators or trodden by animal activity. Samples were obtained opportunistically whilst monitoring local forest productivity by searching along elephant paths or occasionally by collecting dung-piles from the Maya Nord clearing. Dung samples were washed through a 2mm mesh to disperse the matrix and then separated into leaf/fibrous material and fruit remains. The number of different fruit species was noted and identified where possible by VF or research assistant AR (both of whom had previous experience from monitoring gorilla foods in a similar manner) and the total percentage of fruit was estimated. Where very little fruit was found a flat score of 1% was assigned. Thereafter scores were assigned in 5% intervals (5, 10, 15% etc.). As samples were obtained opportunistically and sample sizes varied during the study period, correlations were used to verify that the number of samples obtained was not related to the parameters of interest i.e. percentage fruit content or number of species detected.

3.4.2 Mineral Resources at Maya Nord

All instances of elephants feeding on aquatic vegetation were recorded, to determine whether elephants were acquiring minerals through vegetation feeding rather than geophagy. To assess the mineral availability in the bai soil samples were taken from the elephant pools, from sinkholes where elephants access the soils they ingest and from control sites within and around the bai. Elephants using these mineral pits clearly bypass the upper sandy substrate by digging with their feet and blowing air through their trunks to displace substrate in order to access lower layers. These pits rapidly backfill with sand due to the flow of water through the elephant pools, but are visible as depressions and yield fairly readily to exploration by hand. As it was impossible to replicate the detail of the Klaus et al. (1998) study in this thesis, three minerals were selected for analysis; sodium, potassium and calcium. All of these were demonstrated to be present in higher concentrations at Dzanga geophagy sites compared to control samples and were chosen here for their importance in metabolic and reproductive function.

Sixty seven soil samples were collected and categorised according to whether or not they were taken from a site where elephants were observed to perform geophagy; samples were collected from as many sinkholes as possible, where we could bypass the upper sandy substrate and access the lower layer (n=38). Each sample consisted of between three and five replicates. Some contamination with upper layer substrate was unavoidable and the extent of this was fairly evident during the process of extracting material by hand from the sinkholes. Highly contaminated samples were immediately discarded and samples where contamination was judged to be minimal were immediately marked as “high quality” samples. Some sinkholes proved inaccessible, and even some large adult male elephants had to access these by kneeling as the geophagy layer was so deep. A further 29 samples were taken as controls and included substrate from pools but not in submerged mineral pits where elephants foraged, forest topsoils and bai soils in bare areas where elephants often mud bathed, as well as an exposed clay-like area on one edge of the clearing. This clay zone showed traces of previous elephant activity (tusk marks) but elephants were only twice observed to use this area during the study period. Control sites were thus either bai areas where elephants showed activity but did not perform geophagy, or randomly selected sites in the forest adjacent to elephant paths.

Soil samples were air dried immediately after collection, and then sieved in the field to remove large particles before being stored and shipped in plastic sample bags. Lab analyses were conducted at the University of Stirling after my return to the UK. Approximately 3g of each sample replicate was weighed and transferred to a glass digestion tube. The exact mass was noted and 10ml of 30% HCL and 3.5ml of 65% HNO_3 was added to the tube, before gently agitating the tube to ensure good mixing. Tubes were left in a digestion block overnight without heating. Each batch also contained several blank tubes (i.e. no soil) as controls. The following morning tubes were gradually heated to 140^0C and digested at this temperature for 2 hours. Once cool, replicates were filtered through no. 540 filter paper (pre-washed with 0.5M HNO_3, wash solution discarded) into 100ml volumetric flasks and made up to the mark with distilled water before being transferred to clean plastic bottles for analysis. Sample replicates were analysed using atomic spectrometry (UNICAM 989 AA Spectrometer) using flame emission for sodium and potassium analyses, and flame absorption for calcium. The spectrometer yields three readings, which were averaged for each replicate. All replicates were then averaged to give a reading for each sample.

An analysis of soil geochemistry was conducted by Ben Pears (University of Stirling) to assess particle size via laser granulometry; this method underestimates the proportion of clay (Konert & Vandenberghe 1997) but was the only technology available within the means of this study. The number of samples processed was limited by the availability of equipment and specialist staff. A subset of twenty five samples were assessed for the proportion of clay (defined as particles <2µm in diameter), consisting of control samples (n=9) and high-quality geophagy pit samples (n=15).

Soils form through weathering of rocks and the deposition of organic matter, so the concentrations of individual minerals in soils are not independent of each other. Elemental concentrations were analysed using a MANOVA, using Pillai's trace due to unequal sample sizes. As sodium appetite is claimed to be a driving force in geophagy behaviour (Freeland et al. 1985) sodium preference was expressed as the concentration of sodium (mg/l per gram of soil) divided by the total concentration of all measured minerals. The percentage of clay in samples was assessed using the same sample categories (geophagy sites versus controls) in an ANOVA. However, sample contamination with upper layers (especially of sand) was unavoidable when extracting samples from sinkholes beneath water level without specialist equipment. Clay content was therefore analysed using a 2-tier classification for sinkhole samples ("normal" versus "high quality" samples), according to how well the geophagy layer was captured whilst avoiding contamination.

3.5 Results: Defining Seasonality

3.5.1 Rainfall & Temperature

Rainfall during the study period followed the pattern described by Hecketsweiler et al. (1991), with bimodal rainfall and little temperature variation (Figure 3.1). Hecketsweiler et al. describe a "grande saison sèche" spanning July to August, followed by the "grande saison des pluies" from September to November. From December to February constitutes a "petite saison sèche", and the "petite saison des pluies" lasts from March to May. The Mambili River was particularly low at the start of the study, making initial access to the site difficult, and suggestive of an atypically severe dry season. In addition, the subsequent rainy months had lower total rainfall than would be anticipated from Hecketsweiler et al. (1991), and rains continued into December which is normally a dry month.

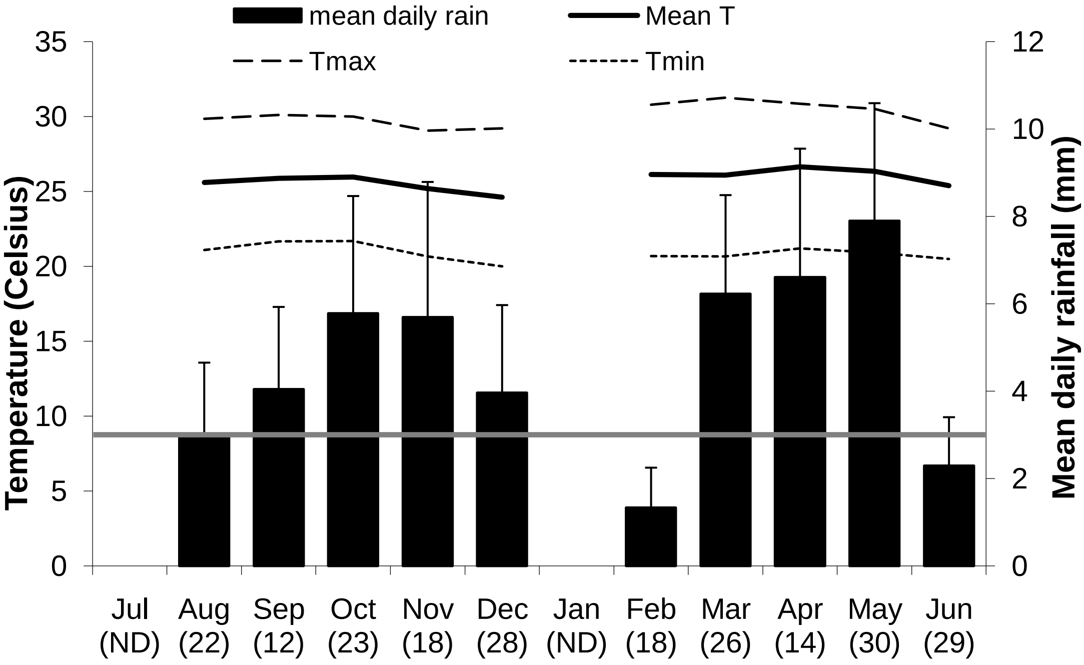

Figure 3.1. Temperature and rainfall data at the Maya Nord clearing for the study period July 2007 – Jun 2008. Error bars show SE. Numbers in parentheses show the number of days present at the site for each month. ND = no data. The solid grey line shows 100mm monthly rainfall, the criterion used to classify months as wet or dry.

Mbeli Bai has a similar climatic regime to that of PNOK, with bimodal rainfall normally peaking in June and October and little annual temperature variation (Mbeli Bai long term records). Examination of the Mbeli long-term rainfall data shows that the study period spanned a relatively wet year at Mbeli, but that the first wet season was quite late, and the second wet season had an abrupt, late onset (Figure 3.2), in agreement with that observed in PNOK. Consistent with this was the high rainfall documented in May 2008 from PNOK, as the result of several large storms. In total, captured rainfall at Maya Nord measured 1,045mm on only 220 days, and seems likely to be representative of a relatively wet year for PNOK, as Hecketsweiler et al. (1991) report annual rainfall exceeding 1500mm.

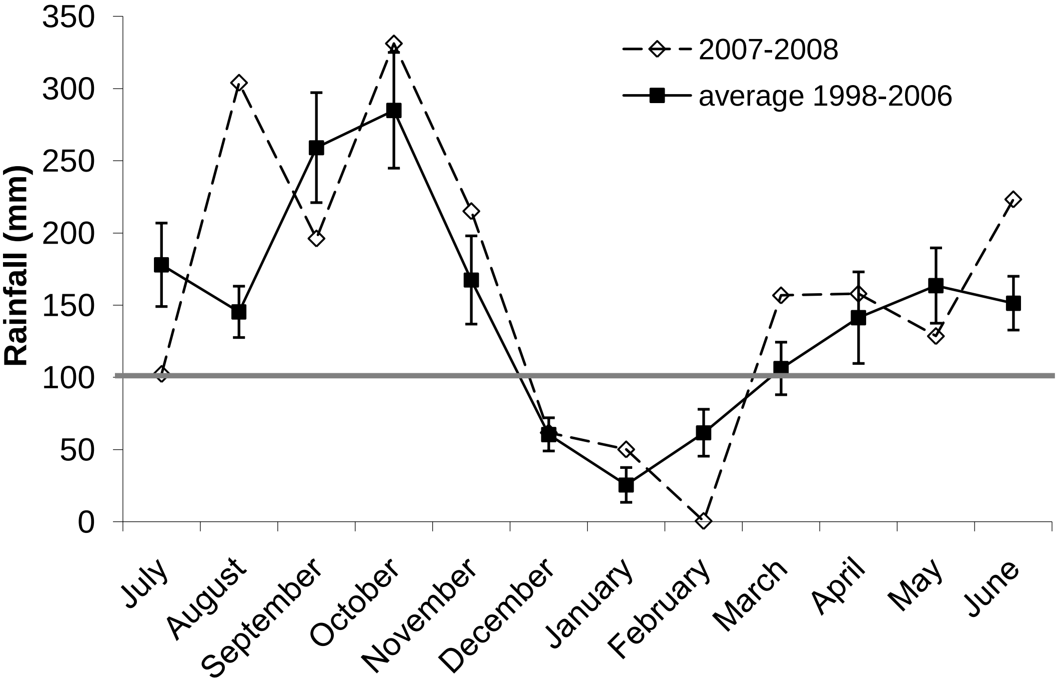

Figure 3.2. Rainfall data from Mbeli Bai, Nouabalé-Ndoki National Park. Error bars show 95% CI. (Source = Mbeli Bai, long-term records). The solid grey line shows 100m rainfall, the criterion used to classify months as wet or dry.

Rainfall during the study period appeared to follow a normal pattern for the region. For the purposes of this thesis, seasons were defined using recorded site rainfall (Figure 3.1). Two wet seasons were defined, falling in October-December 2007 (wet season 1) and a second rainy season in March – May 2008 (wet season 2). Dry season 1 was well advanced at the start of the study having commenced in July 2007, ending in September 2007, dry season 2 was a short dry season in January and February 2008 and dry season 3 was beginning in the final month of study in June 2008. Although rainfall in September 2007 was relatively high (Figure 3.1) this was due to two very wet days recorded at the end of the month and so was overall classified as dry.

3.5.2 Forest Productivity

Fruit scores along the forest paths remained constant and generally low throughout the study period on both paths (Figure 3.3), and no significant changes in fruit crop were seen over time (appendix B1 and B2). Fruit scores tended to be slightly higher on the Maya Centre path where the crops of several large fruit trees contributed to the overall fruit score. The distribution of leaf and visibility scores differed significantly between the two paths (leaf score $Z= 4.264$, $p<0.001$; visibility score $Z= 3.116$, $p<0.001$; appendix B1 and B2) but ripe and unripe fruit scores did not (ripe fruit $Z= 0.098$, $p=1.000$, unripe fruit $Z = 0.442$, $p= 0.990$; appendix B3 and B4). These distributions are almost certainly attributable to the relatively large amount of Marantaceae forest traversed by the Maya Centre path. Both paths showed peak leaf production during wet months (see appendix B1), though this is less clear for the first wet season (October to December), which may be due to the extreme dry season at the beginning of the study period.

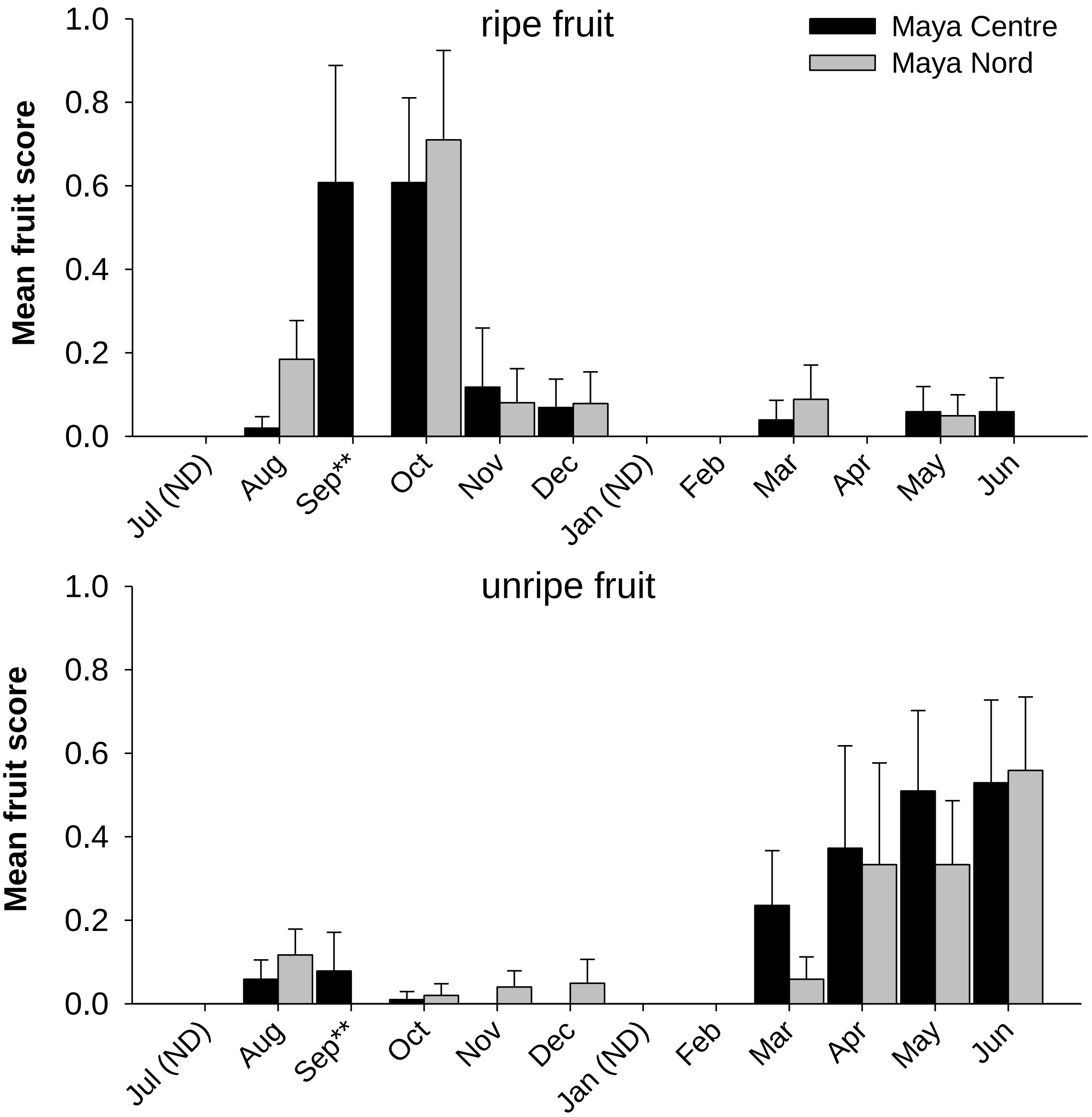

*Figure 3.3. Mean monthly fruit scores by path for ripe (top) and unripe fruit (bottom). Error bars show 95% CI. ND=no data. **For September only one dataset was collected from the Maya Centre path.*

3.5.3 Dung samples

Monthly sample sizes for dung were affected by the ease of finding fresh dung piles in the forest, whilst simultaneously minimising human disturbance in the zone. However, there was no significant relationship between the number of dung samples obtained per month and either the number of different seed species detected in the dung (*r*= 0.495, p= 0.146), or with the percentage fruit content (*r*= -0.014, p= 0.970). Fruit content and the number of different species in samples were unrelated (*r*= -0.12, p= 0.740), and fruit content and the monthly fruit score obtained along fruit fall paths were also uncorrelated (*r*= 0.130, p = 0.721).

All dung piles sampled (n= 82) contained fruit remains which is unsurprising given that elephants are excellent at locating fruit resources whenever and wherever they are available (e.g. Blake 2002; Blake & Inkamba-Nkulu 2004). There was considerable variation in the percentage of fruit in samples (range= 1-98%, mean= 11.31, SD=15.22), and the number of different species found per dung pile (range= 1-12, mean= 3.85, SD=2.18) but there was no consistent temporal pattern to this variation (Figure 3.4).

Nineteen fruit species were identified from seeds and fruit remains in the 82 dung piles examined, and a further 42 species were unknown to observers. Eleven species were observed more than five times but only one fruit species, *Strychnos camptoneura* (Loginaceae)*,* was found in dung piles throughout the sampling period (see Table 3.1). There was no evidence of mast fruiting events that might draw elephants to the Maya zone, either through changes in fruit crops available on fruit-fall paths, abrupt changes in the fruit content of dung, or the dominance of a single species in samples dung-piles. For instance, although *Strychnos* was found in all dung-piles sampled from September to December, the percentage fruit content of these dung-piles was not high.

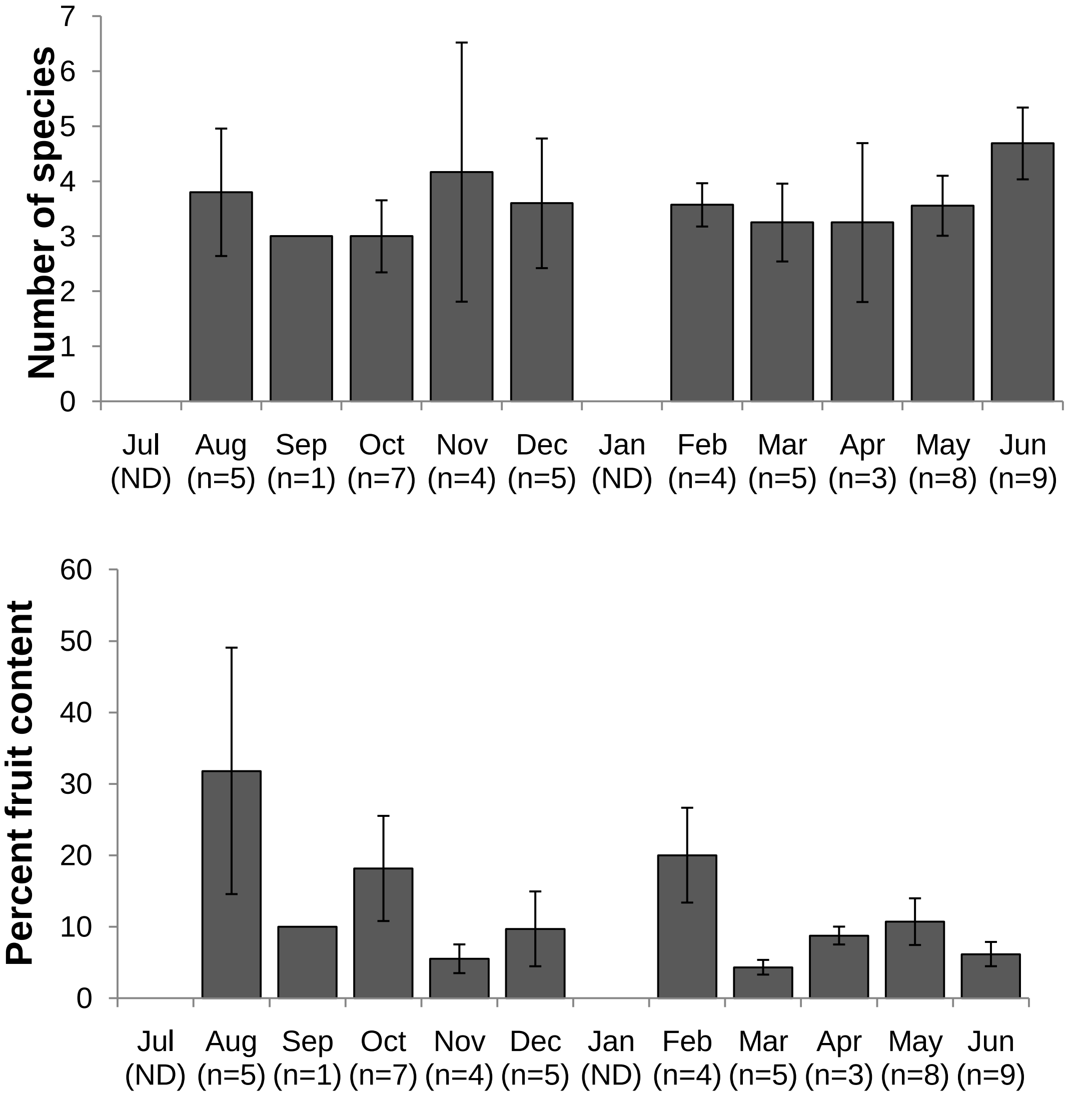

Figure 3.4. Mean monthly fruit content of dung samples (top) and mean number of different fruit species detected in samples each month (bottom). Error bars show 95% CI. Numbers in brackets indicate sample size, ND=no data.

Prevalence (%)

Species	**Total**	**Monthly**										
		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Anonidium mannii	7.3	60			17					25		6.3
Chrysophyllum gambeya	29.3	60				20			13		61	94
Duboscia ?macrocarpa	24.4	40		14	33	70				100	17	31
Grewia coryacea	43.9	20				10		14	75	100	89	63
Irvingia gabonensis	9.8					10		71	13		5.6	13
Keayodendron bridiloides	8.5				33	10					28	13
Klainedoxa gabonenesis	7.3			14	33	10					11	6.3
Myrianthus arboreus	9.8									25	11	38
Pachypodanthium staudii	11.0							100	13			6.3
Panda oleosa	7.3									25	11	19
Strychnos camptoneura	73.2	60	100	100	100	100		71	75	25	33	94
Sample size	51	5	1	7	6	10	0	7	8	4	18	16

Table 3.1 Total and monthly prevalence of eleven fruit species found in more than 5 dung-piles. For clarity, squares are shaded according to monthly prevalence; no shading < 25%; light grey 25-50%; dark grey 50-75% and black 75-100%.

3.6 Results: Mineral Resources at Maya Nord

The behavioural sequence used by Maya Nord elephants matches the behaviours performed at other sites, including the mineral and clay-rich dolerite clearings in CAR (VF pers. obs.). During visits to the clearing elephants mainly performed geophagy behaviours in the pools and did not feed on the aquatic herbs that covered the majority of the clearing, in agreement with observations at other sites (VF pers. obs.; Momont 2007). Vegetation feeding was recorded for 107 elephants in 79 parties, but only 5 of these occasions lasted more than 10 minutes. Overall this represents only 4.28% of elephant parties engaging in any herb-feeding behaviour. The longest herb-feeding session was 2 hours 34 minutes, by an unidentified male aged 5-9 years, who did not aggregate with other elephants during his visit despite the presence of other elephants in the clearing. Elephants thus did not use the Maya Nord clearing in order to feed on aquatic herbs, despite the relatively high sodium content of these plants (Magliocca &Gautier-Hion 2002).

Overall, the three measured mineral levels differed between sink holes and control sites (Pillai's Trace =0.603, $F_{3,57}$=28.912, $p<0.001$), but this was not a consistent relationship for any of the minerals tested. Sodium and calcium were both at extremely low levels in all samples tested, as indicated by the strength of the standard solutions required to calibrate the spectrometer for these minerals (H. Ewan pers. comm.). Sodium levels did not differ between the sink holes and control sites (Na $F_{1,60}$=0.404, p=0.528, R^2 =-0.10), whereas calcium levels were somewhat higher, and potassium levels much higher in control versus sink hole samples (Ca $F_{1,60}$=10.032, p=0.002, R^2 =0.131; K $F_{1,60}$=83.149, $p<0.001$, R^2 =0.555). Expressing the data as a sodium preference shows that sinkholes contained higher levels of sodium relative to the other minerals that were tested (Figure 3.5; $F_{1,61}$ =48.178, $p<0.001$, R^2=0.436).

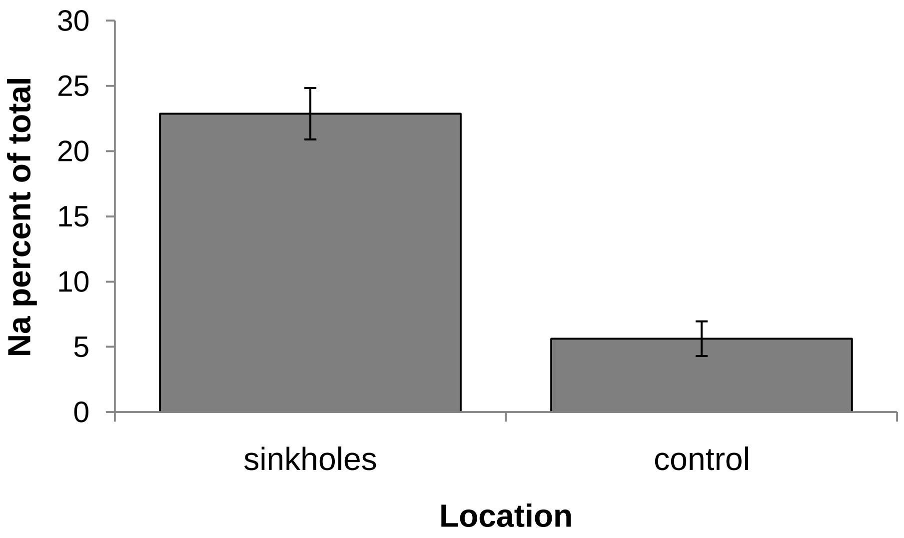

Figure 3.5. Mean sodium levels, expressed as a percentage of total detected elemental concentration (mg/l per gram of soil). Sink holes were samples taken at geophagy sites (n=37); controls were taken from sites in and around the bai (n=28). Error bars show 95% CI.

Control samples contained much higher proportions of clay compared to those taken from geophagy sites ($F_{1,23}$ = 11.011, p=0.003, R^2= 0.303). However this difference was less clear once the two-tier classification was applied to geophagy samples ($F_{2,23}$ =5.426, p=0.013, R^2= 0.278) where the only significant difference lay between control samples and geophagy samples that were not considered to be of particularly high quality (Hochberg post hoc p<0.05; Figure 3.6). Interestingly, when we were able to reach the sub-layer that elephants access, we discovered that many sinkholes had wood lying above an extremely hard layer, the upper surface of which was slick and difficult to extract by hand.

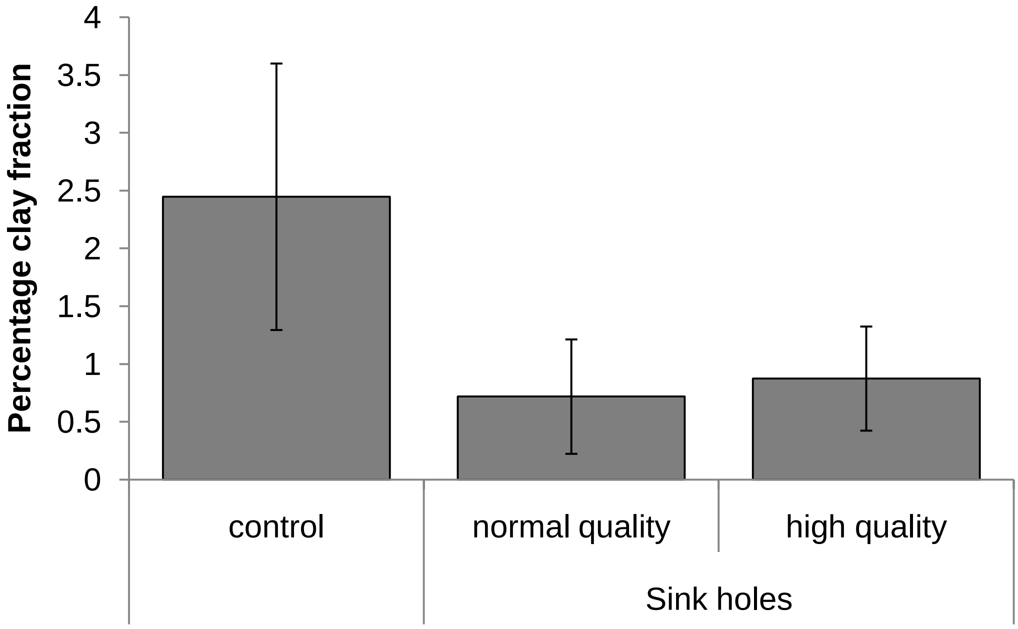

Figure 3.6. Mean percentage clay fraction according to location for soil samples. Sink holes were samples taken at geophagy sites and categorised as normal (n=8) or high quality (n=7); controls were taken from sites in and around the bai (n=9). Error bars show 95% CI.

3.7 Discussion

The data presented in this chapter indicate that seasonal changes during the study period followed patterns known to be normal for the region, and there is no evidence to suggest exceptional ecological conditions that might disrupt elephant ranging or visiting patterns to Maya Nord. Elephants in the Maya region located and consumed fruit throughout the year, although this was highly variable between samples in some months, and also variable between months. This variability and the low detection rate of fruit along monitored paths is consistent with the relatively low abundance of fruit trees in the dense Marantaceae forest that predominates in the north of PNOK (Hecketsweiler et al. 1991; Lejoly 1996). I found no evidence that elephant visiting to Maya Nord was affected by large-scale fruiting events (e.g. *Sacoglottis gabonensis,* White 1994), which would be expected to appear as sudden increases in the fruit content of the majority of sampled dung-piles (Morgan 2000).

Direct observation of the elephants using Maya Nord makes it very clear they come to the bai to obtain nutritional resources, and not for any specific abundance of fruit in the surrounding areas. The behavioural repertoire for accessing soil is a fairly fixed pattern which matches the behaviours performed at other sites, including the mineral and clay-rich dolerite clearings in CAR (VF pers. obs.). However the underlying causality for this remains unclear as both mineral and clay concentrations were low in soil samples. Although geophagy sites did not contain concentrated sodium *per se*, elephants may have been selecting these areas in order to access sodium whilst avoiding other minerals, especially potassium which is known to disrupt mineral budgets for other minerals such as sodium and calcium (Kreulen 1985). However, elephants rarely consumed the sodium-rich plants that were also available in the clearing. Appetite for both sodium and clay have been proposed as driving factors for geophagy amongst large mammals, and specifically for forest elephants (Klaus et al. 1998) who may suffer dietary sodium deficiency and consume significant quantities of secondary compounds. My study could not confirm either of these as important for forest elephants visiting Maya Nord.

Klaus et al. (1998) also found approximately one third of their samples to contain lower concentrations of sodium, magnesium and calcium compared to forest topsoils, and postulated that geophagy is not solely explained by mineral appetite. All of their samples contained more than 35% clay, but this study failed to identify clay as an important factor for elephant use of the Maya Nord clearing, as the clay content from Maya Nord samples was considerably lower than Klaus et al. reported for CAR. Klaus et al. (1998) note the extreme heterogeneity of lick soils and whilst the observed mineral concentrations are consistent with their findings, these somewhat anomalous clay results may be an artefact of an admittedly simplistic sampling regime and the fact the laser granulometry method significantly underestimates the clay fraction (Konert & Vandenberghe 1997). The significant difference between normal quality samples and controls suggests that these sinkhole samples may have been particularly contaminated with upper-level substrate (i.e. sand), thus lowering the overall clay fraction in the samples. Despite this mixing, the extremely low clay fraction in the highest quality samples (around 1%) seems to preclude clay appetite as a factor in elephant visiting.

It is unclear whether the presence of wood in sinkholes affects their nutritive value; African great apes are observed to eat rotten wood, purportedly for mineral (sodium) appetite (M. Bermejo pers. comm.; Reynolds et al. 2009) but we could not extract this wood, or determine if it was rotten. Certainly observations did not suggest elephants were feeding on wood, and a number of tree species noted in the forest edge are known to be extremely slow-weathering timbers (e.g. *Lophira alata* (Ochnaceae)). We never noted natural springs or water upwellings which have been proposed as an alternative resource base that elephants may be accessing (P. Wrege pers. comm.). In fact, a natural spring close to our observation platform showed no sign of usage, despite being located next to several fairly major elephant trails.

Chapter Four

Elephant Visiting Patterns

Chapter 4 Elephant Visiting Patterns

4.1 Abstract

Elephant visits were highly variable over the course of the study period, but the pattern of visits remained constant with elephants most commonly seen early and late in the day. Patterns of nocturnal activity matched the patterns of diurnal variation in visits to the clearing, although aggregations tended to be larger at night. Elephants stayed longer in the clearing during the period from 10:30 to 14:59 (mdn per time block 70-100mins) compared to the rest of the day (mdn per time block 20-40 mins). The Maya Nord clearing was used by most elephants only once per year (or less frequently). For the 200 animals seen on more than occasion, the average interval between revisits was 36.97 days (SD= 57.47 days). Both males and females of all ages used the bai, and visits by parties of different composition were seasonally variable, but no consistent pattern could be detected. April 2008 was unusual in having very high number of elephants using the clearing, but elephants spent approximately the same total amount of time in the clearing during this month. Three levels of elephant visiting (high, medium, and low) were defined during the study period, according to rate at which animals used the clearing. Elephants did not alter their patterns of clearing use during periods of high activity, either through the timing or duration of their visits, and therefore did not minimise competition during these periods, with the net result that elephants were found in larger aggregations, and in larger parties within aggregations.

4.2 Introduction

Little information is published regarding patterns of bai use by elephants, although researchers in the region note that clearings can vary considerably in their size, topography and levels of frequentation by elephants (Blake 2002; Inkamba-Nkulu 2007; Vanleeuwe et al. 1997). Most studies have instead focused on the population structure and grouping patterns of elephants at forest clearing (Querouil et al. 1999; Turkalo 1996; Turkalo & Fay 1995, 2001). Elephant ranging is highly individually variable, both in savannah and forest elephant populations (e.g. Blake 2002; Charif et al. 2005; Graham 2006), and is known to be affected by gender (Graham 2006), season (Loarie et al. 2009) and reproductive status (Momont 2007). Momont (2007) found that elephants inhabiting a forest-savannah mosaic in Gabon increased their daily travel distances during wet seasons.

Seasonality in bai use has been documented elsewhere in Central African (e.g. Fishlock et al. 2008) and is usually assumed to relate to changes in resource availability; either through the availability of fruit crops or changes in forage quality (Blake 2002). Changes in primary productivity generally respond to rainfall in lag terms and satellite imaging data suggests that plant primary productivity peaks weeks or months after rainfall (Rasmussen et al. 2006) although this is variable between vegetation types, and the effects of rainfall on primary productivity may be less marked in tropical rainforests than in the arid savannahs of East and Southern Africa (Davenport & Nicholson 1993). Central African bai studies generally report a mixture of “resident” and "roaming" individuals amongst their identified population (Mbeli Bai long term data; L. Momont pers. comm.; A. Turkalo pers. comm.), where "residents" are sighted regularly throughout the year, and "roamers" are known to visit clearings during a particular period, but are absent for periods of months at a time.

On a finer temporal scale, circadian activity patterns also influence clearing use; many sites report increased elephant activity during the hours of darkness (e.g. Mbeli Bai, Congo: long term data; Langoué Bai, Gabon: Momont 2007; Dzanga Bai, CAR: Turkalo & Fay 1995) and acoustic monitoring suggests that up to 80% of elephant activity in bais takes place during the hours of darkness (P. Wrege pers. comm.). GPS collar data suggest that elephants spend most of their daylight hours focused on forest feeding, with a rest period around midday (Blake 2002). Elephants' decisions to visit bais may be related to the risks of entering these open spaces where poachers operate (Blake 2002; Chapter 8) as well as daily activity patterns. Unfortunately, we do not know of any truly undisturbed forest elephant populations in order to document undisturbed clearing visiting patterns. However, the number of elephant visits recorded during daylight observations has steadily risen at Mbeli Bai over a decade of effective protection in Nouabalé-Ndoki National Park, Congo (Mbeli Bai, long-term data).

4.3 Chapter Aims

4.3.1 Describe temporal variation in elephant visits to the clearing

This chapter describes changes in elephant visiting patterns over the study period on daily, monthly and seasonal scales. I use several measures to describe elephant visits; the proportion of 30 minute counts where elephants were present in the clearing, the number of elephants seen per observation hour and the amount of time individuals spent in the clearing. Changes in elephant visit rate were correlated to a series of rainfall lags, selected as one, two, three and four-weeks post rainfall, as changes in rainfall probably provide elephants with environmental cues for seasonal shifts in ranging patterns (e.g. Blake 2002). The amount of time that an individual chose to spend in the clearing could be affected by a number of factors, most notably the presence and behaviour of conspecifics. This section describes temporal variation in visit duration before analyses in relation to social dynamics (Chapter 6) and risk perception by elephants (Chapter 8). Issues of autocorrelation relating to sampling intervals (i.e. observation days) are also explored.

4.3.2 Describe temporal variation in socio-spatial organisation within the clearing

The absolute number of elephants observed within the clearing is only one measure of clearing use. Evaluating the social role of clearings requires examination of the socio-spatial arrangement of animals using the clearing, and these grouping decisions may change according to how many conspecifics are present, and the levels of competition for the nutritional resources elephants acquire within the bai. To describe temporal changes in grouping patterns over the study period I examine daily, monthly and seasonal changes in aggregation size (defined as all elephants present in the clearing) and party size (elephants associating with one another, as defined in Chapter 2). Aggregations were evaluated through changes in aggregation size over the course of an observation day, and via monthly and seasonal changes in maximum daily aggregation sizes. The maximum daily aggregation size was selected as a proxy for the amount of social opportunity available to elephants within the clearing. A brief description of temporal changes in the types of parties observed is also presented.

4.3.3 Describe individual visiting patterns of identified elephants

To quantify the presence of "resident" animals, and the number of times elephants made multiple visits on the same observation day, the visiting patterns of individually identified elephants are described. I examine potential age-sex differences in patterns of clearing use, assessed through the number of sightings of individuals. I also examine the relationship between body condition score and the interval between sightings of individuals over the study period as it was hypothesised that animals with low body condition scores (see Chapter 5) might use the clearing more frequently, as they lacked the energy reserves to range further afield in search of patchy but profitable fruit crops.

4.4 Methods

These analyses use all elephant visits recorded during the study period. Data are plotted using absolute proportions, means with 95% confidence intervals (hereafter 95% CI), medians with 95% CI or box and whisker plots, where boxes show medians and inter-quartile ranges (IQR) and whiskers represent the 10th and 90th percentiles. In places extreme outliers changed the y-axis scale to such an extent as to make it hard to see changes in central tendency on box and whisker plots; in these cases extreme outliers were excluded from graphs by excluding the upper and lower 5% of data, and the maximal values marked on graphs. These manipulations did not change the values of medians and IQRs and only apply to the graphs presented, not to the analyses conducted. Parametric statistics were used on transformed data (log, reciprocal root or reciprocal square), which reduced skew to acceptable levels for the large sample size here (see Chapter 2). Where type I ANOVA models were applied, models are tabulated and report the mean square to show the relative contribution of all factors. Autocorrelation tests (Minitab v.15) were used to explore potential statistical bias introduced by the visit patterns of certain individuals who may have contributed disproportionately to the dataset.

4.4.1 Temporal Variation in Clearing Use

The same analytical approach was taken to examine temporal variation in both elephant visits to the clearing, and in the socio-spatial organisation of animals within the clearing. It was considered important to explore temporal variation on both monthly and seasonal (wet/dry season) scales. Since these could not be modelled together (as months were by definition either wet or dry), factorial ANOVAs were run separately, and a Bonferroni correction applied (so effects were considered significant where $p<0.025$). Months were assigned to wet or dry seasons as defined in Chapter 3 according to total rainfall.

To explore temporal variation in elephant visits, daily patterns of clearing use were examined using the proportion of 30 minute scans with elephants present, irrespective of how many elephants were counted, and the distribution analysed using a chi-square test. The 30 minute scan sample data from time block 0 were excluded due to the low number of observation samples in this time period. To explore monthly and seasonal changes in clearing use the rate of visits was calculated as the total numbers of individual elephants seen per day, corrected for observation duration (generating an “elephants per hour” measure). These monthly and seasonal changes in elephant visit rate were analysed using ANOVA models on log transformed data; seasonal changes in visit rate used a type I ANOVA to control for the change in observation point that occurred in December 2007. As explained in Chapter 2 no data were collected in January 2008, and nocturnal observations were made whenever possible. Monthly changes in elephant visit rate were correlated to rainfall using a series of lags, using a Spearman’s correlation. Monthly changes in morning dung counts, used as an index of nocturnal activity, were also analysed using an ANOVA, and correlated to diurnal visit rates, using a Spearman’s correlation.

Elephants often fled the clearing (Chapter 8) and could be present when observers arrived at the clearing, or when observations ended. To examine if these conditions affected the recorded visit duration, data were partitioned according to whether or not visits were complete (i.e. both entrances and exits were recorded) and whether or not animals fled the clearing. An ANOVA was used to examine diurnal variation in the duration of elephant visits, where visits were assigned to time blocks according to the time individuals were first observed and time blocks were defined as outlined in Table 2.5 (where blocks were considered independent after log survivorship analysis, see Chapter 2). Visit durations were strongly affected by the time of day in which visits occurred, so monthly and seasonal changes in visit duration were examined using type I ANOVA models with time block as a factor (see also Section 2.4).

To explore temporal variation in elephant grouping patterns, I examined changes in aggregation and party sizes. Aggregation refers to all elephants present in the clearing at any one time, and for daily changes in aggregation size data were obtained from 30 minute scans. For monthly and seasonal changes in aggregations, maximum aggregation size during the observation day was selected as the dependent variable, with data obtained from continuous recording of elephant visits. Time block was not used as a controlling factor in these models, as only 7% of maximal aggregations were recorded to occur between 07:30 and 13:29. Instead, to examine if monthly and seasonal changes occurred in the time of day at which the maximum aggregation was observed, I used factorial ANOVAs where the time of the maximum aggregation was the dependent variable, with month and then season as factors.

Parties, as defined in Chapter 2, were used here to indicate the ways in which elephants grouped when using the bai. Of the observed parties, 473 were “transitory” in nature, lasting 1 minute or less, and were removed from the analysis, although this had little effect on the overall distribution of party sizes. Party sizes were examined on daily, monthly and seasonal scales, using type I ANOVA models for monthly and seasonal changes whilst controlling for time of day effects. Changes in party type on temporal scales were described.

4.4.2 Individual Visiting Patterns

To examine individual patterns of clearing use, males and females were grouped by age class and visit patterns described according to the number of sightings and the interval between sightings (number of days) over the study period. Both number of sightings and interval between sightings were examined using type I factorial ANOVAs to hierarchically examine the effects of age and sex on visiting patterns. As an individual's ranging may be affected by body condition, inter-visit intervals were also examined according to body condition score. The majority of animals scored a 3 according to the Foley scale (see Chapter 2 and Section 5.3) and there were seasonal differences in body condition amongst the elephants using the clearing (Chapter 5). Animals in poor body condition (≤2 Foley score) were compared to animals judged to score high (≥4) on the Foley scale, using an ANOVA to examine differences in the number of days between visits. Calves younger than 5 years old were excluded from these analyses as it was assumed their ranging decisions are determined by their mothers. The number of instances that individuals made multiple visits on the same day was described, using a 90-minute criterion to classify visits as separate from one another: This criterion was used as it agreed with the partitioning of daily time blocks as determined by visit duration data (Chapter 2), and with a log survivorship analysis of the interval between visits (where a break in slope occurred at 1hr 45 mins).

4.5 Results: Sampling Intervals & Autocorrelation

Autocorrelation tests were run on the interval between sightings of known individuals by observation day, and showed significant autocorrelation for lags of up to two sequential observation periods (Figure 4.1). This autocorrelation was evident in some but not all ranging units (defined as either family units or dispersed and socially independent individuals); only 30.3% of known ranging groups were re-sighted within 2 successive observation days. Within family units, visiting patterns varied greatly; for example adult female Naomi was never re-sighted within two successive observation days while her close female associates Nicola and Natalie both were. The proportion of sightings that occurred within the autocorrelation time window was unrelated to the total number of sightings of individuals (r_s= -0.189, p=0.06, n=99 individuals from different ranging units). To minimise potential statistical bias introduced by the re-sighting of certain individuals within the two day autocorrelation period, the ANOVA models on monthly sightings presented in this chapter were re-run using a random subsample of 70% of observations (since an autocorrelation term as determined in spatial analyses [Augustin et al. 1996; Sitati et al. 2003] could not be calculated for each sighting as opposed to each individual, which was the unit of dependence). Random models produced the same effects as those using all data so analyses of the full datasets are presented in this chapter.

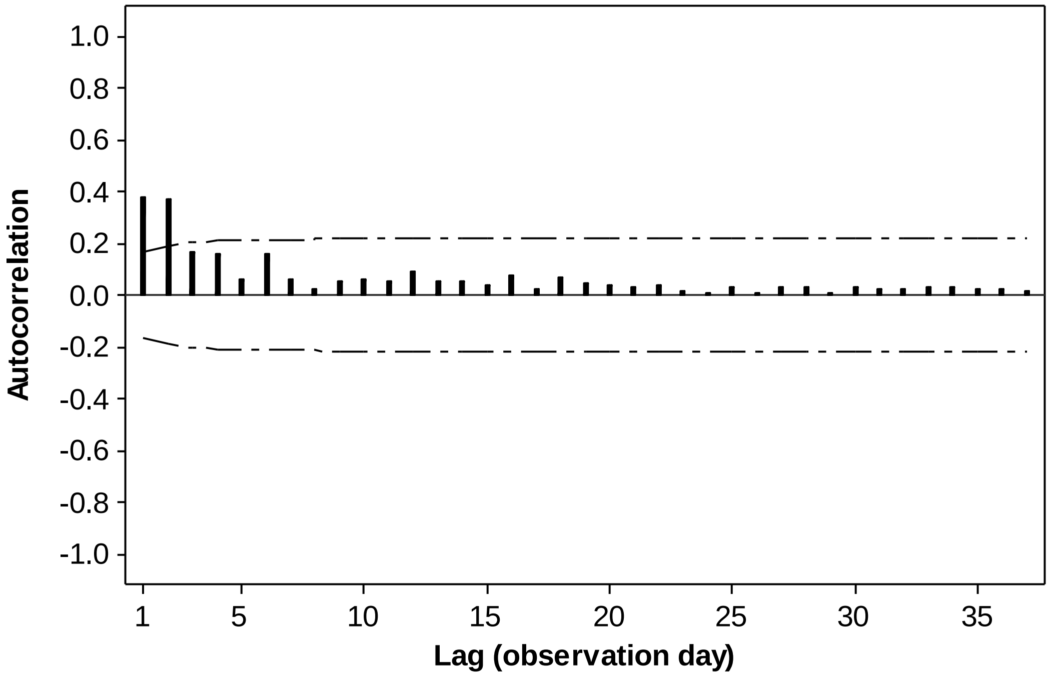

Figure 4.1. Autocorrelation function of intervals between sightings of known individuals by observation day. Significant values of autocorrelation are indicated when T-statistic is ≥3. T= 4.60 at lag one; T= 3.96 for lag 2; T=1.58 for lag 3, all other lags also NS. Dashed line indicates 5% significance limits for autocorrelations.

4.6 Results: Temporal Variation in Elephant Visits

A total of 1599 elephant visits were observed over the 11 months of data collection. Of these 1055 were in parties and 544 were solitary elephants.

4.6.1 Elephant Visit Rates

Elephant visits were not equally distributed throughout the daily time blocks (χ^2= 1545.73, df=7, p<0.001) and peak visits occurred in the early morning and late afternoon as represented by the number of half-hourly counts where elephants were present in the clearing (Figure 4.2).

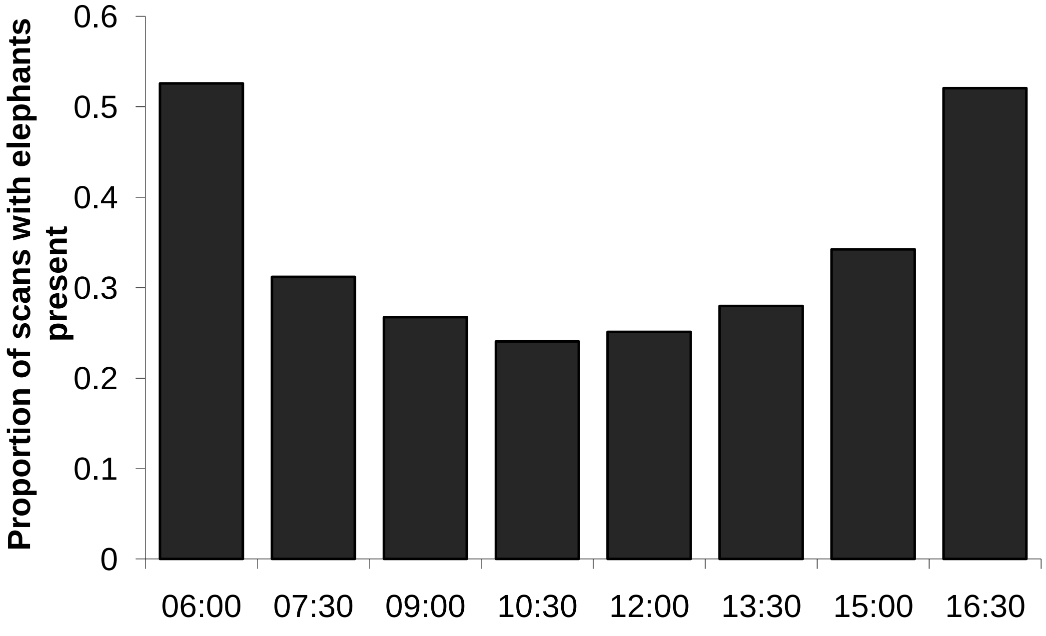

Figure 4.2. Daily elephant presence in the clearing from the proportion of scans with elephants present by time block. Data are from all 30 minute scans made over the study period, n=3598 scans on 187 observation days.

The total number of elephants seen per month, corrected by observation duration, varied enormously over the course of the study period ($F_{10,186}$ = 7.211, p<0.001,

R^2=0.250; Figure 4.3). Visit rate in August was significantly lower than those from December through to May (Hochberg post hoc tests, all p<0.05), and visit rates were higher in February and April than October and June (all p<0.05). In August only one visit was observed over 5 days, whereas during peak visiting in April 2008, 117 animals were recorded in a single day, although this period of intense activity was relatively brief (see Figure 4.3). Three intensities of elephant visiting were defined according to monthly scores: low (July to October 2007, June 2008), medium (November-December 2007, March 2008 and May 2008) and high (February and April 2008).

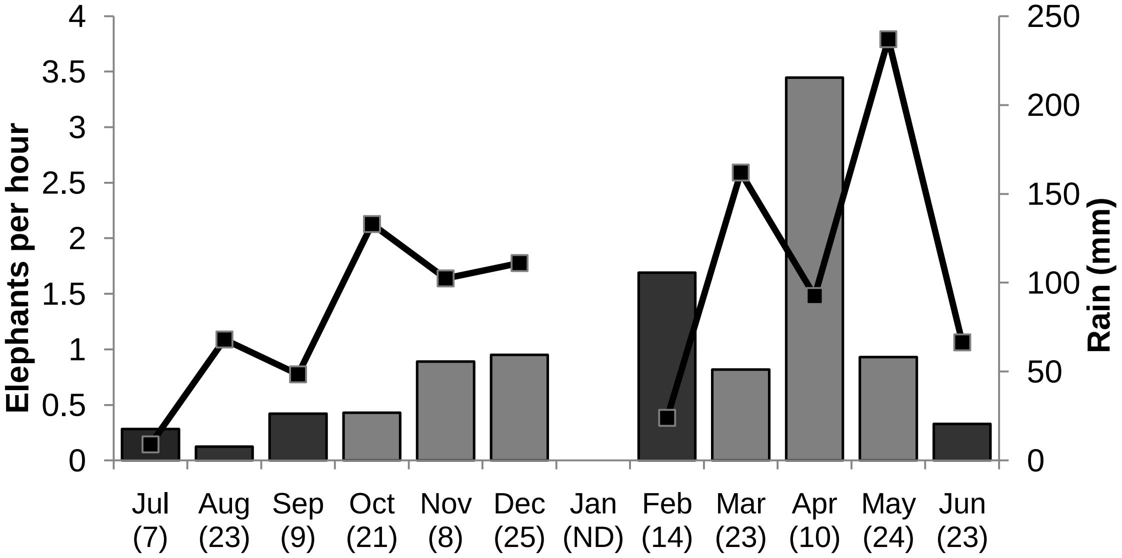

Figure 4.3. Visit rate as defined by total number of elephants per hour by month (corrected for observation duration). Bars = elephants per hour (light grey = wet season months, dark grey = dry season months). Numbers in brackets indicate number of observation days per month, and ND= no data for that month. Line = total recorded rainfall.

There was a significant correlation between elephant visit rate and daily rainfall (Table 4.1 with all correlations), with the strongest relationship occurring between rainfall and elephant visit rate 21 days later. This lag duration may be related to changes in plant primary production in response to rainy periods 3 weeks earlier (e.g. Rasmussen et al. 2006). However, February was also a high activity month, despite being preceded by low rainfall.

Rainfall	Rate+7days	Rate+14days	Rate+21days	Rate+28days
r_s	0.447	0.544	0.621	0.427
Sig. (2-tailed)	<0.001	<0.001	<0.001	<0.001
N	149	124	102	93

Table 4.1.Correlations between rainfall and elephant visit rates 7-, 14-, 21- and 28- days post-rainfall.

Dung counts made at the beginning of the observation day varied by month (Figure 4.4; $F_{7,111}$= 7.635, p<0.001, R^2= 0.295). There was a strong correlation between the mean number of dung piles per month and the monthly mean elephant visit rate (r_s= 0.952, p<0.001, n=8).

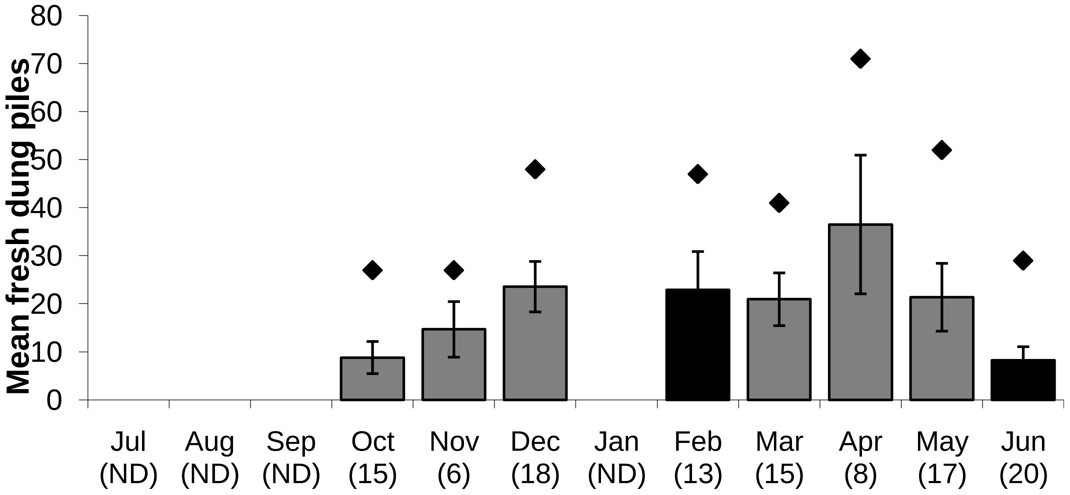

Figure 4.4. Mean number of fresh dung piles by month. Error bars show 95% CI. Grey bars show wet season months, black bars dry season months. Diamonds show monthly maxima. Numbers in brackets indicate the number of observation days contributing to that month, ND indicates no data available for that month.

Monthly changes in diurnal visit rate were also mirrored in seasonal differences; elephants visited the clearing more often during wet seasons (Table 4.2, Figure 4.5).

This was not due to the change in observation point, although this also had affected elephant visit rate (Table 4.2). Thus elephants visited Maya Nord more often in wet than dry seasons and more often after we constructed the new observation platform.

Model Factors	df	Mean Square	F	Sig.	Model Adjusted R^2
Season (wet/dry)	1	0.542	13.516	**<.0001**	0.112
Observation point (old/new)	1	0.508	12.650	**<.0001**	
Season*Observation point	1	0.008	0.191	0.663	
Corrected Total	*186*				

Table 4.2. Factorial ANOVA model for seasonal changes in hourly elephant visit rate, controlling for change in observation point using Type I sums of squares (n=187 observation days).

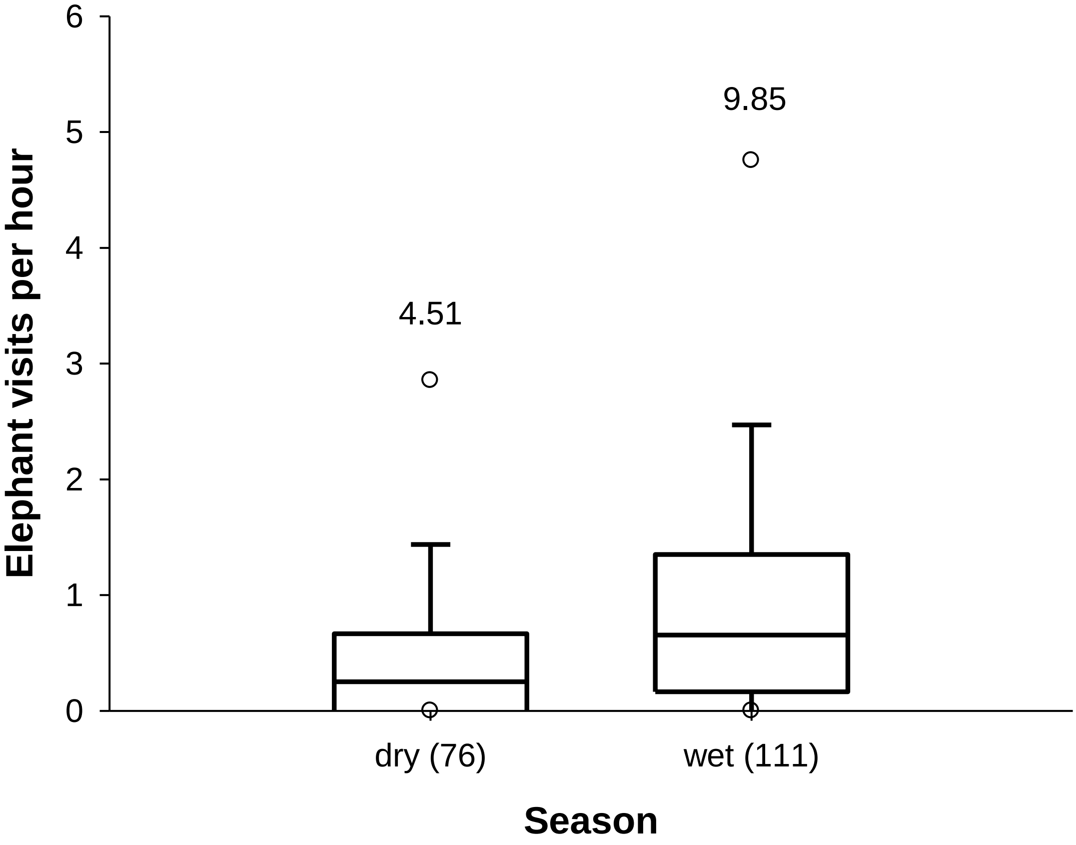

Figure 4.5. Median and IQR of visit wet and dry seasons. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of observation days).

4.6.2 Elephant Visit Durations

Data were first examined according to whether or not elephants were observed entering and leaving the clearing ("complete" visits) or not, and then according to whether or not animals fled the clearing. Neither of these factors changed the patterns of visit durations (Figure 4.6a and b) and so both were excluded from subsequent analysis of visit durations. Median visit duration was 32 minutes (IQR = 46 mins, range 1-325 mins). Visit durations were strongly related to the time block in which they occurred ($F_{9,1722} = 44.74$, $p < 0.001$, $R^2 = 0.294$), with longer visits occurring in the middle of the day, between 10:30 and 14:59 (Figure 4.7).

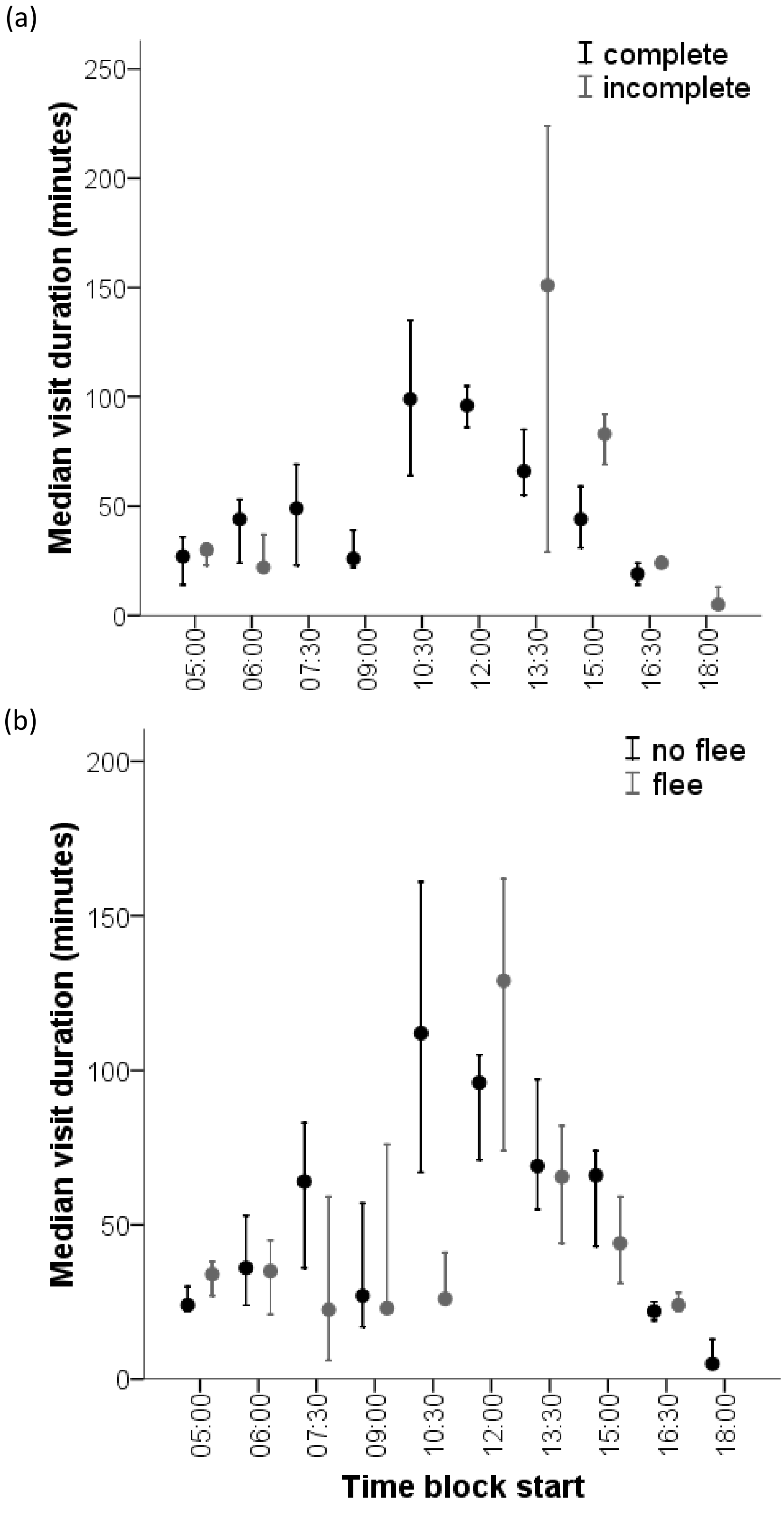

Figure 4.6. Median and 95% CI of visit durations by time block, split by (a) incomplete visits and (b) flight events.

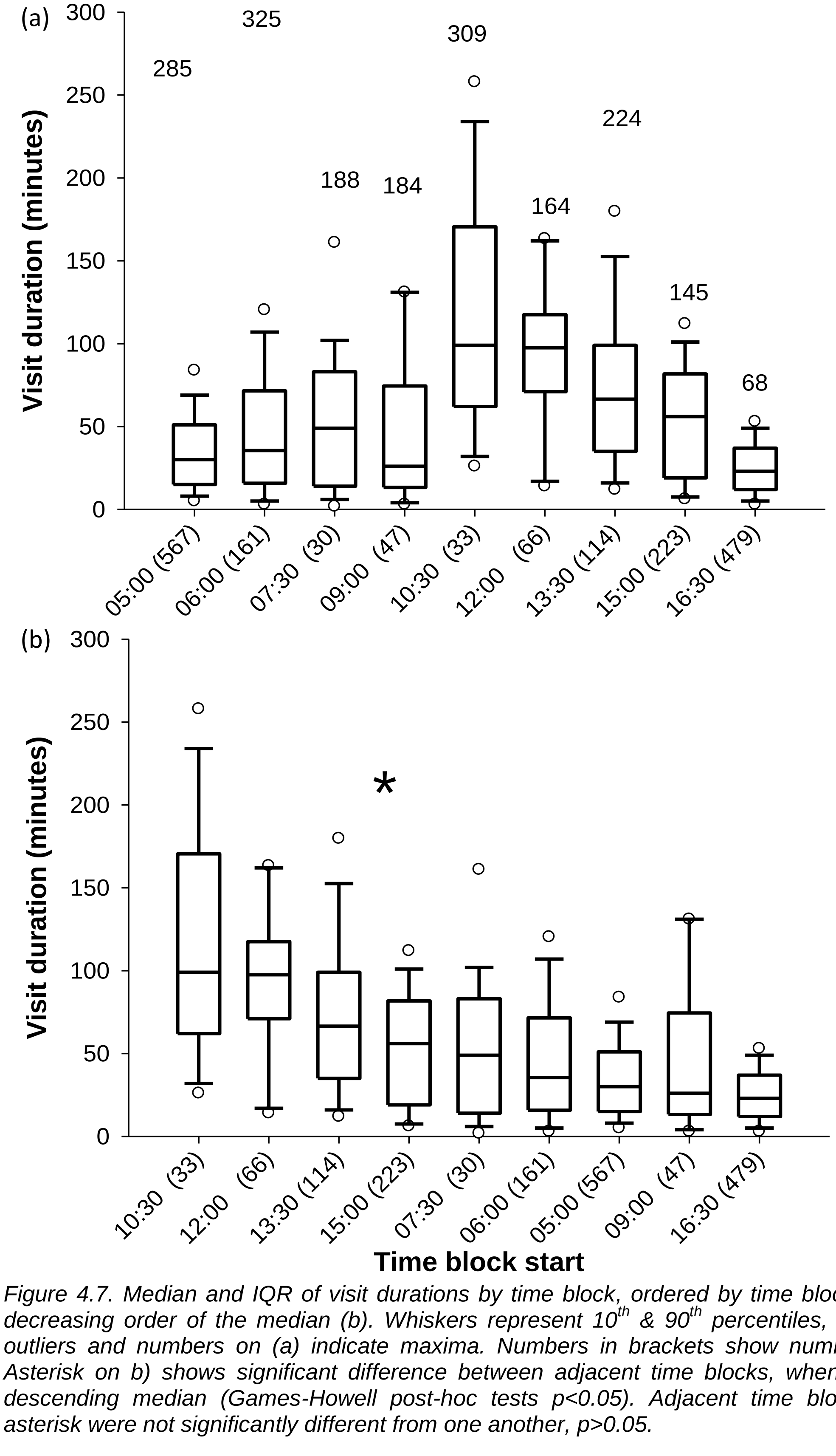

Figure 4.7. Median and IQR of visit durations by time block, ordered by time block (a) and in decreasing order of the median (b). Whiskers represent 10th & 90th percentiles, circles show outliers and numbers on (a) indicate maxima. Numbers in brackets show number of visits. Asterisk on b) shows significant difference between adjacent time blocks, when ordered by descending median (Games-Howell post-hoc tests p<0.05). Adjacent time blocks with no asterisk were not significantly different from one another, p>0.05.

There was a clear effect of month on visit duration (Table 4.3), but there was no consistent patterning; visits appeared to be markedly shorter in November (November to all other months Games-Howell post hoc tests p<0.05; Figure 4.8). Visit durations did not vary according to the number of elephant visits observed in the month i.e. whether many or few elephants were using the bai in any month was unrelated to the time they spent there. This is visible in Figure 4.8, where there is no marked difference in the distribution of visit durations in April and May compared to other months, despite the high numbers of elephants visiting the clearing during this period.

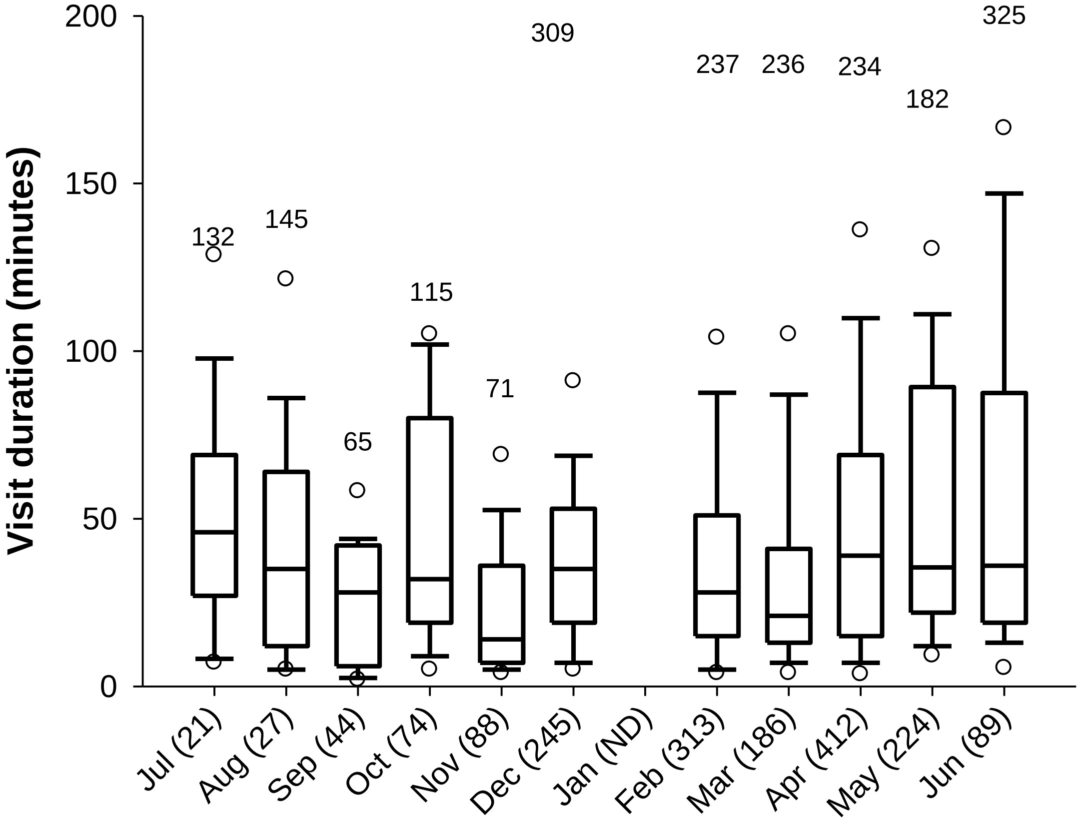

Figure 4.8. Median and IQR of visit durations by month. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of visits).

Monthly Effects					Seasonal Effects (wet/dry)				
Factor	df	Mean square	F	Sig.	Factor	df	Mean square	F	Sig.
Time block	9	5.955	44.74	**<0.001**	Time block	9	5.955	38.193	**<0.001**
Month	10	2.030	15.25	**<0.001**	Season	1	0.026	0.165	0.684
Time block * month	64	0.507	3.81	**<0.001**	Time block *season	9	0.593	3.804	**<0.001**
Corr. Total	*1722*				*Corr. Total*	*1722*			
Model R^2	0.294				Model R^2	0.173			

Table 4.3. Factorial ANOVA models for temporal variation in visit durations according to month and season, controlling for time block effects (n=1723 elephant visits over the study period in both models).

Visit durations did not vary according to whether they fell in wet or dry periods, (Table 4.3, Figure 4.9), in agreement with the lack of consistent monthly differences.

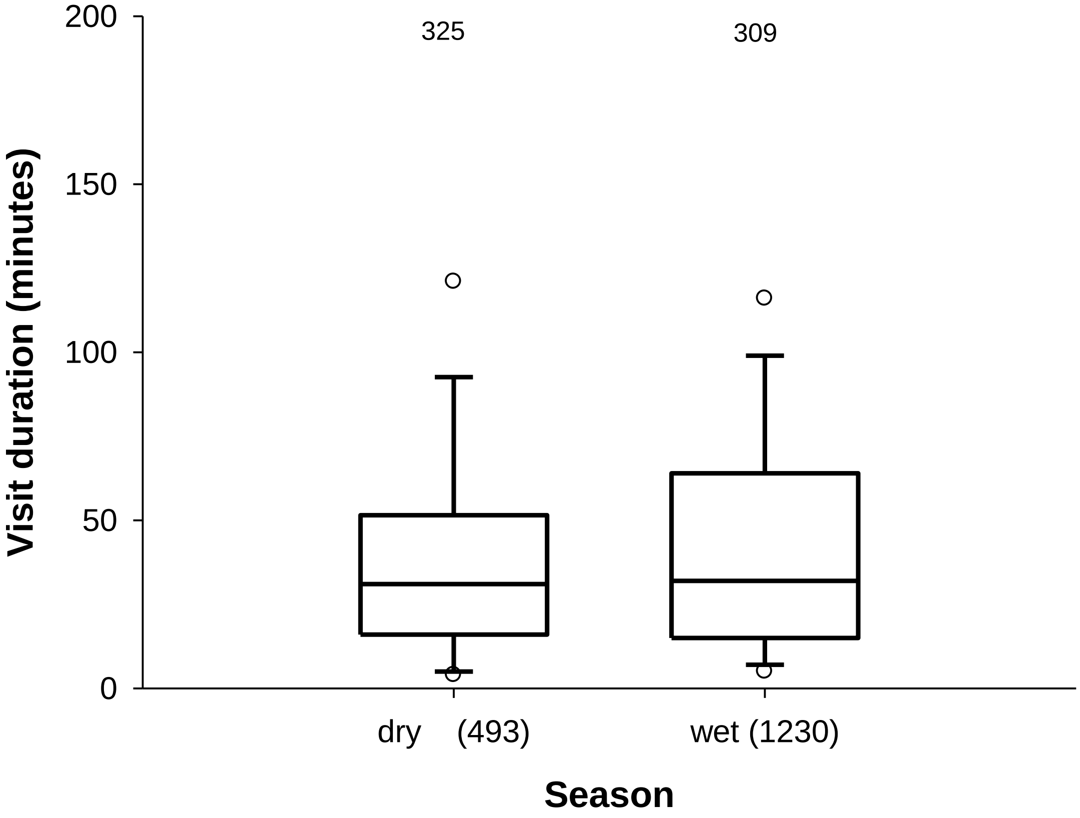

Figure 4.9. Visit duration by season; median, IQ. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of visits).

4.7 Results: Temporal Variation in Socio-Spatial Organisation

4.7.1 Aggregation Sizes

Aggregation counts (made every 30mins during diurnal observations) counted 2521 elephants in 634 aggregations over the study period. Mean aggregation size was 3.97 (SD= 5.25) and aggregation size ranged from one to 65 elephants.

Changes in aggregation size over the time of day are shown in Figure 4.10. Following a similar pattern to elephant presence, aggregations were larger in the early morning and late afternoon (Figure 4.10a), with a small peak around the middle of the day although this time of day effect was not particularly strong ($F_{7,626}=6.300$, $p<0.001$, $R^2=0.056$, Games-Howell post hoc tests all $p<0.05$). Night observations gave sufficiently good observation conditions on five separate evenings, where it was possible to make counts of all elephants in the bai (recorded continuously every 15 minutes; see Chapter 2). Aggregations tended to be larger at night than during daylight observations (Figure 4.10b), although sample sizes between daylight and nocturnal counts were very unequal, and Figure 4.9b does not include nights where fog obscured observations but we heard no elephants using the pools.

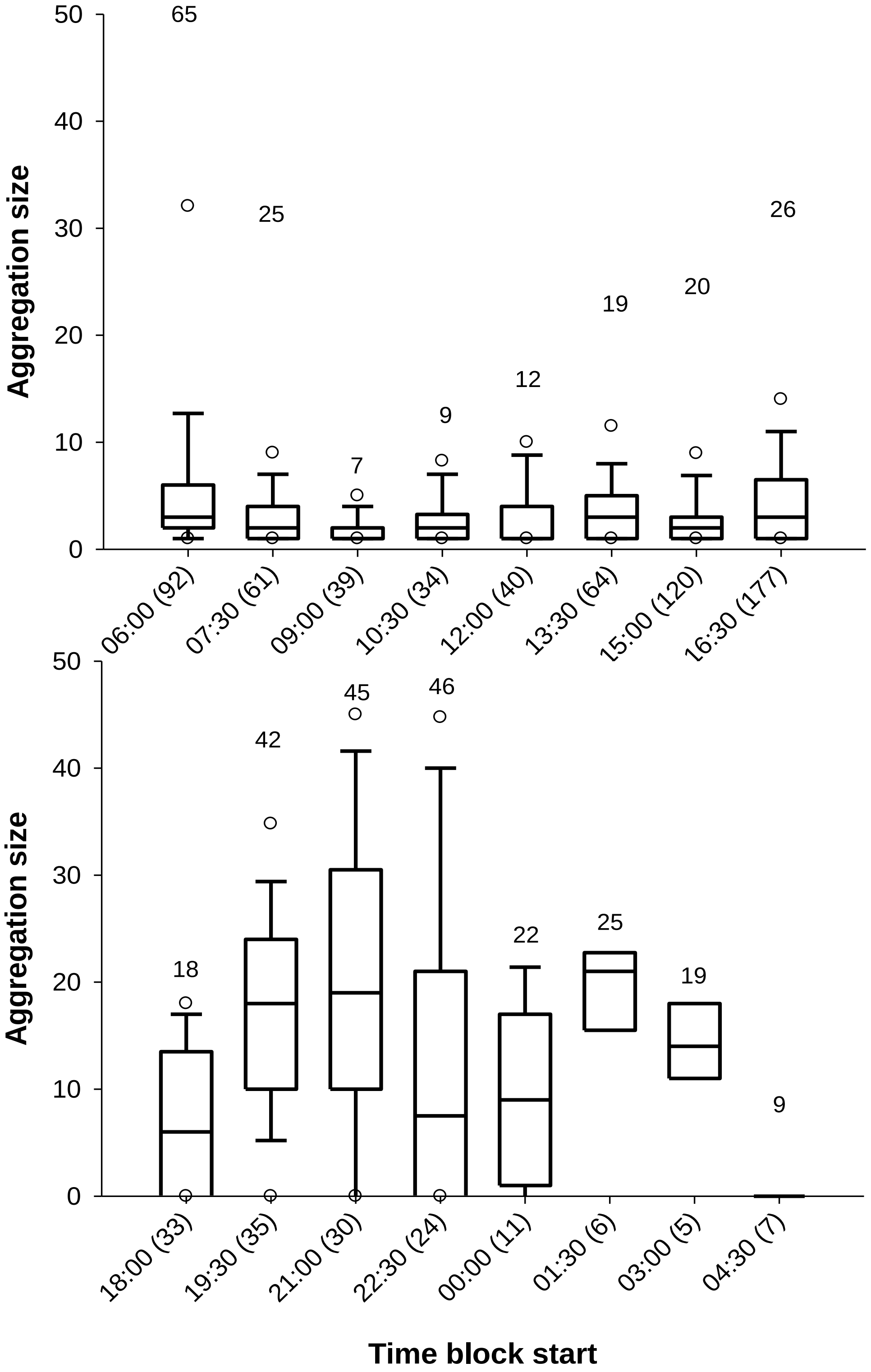

Figure 4.10. Median and IQR of aggregation sizes by time of day for diurnal observations (a) and nocturnal counts from 5 nights (b). Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of 30 minute scans in (a) and number of 15 minute scans in (b)).

Night-time aggregations were dominated by visits from females and immature animals (see Figure 4.11), which mirrored the pattern of diurnal observations and identifications (see Chapter 5). Figure 4.11 shows that the mean number of animals in each life-history class appeared to be slightly higher during night-time aggregations than during day-time aggregation counts.

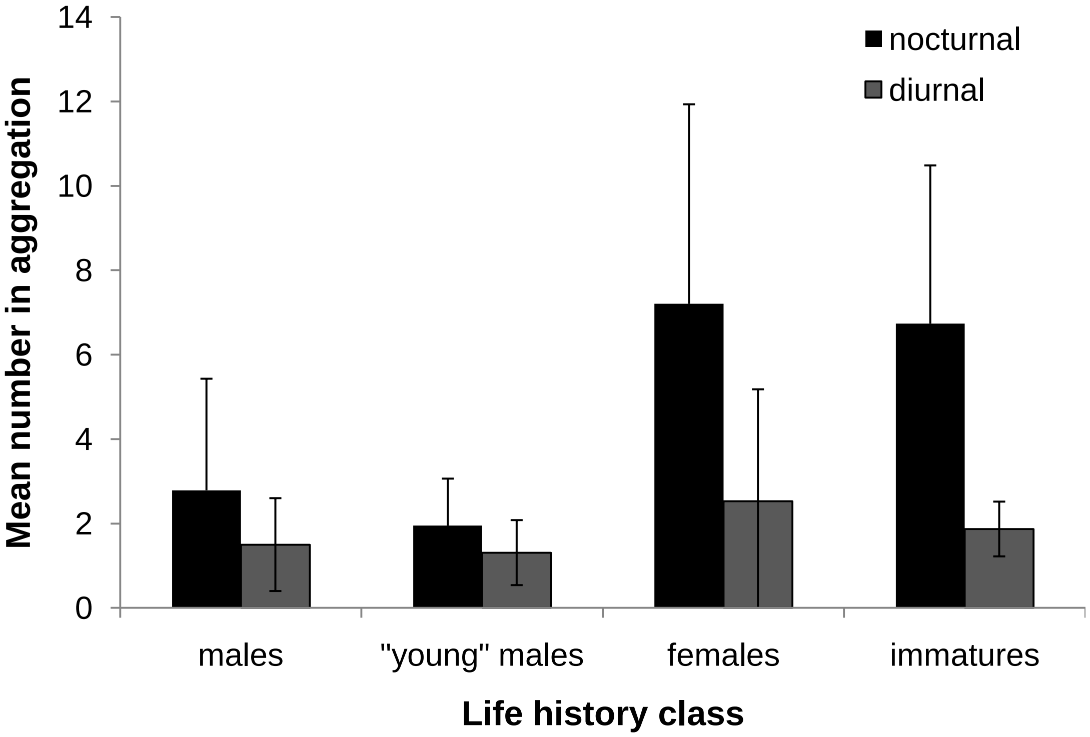

Figure 4.11. Composition of night-time aggregations by life-history class, represented by mean number of animals in 116 nocturnal aggregations (counts made every 15 minutes) and 629 diurnal aggregations (counts made every 30 minutes). Error bars show SD. “Young” males = old sub-adults and young adult males (aged approximately 15-24).

Significant monthly changes in maximum daily aggregation sizes were observed($F_{10,141}$= 4.699, $p<0.001$, R^2= 0.208), mainly due to the large aggregations observed in April (Hochberg post-hoc tests, all $p<0.05$ Figure 4.12). There was no effect of month on the time of day at which maximum aggregations were observed

($F_{10,141}$=1.371, p= 0.201, R^2= 0.026) i.e. maximal aggregations were not observed at different times of day in different months.

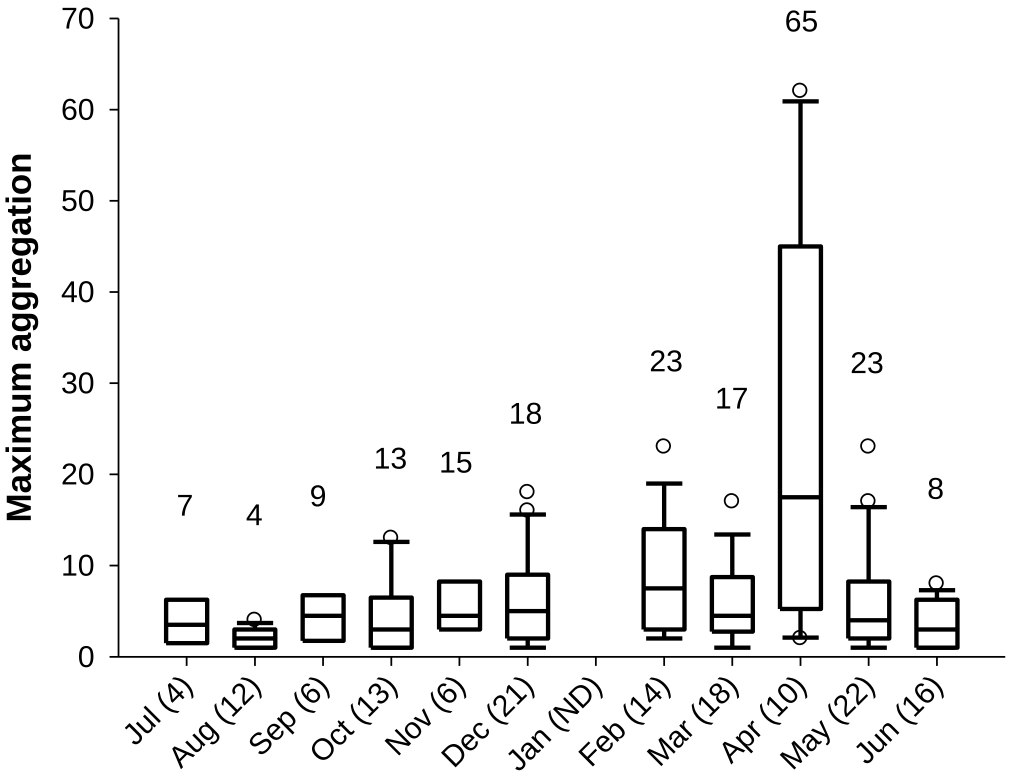

Figure 4.12. Median and IQR of maximum aggregation sizes by month. Whiskers represent 10^{th} and 90^{th} percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of 30 minute scans). ND = no data.

Monthly effects on maximum aggregation size translated into a weak seasonal trend with the largest aggregations tending to occur in wet season months ($F_{1,141}$ = 4.237, p=0.041, R^2=0.022; Figure 4.13). There was no effect of season on the time of day at which maximal aggregations were observed ($F_{1,141}$= 1.659, p=0.200, R^2= 0.005).

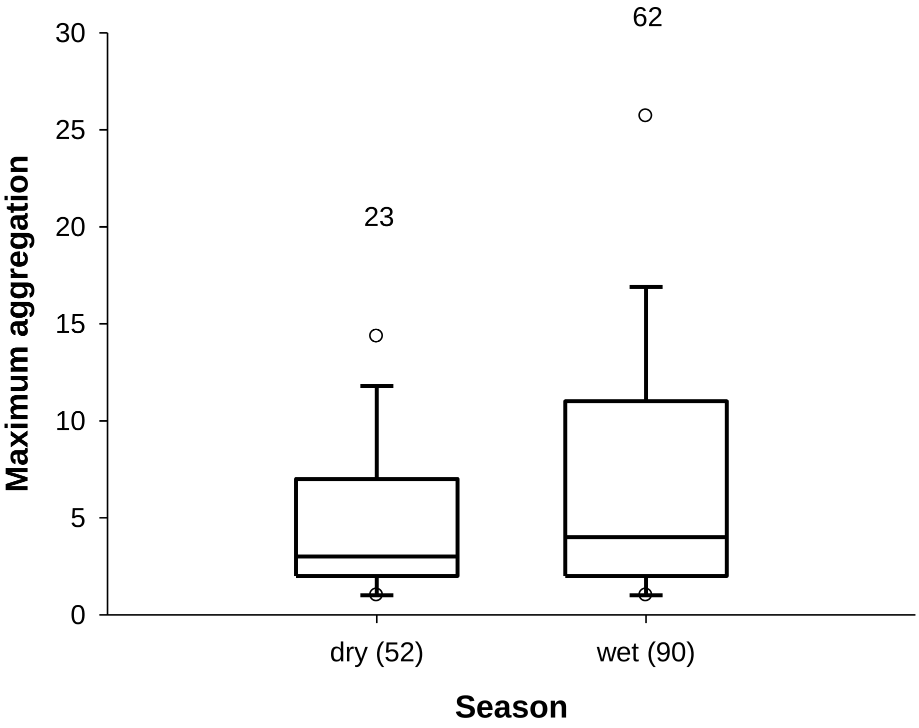

Figure 4.13. Maximum aggregation size by season; median, IQ. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of 30 minute scans).

4.7.2 Party size

In total, 1754 parties lasting more than one minute duration were recorded during the study, with a mean size of 3.94 (SD= 4.56). Party sizes showed variation according to time block ($F_{7,1753}$ = 9.42, $p<0.001$, R^2= 0.109; Figure 4.14) and tended to be larger in the early morning (between 05:00 and 07:29; Games-Howell post hoc tests, $p<0.05$), following the patterns showed by both visit rate and aggregation size.

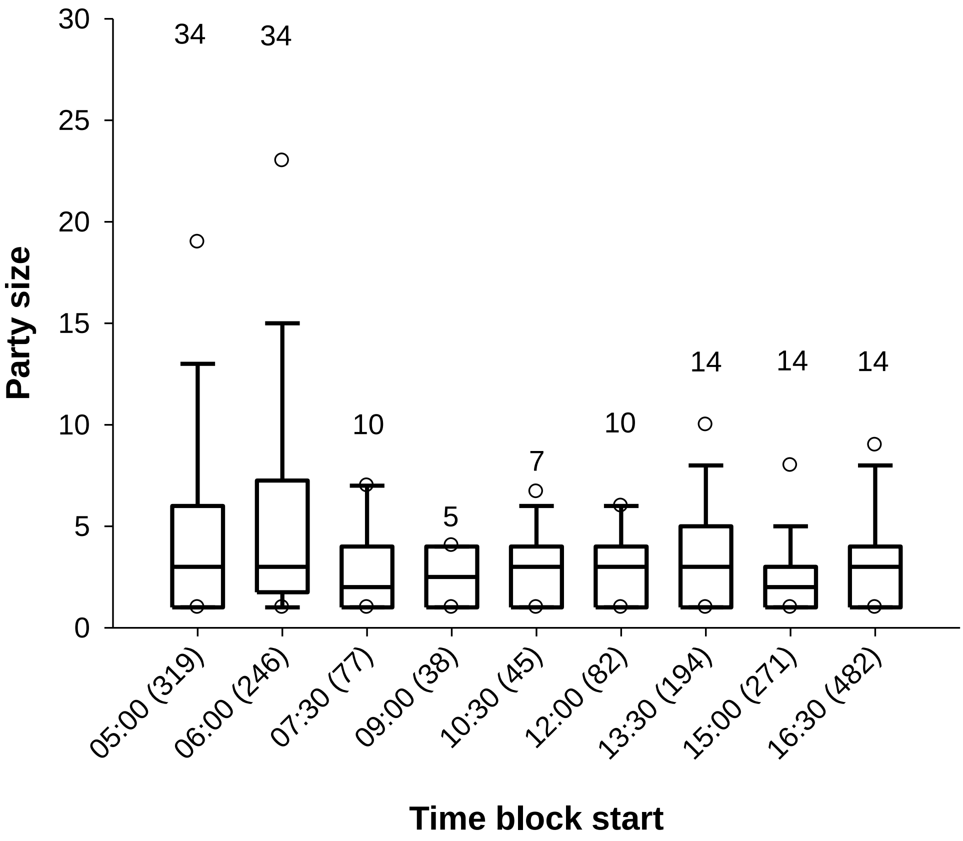

Figure 4.14. Median and IQRs of party size by time block. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of parties).

Party sizes also varied on a monthly basis (Table 4.4), due to large parties observed in April (Games-Howell post hoc tests April versus all other months, p<0.05; Figure 4.15).

Model Factors	Df	Mean Square	F	Sig.	Model Adjusted R^2
Time block	8	1.133	9.415	**<.0001**	0.109
Month	10	1.279	10.633	**<.0001**	
Time block*Month	63	.215	1.789	**<.0001**	
Corrected Total	*1753*				

Table 4.4. Factorial ANOVA model for monthly variation in party size, controlling for time block effects (n=1754 elephant parties over the study period).

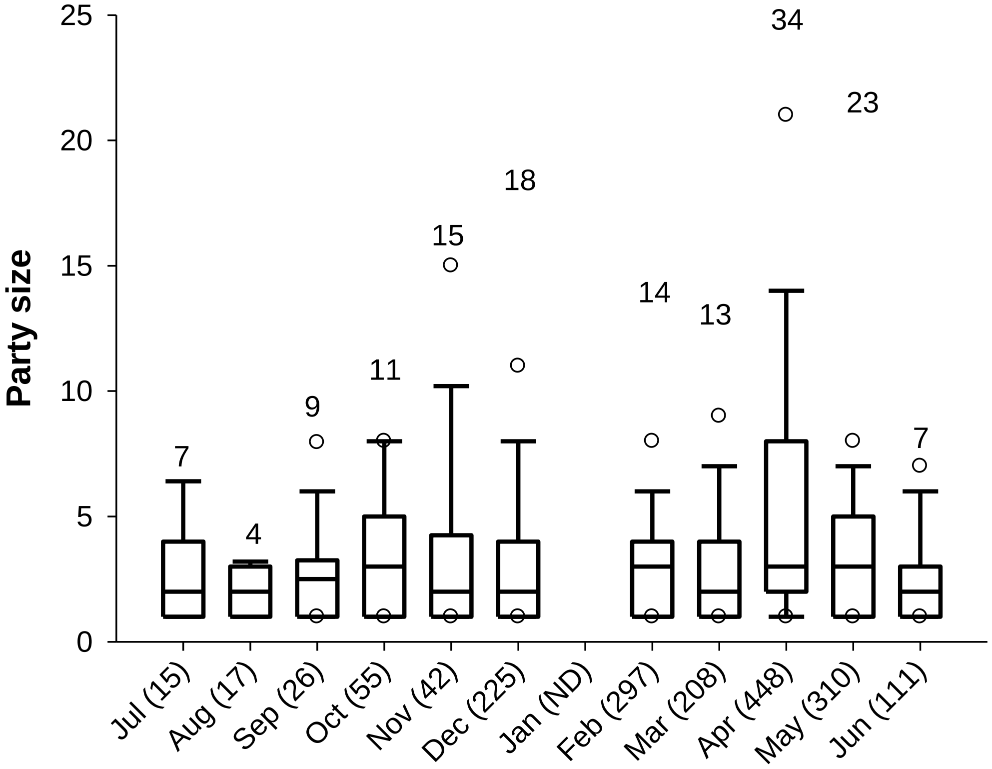

Figure 4.15. Median and IQR of party sizes by month Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of parties).

Party sizes were significantly larger in during wet seasons, (Table 4.5; Figure 4.16) however this effect was attributable to the large party sizes observed in April (a wet season month) as shown by the lack of explanatory power in the model when April data were removed from the analysis (Table 4.5).

Monthly Effects					Seasonal Effects (wet/dry)				
Factor	df	Mean square	F	Sig.	Factor	Df	Mean square	F	Sig.
Time block	8	1.133	8.838	**<.0001**	Time block	8	0.290	2.722	**0.006**
Season	1	2.462	19.21	**<.0001**	Season	1	0.288	2.709	0.100
Time block *season	8	0.319	2.489	.011	Time block *season	8	0.065	0.614	0.767
Corr. Total	*1753*				*Corr. Total*	*1305*			
Model R^2	0.050				Model R^2	0.009			

Table 4.5. Factorial ANOVA models for temporal variation in party size according to season, controlling for time block effects, for all months (n=1754 elephant parties) and excluding large parties seen in April (n=1306 elephant parties).

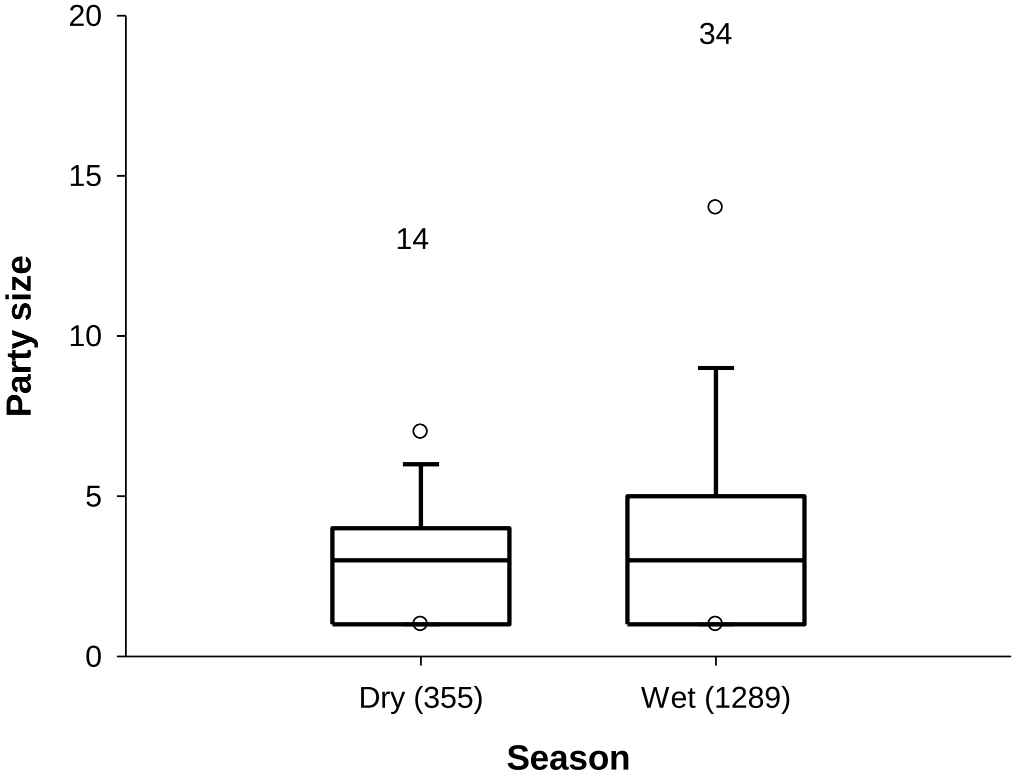

Figure 4.16. Median and IQR of party sizes by season. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (i.e. number of parties).

4.7.3 Party types

It was not possible to discriminate changes in the proportion of party types on either a daily or monthly basis due to large variation inherent in the data, but at a seasonal level a clearer pattern began to emerge (Figure 4.17). As with visit duration data, there was no difference in the distribution of party type according to whether or not groups fled the clearing. The effects of party types are explored in detail in Chapters 6 and 7 which examine elephant gregariousness and socio-spatial organisation in detail.

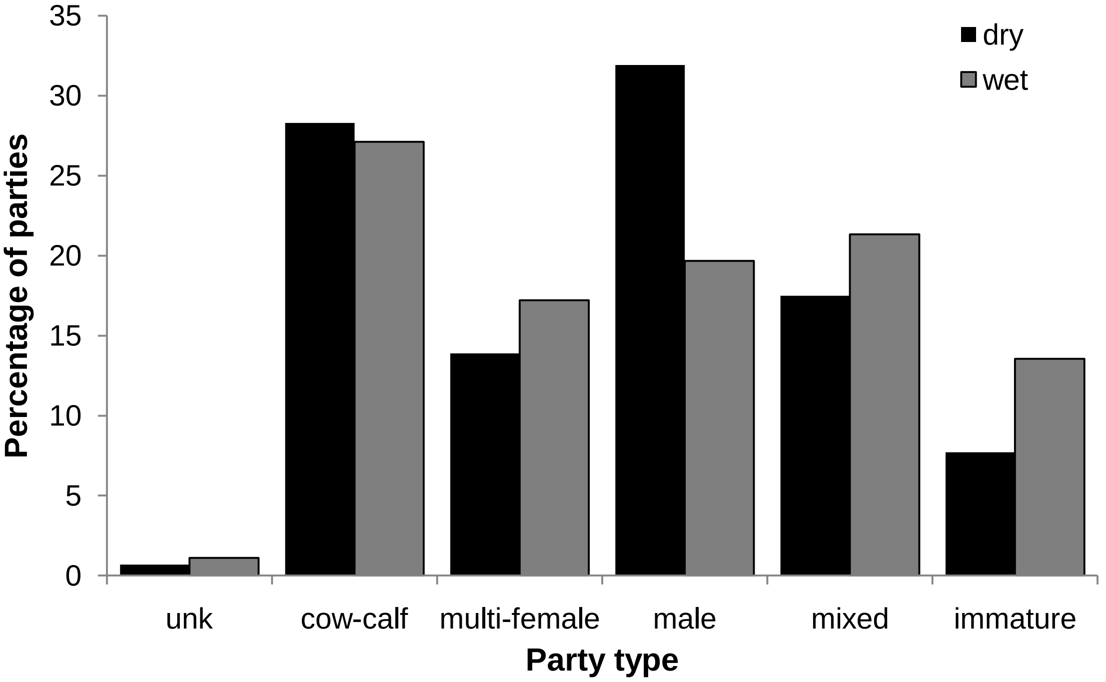

Figure 4.17.Seasonal changes in party types measured as percentage of parties of each age sex class. Unk= unknown; cow-calf = one adult female, alone or with immature animals; multi-female= 2 or more adult female; with or without immatures, male=adult males only; mixed = both adult males and females present; immature = no adults present in the party. Data are based on 583 parties observed in dry season and 1261 parties observed in wet season months.

4.8 Results: Individual Visiting Patterns

Over the study period 454 animals were individually identified. Of these, 44% were seen more than once, with a mean re-sighting frequency of 1.72 (SD =1.48, range =1-14). The most frequently sighted individual was an adult male, Akoa who was seriously wounded (see Chapter 8) and whose ranging was presumed to be affected by his injuries. For non-wounded animals the maximum number of sightings was 10. The number of sightings of individual elephants did not vary as a function of either age class or sex (Table 4.6). Although Akoa was seen most frequently when wounded, for other individuals there was no difference in inter-visit intervals between animals with low and high body condition scores ($F_{1,85}$= 0.008, p=0.929, R^2=0.112).

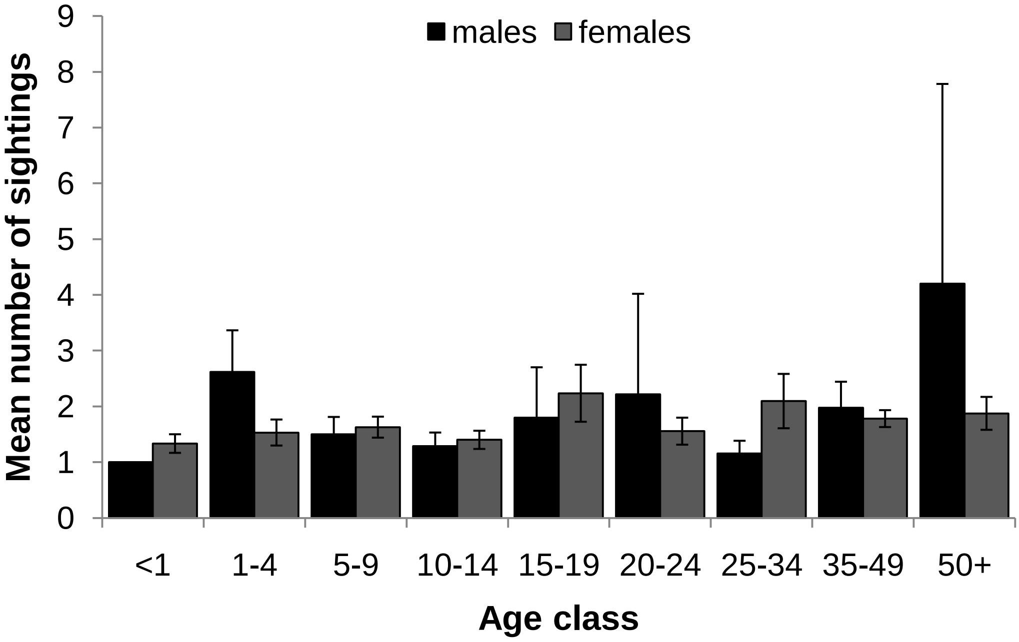

Figure 4.18. Mean number of sightings of individuals identified elephants according to age class and sex (n=454). Error bars show 95% CI.

Number of Sightings					Interval Between Sightings (days)				
Factor	df	Mean square	F	Sig.	Factor	df	Mean square	F	Sig.
Age	8	0.198	1.259	0.263	Age	7	1.530	2.616	**0.012**
Sex	2	.269	1.709	0.182	Sex	1	0.117	0.199	0.656
Age*Sex	10	.242	1.538	0.123	Age*Sex	7	0.976	1.669	0.116
Corr. Total	*437*				*Corr. Total*	*368*			
Model R^2	0.020				Model R^2	0.040			

Table 4.6. Factorial ANOVA models for temporal variation in number of sightings (n=438) and interval between sightings (n=368) according to age and sex all sightings of known individuals over the study period. Note that the unbalanced sample size between models is attributable to the number of individuals who were only seen once.

Overall, the interval between sightings showed a weak effect of age class but not sex, (Table 4.6). This effect appears to be due to longer intervals between sightings of young males aged 15-19, as this class differs from the youngest and oldest age classes (Games-Howell post hoc tests all $p<0.05$). One young male provided an extreme outlier, having visited the clearing after an interval of 358 days but the effect in this age group is not entirely due to this individual, as the model results did not change when he was excluded from the analysis.

Elephants normally made only one visit to the clearing on each observation day; only 132 of 1724 visits by individual animals were repeat visits in a day. Of these, 33 (2% of total visits) were considered as truly separate visits, being separated by 90mins or more. When considering independent social units i.e. excluding closely bonded adult females or females with dependent offspring, only 20 repeat visits were made (1.1% of observed visits). Animals nearly always visited the clearing only once in any given observation day and then if they were seen again it was only after an average interval of 36.97 days (SD = 57.47 days).

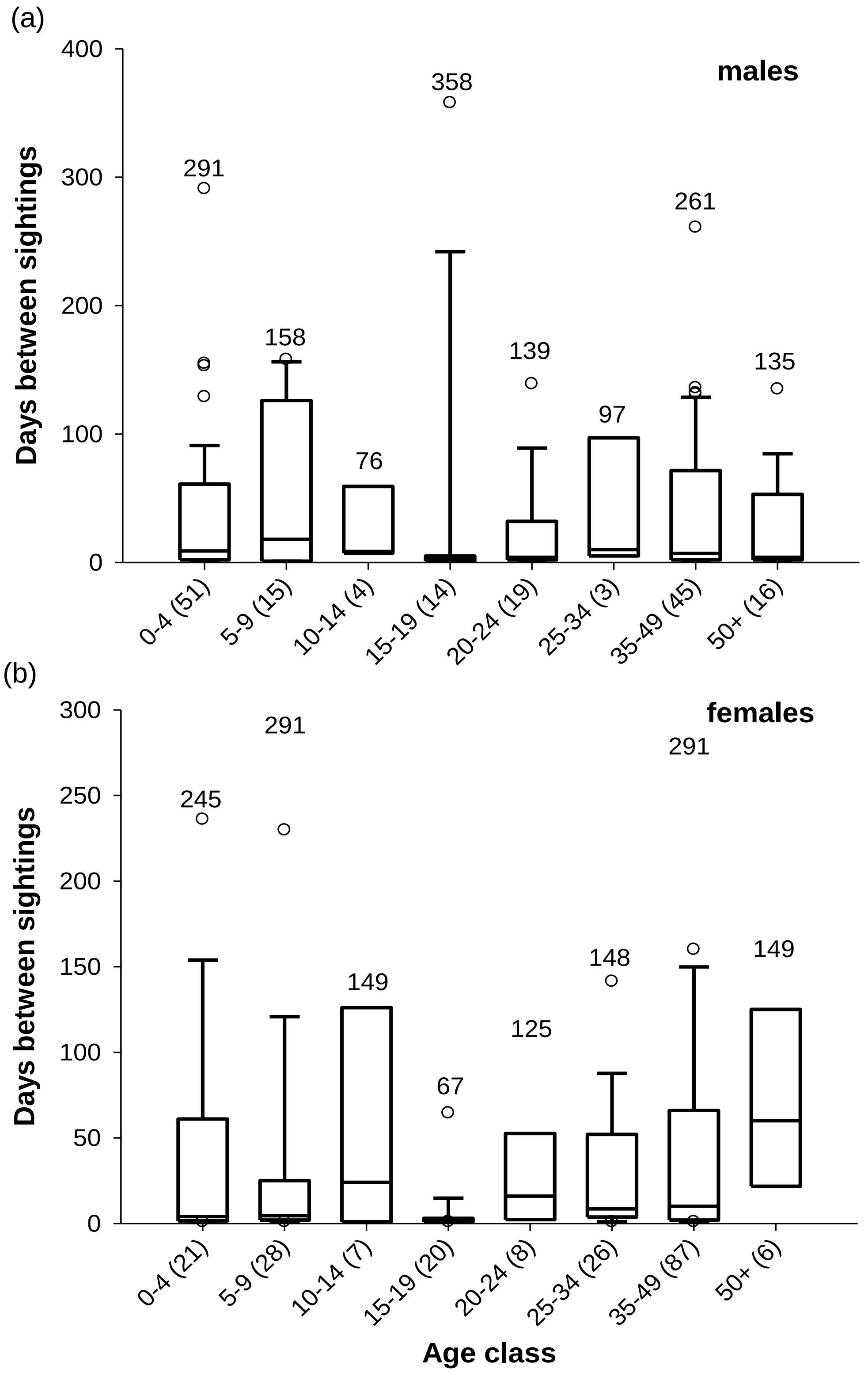

Figure 4.19. Inter-visit intervals by age class for (a) males and (b) females; median, IQR. Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima. Numbers in brackets show sample size (number of intervals between visits).

4.9 Discussion

The diurnal pattern of visiting by elephants to Maya Nord was consistent with that observed at other forest sites, where elephants are more commonly seen in early morning and late afternoon (e.g. Momont 2007; Mbeli Bai long term data) and also with GPS telemetry data suggesting that during daylight hours elephants focus on forest feeding with a midday rest period (Blake 2002). This circadian pattern suggests that elephants visit the bai outside peak feeding times (in the mid- to late- morning and early- to mid-afternoon), consistent with the observation that relatively few visits encompass activities other than geophagy (see Section 3.4).

Using dung counts as an index of nocturnal activity suggests that nocturnal and diurnal visiting patterns show similar patterns on monthly and seasonal scales; both showed a high activity period from November to May and low visiting during the driest seasons. Even with a limited dataset it is clear that much elephant activity at Maya Nord occurred during the hours of darkness, as reported at other sites (e.g. Momont 2007). As recorded from GPS collar data (Blake 2002) peak elephant activity in this area occurred in the hours before midnight, and then dropped off in the early hours of the morning. Acoustic monitoring suggests that up to 80% of elephant activity in bais takes place during the hours of darkness (P. Wrege pers. comm.). Although aggregation sizes were larger during the night, elephants showed similar patterns of clearing use during nocturnal observations, with activity strongly concentrated on the pools and very little vegetation feeding.

Elephant use of the Maya Nord clearing was highly variable during daylight hours. There were many occasions when no elephants were present, but when elephants did use the clearing the patterns of grouping were relatively independent of the number of individuals present. The patterning of aggregation size closely mirrored that of the overall visiting rates; periods of high overall activity thus reflect episodes of intense elephant activity, with large aggregations, rather than a steady flow of visits to the clearing. Elephants did not appear to minimise competition at the bai during these "busy" periods by altering the timing or duration of their visits, and the net result was that aggregations become larger at these times of the year (maximum= 65 animals). Overall, these patterns suggest that elephants did not change their visiting patterns in response to how many other animals were using the clearing, and that periods of low activity in the clearing reflected lower elephant presence in the zone.

Elephants are expected to range over the landscape, and due to the large number of clearings in the North sector of PNOK, here they are not limited to using one particular clearing, a situation which is perhaps unlike some other Central African sites. During periods of low visiting, elephant sign disappeared from the surrounding forest, as evidenced by the number of dung-piles counted on the Maya Centre fruit fall path (see Chapter 2) and by the amount of elephant sign and encounters by team members when travelling to and from the Mambili River for logistical purposes. It therefore appears that when elephants are present in the zone they visit the clearing and that their absence from the bai reflects an absence in the surrounding zone, rather than behavioural shifts such as less frequent diurnal visits and/or increasingly common nocturnal visits. It was not possible for this study to monitor multiple clearings in

PNOK, but elephants did tend to use the Maya Nord clearing more during wet seasons, when the large clearings and geophagy sites close to the major rivers in the Park were inundated and inaccessible to them.

Most elephants (n=1055, 66.0%) used the clearing in parties, rather than as solitary animals. Parties on average contained 3.94 elephants (SD= 4.56) and elephants stayed in the clearing for an average of 43.14 mins (SD= 39.32 mins). Party size was highly variable over the course of the study period; median party sizes were relatively stable but the maximum party sizes changed dramatically over the year. During the period in April when a “superabundance” of elephants visited the bai not only were elephants were found in larger overall aggregations but also in larger parties within these aggregations. Visit durations showed clear variation on daily but not monthly and seasonal level, although there were no a priori reasons to suppose this would be the case. It was clear that while more elephants used the bai at early morning and late afternoon they tended to remain in the bai for longer between 10:30 and 13:30. Party types remained fairly constant over the study period except that fewer male parties and more immature parties were observed during wet season months. Males were not absent from the clearing during these wet season months however, as the proportion of mixed parties did not change.

The number of elephants using the clearing appeared to be a lagged response to rainfall, and is presumed to relate to primary productivity changes in the surrounding forest, as surface water is not limiting. Elephant ranging is a complex function of individual strategy, experience and local ecological pressures (e.g. Momont 2007), so it is unsurprising that whilst rainfall had some relationship to visits, the effect was not direct. The most severe drying period of the year fell at the start and end of the study period when elephant visits were lowest, and although surface water was not limiting during these periods, browse quality may have been affected during these times. Elephants in the Nouabalé-Ndoki National Park (100km NE of PNOK) tend to move southwards towards Raphia swamps during the driest months of the year, probably to feed on the moisture-rich vegetation found there (Blake 2002). PNOK elephants might follow a similar pattern of seasonal movements, although as yet there are no data to support this suggestion. This study did not detect evidence of mast fruiting that could attract elephants to the Maya Nord zone (see Chapter 3).

Maya Nord seems to be more strongly seasonal and irregular in elephant activity by comparison to other clearings where elephants have been studied (Dzanga, A. Turkalo pers. comm.; Langoué, Momont 2007; Mbeli Bai, long term data). Observations at other Central African sites have suggested some animals may be resident within a relatively small zone, and are regularly observed at a particular bai (Langoué Bai (Momont 2007); Mbeli Bai long-term data). This was not the case at Maya Nord during this study, where the re-sighting frequency was low and inter-visit duration was highly variable, in some cases involving intervals of up to 12 months. Most elephants (66%) identified during this study only visited the clearing once. For the elephants who were seen on more than one occasion, the average inter-visit interval was 36.97 days (SD = 57.47 days). Males aged 15-19 showed the longest inter-visit intervals, which may be related to a period of social and locational dispersal related to adolescence (Evans 2006; Isbell 2004; Poole 1996).

The intensity of elephant use of the clearing and the sizes of aggregations observed in this study do not seem to reach the levels observed by previous researchers at the site. Querouil et al. (1999) reported some exceptionally large aggregations of around 100 animals and films, photographs and field reports from this period also appear to show larger aggregations than were common in my study (e.g. Cajani et al. 1998). It is difficult to compare this quantitatively to the data obtained in this study (although see Chapter 5 for a discussion of population structure), but it does appear that Maya Nord is somewhat less frequented by elephants than previously (R. Andembo pers. comm.). In light of the large population estimate calculated for PNOK prior to my studies (Blanc et al. 2007) it is unlikely that this drop in visiting is entirely due to a decline in the elephant population: heavy poaching was known at other clearings in PNOK during the 1980s and 1990s during Querouil et al.'s observations. It may be that elephants were compressed into a zone of relative security around Maya Nord during the heavy poaching period, and have subsequently resumed a more relaxed ranging pattern. However, from observations of elephant behaviour at the clearing, and of poaching wounds animals sustained during the study period, it is clear that the human threats to PNOK elephants persist. These issues are further discussed in Chapter 5 and Chapter 8.

Chapter Five

Population Demography & Health

Chapter 5 Population Demography & Health

5.1 Abstract

52.1% of all elephants seen were assigned individual identities and 79.7% of elephants who remained in the clearing long enough to permit good observations were individually identified. Over the study period 454 elephants were identified, and the visiting population was estimated to be between 870 and 1193 individuals. 310 elephants were identified as belonging to 100 family units, the mean size of which was 3.08 (SD= 1.30, range 2-9). Family unit size and structure did not vary as a function of matriarch age. My study did not find a balanced sex ratio among adults, as previously reported for elephants using Maya Nord; sex ratios for animals over the age of 5 were significantly different from 1:1, with a male:female ratio of 1:1.63 amongst adults (over 15 years old) and 1:1.55 amongst elephants aged 5-14. Body condition scores varied during the study but this was unrelated to measured rainfall and only weakly related to the fruit content of examined dung-piles (Chapter 3). Highly individual ranging patterns and the existence of age- and sex- effects on body condition, and a small sample size may have weakened this relationship. High pre-weaning survival among calves and a high proportion of reproductively active females suggest that PNOK elephants are not reproductively constrained either by ecological stressors such as limited food availability, or chronic social stressors resulting from heavy and sustained poaching pressure (Gobush et al. 2008). A high proportion of adult females were reproductively active, although females in PNOK appear to begin reproducing

relatively late as pregnancies were only observed in females over the estimate age of 15. Pre-weaning calf survival was high (for calves below the age of 5), although maternal experience was also important. Musth bulls and oestrous females were rare in daylight aggregations, indicating that Maya Nord does not function as a mating arena for PNOK elephants

5.2 Introduction

The structure of the visiting elephant population affects both the potential for bais to act as social arenas, and the behavioural profiles and interactions exhibited by individuals in the bai (e.g. Mitani 2006). The types of associations and interactions that occur depend on the physiological and reproductive state of individuals, which are known to be important for elephant ranging decisions, and may therefore also underpin their decisions to use forest clearings. Savannah elephants show sexual segregation; males use “bull areas” in which they associate with other males, and generally only enter female areas and associate with females when sexually active (usually when in the state of musth; Poole 1994).

Shannon et al. (2006b) concluded that forage selection was enough to drive sexual segregation of savannah elephants in South Africa, with females showing highly selective foraging in relatively short bouts. Savannah females are usually constrained in their ranging by access to water, which is a limiting resource for lactating females especially mothers of calves aged between 6 and 12 months, whose suckling demands are at their highest but whose independent feeding and drinking are still limited (Moss

& Lee in press b). Males can make independent, rather than group-based foraging decisions, and are not hindered in their movements by slow-moving calves. Amongst forest elephants, the degree of sexual segregation remains largely unquantified, although telemetry studies have demonstrated that males tend to range more widely than females (Blake 2002; Powell 1997). Whilst not limited by the availability of surface water, forest elephants must sometimes move over large distances in order to exploit highly profitable fruit crops (e.g. White 1994; White et al. 1993), and in dry periods may show strong preferences to remain close to watercourses which may be related to forage quality (Blake 2002). Forest elephants do not experience the same degree of (non-anthropogenic) predation pressure that is hypothesised to drive the formation of large multi-female groups in savannah elephants (e.g. Wittemyer et al. 2005).

Individual body condition can also affect ranging decisions and influence associations and interactions with conspecifics. Male elephants lose body condition during metabolically costly musth episodes, as assessed by a decline in the ratio of body width to height (Poole 1989a). Examination of culled animals has demonstrated that the lumbar depression on elephants is a useful and reliable indicator of body condition which corresponds well with kidney fat levels and increases in depth across all age-sex classes in resource limited savannah populations during dry periods (Albl 1971). Foley et al. (2001) expanded on Poole's earlier work, and developed a scale of body condition based on lumbar depression depth and other markers to categorise changes in individual body condition.

PNOK has been demonstrated to harbour a numerically large population (see Chapter 2), but absolute elephant numbers are not the only factor in determining the health and consequent viability of a population. This chapter is the first detailed examination of the PNOK elephants since Querouil et al.'s (1999) study. In the intervening 10 years, human pressures on elephants in the Central African forest block have intensified (Blake et al. 2008). These pressures can have effects on the reproductive capacity of populations (Abe 1994; Gobush et al. 2008; see also Chapter 8). If Maya Nord functions as a reproductive centre, risk perception by elephants using the clearing may affect individual reproductive success. Quantifying the visiting population structure is a preliminary step in assessing the social function of a clearing: A high proportion of musth males would indicate that males are using this area to search for receptive females. Conversely, few females might indicate that this clearing is part of a "bull area", containing a high number of reproductively inactive males. Assessing the health of individuals using the clearing permits an assessment of general population health and reproductive capacity, and also provides key information for interpreting the associations and behaviour of elephants within the clearing.

5.3 Chapter Aims

5.3.1 Assess the age-sex structure of the Maya Nord elephant population

This chapter describes the age-sex structure of elephants using Maya Nord to establish whether Maya Nord constitutes a sexually segregated area, either as a core female area or as a "bull" area for sexually inactive males. I compare the observed age-sex structure to previous published study from this site, and assess how many individuals might be represented in the visiting population over the course of the study period.

5.3.2 Assess the health and reproductive status of Maya Nord elephants

Population health and viability does not depend solely on absolute population size, but also on the demography, reproductive status and health of a population. Clearings might function as mating arenas, and if so a high proportion of males observed in the area would be expected to exhibit signs of sexual activity, including musth. This chapter describes the reproductive status of males and females and assesses changes in body condition as a result of ecological variability and age-sex effects. Social interactions associated with reproduction such as allomothering and male testing of female reproductive status are discussed in Chapter 7. Oestrus was also determined via behaviour cues and is therefore also discussed in Chapter 7. Family unit descriptions are presented under the general heading of female reproduction, as the availability of allomothers for communal calf care is known to affect female reproductive success amongst savannah elephants (Lee 1987).

5.4 Methods

Observational methods relating to general elephant observations and age estimates were presented in Chapter 2, and putative family units and bond groups were assigned on the basis of proximity, tolerance and affiliation (see Table 2.4). These methods specifically outline data relating to evaluating the Maya Nord population structure, elephant health and reproduction. As the analyses used here required considerable manipulation of the data, the data used and the tests applied are summarised in Appendix C1.

5.4.1 Population Structure

Individuals were classed according to life history stage in the field, and were often assigned more precise age-estimates, either for identified animals (n=404) or unknown animals (n=151) (see Chapter 2). Differences in the underlying distribution of age-sex classes between the identified and non-identified populations were examined using Kolmogorov-Smirnov 2 sample tests (Siegel & Castellan 1988) for males and females separately. The test statistic D_{max} was calculated as the absolute maximum difference at any interval between the two cumulative frequency distributions for samples *m* and *n*. Critical values of K were calculated at p=0.05 significance level as;

$$K = 1.36 \times \sqrt{(}{}^{m+n}\!/_{mn})$$

The observed age-sex structure was compared to a previous study at this site, where data were collected between 1996 and 1997 (Querouil et al. 1999), and the rate of identifications over the study period was described and used to provide a broad estimate of the size of the visiting population.

5.4.2 Elephant Health: Body Condition Scoring & Wounds

When observation conditions permitted, elephants were assigned body condition scores (Table 5.1) following the scale developed by Foley et al. (2001). All age-sex classes of savannah elephants lose body condition in periods of resource limitation, and this is visible via changes in the lumbar depression (Albl 1971) and through other cues. The distribution of monthly scores is presented in Appendix C2. To explore temporal variation in population body condition scores amongst elephants visiting Maya Nord, all scores assigned within a month were averaged. Individuals that suffered major trauma were excluded from analysis after their injuries occurred, and each known individual only contributed one score in each month. Health scores were assigned to 100 individual males and 160 individual females who had been assigned age estimates, in all age-classes. Newborns (animals <6mo old) were not scored for body condition, as their lack of body fat renders the Foley (2001) scale inappropriate. The low re-sighting frequency of known animals, and long inter-visit intervals did not permit analysis of the repeatability of scores, as I refrained from re-scoring those few animals seen on successive observation days (as I could generally recall the scores that had been assigned).

Body Condition Score	Description
1	Emaciated: clearly protruding bone structures around face, ribs, ilium and pelvis
2	Ribs not visible but depression around wing of ilium and lumbar region clearly apparent, highly concave skin on pelvic area
3	Depression around wing of ilium and lumbar region clearly visible, with skin on pelvic area shallowly concave
4	Lumbar depression flat or broadly convex and wing of ilium barely visible
5	Scapular and pelvic bones not visible

Table 5.1. Scale used to assign body condition scores (after Foley et al. 2001).

Month and age-sex effects on health score were assessed using ANOVA models. Field observations suggest that animals visiting the clearing in June seemed to be in poorer body condition than in other months, and it was therefore necessary to distinguish whether these lowered scores were the result of individuals losing condition at this time, or whether more elephants with lower body condition were visiting the bai. June scores were compared to scores from at least one previous visit for 11 known individuals using a one-tailed Wilcoxon signed-rank test. Body scores in September seemed to be higher than other months of the year but animals seen at this time were not re-sighted often enough to permit statistical analyses.

All wounds were noted, along with the age-sex class of the individual, the body part affected and the nature of the injury, along with a judgement on the severity of any compromise to individual welfare.

5.4.3 Reproduction

Reproductive status was assigned to females wherever possible, to assess the proportion of females currently reproducing. Reproductive status was assigned to 169 known females over the age of 10 (Table 5.2; minimum age at reproductive maturation is around 8, with a 22 month gestation; see Sukumar 2003 for a multi-site comparison). Females were assigned as parous or nulliparous based on breast development (Moss 1996), and pregnancies were classified as either suspected or definite. Late-stage pregnancies were relatively easy to determine by female body morphology and breast development, and nulliparous females were easy to identify by their lack of breast development (Moss 1996). Females not judged to be pregnant and without a calf under 4 years old were classified as not engaged in a current reproductive effort since lactational anoestrous lasts 12-18 months and gestation is 22 months (Moss & Lee in press a), so a minimum 3.5-4 year inter-birth interval is expected between surviving calves. No instances of twinning were suspected for PNOK elephants, consistent with the rarity of twinning rates known for elephants elsewhere (<0.01% of all elephant births, Moss 2001; but see also Foley 2002). An overall measure of female reproductive activity was calculated as the proportion of females of reproductive age (i.e. ≥10 years old) who were currently reproducing i.e. who were pregnant or who had a calf under four years old. Annual fecundity was estimated by dividing the number of known females of reproductive age with calves ≤2 years, by the number without. An inter-birth interval for PNOK females was estimated by adding a 22 month gestation to the inverse of the annual fecundity.

Measure	Categories	Diagnostic cues/ Description
Parity	Nulliparous Parous Unknown	Based on breast development: Flat breast and nipples indicate have not previously suckled a calf; pendulous nipples with flat breasts suggest reproductive experience but no current lactation (Moss 1996).
Pregnancy	Suspected Confirmed No judgement	Body profile and breast swelling.
Calf <2years old	Yes Yes; gave birth during study No	Includes infants known to have died and presumed stillbirths.

Table 5.2.Classification system and criteria used in describing female reproductive status.

Calf survival was estimated via observations of known losses to the population along with observations of apparent orphans, seriously compromised health amongst calves, and the proportion of calves less than 5 in the known population. An overall proportion of calves surviving the study period was estimated from;

$$calf\ suvival = \frac{N_{ind<5} - \ total\ deaths}{N_{ind<5}}$$

Where $N_{ind<5}$ indicates the number of calves under 5 years old who were seen more than once (in different months), as a measure of the number of these calves that survived over the study period.

The low re-sighting rate of known individuals and the correspondingly low association indices did not permit statistical classification of multi-level organisation amongst forest elephants using Maya Nord (Wittemyer et al. 2005). Instead animals were assigned to putative family units or bond groups according to behavioural measures such as proximity, co-ordination and affiliation (Table 2.3). Solitary females were counted as all females over the age of 10 with no associates and no dependent calves, and matriarchs were defined as the eldest (and usually most dominant) female present in a family unit.

Temporal gland secretion (TGS) was recorded whenever observed for males and females alike. This secretion contains volatile compounds and hormonal by-products suggestive of arousal or stress as well as musth (Buss et al. 1976; Rasmussen et al. 1996; Rasmussen & Schulte 1998). Musth in males was scored using three separate cues; temporal gland enlargement (TGE), temporal gland secretion (TGS) and urine dribbling (Ganswindt et al. 2005; Poole 1987; Poole & Moss 1981) as males may show some or the entire suite of musth characteristics as they shift in or out of peak musth condition. This three-point scale (TGS, TGE, urine dribbling) was used to attribute definitive musth status. When considering the co-occurrence of these signs in the population, 324 sightings were used, including multiple sightings of known males. When calculating the proportion of the known population exhibiting musth behaviours, only males above 35 were considered. The age of onset and the duration of a regular musth cycle are variable amongst elephants, but by the age of 35, nearly all savannah males are fixed in a regular annual musth pattern (Poole 1989a, 1989b; Poole & Moss 1981). Males below the age of 10 were excluded from analyses of reproductive behaviours. One adult male, Akoa suffered major trauma (see also Chapter 8) and was excluded from analyses after his injuries occurred.

5.5 Results: Population Structure

5.5.1 Population Age-Sex Structure

Overall there were 176 males and 266 females amongst the 454 animals assigned individual IDs (and 12 animals where gender remained undetermined for animals aged 0-9). Over the study period 833 sightings were made of unidentified animals (230 males; 442 females, 158 gender unassigned) and amongst these animals 151 were assigned age estimates (61 males; 76 females and 14 gender undetermined for animals aged 0-9). No difference was detected in the overall age distributions for males or females according to whether or not animals had been identified (males;

D_{max}= 0.189 < K = 0.206, for p= 0.05: females; D_{max}= 0.149 < K = 0.179, for p= 0.05, Figure 5.1). Thus the known population may be considered to be representative of the visiting population as a whole, and the following analyses do not differentiate between animals known to observers and unidentified elephants.

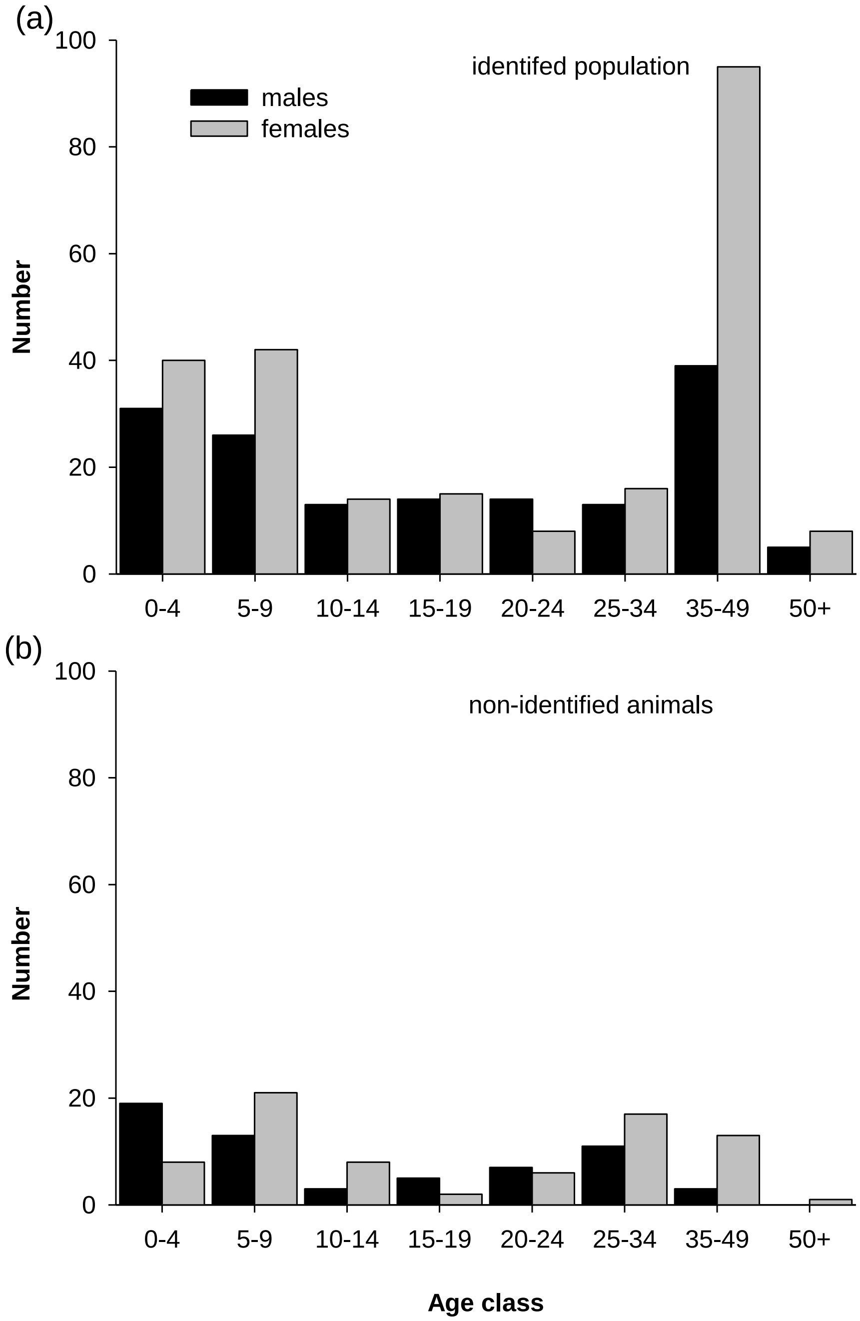

Figure 5.1. Age-sex structure of (a) known population, n=404 and (b) 151 unidentified animals.

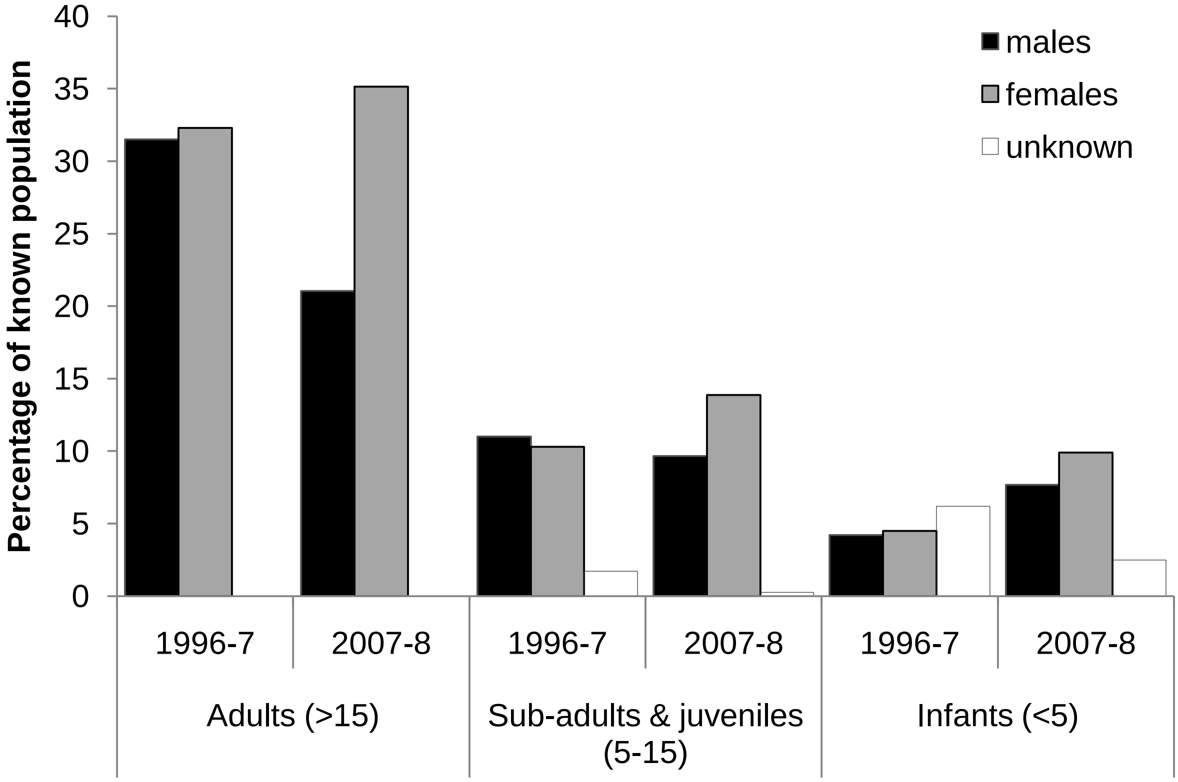

Figure 5.2. Comparison of the age-sex structure of the population in 2007-8 (this study, n=555) and 629 elephants identified in 1996-7 (Querouil et al. 1999). Age classifications follow those of Querouil et al. for comparative purposes.

This study clearly identifies a female bias amongst adults and sub-adults & juveniles; male:female sex ratios adults 1:1.63, binomial test $p<0.001$; sub-adults 1:1.55 binomial test $p= 0.014$; juveniles and infants 1:0.96, binomial test $p= 0.920$. This is in clear contrast to the 1996-7 data (Figure 5.2)

5.5.2 Identification Rates & Population Size

Of 1552 elephant visits observed in the clearing, positive identities were assigned on 809 occasions, which corresponds to a 52.1% identification rate (see also Section 4.4). Most often, elephants were not identified because observation conditions were poor, or because they failed to remain in the clearing long enough to allow clear identification, although life history class could be rapidly assigned. Overall, these "incomplete" identifications accounted for 539 of the 1552 elephant visits (34.7%). Excluding these visits, the identification rate increases to 79.7%, and only 13.3% (n= 206) elephants were well observed but had insufficient distinguishing features to assure positive identification upon re-sighting. New elephants continued to be identified throughout the study period (Figure 5.3a) at a relatively constant rate. Elephants did not use the clearing steadily throughout the year (Chapter 4) and the shape of the curve partially reflects extreme changes in visiting rates (see Figure 5.3b): The curve appears to approach an asymptote, but this is confounded by a drop in visiting rate at the end of the study period.

The lower bound for the size of the visiting population was calculated by using the ratio of visits made by known elephants (=454/809) and applying this to the 743 visits where IDs were not assigned, giving an estimate of 417 animals. The upper bound was simply made by assuming each of those visits were made by different animals (which is reasonable given the extremely low re-sighting frequency of known elephants: see Section 4.4). Hence the observed visiting population was estimated to be 870 - 1193 individual elephants over the course of the study period.

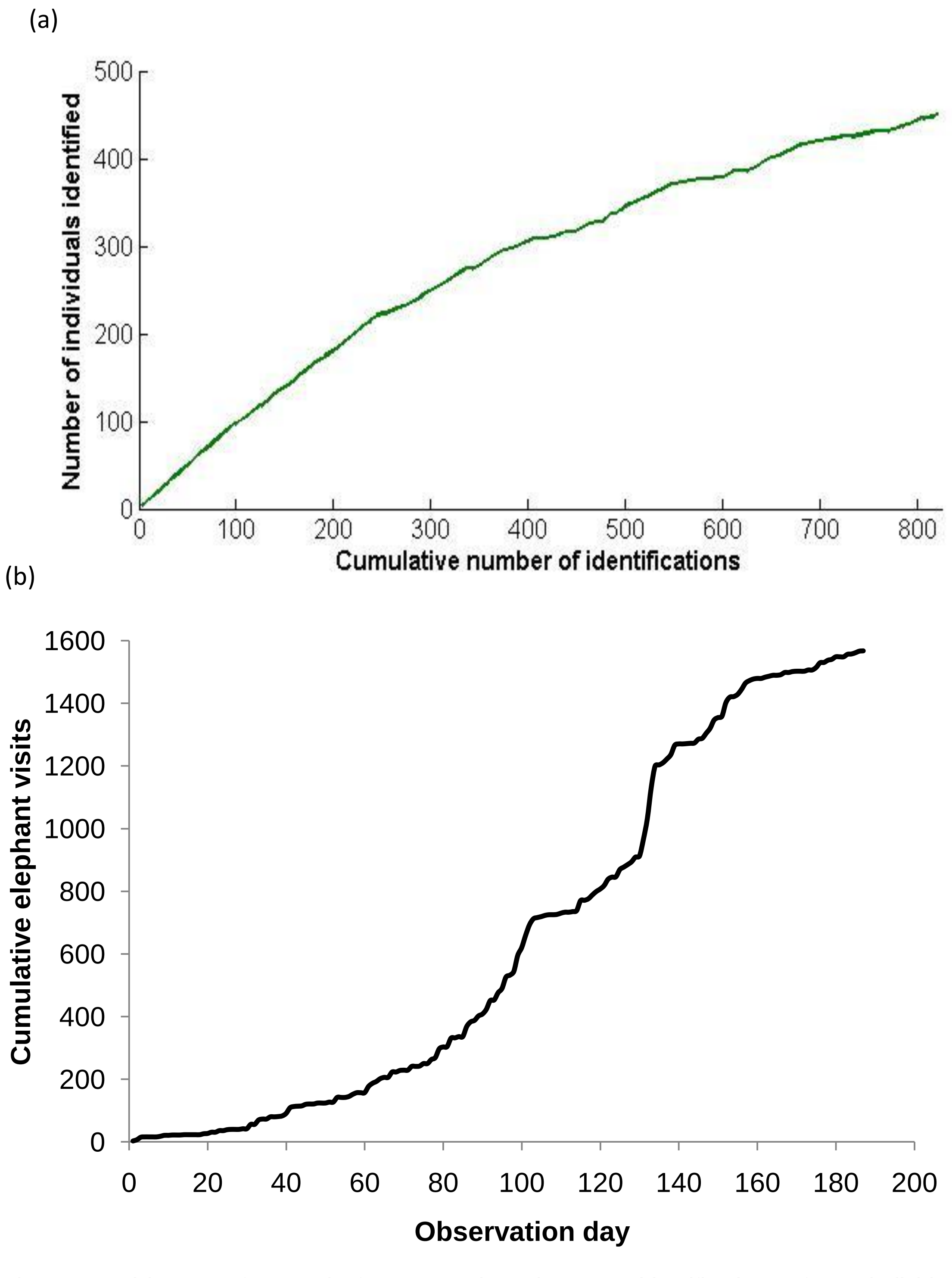

Figure 5.3. (a) Rate of accrual of new IDs, based on 809 identifications of 450 individuals observed during diurnal sampling.(b) cumulative number of elephant visits during the study period for comparison with Figure (a).

5.6 Results: Elephant Health

5.6.1 Body Condition Scoring

The distribution of body condition scores were generally similar for males and females (males: mean= 2.590, SD= 1.0574, mdn= 3.000; females: mean= 2.731, SD= 0.8163, mdn= 3.000). The highest scores (≥4) were more commonly assigned to males (22% of males; 12.5% of females) and of these most were amongst prime age males (n= 14).

There were significant monthly differences in body scores ($F_{10,556}$= 7.974, p<0.001, R^2= 0.112; Figure 5.4), with the highest scores occurring in September 2007 and the lowest scores in June 2008 (Games-Howell post-hoc tests, all p<0.05). June scores for known individuals were significantly lower than the average score from sightings in other months (June mdn= 1.5*,* other months mdn= 2.0, z= -2.675, p= 0.04*, r*= -0.57*)*.

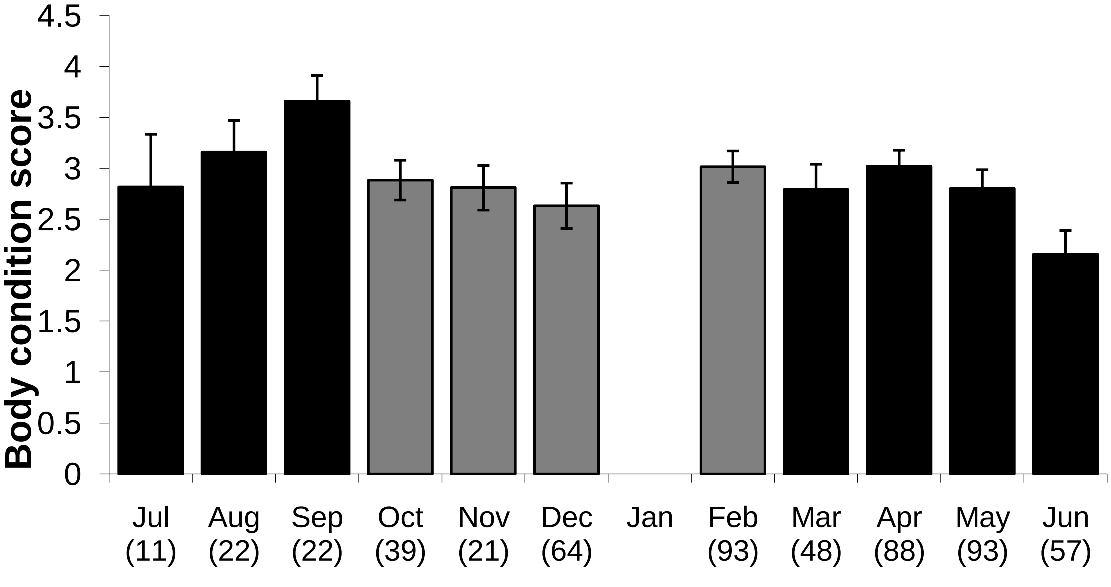

Figure 5.4. Mean body condition score by month. Error bars show 95% CI. Black bars are dry months, grey bars show wet months. Numbers in brackets indicate the number of scores made in each month.

The only relationship between body condition and seasonality measures (Chapter 3) was a trend towards a positive relationship between mean monthly body condition score and the monthly average fruit content detected in dung-piles (r_s= 0.539, p= 0.108, n= 10). There was no significant relationship between mean monthly body condition score and rainfall, measured either as mean daily rainfall per month (r_s= -0.006, p= 0.987, n= 10) or mean daily rainfall in the preceding month (r_s= -0.333, p= 0.420, n =8). Monthly fruit content of dung-piles was unrelated either to mean daily rainfall per month (r_s= -0.309, p= 0.385, n= 10) or mean daily rainfall in the preceding month (r_s= 0.048, p= 0.911, n =8).

Age effects on body condition were evident for both males and females ($F_{7,259}$= 4.114, p<0.001) and sex did not predict changes in body condition score ($F_{1,259}$=2.058, p=0.153) although an interaction between age and sex was important ($F_{7,259}$= 5.391, p<0.001, R^2=0.210). Thus age effects on body condition differed for males and females (Figure 5.5). Elephants aged 20-24 appeared to show a dip in mean body condition before a recovery in animals aged 25-34 which was particularly noticeable amongst males.

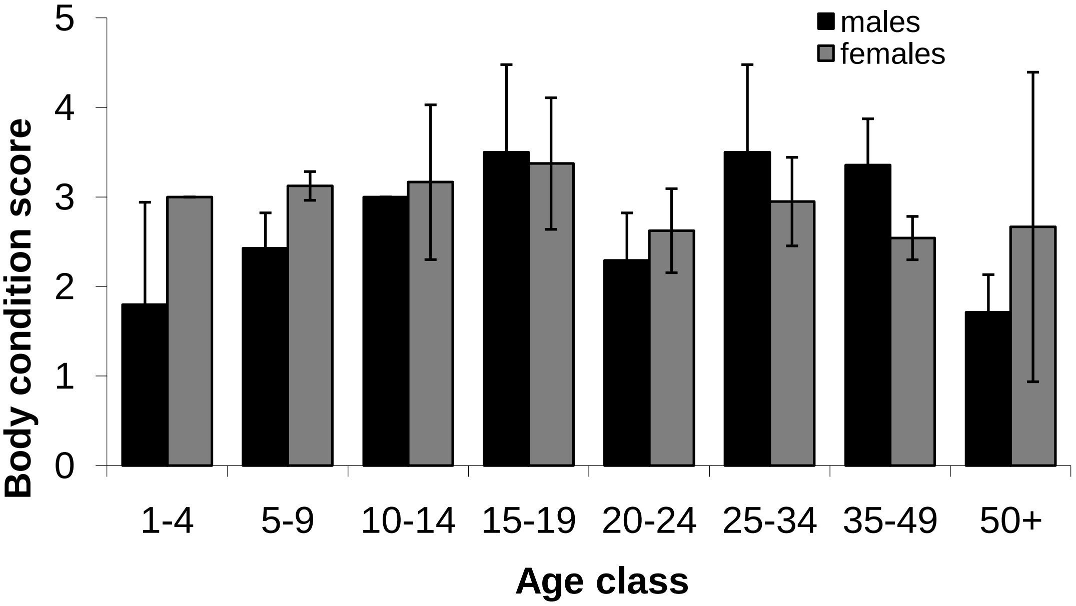

Figure 5.5. Distribution of mean body condition scores for males and females according to age-class. Black bars= males (n=100), grey bars = females (n=160). Error bars show 95% CI.

5.6.2 Wounds

Seventy eight animals of all age-sex classes were seen with injuries over the course of the study, of which 58 (74.4%) were considered to have seriously compromised the wellbeing of the individual when they occurred. Animals either sustained wounds during the study period (n= 23), or showed evidence of past wounding (n= 51; in 4 cases the age of the wound could not be determined). Serious injuries generally occurred as wounds to the flanks and abdomen (n= 17), or partial amputations of the trunk or tail (n= 29). Both males and females were seen with these kinds of serious injuries that were most likely to be human induced, and in total the injuries on 25 animals (32.1%) were categorised as human-induced (see Table 8.1). The indications are of strong human pressure on the Odzala elephant population, and these are discussed further in Chapter 8, along with other non-human mediated risks.

5.7 Results: Female Reproduction

5.7.1 Female Reproductive Status

Several relatively young females in the population were suspected to be parous and conversely several relatively old females (age class 20-24) where judged to be nulliparous or reproductively inactive (see Figure 5.6a). In total, 14 pregnancies were confirmed over the study, and a further 18 suspected, corresponding to a 14.6% potential or 8.3% confirmed pregnancy rate amongst known females aged 10 or above. Pregnancies were distributed across all female age classes (Figure 5.6b), but were commonest in younger females. This may be an artefact however, as changes in breast and body morphology are easier to detect on smaller, younger females than for larger multiparous older females.

Calves below the age of 2 were rare amongst the younger classes of female (Figure 5.6c). This is consistent with the higher proportion of nulliparous females, and the number of first-time pregnancies amongst this group. There were females in all age classes that were not investing in a current reproductive effort (Figure 5.6d), although the proportion of reproductively inactive females was lowest for those aged 35-49, where only 6 (6.2% of females in this age class) were not accompanied by calves. Overall, 81.0% of known females showed evidence of past or current reproductive effort, and were judged to be reproductively active.

The annual fecundity for the population was calculated to be 0.341 (proportion of females with calves <2, versus number of females without calves <2). The inter-birth interval for PNOK females was estimated to be 4.76 years.

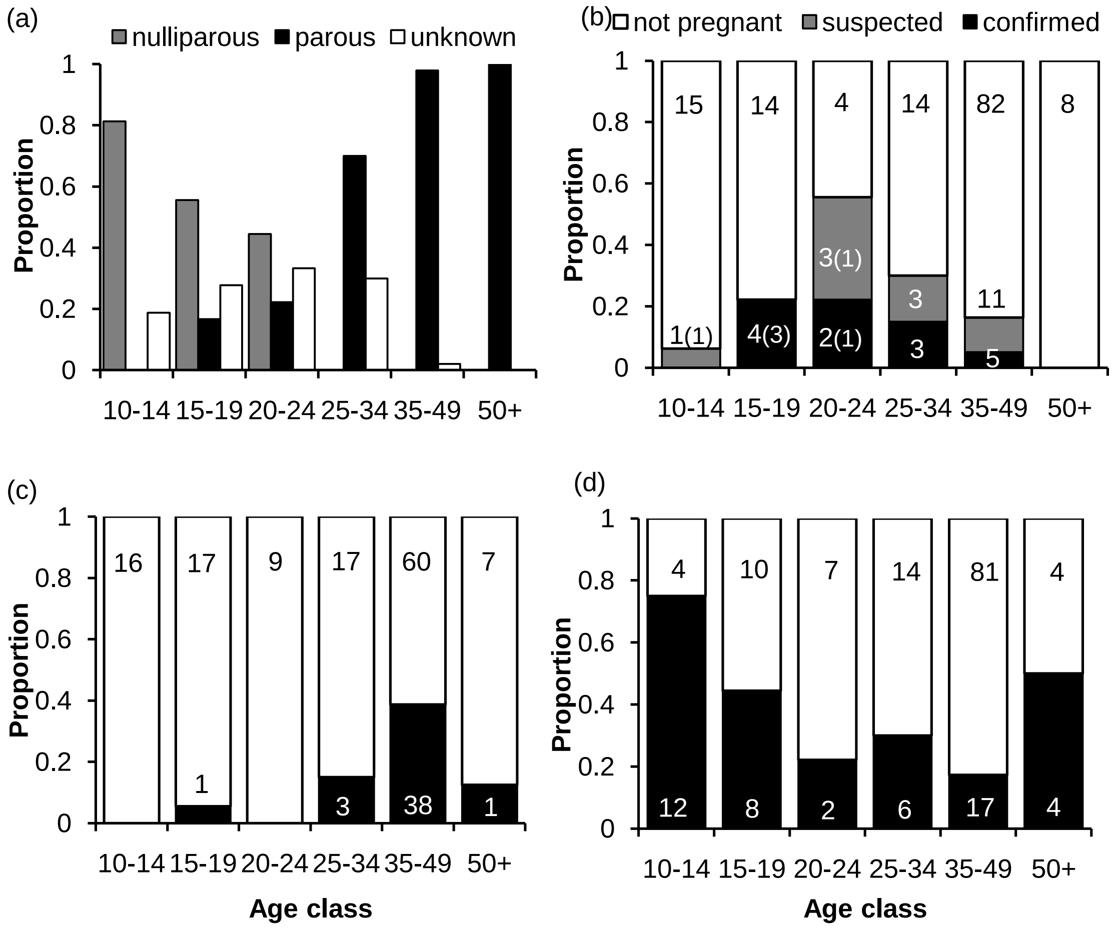

Figure 5.6. Female reproductive parameters for 169 known females aged ≥10 years. Numbers marked on Figures (b)-(d) show the number of females in each category. (a) parity, (b) pregnancies; small numbers in brackets indicate the number of these classified as primiparous, (c) females with calves aged ≤2 (black bars), (d) females classified as having no current reproductive effort (black bars; see text for definition). Sample sizes; 10-14 n=16; 15-19 n=18; 20-24 n=9; 25-34 n=20; 35-49 n=98; 50+ n=8.

5.7.2 Calf Survival

Several calves were seen to be severely injured and in very poor condition, while others seemed to be coping with or recovering from injuries (see Chapter 8). Although small calves were observed visiting the clearing alone on five occasions (see also Section 6.3) only once was the calf in question suspected to be an orphan: A young male estimated to be around 2-3 years of age visited the clearing several times, always alone and in poor body condition. He approached other elephants during these visits, but was not well tolerated by them.

Three known calves died during the study period, and one heavily pregnant female, Nicola was later seen without any calf, which was presumed to have died immediately pre- or post-partum. She had sustained a serious injury which was possibly related to the loss of her infant (see Chapter 8). Of the three known calves that disappeared and were therefore presumed dead, the youngest was the newborn calf of a relatively young female, Miranda, who was pregnant at the start of the study and who was sighted 4 months later without her infant. The other two calves were estimated to be 6 months and 18 months old, the second of these belonged to an old (and therefore experienced) mother, Hester, who was amongst the oldest females in the population (50+ years old). None of these calves was recorded as in particularly poor health prior to their disappearance.

To consider calf survival more broadly, the age-sex structure of calves below the age of 5 was examined (Figure 5.7). Balanced sex ratios were observed amongst calves between 1 and 4 years old, but diverged for infants younger than a year, and in the 3-5 year age range (0.22:1 and 0.75:1 respectively). Although a 1:1 ratio might be expected at birth, annual sex ratios can vary considerably, for example in Amboseli annual birth skews as extreme as 0.4:1 have been observed at least twice (Lee et al. in press a), so the ratios seen here may simply be a result of the low sample size in this study (n=84). In this study, the number of calves in each age category varies between 18 and 23. With similar sample sizes, Amboseli data have shown birth skews ranging from 0.8 to 2.0, although over the 38 years of study the overall ratio is not significantly different from 1:1 (Lee et al. in press a). Survival of male calves to two years old, born to young or inexperienced mothers, is lower than that of female calves (Moss & Lee in press a).

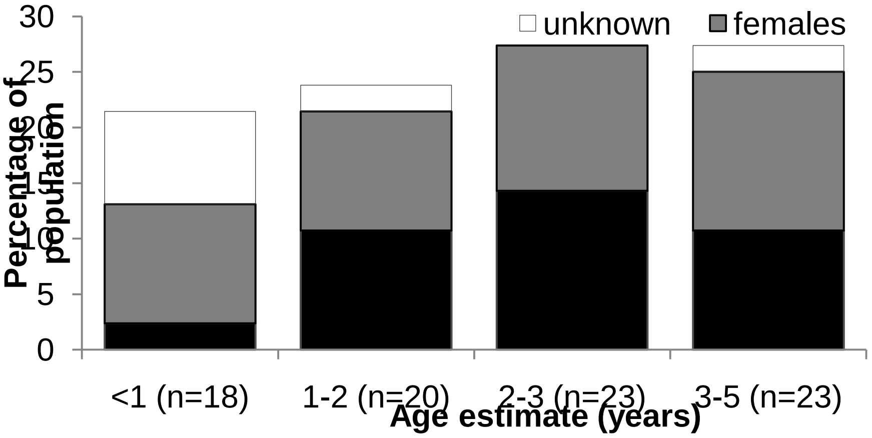

Figure 5.7. Age-sex structure for 84 known calves below the age of 5.

Calf survival over the study period was estimated as;

$$calf\ suvival = \frac{N_{inf} - total\ deaths}{N_{inf}} = \frac{28 - 4}{28} = 85.7\%$$

Coupled with the constant number of calves in each age-bracket, the data suggest high pre-weaning calf survival amongst PNOK elephants.

5.7.3 Female Temporal Gland Activity

Temporal gland activity was uncommon amongst females, and only four adult females were observed secreting from temporal glands. Two of these females were always observed with TGS (2 and 3 visits respectively) which may indicate either high social arousal in the bai context, or underlying physiological arousal. Notably, both females had very young infants and were noted to be especially dominant. A third, unknown female also showed TGS, and also had a newborn calf. The fourth female was Nicola; a female who lost a late-stage pregnancy or newborn calf due to human wounding. She made six visits to the clearing after her injury occurred, and two months after the injury was observed with TGS which may have indicated the onset of oestrus, as she had regained body condition and the wound appeared to be healing well. She was in the company of several adult males over the course of the visit, none of whom paid her particular attention.

5.7.4 Family Units

Solitary females with no associates or dependent calves accounted for 11.67% of identified females and were all aged 15 or more (Figure 5.8). Excluding these solitary females, 310 elephants from the identified population were classified as belonging to 100 family units. Mean family unit size was 3.07 (SD= 1.30, range 2-8). All matriarchs were aged over 25, and most of these were aged 35-49 (85%). A further 20 animals associated more loosely with these units in the style of bond group relationships and ranged in age from to 4 to 24 years old (Table 5.2). Forty-six percent of families contained more than one female over the age of 10, and 23% contained more than one female over the age of 20. On average families contained 1.63 females aged 10 or more (range 1-5) and 1.29 females aged 20 or more (range 1-3; Figure 5.9). Family unit composition did not vary consistently as a function of matriarch age (Figure 5.9) although the family units of "prime" matriarchs aged 35-49 showed the most even distributions of ages.

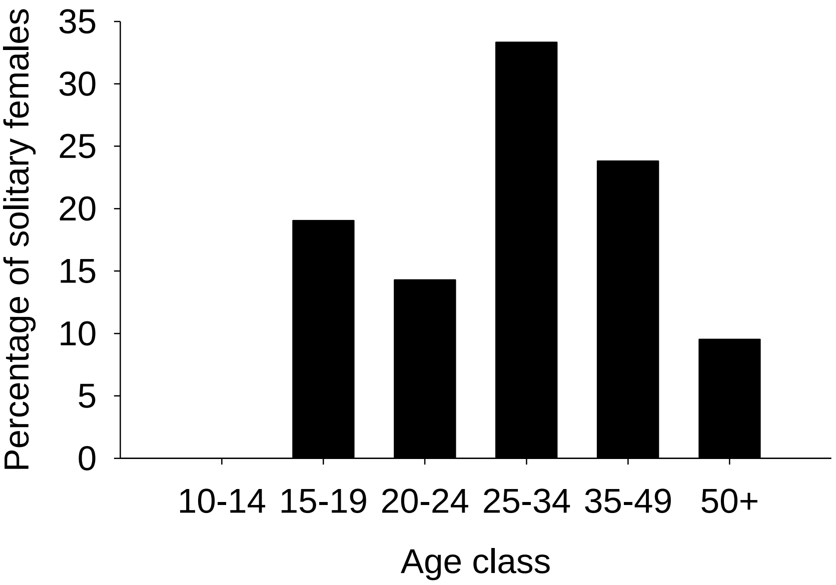

Figure 5.8. Age distribution of solitary females (n=21 elephants).

Family Unit				**Bond Group Members**		
Matriarch	**N calves**	**N females >10**	**FU size**	**ID**	**Age class**	**Sex**
Aisha	2	3	5	Adam	15-19	M
Anastascia	4	2	6	Anastascia III	0-4	uk
Caroline	2	1	3	Caroline II	5-9	F
Claire	1	2	3	Charlie	5-9	M
Erin	2	1	3	Erin III	5-9	F
				Erroll	10-14	M
Esther	1	1	2	Edgar	15-19	M
Fiona	2	1	3	Freda	10-14	F
Hazel	2	1	3	Holly	20-24	F
Kalli	1	2	3	Anya	20-24	F
				Kalia	5-9	F
Kiera	1	1	2	Kietzi	5-9	F
Kristina	2	1	3	Kelly	5-9	F
Louise	1	2	4	Lolly	0-4	F
				Leah	15-19	F
				Lucas	15-19	M
Matilda	2	1	3	Melanie	5-9	F
Motaba	2	1	3	saf	10-14	F
Tessa	2	1	3	Tina	5-9	F
Yvonne	1	2	3	Yves	15-19	M

Table 5.3. Details of family units seen with bond group individuals.

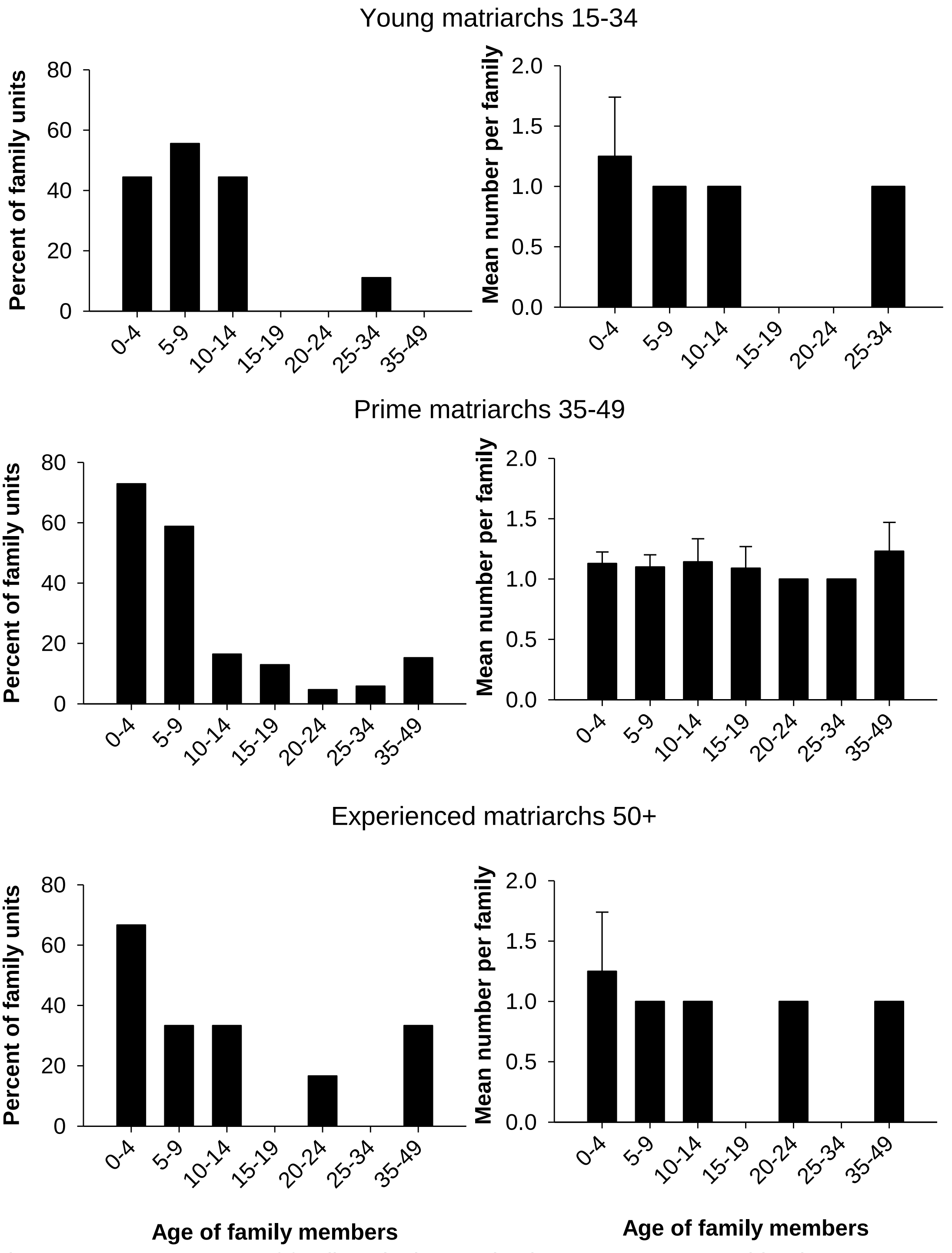

Figure 5.9. Age structure of family units by matriarch age as represented by the percentage of family units with members of each age class, and the mean number of individuals per age class (n=100 family units where matriarchs were aged over 25). Error bars show 95% CI.

5.8 Results: Musth

Sexual activity among bulls was assessed by the presence of specific characteristics associated with the sexually active state of musth. The distribution of data did not permit a chi-square analysis, although temporal gland secretion and enlargement in males were generally associated with one another (Table 5.3), and are hereafter referred to as temporal gland activity (TGA). Musth signs were rare amongst males visiting the clearing; 19.6% of known males aged 35 or more were seen with TGA, on 10.9% of visits by these males (n= 9 males; n= 13 observation days; sightings of males ≥35years old n= 82). Males dribbling urine were always seen with TGA and were thus considered to be in full musth (n=5 males, n=6 sightings).

		TGE			
		Present	Absent	Unsure	**Total**
TGS	Present	13	1	0	14
	Absent	4	291	6	301
	Unsure	1	2	6	9
	Total	18	294	12	324

Table 5.4. Patterns of temporal gland activity patterns in males, based on 324 sightings of 112 known and 115 unknown males ≥10 years old. "Unsure" was recorded when it was not possible to score presence or absence of the characteristic with certainty; most often this occurred when elephants were wet. TGE = temporal gland enlargement; TGS = temporal gland secretion.

In twelve of the 13 instances where males were recorded with full TGA, the males in question were aged 35-49. One male aged 20-24 was also recorded with full TGA. These males may well have been in the early stages of a musth episode. One musth male, Huxley, was observed to begin urine dribbling over the course of several visits, and thus move into full musth phase. Males observed in full musth were all aged 40 or above. Three musth males were also observed in consortships with the same oestrous female on different days (see also Chapter 7).

5.9 Discussion

5.9.1 Population Structure

This chapter describes the age-sex structure and size of the current Maya Nord elephant population and demonstrates unbiased sampling of the population when assigning individual identifications. For elephants, environmental stochasticity can produce apparently high variation in population structure and dynamics over the short term, although these are in fact stable over the long-term (Lee et al. in press a; Whitehouse & Hall-Martin 2000). Conclusions from this short-term dataset regarding the PNOK population structure should therefore be drawn with care, however elephant use of the Maya Nord clearing has clearly changed over a ten year period. Querouil et al. (1999) reported large aggregations as a regular occurrence (see also Chapter 4), and a balanced sex ratio among adults. These features were not observed during this study, which found a skew against adult males. In addition, Querouil et al. found a higher proportion of their population to be adult (63.8%) compared to this study (52.6%). Their relatively crude age scale makes it impossible to make a detailed comparison and thereby determine whether a particular cohort of males is missing, or whether this effect is similar across all males over the age of 15. Age-graded mortality is known to be more severe for male elephants compared to females (Lee & Moss 1986), especially when there is hunting or poaching pressure (see also Chapter 8), suggesting that Querouil et al.'s even sex ratio is unexpected. Given that there is poaching pressure on this population, a skew towards females is to be expected.

In addition, male elephants tend to range more widely than females (e.g. Douglas-Hamilton 1972; Moss & Poole 1983; Smit et al. 2007), and often disperse from their natal area; the difference between studies might possibly reflect the natural dispersal of a large cohort of young adult males. Certainly, the classification of all animals aged 15 years or older as "adult males" encompasses large changes in an individual's life history, such as the onset of musth and the establishment of settled bull areas, which affect ranging decisions. Alternatively, the skew may reflect an avoidance strategy by adult males who prefer to visit the clearing during the night. Acoustic monitoring suggests that most elephant activity occurs during the hours of darkness (P. Wrege, pers. comm.), and nocturnal observations did indicate that it was commoner to see the largest males, and a larger number of males in aggregations at these times (see Section 4.2.3).

A final hypothesis is that this skew reflects a genuine removal of large numbers of adult males from the population, and this seems highly likely, given a lack of protection in PNOK during and prior to the study period, a burgeoning ivory trade and increased access to the forests around Odzala as active logging concessions are exploited. Further modelling is required to determine if the observed age-sex structure could result from natural mortality and stochasticity in demographic processes. The presence of a number of old individuals suggests that a catastrophic population disruption has not occurred since the Querouil et al. study. However, the apparent rarity of adult males is cause for concern when coupled with observations of high elephant vigilance and fearfulness when confronted with human observers (see Chapter 8).

5.9.2 Elephant Health

I detected changes in elephants' body condition over the course of the study but these were not related to measures of seasonality as detected by elephant fruit consumption (i.e. examination of dung-piles) or rainfall. These changes were likely to be related to the availability of high-quality fruit resources but this relationship was not significant, probably due to the relatively small sample size (n= 10 months) and the interacting effects of age and sex on individual body condition. The particularly low scores in June, coupled with the overall drop in visit rate suggest that those individuals that remain in the Maya zone may not have had the energy availability to range in the same manner as the rest of the population. Since this study failed to detect any "resident" individuals (see Chapter 4), this decline in scores is not attributable to "roaming" versus "resident" ranging strategies for these elephants. Known individuals who visited during the month of June were in poorer condition than previous visits earlier in the study.

The highest body condition scores were observed amongst "prime" males, as would be expected; these males are competitively superior and are expected to invest in body mass to achieve peak condition prior to beginning metabolically costly musth episodes (Poole 1982, 1989a; Schulte & Rasmussen 1999). Males aged 20-24 appeared to have low body condition, before a recovery in condition amongst males aged 25-34. This "dip" may be related to a lack of competitive ability, high investment in growth or tusk development, or reduced foraging efficiency after dispersal from natal areas. Females showed less clear effects of age on body condition than did males, probably due to their sustained investment in costly lactation across their lifespan (Clutton-Brock et al. 1989).

5.9.3 Reproduction

The majority of known females were actively reproducing, suggesting that PNOK elephants are not reproductively constrained either by ecological stressors such as limited food availability, or chronic social stressors resulting from heavy and sustained poaching pressure (Gobush et al. 2008). Age at first birth is known to be a highly variable parameter for elephants, varying substantially according to population (Sukumar 2003) and also over time within populations (Moss 2001; Lee et al. in press a). Females in the PNOK population appear to start reproducing relatively late according to these data, with pregnancies only observed after the estimated age of 15. The rarity of calves below two with females younger than 25 years old suggests that a number of these first pregnancies may abort or result in neonatal deaths (Moss 2001).

A small number of females were known to lose calves over the study period, and the relatively old females (>20 years) judged to be nulliparous probably also suffered failed reproductive events. Overall however, pre-weaning calf survival appears to be high in the population based both on the re-sightings of known calves and on their age structure; for calves below the age of five, there were approximately constant numbers across age classes. I estimated calf survival over the study period to be 0.857, which is broadly equivalent to calf survival reported from Amboseli (males 0.785, females 0.836; Lee et al. in press a). Maternal experience is a factor in calf survival, as has been documented for savannah populations (Lee & Moss 1986; Moss & Lee in press a). Family units were small in size, consistent with reports from other studies (Momont 2007; Morgan & Lee 2007; Theuerkauf et al. 2000; White et al. 1993). The observed family unit size was also consistent with Querouil et al. (1999) who reported that groups larger than 6 were never seen more than twice with same composition, and they hypothesised these were formed from multiple family units (but see also Section 8.5).

Musth bulls were rarely observed in the clearing. Albeit that musth males may be rare in a population at any given point in time (with one or two in any month), these data may exaggerate this rarity, as it was more common to see the largest males during nocturnal observations than during the day (Chapter 4) suggesting that males may avoid using clearings during daylight hours (Vanleeuwe et al. 1997). In addition, oestrous females are likely to be patchily distributed in both space and time in forest ecosystems, unlike in savannah areas where a period of resource limitation followed by resource proliferation causes a degree of synchrony in the availability of oestrous females (Laws et al. 1975; Moss 2001; Wittemyer et al. 2006). This in turn leads to a peak in male-male competition, and the largest and most dominant males enter musth during this peak season; the presence of these dominant males in musth also leads to reproductive suppression of more subordinate males (Poole 1989b). This complex synchrony/asynchrony of reproductive activity is underpinned by clumped resource availability. Where resources (and therefore oestrous females) are more evenly distributed synchronisation may disappear. The rarity of oestrous females is further underlined by the low frequency of flehmen behaviours (see section 7.5). This bai appears not to act as a mating arena for PNOK elephants, although behaviours associated with reproduction were observed (Chapter 7).

Chapter Six

Sociality: Associations

Chapter 6 Sociality: Associations

6.1 Abstract

Forest elephants at Maya Nord exhibited non-random associations at both aggregation and party levels, and patterns differed between these levels, so that elephants showed multi-level social organisation in the bai. The non-random nature of aggregation-level organisation suggests that social decisions to associate and aggregate were made at least in part before elephants entered the clearing. Both inter- and intra-sexual relationships were important, and intra-sexual relationships were maintained by directly associating with conspecifics, rather than by "eavesdropping" through observing those conspecifics interact with others (Bonnie & Earley 2007). Relationships were structured by age and sex, and all network measures showed significantly high variation, suggesting the potential importance of individual identity in the structuring of forest elephant relationships. Female associations structured many of the observed relationships and old matriarchs (those aged 50+) appeared to play a central role. Active choice of associates and avoidance of other conspecifics underlines the importance of individual identity for forest elephants, and demonstrates the importance of clearings as social centres as well as points of access for nutritional resources.

Elephants using Maya Nord associated at above-chance levels, although AIs were low. All networks showed high clustering, indicating a "friends of friends" scenario, suggestive of matrilineal relationships for females, and a male society also structured

by age and individual identity. Females were more gregarious than males and showed stronger preferences for companions and more active avoidance of other conspecifics than did males. Males were socially more explorative than females, consistent with observations for savannah elephants (Lee & Moss 1986, 1999, in press). 10-14 year old animals of both sexes were highly socially explorative, which may be associated with minimising the costs of social dispersal. Males were more connected to each other than to females, although between males, 20-24 year olds and the oldest males (50+ years) were unconnected in the network. For 20-24 year olds this may because these males have undergone social and locational dispersal from the natal group and natal range, and have not yet firmly established themselves in the male society and dominance hierarchy. For the oldest males, this lack of connectedness may be related to the strong deference shown to them by all other age-sex classes.

Most animals associated with other elephants while in the clearing, and in doing so lengthened their visits by approximately 50% compared to elephants who did not associate outside their ranging parties. Mixed parties were common, despite the female bias in the visiting population; thus when males were present they sought to associate with females. These mixed parties could be large and provided elephants with rich social opportunities not available in small, same-sex ranging parties. Elephants were attracted to larger parties. Females were attracted to older individuals, but males did not show preferences for the age of individuals they associated with.

6.2 Introduction

In clearings, forest elephants have the visual and olfactory as well as the auditory opportunity to choose their spatial associates. They can choose to be in close proximity, or they can (and do) exclude conspecifics from resource access points within the clearing. Hence, the socio-spatial arrangement of elephants in the clearing can reveal much about individual relationships and thereby the surface structure of the population (Hinde 1976). Historically researchers have failed to quantify forest elephant social structure due to the sparse nature of association matrices produced at fixed point studies: Datasets are constrained to the dyads observed during diurnal observations, and all observations are inherently dependent on individual ranging decisions, which are the outcome of dynamic interactions between resource availability, reproductive status and individual experience (e.g. Blake 2002; Momont 2007). Association indices have been widely used in studies of sociality and gregariousness (Ginsberg & Young 1992) but as discussed in Chapter 1, network analysis is a relatively new technique for revealing structures within aggregations (e.g. Lusseau & Newman 2004; Wey et al. 2008; Whitehead 1995; Whitehead 1997; Whitehead 2008a; Whitehead 2009).

Studies of forest elephant acoustic communication have shown levels of complexity that directly parallels those of savannah elephants (Payne 2003; Thompson 2009), indicating that forest elephants are also capable of high-level individual discrimination over a large number of individuals (McComb et al. 2000, 2003; Soltis et al. 2005). Since forest elephants can discriminate, they should also choose their associates, and it is most parsimonious to assume that their relationships would be structured by the same organising principles as for savannah elephants i.e. by age and sex. If elephants use forest clearings as social arenas to acquire social information, individuals can either associate directly with conspecifics (in parties) to acquire information, or they can “eavesdrop” on interactions between other elephants. Such eavesdropping should be an efficient method of extracting social information (Bonnie & Earley 2007), and elephants might eavesdrop on others in their party, or observe interactions occurring in other parties i.e. aggregation level associates.

Thus if forest elephants use clearings as social arenas in order to maintain a complex fission-fusion system, a number of expectations are generated regarding their patterns of socio-spatial organisation within a clearing. Specifically it is predicted that;

1. Elephant associations within the clearing are non-random.
2. If multi-level organisation is present, patterns of association should differ between party- and aggregation-level organisation, as individuals should discriminate between party-level associates more closely than aggregation-level associates.
3. Associations should be structured by age and sex, which are key organising principles for savannah elephant sociality.
4. Elephants that associate with conspecifics whilst in the clearing should differ in their clearing visits compared to animals that use the clearing alone.

6.3 Chapter Aims

6.3.1 Describe socio-spatial organisation of elephants using Maya Nord

This chapter describes the social component to bai use by quantifying gregariousness amongst elephants in the clearing, and then describing the dynamics of gregariousness. Gregariousness is used here to describe the propensity of individuals to spend time with conspecifics, thus creating the opportunity for interactions. Gregariousness measures used both party- and aggregation-level data: Parties were considered independent units for these analyses since they represent choices by individuals regarding immediate close proximity to conspecifics. Aggregations were considered to provide the opportunity for animals to acquire social information by “eavesdropping” on third party interactions. This chapter uses association indices between individually identified animals to construct social networks, and both association indices and networks were permuted to test for non-random patterns of association.

6.3.2 Quantify the dynamics of gregariousness

The second part of this chapter explores the dynamics of gregariousness, by examining the effects of associating with conspecifics in the bai. If bais function as social arenas, animals would be expected to modify their visiting patterns depending on whether or not they associated with individuals outside their ranging party (individuals who arrived and left together, often but not always based around family units). The dynamics of gregariousness are described using data from both identified and unknown animals, with data examined according to age-sex class, rather than at the individual level (Fishlock et al. 2008). Visits by elephants who did not change party whilst in the clearing are described before the dynamics of party change are examined, exploring how parties formed in the clearing differed from animals who arrived and left together (ranging parties), and how life history stage and the social situation affected elephants' decisions to associate.

6.4 Methods

6.4.1 Descriptors of Gregariousness

Association analyses were conducted using SocProg v.2.4 (for MATLAB 7.7.0.471, release 2008b; Whitehead 2009) and were based on 292 individually identified elephants aged 10 or over (Table 6.1). Associations between identified individuals were calculated in using a half-weight index (HWI) (Cairns & Schwager 1987; Whitehead 2008a). This index was chosen as it reduces bias when not all associates are identified (which often occurred during very busy periods; Whitehead 2008a). It is calculated as;

$$HWI = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$$

Where x is the number of times individuals A and B were seen associated, y_A is the number of times A was identified without B, y_B is the number of times B was identified without B, and y_{AB} is the number of times both A and B were identified in a sampling period, but were not associated with one another. Associations were defined on the basis of party membership, except for social networks, which were also constructed on the basis of aggregation membership (see below).

Age class	N males	N females
10-14	16	17
15-19	17	18
20-24	17	8
25-34	20	22
35-49	104	40
50+	5	8
Total	115	117

Table 6.1. Age-sex distribution of 292 identified animals used in permutation tests and network analyses.

Permutation tests were used to generate random datasets against which to test the null hypothesis that the observed patterns were random associations between individuals. These tests control for the pattern of field effort, individual differences in gregariousness and the likelihood an individual is identified. The process then takes random data pairs in the observed association matrix and “flips” them (swaps them over) a specified number of times, in order to create a new matrix with the same properties as the real data (overall age-sex structure, level of association etc.). This procedure is repeated over thousands of permutations, to generate a population of random data matrices which are then evaluated against the observed data. The number of permutations required is assessed by inspection of random standard deviation values; the permutations and flips are increased by the experimenter until the standard deviation values stabilise, which occurred at 5000 permutations and 1000 flips. For this thesis, the “associations within samples” method of permutation was used, as this makes fewer assumptions about underlying social structure than alternative methods, such as permuting groups within samples (Whitehead 2008a, 2008b).

Permutation tests were performed for the identified population using individuals over 10 years old, and then separately for males and females, both at a party and aggregation level. Aggregation level associations were defined as all animals in the bai within 90 minutes of each other (based on log survivorship analyses as described in Chapter 2). Permutation tests were also run on an inter-sex basis to identify preferred and avoided associates of males amongst females and vice versa. The p-values generated from these tests are not statistical p-values, but rather p values from randomisation tests, and are denoted as $\hat{p}$ to separate them clearly from statistical Probability values. These $\hat{p}$-values are the proportion of iterations where the generated random value was greater than the observed value: if random values are always greater than observed data, then $\hat{p}$ = 0, if the real data are always greater than random values, $\hat{p}$ = 1. Values of $\hat{p}$ were considered significant when the proportion of iterations identified as significantly different was within 5% of the extreme (when 0.95 ≥ $\hat{p}$ ≤ 0.05; Whitehead 2008a). Observed data were thus considered significant if less than 5% or more than 95% of random data sets differed from the observed data.

Networks of association were calculated for all individuals over the age of 10, and for males and females separately, for both party- and aggregation- level associations. SocProg generates several highly correlated test statistics that describe the mathematical properties of the network, which are calculated for both real and randomly generated data: Here the mean of Association Indices (AI), Coefficient of

Variation (CV), and the proportion of non-zero AIs were used to evaluate the observed data (see Table 6.1 for explanation and interpretation of these measures). SocProg also offers the possibility to carry out temporal analyses which examine how long individuals were associated for. Such analyses were not conducted in this thesis since basic descriptive statistics showed that elephants often entered and exited with the same individuals, and since the re-sighting frequency of known individuals was so low it was considered to limit the resolution and therefore the value of these analyses (Whitehead 1995).

The series of network measures describe related but distinguishable qualities of the network (Table 6.1). Network measures are not directly comparable between different networks in a quantitative sense (Whitehead 2008a) i.e. it is not correct to assume that a Reach score of 4 is double that of a score of 2, if the networks are generated using different data. However, general patterns are comparable, and here I compare network measures between age-sex classes and relate these to aspects of social development and reproduction. Networks were permuted to test the null hypothesis that individuals are randomly connected in the network, given the structure of existing data. Random standard deviation values for networks stabilised at 5000 permutations and 1000 flips. Network measures are graphed and the full data tables and all associated $\hat{p}$-values are attached in Appendix D.

Measure	Interpretation
Coefficient of Variation (CV)	Standardised measure of dispersion (=SD/mean). E.g. for AIs shows how differentiated AIs are for an individual. If some individuals preferentially associate, then CV will be higher in real, compared to random datasets.
Proportion of non-zero AIs	If some individuals preferentially avoid conspecifics, then will be lower in real, compared to random datasets.
Strength	The sum of all AIs. Directly equivalent to gregariousness: how connected individuals are to others in the network
Reach	The overall strength (connectedness) of neighbours.
Eigenvector Centrality	How well connected an individual is in the network, as an overall measure of the number and strength of connections and to whom (and is therefore a function of reach).
Clustering coefficient	The measure of likelihood that triads exist, i.e. how well connected neighbours are to each other. Measures total number of triads against the possible number, and is standardised by the maximum weight in the network.
Affinity	Weighted mean strength of neighbours: equivalent to reach divided by strength.
Assortativity	Correlation between strength and affinity. When positive, indicates tendency for highly connected individuals to preferentially associate: a common situation in social networks.

Table 6.2. Interpretation measures used for permutation tests of preferred/avoided associates and for social networks (Whitehead 2008a;Whitehead 2009).

6.4.2 Dynamics of Gregariousness

I categorised elephants according to their social experience whilst using the clearing, either as gregarious “changers”, who contacted other elephant parties during their visit, or as “non-changers”. These “non-changers” were either non-changing parties, or solitary animals who visited alone and did not join other elephants in a party. Elephants were not considered to be solitary if they made a second clearing visit within 90 minutes, where they contacted other individuals. To determine if solitary animals used the clearing differently to animals who visited with conspecifics, visits by solitaries were compared to 278 visits by non-solitary animals who changed groupings (all these animals were in different parties, since animals often entered and exited with the same individuals: Section 6.3.2). Differences in visit duration (overall time in the clearing) according to social experience were examined using a type I ANOVA controlling for month and time block.

For animals who changed parties during bai visits, differences between party types in the size and duration of parties (time in a party) were assessed using type I ANOVAs, controlling for month and time block. Party sizes when elephants joined others were assessed relative to their current party size using Wilcoxon signed ranks tests (with Bonferroni correction applied) for different intensities of elephant visits (low, medium or high as defined in Chapter 4, p89). Party sizes were also assessed according to where they formed; parties entering or exiting the clearing were compared to those that formed in the clearing, using a Mann-Whitney U test (with Bonferroni correction) for all levels of visit intensity.

Logistic regression models were used to examine age-sex differences in decisions to associate, by examining the creation of multi-male, multi-female and mixed parties. Same-sex parties were examined by creating a one-zero response variable for individuals who did or did not join same-sex conspecifics. Only one individual per ranging party contributed to these analyses; for multi-female parties I used the matriarch on the assumption that matriarchs guide social decisions for savannah elephants (e.g. McComb et al. 2001). Predictors were either related to the individual (age) or to the social situation (size of party, relative age of conspecifics i.e. older/younger, visit rate intensity i.e. low/medium/high as defined). To examine the creation of mixed groups, individuals were coded as one-zero according to whether or not they joined to mixed groups to create the response variable. Predictors were individual age, sex and visit rate intensity. Logistic regressions were run using a forward stepwise procedure to determine the relative importance of predictors, and were also run using a backward procedure to check for suppressor effects. Predictors were retained or dropped from logistic regression models due to their respective Wald values during the model fitting process; predictors dropped from the model (i.e. who did not contribute to the explanatory power of the model) are reported in table legends throughout.

6.5 Results: Describing Gregariousness

6.5.1 Association Indices

Party-based association indices (AIs) were low for all age-sex classes (Figure 6.1) as expected, due to the low re-visit frequency coupled with imperfect identification rates (especially during periods of high visit rate when aggregations were large). Association rates differed overall according to age-sex class (n=450 animals; two-tailed Mantel test with 1000 permutations: t=-1.886, p=0.019). When infants (<5 years old) were excluded from the analysis, this difference disappeared (two-tailed Mantel test with 1000 permutations: t=-0.1118 p=0.457), suggesting that the differences detected by this test were due to strong bonds between mothers and dependent offspring. Males showed consistently lower AIs regardless of age class (Figure 6.1) and an apparent trend for decreasing AI with age.

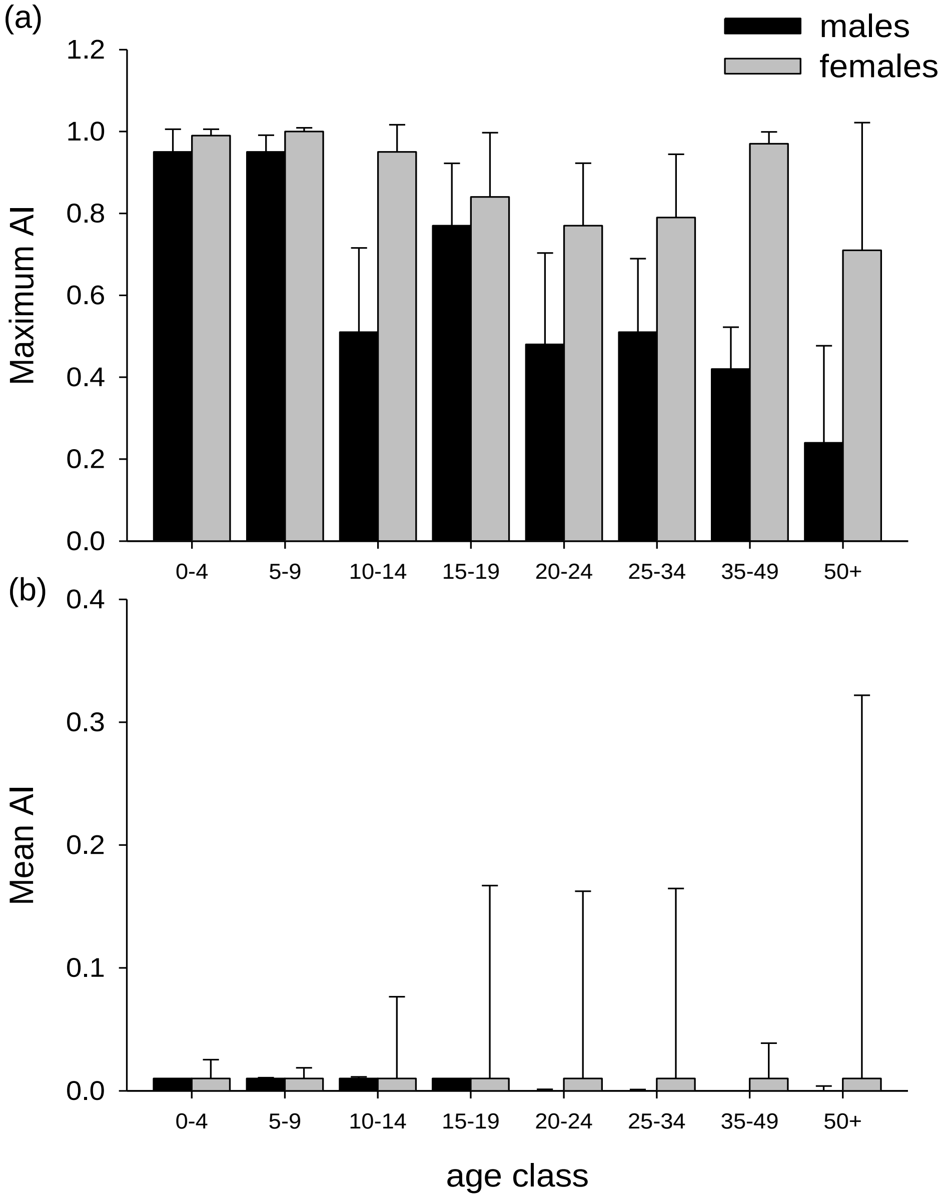

Figure 6.1. (a) Maximum AI and (b) mean AI by age-sex for 450 known individuals, calculated using a Half Weight Index. Maximum AI values are presented as a measure of the closest associates of each age-sex class, for comparison to the mean scores which show a measure of the general gregariousness of each age-sex class.

Party-level permutation tests showed AIs were higher than expected by chance, with a high CV and low proportion of non-zero elements compared to random data (Table 6.2), indicating that elephants actively chose certain associates while actively avoiding other conspecifics. Female-female relationships showed the same patterns, while males associated with other males at levels that were not different from random. The overall effects could therefore be due to the strong tendencies for females to choose associates. At an aggregation level, elephants showed active choice for associates, and active avoidance of conspecifics (Table 6.2), but mean association levels did not differ from random. Once again these patterns were only true for inter-sex associations and for female-female relationships.

PARTY-LEVEL ASSOCIATIONS		Both	Males only	Females only
AI mean	Observed	0.00621	0.00545	0.00818
	Random	0.00614	0.00545	0.00796
	$\hat{p}$	**0.9956**	0.4598	**0.9998**
CV	Observed	10.66813	10.67454	9.75241
	Random	10.40114	10.67392	9.41724
	$\hat{p}$	**1**	0.5202	**1**
Proportion non-zero elements	Observed	0.01156	0.01236	0.01297
	Random	0.01234	0.01228	0.01461
	$\hat{p}$	**0**	0.7672	**0**
AGGREGATION-LEVEL ASSOCIATIONS		Both	Males only	Females only
AI mean	Observed	0.01262	0.01188	0.01598
	Random	0.0126	0.01188	0.01593
	$\hat{p}$	0.7926	0.442	0.847
CV	Observed	7.31958	7.54731	6.66429
	Random	7.25083	7.54233	6.59994
	$\hat{p}$	**0.9998**	0.693	**1**
Proportion non-zero elements	Observed	0.02464	0.0241	0.02915
	Random	0.02514	0.02402	0.02989
	$\hat{p}$	**0**	0.767	**0.0002**

Table 6.3. Permutation test results for preferred and avoided associates at party level and aggregation level organisation. N= 292 identified individuals aged 10 years or older. NB where $\hat{p}$*=1, observed data > all randomly generated values. Bold values are significant.*

Permutation tests examining inter-sex preferences showed party-level associations were lower between males and females than expected from random (Table 6.3), signifying a degree of sexual segregation. At an aggregation level, males were with females less than expected by chance, while females were with males at chance levels. Females showed high CV in their associations with males, indicating active choice, coupled with a non-significant tendency to avoid certain males.

PARTY-LEVEL ASSOCIATIONS	Observed inter-sex AI	Males to females	Females to males
AI mean	0.01029	0.01033	0.01032
$\hat{p}$		0.0582	**0.01266**
CV	7.85466	7.83708	7.83303
$\hat{p}$		**0.9858**	**0.996**
Proportion non-zero elements	0.02137	0.02142	0.02144
$\hat{p}$		0.2122	0.153
AGGREGATION-LEVEL ASSOCIATIONS	Observed inter-sex AI	Males to females	Females to males
AI mean	0.00494	0.00498	0.00496
$\hat{p}$		**0.004**	0.25
CV	11.4277	11.41176	11.38737
$\hat{p}$		0.8574	**0.996**
Proportion non-zero elements	0.01022	0.01028	0.01029
$\hat{p}$		0.11	0.0872

Table 6.4. Permutation tests for preferred and avoided associates for males amongst females and vice versa, at party and aggregation level organisation. N= 292 identified individuals aged 10 years or older. NB where $\hat{p}$=1, observed data > all randomly generated values. Bold values are significant.

6.5.2 Social Networks

All networks were characterised by high clustering coefficients with high CV (Table 6.4). These clustering coefficients are equal to the proportion of observed triads; it appears that forest elephants show associations between “friends of friends”, but with a high degree of individual variability in the extent of these associations (resulting in a high CV). The low eigenvector centrality values observed suggest that these networks were not centred on a few key individuals, while a high CV indicates this measure was highly variable between individuals. Consistent with this observation, affinity measures were lower than expected for all networks, with high CVs, indicating that most individuals were not connected to highly connected neighbours. These low affinity measures might reflect attraction between animals of dissimilar age as low affinity suggests social connections between animals occupying different social roles, which for elephants are principally structured by age and sex (e.g. Wittemyer et al. 2005). However, assortativity measures were positive for all networks, indicating that the neighbours of well-connected individuals are themselves well-connected.

Measures of strength and reach were far more variable between the networks. Males appeared to be more gregarious than expected within parties but not within aggregations, both with other males and with females. Female gregariousness did not differ from random expectations, although at an aggregation level there was a tendency for more individual variation than expected by chance (high CV). Males are thus more socially exploratory than females, who are more often found with conspecifics than males (see AI permutation tests above), but who express stronger choice for their social partners.

The gregariousness of neighbours in the network (reach) varied according to the sex included in the network, and the association level used: the inter-sex network showed high reach and with high variation in party- and aggregation-level associates. Intra-sexual networks showed sex-specific patterns: male-male relationships showed high party-level but low aggregation-level reach whereas females showed party-level reach at random but higher than expected reach at an aggregation level. All reach values showed higher than expected CVs, again underlining strong individual differences in these measures.

PARTY-LEVEL ASSOCIATIONS		Inter-sex	Males only	Females only
Strength	Observed	1.81	1.44	0.62
	$\hat{p}$	**0.99**	**1**	0.45
	CV test	0.08	**0.03**	0.32
Reach	Observed	5.89	3.47	1.03
	$\hat{p}$	**0.95**	**1**	0.37
	CV test	**1**	**1**	0.76
Eigenvector Centrality	Observed	0.01	0.01	0.02
	$\hat{p}$	0.72	**0.01**	**0**
	CV test	0.28	**0.99**	**1**
Clustering coefficient	Observed	0.52	0.6	0.32
	$\hat{p}$	**1**	**1**	**1**
	CV test	**0**	**0**	**0.05**
Affinity	Observed	2.58	1.93	1.4
	$\hat{p}$	**0**	**0**	**0.04**
	CV test	**1**	**1**	0.94
Assortativity	Observed	0.7277	0.895	0.59
	$\hat{p}$	**1**	**1**	0.7423
AGGREGATION-LEVEL ASSOCIATIONS		Inter-sex	Males only	Females only
Strength	Observed	3.67	1.35	2.81
	$\hat{p}$	0.79	0.43	0.85
	CV test	0.51	0.27	0.91
Reach	Observed	22.8	5.69	12.45
	$\hat{p}$	0.9	0.07	**1**
	CV test	**1**	**0.99**	**1**
Eigenvector Centrality	Observed	0.01	0.03	0.02
	$\hat{p}$	**0**	0.8	**0**
	CV test	**1**	0.2	**1**
Clustering coefficient	Observed	0.52	0.34	0.57
	$\hat{p}$	**1**	**1**	**1**
	CV test	**0**	**0**	**0**
Affinity	Observed	4.74	2.33	3.56
	$\hat{p}$	**0**	**0**	**0**
	CV test	**1**	**1**	**1**
Assortativity	Observed	0.8036	0.9151	0.8132
	$\hat{p}$	**1**	**0.993**	**0.9998**

Table 6.5. Overall means of network measures for all association networks. N= 292 identified individuals aged 10 years or older. NB where $\hat{p}$*=1, observed data > all randomly generated values. Bold values are significant.*

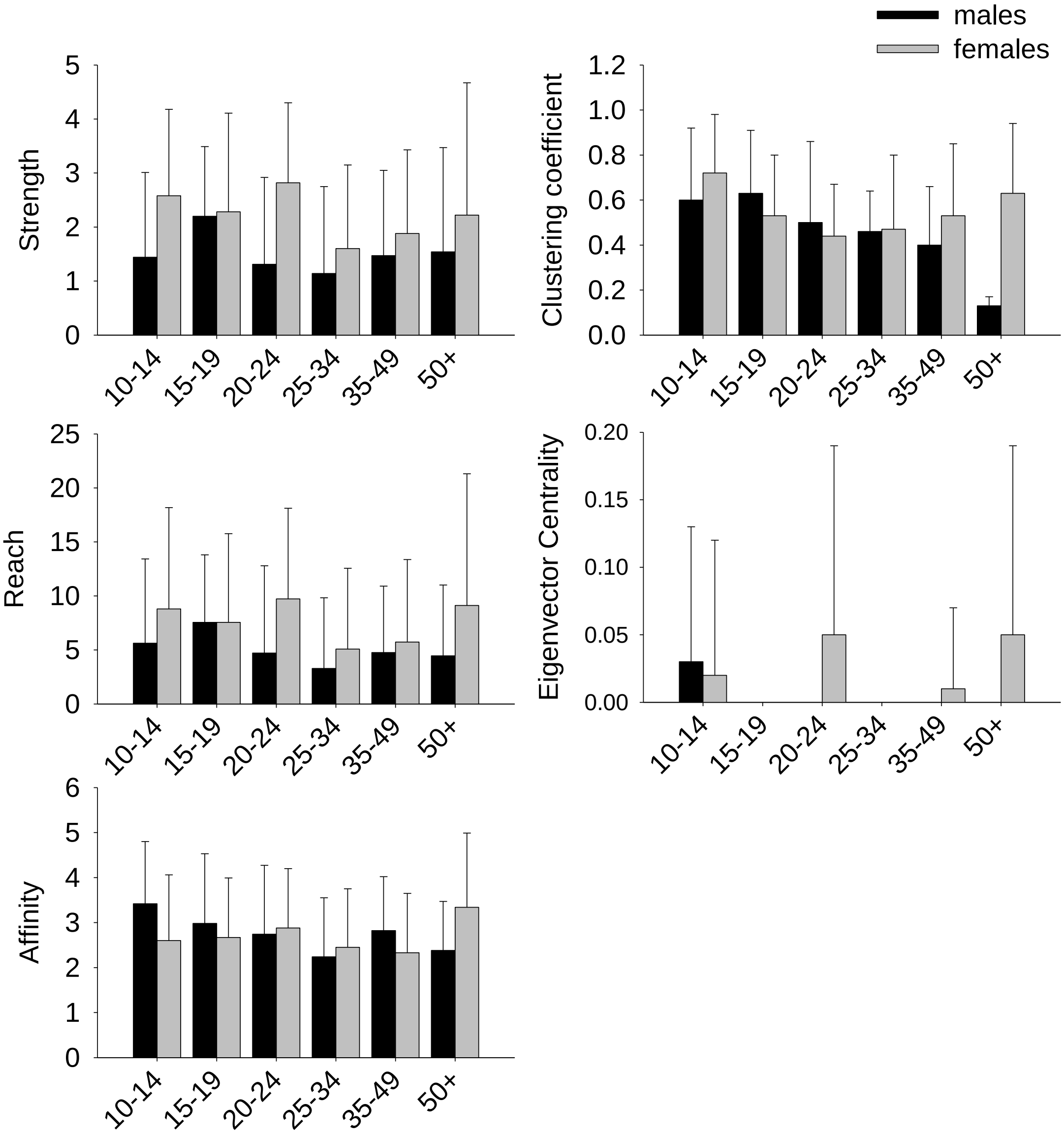

Figure 6.2. Observed network measures for a party-based network for males and females together. Error bars show SE. N= 292 identified individuals aged 10 years or older.

Closer examination of age-sex structuring in associations showed that females scored higher than males on all network measures at party-level organisation (Figure 6.2). All age-sex classes showed gregariousness tendencies close to random expectations, although there were small but significant differences for females aged 10-14, 35-49 and 50+ who showed higher than random strength values, and for males aged 20-24 who showed lower than random strength. This was also true for reach, except that 35-49 year old females did not differ from random, and 10-14 year old males and 15-19 year old females showed lower than expected values. On reach measures, all age classes except 50+ females and 10-14 year old males had larger CVs than expected by chance, highlighting strong individual differences in neighbour gregariousness existed for the majority of the population. The oldest (50+) and youngest adult females (10-14 years) had the highest reach values, indicating these are the classes which may be either "social glue" or socially explorative individuals (Whitehead 2008a; Williams & Lusseau 2006). Males aged 25-34 had lower than expected reach. Eigenvector centrality measures found that males were unconnected in the network, except for the 10-14 year old males. Female eigenvector centrality measures were also low and did not differ from random, although 10-14 year old, 20-24 year old and 50+ females showed higher than expected variation indicating that some of these individuals hold key roles within the network. Clustering coefficients were higher than expected for all age-sex classes with smaller than expected CVs, indicating that all classes contain some animals which exhibit high levels of linkage between their associates ("friends of friends"). Affinity measures for females had lower than expected CVs, and values were lower than expected for all females except for the oldest (50+) females who showed a small but significant increase in affinity compared to random. Males did not differ from random on affinity measures except for 25-34 year olds and 50+ year olds, whose affinity was lower than expected. Thus, only the eldest females are apparently connected to well-connected individuals more than chance, and these are also the individuals with the highest reach measures.

Overall, results at a party level suggest a female-based association network where males do not play a central role. The strongest attractive roles in this network appeared to belong to the eldest females and to young females aged 20-24. Males and females aged 10-14 years were both active in the network, whilst the oldest males and 25-34 year old males were more peripheral than expected. For 25-34 year old males, this may be because they are not aggressive but they also lack competitive ability with respect to older males, and are poorly tolerated due to their sexually active behaviours (see Chapter 7).

Measures were lower in same-sex party networks than the inter-sex network (Figure 6.3), suggesting that some of the variation in social relationships was driven by inter-sex relationships. Both males and females had higher than expected clustering coefficients with low CVs, indicating same-sex neighbours are themselves linked to each other. Male-male relationships showed very similar patterns to those described for males in the inter-sex network: strength measures did not differ from random, reach was low for 10-14 year old and 25-34 year old males and clustering coefficients were generally higher than expected, except for 10-14 year olds (Figure 6.3). However, eigenvector centrality measures were higher than for the inter-sex network, suggesting that males are more connected to other males than they are to females. The oldest males remained unconnected in the network despite behavioural evidence that they were attractive to conspecifics (see Chapter 7), as did 10-14 year old males. Affinity measures were generally at random levels for males, but 20-24 year old males showed higher affinity than expected, indicating well-connected elephants have well-connected neighbours. Males aged 25-34 showed lower affinity, coupled with a low CV, in keeping with their peripheral role within the inter-sex network.

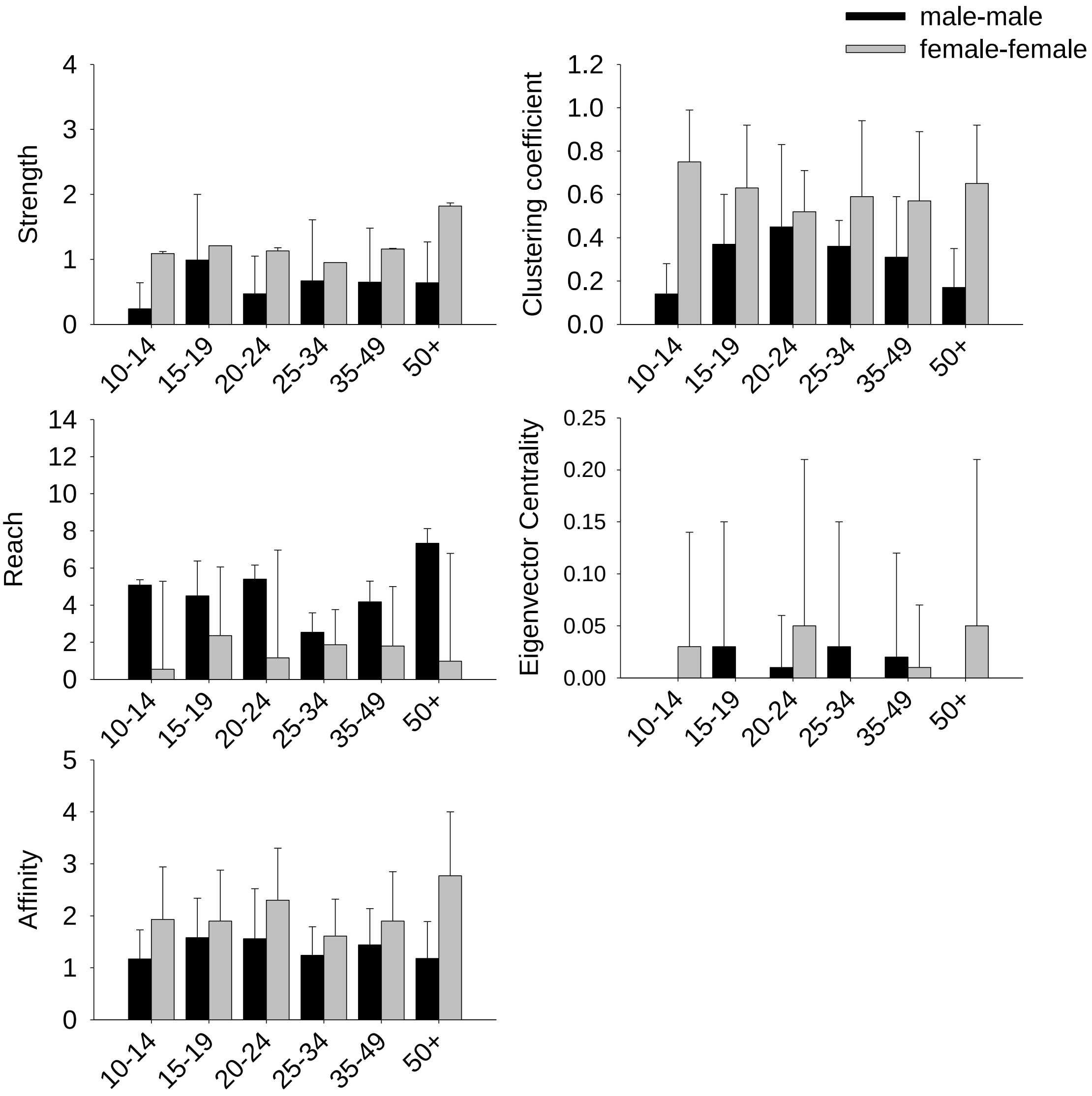

Figure 6.3.Observed network measures for a party-based network for males and females separately. Error bars show SE. N= 292 identified individuals aged 10 years or older.

Female-female relationships (Figure 6.3) were also similar to the female relationships described by the inter-sex network; strength values followed the same pattern although 25-34 year old females also had higher than expected strength. Reach measures also changed, with 10-14 year olds and females over 35 showing higher than expected values, again indicating these females are the “social glue” for female-female relationships. Eigenvector centrality measures illustrated the inverse relationship; females aged 15-34 were either unconnected in the network or less connected than expected, representing clusters of females that were linked together but not necessarily linked to other clusters. Consistent with this observation, all classes showed higher than expected clustering coefficients with low CV in this measure, suggesting that neighbouring animals in the network are themselves linked: this may correspond to a matrilineal or bond group structure, and the same pattern was also observed amongst males. Affinity measures were lower than expected, except for 20-24 year females who were connected at random, and for the oldest females where affinity was higher than expected. Overall, the evidence again suggests that the oldest females occupy key positions in the social network.

Aggregation-level networks of association illustrate broadly similar patterns to party-level networks when considering males and females together (Appendix D1). However eigenvector centrality measures for males were higher than those for the party-level network, existing for all age classes except 10-14 year olds. Female patterns of network measures did not change. For intra-sex networks, no age classes showed strength values that differed from random expectations but there were strong changes in eigenvector centrality measures for both sexes and in clustering coefficients between males (Figure 6.4). Between males eigenvector centrality was significantly higher than expected for males aged 15-24, and between females it was lower than expected for animals aged 35-49, while females over 20 were totally unconnected in the network. These changes in the connectedness of individuals suggest that intra-sexual relationships were maintained by direct interactions (i.e. party-level associates) rather than by eavesdropping on third party interactions (aggregation-level associates). Between males, clustering coefficients for aggregation-level associates were lower than expected for 20-24 year old and 50+ year old males, which differed from all the other networks examined. This might indicate that these young males are not yet firmly established in a hierarchy especially after dispersal from their natal home range. For the oldest males this could be a function of the very few number of individuals in this age category, coupled with their highly dominant status and risk avoidance strategies (see Chapters 7 and 8).

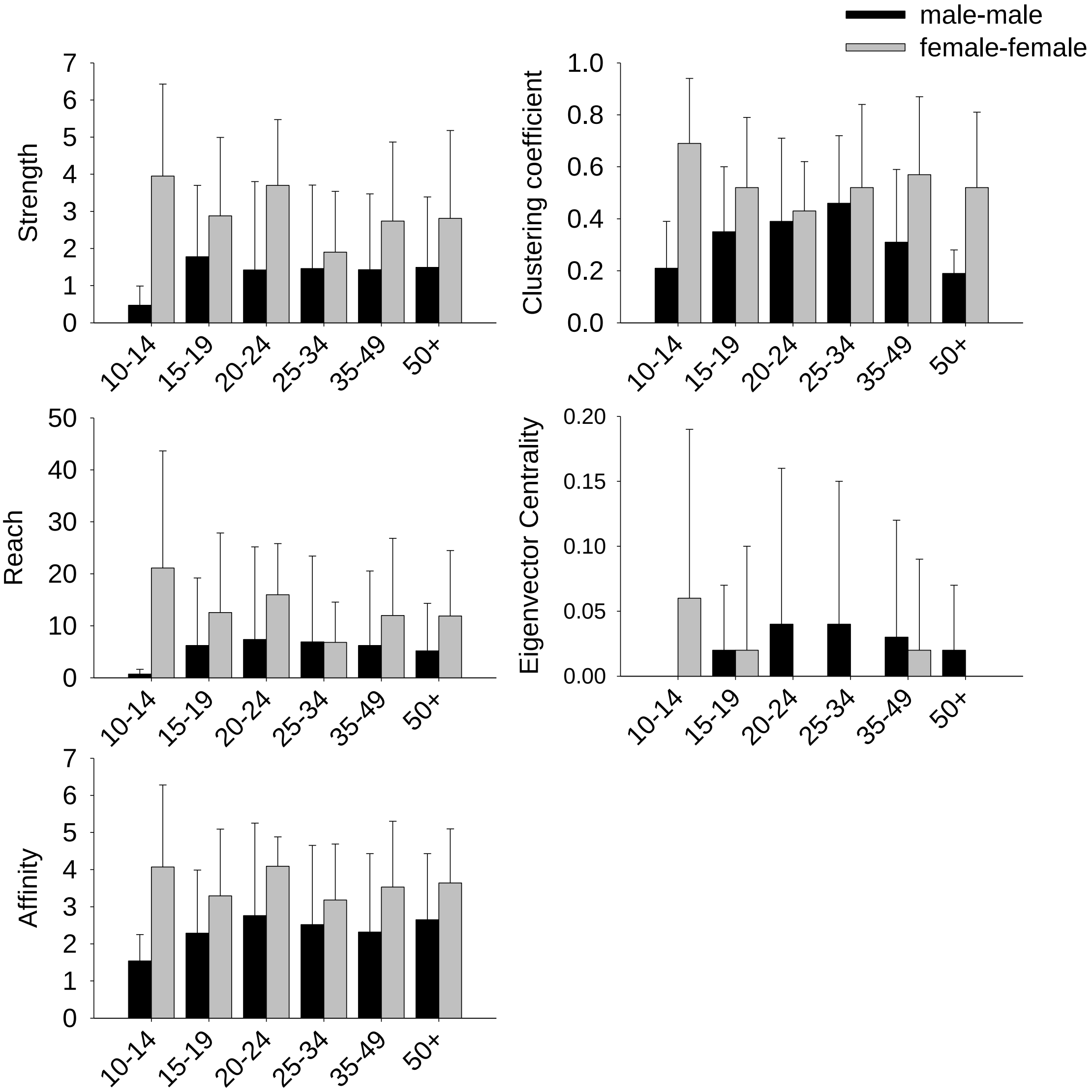

Figure 6.4. Observed network measures for an aggregation-based network for males and females separately. Error bars show SE. N= 292 identified individuals aged 10 years or older.

6.6 Results: Dynamics of Gregariousness

6.6.1 Solitary animals

Solitary animals accounted for 31.0% (n= 544) of parties lasting more than one minute. Of these individuals, 28.5% (n= 155) did not join other animals in the clearing. These non-changing solitaries were predominantly male (35-49 years), although all age-sex classes except sub-adult (10-14 years) and young adult females (15-19 years) were represented (Figure 6.5). Notably some very young animals (aged 2-3 years) were observed to use the clearing alone (see also Chapter 8).

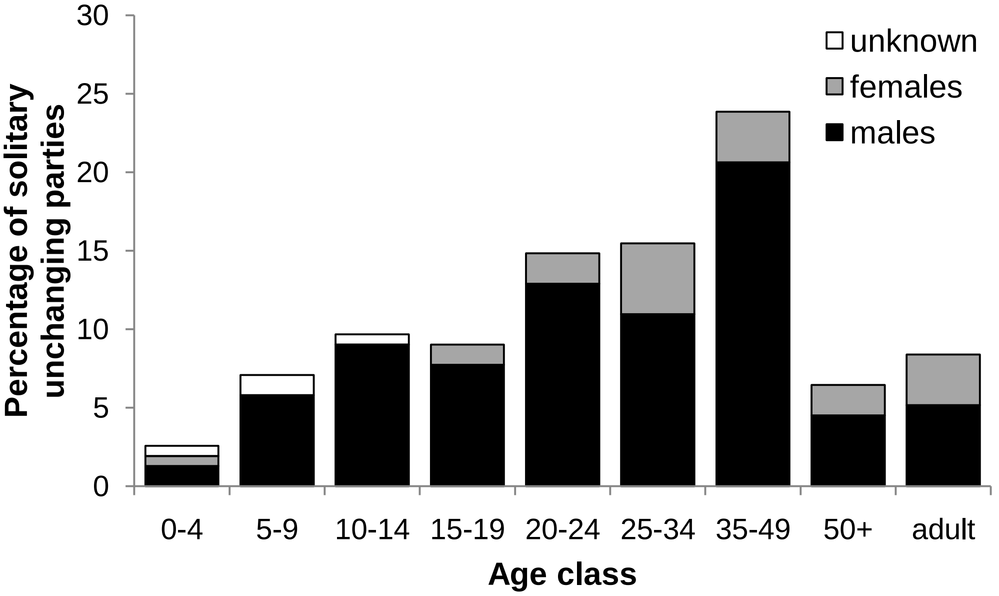

Figure 6.5. Age-sex distribution of 155 solitary elephants who did not contact conspecifics during their clearing visits.

Model Factors	df	Mean Square	F	Sig.	Model Adjusted R^2
Time block	8	2.370	27.004	**<0.001**	0.423
Social experience	2	3.211	36.587	**<0.001**	
Month	10	0.237	2.695	**0.003**	
Time block * social experience	16	0.086	0.983	0.475	
Time block * month	62	0.141	1.602	**0.005**	
Social experience * month	19	0.133	1.511	0.079	
Time block * social experience * month	47	0.140	1.598	**0.010**	
Corrected Total	*507*				

Table 6.6. Factorial ANOVA model for changes in visit duration according to social experience (solitaries, unchanging parties and "changers"), controlling for time of day and month effects using Type I sums of squares (n=508 elephant visits).

Elephants' social experiences strongly influenced visit duration: animals who changed social group stayed longer in the clearing than those who did not change (Table 6.6,

Figure 6.6). There was a positive correlation between the number of elephants present per hour and the percentage of parties that changed composition or size (Figure 6.7; R_s=0.6852, p=0.021).

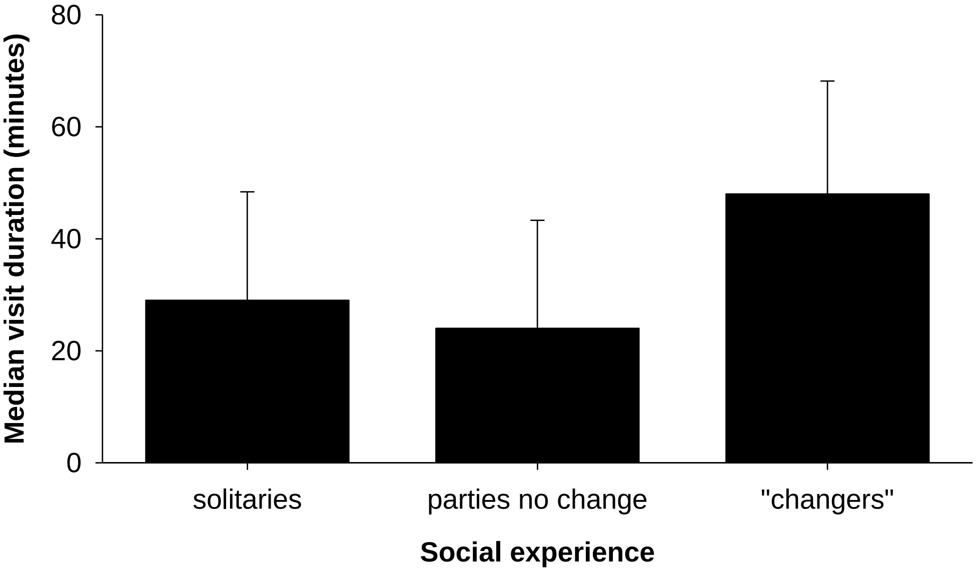

Figure 6.6 Visit duration according to social experience for animals who used the clearing alone (n=153), parties who did not contact other elephants (n=106) and elephants who contacted conspecifics during clearing visits (n=278).Error bars show 95% CI.

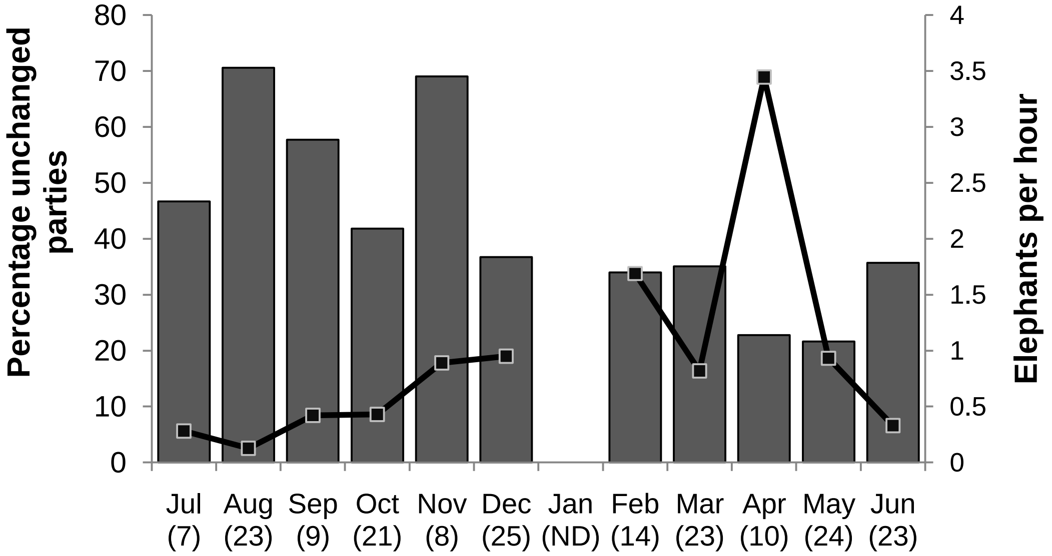

Figure 6.7. Relationship between the percentage of parties that did not contact conspecifics during bai visits (bars) and visit rate (line) by month. Data are based on 552 groupings (parties and solitary elephants).

6.6.2 Party Dynamics: Size, Duration and Instigators of Change

6.6.2.1 *Party Types and Structure*

All party types were represented among elephants who changed parties. Cow-calf parties were the most frequent, but mixed parties were also common in the clearing (Figure 6.8) despite the unequal sex ratio and underrepresentation of adult males in the elephant population (see Chapter 5).

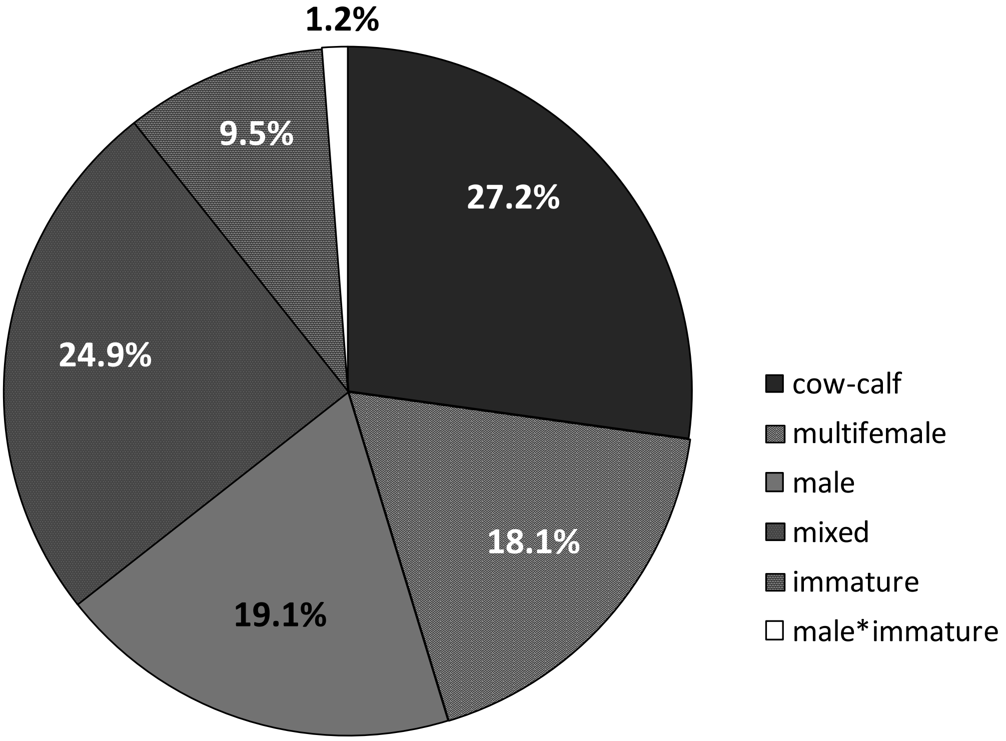

Figure 6.8. Distribution of party types for elephants who changed social groupings in the clearing (n=1207 parties).

In total, 283 mixed parties were recorded with males over 10 years old, with a median size of 5 (IQR= 5, range= 2-35; Figure 6.9a). The median number of males in a mixed party was 1 and the maximum was 6. The number of females over 10 years old in mixed parties varied from 1 to 24, with a median of 3 (IQR= 3). Mixed groups containing younger males were generally larger and most commonly contained either 15-19 year old or 35-49 year old (prime) males (Figure 6.9b). Males aged 15-19 years old were disproportionately represented in mixed groups (Figure 6.9b), and these males were also particularly aggressive in their interactions with conspecifics (see Chapter 7).

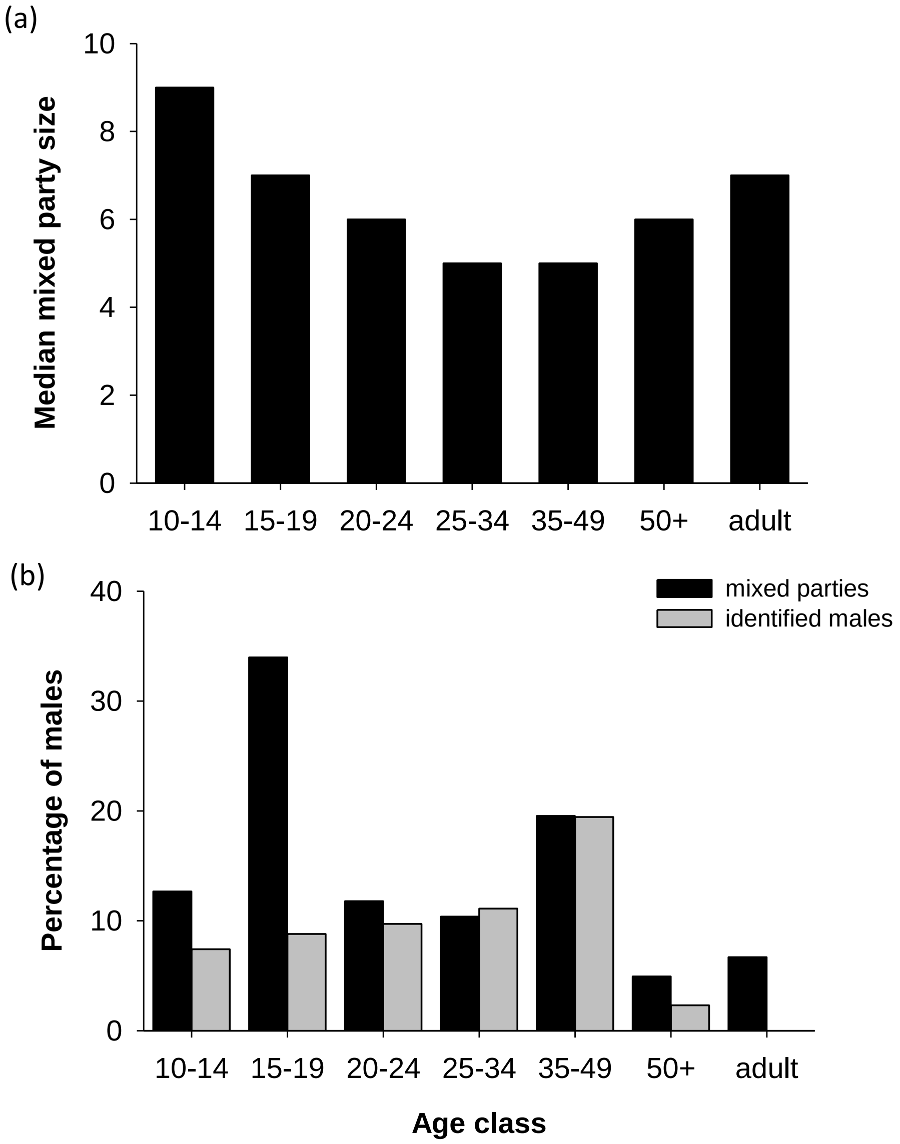

Figure 6.9. Median mixed party size by male age (a) and age distribution of males in mixed parties against distribution of male ages for identified animals (b). N=568 instances of males in 378 mixed parties; identified population n= 127 males aged over 10 years old.

The majority of parties changed composition during clearing visits creating new opportunities for social interactions (71.5% of all parties; 68.6% parties >1min duration). Party size varied strongly as a function of the party type, controlling for time of day and month (Table 6.7; Figure 6.10a). Mixed parties were largest, although there were significant differences between all party types (Games-Howell post hoc tests all p<0.05). Party duration was not strongly influenced by party type (Table 6.7; Figure 6.10b), and there were no consistent differences in the durations that parties of each type persisted (Games-Howell post-hoc tests all p>0.05).

PARTY SIZE

Model Factors	df	Mean Square	F	Sig.	Model Adjusted R^2
Party type	5	13.946	318.545	**<0.001**	0.658
Time block	8	0.177	4.052	**<0.001**	
Month	10	0.190	4.339	**<0.001**	
Party type * time block	36	0.085	1.945	**0.001**	
Party type * month	41	0.063	1.430	**0.042**	
Time block * month	43	0.058	1.331	**<0.001**	
Party type*time block* month	73	0.044	1.011	.456	
Corrected Total	*890*				

PARTY DURATION

Model Factors	df	Mean Square	F	Sig.	Model Adjusted R^2
Time block	8	0.499	3.498	**0.001**	0.134
Month	10	0.587	4.117	**<0.001**	
Party type	6	0.254	1.785	0.100	
Time block * month	44	0.280	1.968	**<0.001**	
Time block * party type	36	0.219	1.534	**0.025**	
Month * party type	41	0.126	0.886	0.675	
Time block * month * party type	73	0.193	1.351	**0.033**	
Corrected Total	*894*				

Table 6.7. Factorial ANOVA models for variation in party size and duration according to party type, controlling for time block and month effects (n=1723 elephant visits over the study period in both models).

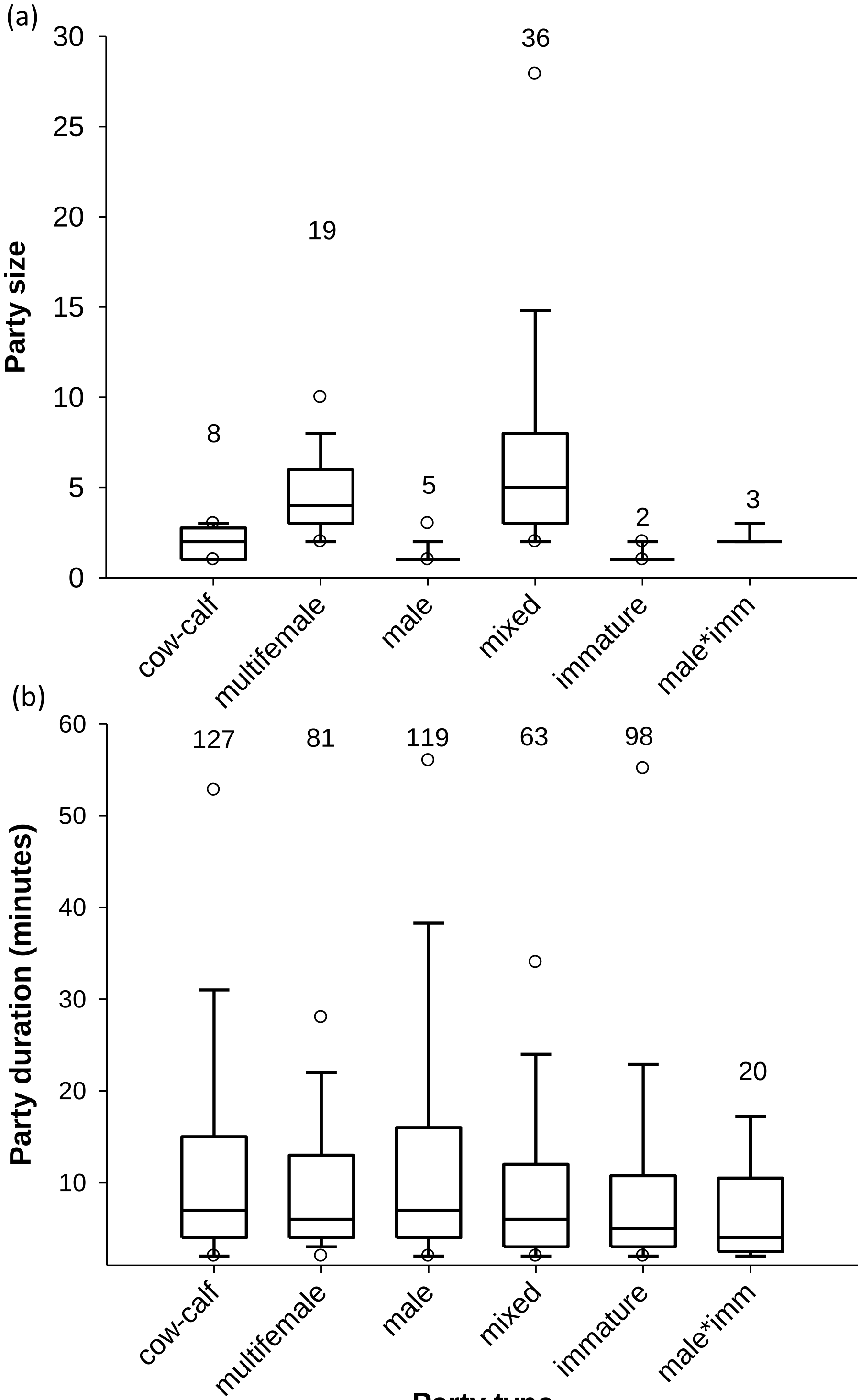

Figure 6.10. Median and IQR of (a) party size and (b) party duration by type for animals who changed social groupings while in the clearing (n=891 parties). Whiskers represent 10th and 90th percentiles, circles show outliers and numbers indicate maxima.

Most animals entered and exited the clearing in the same party compositions, regardless of their age-sex class (see Table 6.8). For all observed exits where composition changes could be scored, 78.53% of parties did not change (n= 278 parties). For those 76 parties who did change composition when exiting, 40.7% (n= 31) were fleeing the clearing (for further discussion, see Chapter 8).

Exit Seen	N parties (% of all parties)	N elephants
No	152 (8.25%)	453
Yes	575 (31.20%)	1578
unchanged	*278*	*601*
changed	*76*	*342*
unknown	*221*	*635*

Table 6.8. Exit composition data for 727 elephant parties (all other parties occurred within the clearing). Unknown compositions for observed exits were for elephants already present in the bai when observations began.

Mixed groups and multi-female groups were most commonly formed within the clearing, and this pattern did not change according to elephant visit rate (Figure 6.11).

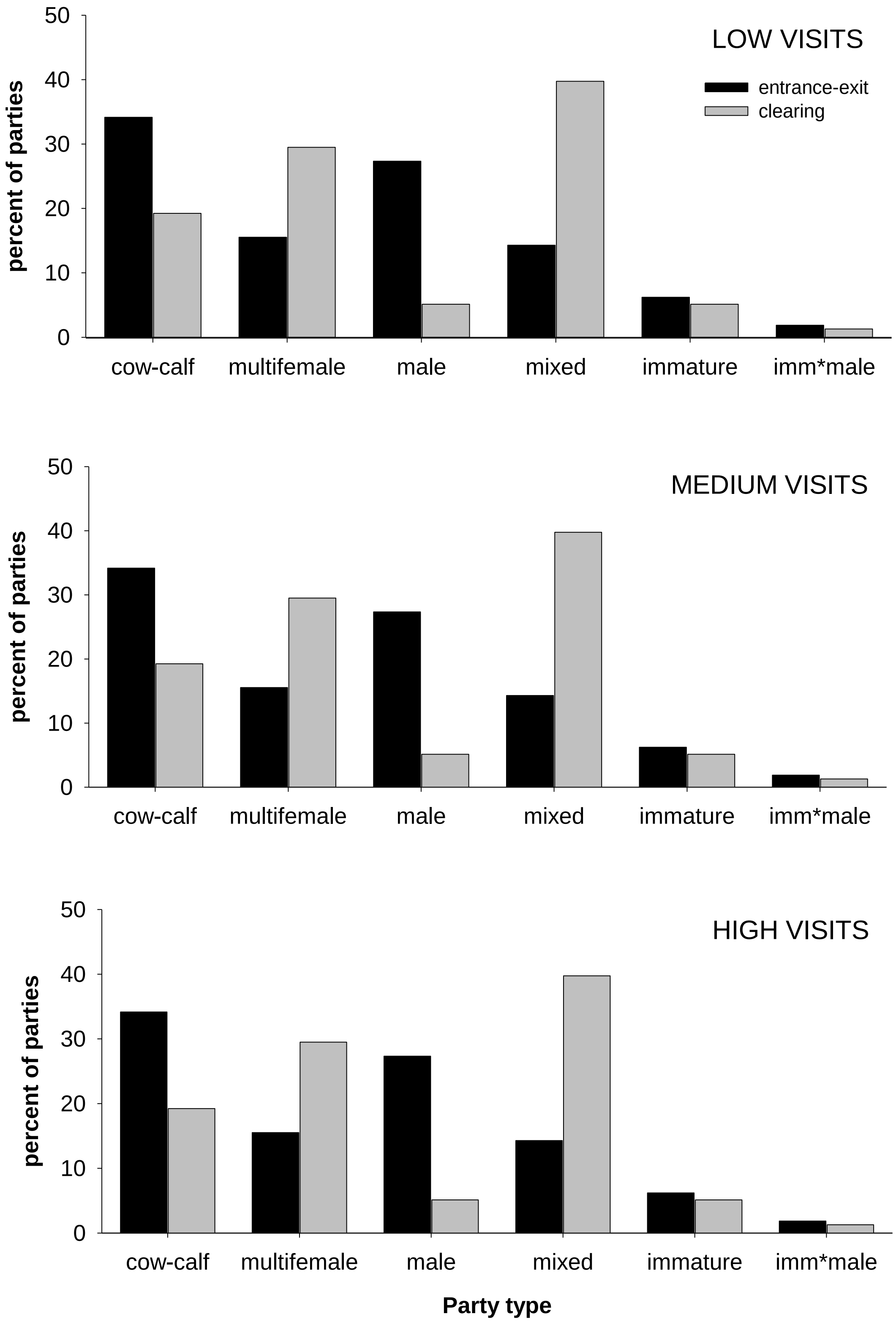

Figure 6.11. Party types by location, by elephant visit intensity (low n=239 parties, medium n=841 parties, high n=764 parties; see Section 4.2 for definition of visit intensity).

When animals joined conspecifics, they joined parties that were larger than their current party at all levels of visit intensity (Wilcoxon signed ranks test for low n= 239, Z= -4.561, p<0.001, r= -0.604; medium n= 841, Z= -8.645, p<0.001, r= -0.580; high n= 764, Z= -8.184, p<0.001, r= -0.617). Parties formed in the clearing were larger than entrance/exit (ranging) parties, for all levels of visit intensity (Figure 6.12; Mann Whitney U test for low U= 9635, Z= -2.436, p= 0.015 r= -0.135; medium U= 85299, Z= -3.317, p= 0.001, r= 0.111; high U= 33786, Z= -5.259, p<0.001, r=0.210). Visit intensity therefore did not apparently affect elephant decisions to aggregate.

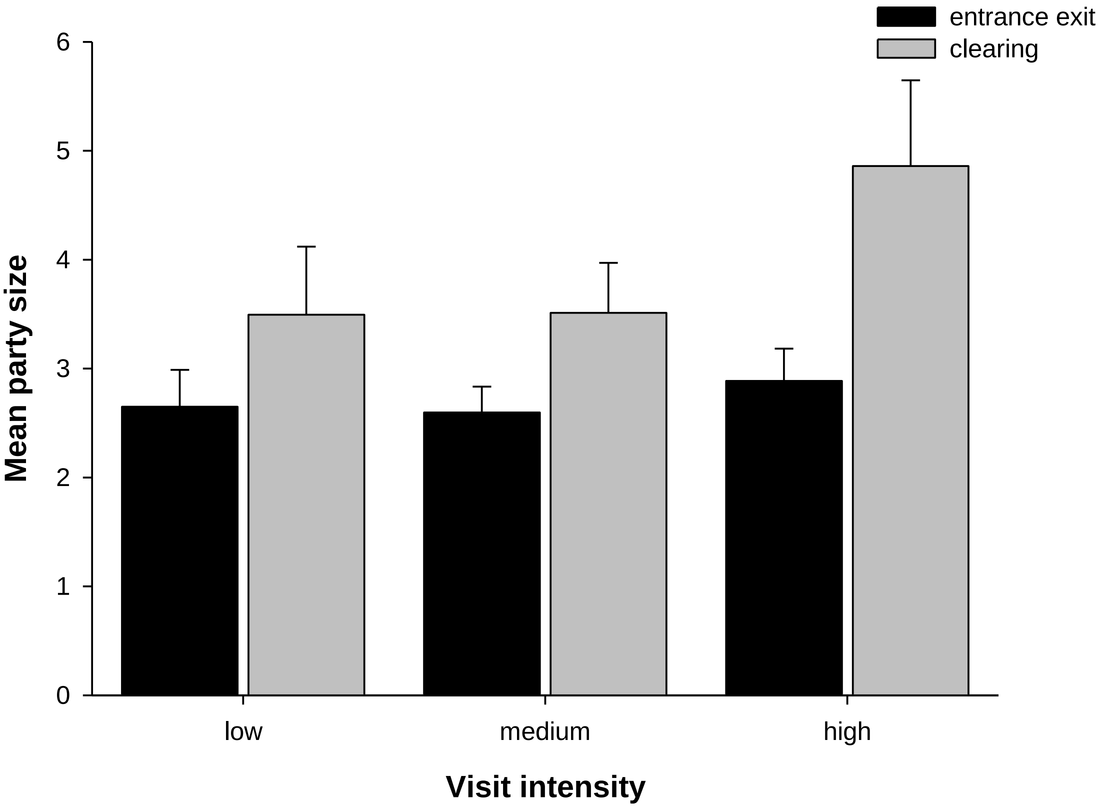

Figure 6.12. Party size comparisons according to location for 1806 parties where location was known. Error bars show 95% CI. See section 4.2 for definition of visit intensity.

6.6.2.2 Age-sex dynamics of gregariousness decisions

Individual decisions to join conspecifics, and which groups to join, varied as a function of age and sex (Table 6.9).

group type	**join conspecifics**		**joins (%)**				
	N	%	females	males	mixed	immature	males* imms
cow-calf	192	*58.36*	51.04	17.71	23.44	6.25	1.56
multi-female	53	*24.65*	43.40	13.21	37.74	3.77	1.89
male	131	*56.47*	35.11	29.01	29.77	5.34	0.76
mixed	21	*6.95*	47.62	23.81	28.57		
immature	82	*71.30*	57.32	9.76	24.39	8.54	
imm*males	4	*25*	50		50		

Table 6.9. Percentage of parties who joined conspecifics by party type, and who they chose to join (n=484 parties).

Males were most likely to join other males during periods of medium visit intensity (Table 6.10) but their age did not affect the likelihood that males would form multi-male parties, either by the age of the initiator or the age of the male they joined. Sample sizes for males who left multi-male groups were too small for statistical analysis (n= 25), but showed no clear age-related pattern.

Predictors added	B	S.E.	expB	Wald	Df	Sig.
Visit rate (baseline = low)				11.157	2	**0.004**
medium vs. low	2.744	0.950	15.556	8.347	1	**0.004**
high vs. low	0.591	0.833	1.806	0.503	1	0.478

Table 6.10. Logistic Regression model for males joining males (n=299 male parties). Model $X^2=14.585$*, df=2, p=0.001. Nagelkerke's* $R^2=0.287$*. Predictors dropped from the model: male age, difference in male ages (older/same/younger).*

Predictors added (in order)	B	S.E.	expB	Wald	Df	Sig.
Party size	-0.346	0.091	.707	14.399	1	**<0.001**
Female age (baseline 35-49)				15.188	5	**0.010**
10-14 vs. 35-49	1.324	0.513	3.758	6.658	1	**0.010**
15-19 vs. 35-49	0.518	0.414	1.678	1.562	1	0.211
20-24 vs. 35-49	0.945	0.407	2.572	5.377	1	**0.020**
25-34 vs. 35-49	0.732	0.292	2.079	6.267	1	**0.012**
adult vs. 35-49	-0.020	0.299	0.980	0.004	1	0.947

Table 6.11. Logistic regression model for females joining females (n=744 female parties, for females aged less than 50). Model X^2=45.66, df=6, p<0.001. Nagelkerke's R^2=0.109. Predictors dropped from the model: visit rate intensity (low/medium/high).

Females were more likely to join females when their own groups were small (Table 6.11). Age also affected the likelihood that females would join other females: Females aged 35-49 were less likely to join females compared to other age classes. Females in the oldest class (aged 50+) and the difference in female ages could not be entered as predictors in the model because old females never joined other females, and all other age classes showed clear preferences: females below 24 joined females older than themselves, females aged 25-34 always joined females younger than themselves and females aged 35-49 showed less of a preference (Table 6.12). It should be noted that old females were rare and therefore relatively unavailable (see also Chapter 5). The decisions to leave multi-female parties were often made by immature animals (0-9 year olds; males and females included) or by individuals over the age of 25 (Figure 6.13).

	Joins			
Female age	Older	Same	Younger	**Total**
10-14	10			10
15-19	9	1		10
20-24	10			10
25-34			25	25
35-49	3	17	18	38
50+				
Adult	1	14	1	16
Total	33	32	44	109

Table 6.12. Age preferences for females joining other females.

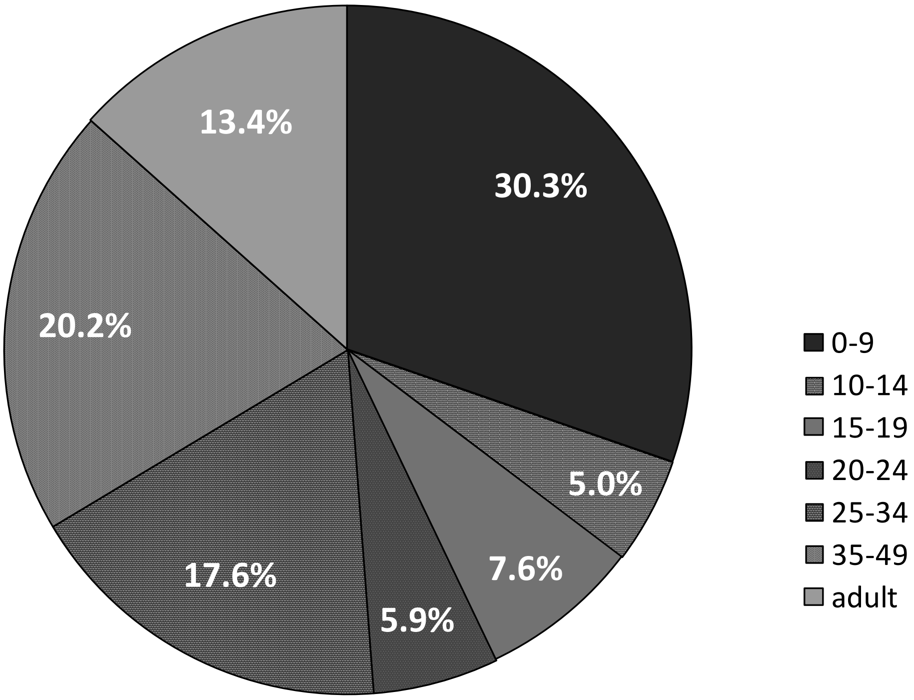

Figure 6.13. Age distributions of the first individuals to leave multi-female groups (n=119 parties).

Males were significantly more likely to be responsible for forming mixed parties than were females (Table 6.13) while the individuals who left mixed parties were most often females (54.0% of 176 mixed parties).

Predictors added	B	S.E.	expB	Wald	Df	Sig.
sex	0.806	0.163	2.239	24.446	1	**<0.001**

Table 6.13. Logistic Regression model for creation of mixed parties (n=1069 parties). Model X^2*=23.72, df=1, p<0.001. Nagelkerke's* R^2*=0.035. Predictors dropped from the model: age, visit rate (low/medium/high).*

6.7 Discussion

The SocProg analyses showed clearly that association patterns within the bai were non-random and represented conscious and active social choices by individuals. These associations were structured by age, sex and individual identity and elephants showed multi-level organisation, where association patterns differed between party- and aggregation-level associates, and within- and between- sexes. All networks showed high levels of clustering indicating “friends of friends” style relationships between elephants, where the associates of an individual were themselves associated. The strongest structuring roles were held by the eldest females, in a striking similarity to the roles held by experienced savannah elephant matriarchs as “repositories of social and ecological knowledge” (McComb et al. 2001). Female-female relationships were stronger than male-male relationships, and for networks incorporating both sexes, males appeared superimposed on the network of female relationships, consistent with previous findings for forest elephants (Fishlock et al. 2008). For savannah elephants, male social relationships change in a dynamic landscape involving age, rank and reproductive status and individual associations are important (Evans & Harris 2008; Lee et al. in press b ; Poole et al. 1988, in press). When male-male relationships were considered separately, males were more connected to each other than to females, suggesting sociality is also important for male forest elephants. The oldest males and

20-24 year old males were more peripheral than expected in the male network. For 20-24 year old males, this may be because they have dispersed from their natal group but were not yet well established within male society. For the oldest males, this lack of connectedness may be a result of the strong deference shown to them by all other age-sex classes, including prime-age males (see also Chapter 7).

Males and females aged 10-14 years were both active in the network, which was due to the socially explorative tendencies of these individuals to move from party to party, possibly as a strategy to cope with social dispersal from the natal group. In using the bai to establish relationships with conspecifics, young animals may be able to minimise the costs associated with social dispersal, which include aggression from strangers, loss of alliance (maternal) support and the time and energy involved in establishing new relationships (Isbell & van Vuren 1996).

Elephants changed their visiting pattern according to their social experience and increased their time in the clearing by almost 50% when they contacted conspecifics in the bai. Individuals were attracted to large parties and were more likely to associate with conspecifics when visiting rates were high, and more partners were available, and coupled with the non-random nature of aggregation-level organisation this suggests that decisions to aggregate were made at least in part before individuals entered the clearing. Animals did not appear to use the clearing to meet up with conspecifics with whom they then continued ranging, as most animals exited the clearing with those same conspecifics that they arrived with. Elephants did not minimise competition by altering their aggregation patterns during intense visit periods. However, individual choices to associate may have been affected by health status, as individuals in poor condition were observed to avoid joining with other elephants (see Chapter 8).

Forest elephants range in group sizes of approximately 3 individuals, excluding solitary animals (reviewed in Morgan & Lee 2007). The maximal party sizes observed at Maya Nord (up to 35 individuals) were demonstrably larger than these ranging groups and 34.3% of parties in the clearing contained four or more individuals. Both inter-and intra-sexual relationships were maintained within the bai, where individuals had the chance to associate with conspecifics who they did not forage with. This created novel social opportunities in the form of large multi-female parties which were attractive to males who then joined them to create mixed parties. Young elephants probably have no richer opportunity to learn social rules than in these large dynamic groupings. Among elephants older individuals of both sexes function as role models and repositories of social knowledge (Evans 2006; Evans & Harris 2008; McComb et al. 2001) and removal of old individuals can have catastrophic consequences for individual welfare and fitness (Abe 1994; Bradshaw et al. 2005; Gobush et al. 2008; Slotow & van Dyk 2001; Slotow et al. 2000).

These analyses form a prelude to being able to examine social roles in forest elephants: there is some evidence to suggest that old females played important roles as “social glue” or attractive centres to an aggregation or party. Relationships were structured by age and sex, but individual identity also played an important role for forest elephants, as underlined by active choice of associates and avoidance of other conspecifics, and high variation in all network measures. These analyses show characteristics of social organisation among forest elephants that clearly correspond to patterns of savannah elephant sociality, including matrilineal and multi-level organisation for females (e.g. Wittemyer et al. 2005). The resolution in this dataset was limited by a low recapture rate for known individuals, compounding the problems of assessing social relationships for such long-lived mammals in a short-term dataset. Some of this knowledge gap may be addressed by examining interactions between individuals which provide more detailed information on the nature of dyadic relationships and these form the subject of the next chapter.

Chapter Seven

Sociality: Interactions

Chapter 7 Sociality: Interactions

7.1 Abstract

Interaction rates were high in the Maya Nord clearing (11.22 interactions per hour of elephant presence) and were positively correlated with elephant visit rate. Competitive interaction rates in this study were high at 5.88 per hour of elephant presence over the year, in comparison to the rates of competitive interaction seen in savannah elephants (0.70 per hour: Archie et al. 2006a; 0.34 per hour: Lee 1987). Interaction types were evenly distributed between parties, but socio-sexual behaviours were rarest overall, again underlining that Maya Nord does not function as a mating arena for PNOK elephants (Chapter 5). Rates of affiliation were highest among family members. Between females affiliative interactions occurred at a rate of 1.9 per hour of elephant presence, a level comparable to the 2-4 interactions per hour seen in savannah elephants (Lee 1987). While the age and sex of individuals in aggregations and the duration of parties were able to predict the occurrence of specific interaction types, the likelihood models often showed relatively low explanatory power suggesting that elephants using the Maya Nord clearing do not make social decisions based purely on aggregation “rules” such as party size or type. Social interactions probably emerge at least partly as a function of individual identity, both from the knowledge of initiators and individual recognition of conspecifics (recipients). These analyses show that age-, sex- and kin-structuring of behaviour are all important for forest elephants. Forest elephants at Maya Nord showed a suite of interactions which have direct parallels to those recorded for savannah elephants,

indicative of valuable relationships and consistent with the findings of preferred and avoided associates as shown by analyses of association presented in Chapter 6.

7.2 Introduction

Elephants have slow life histories, and even the longest-running field sites have yet to see an entire cohort of individuals be born, mature, reproduce and die a natural death (Moss et al. in press a). Reproductive strategies may cause divergence in life history and social environment between males and females, but both sexes have relationships that extend well beyond their family kin-group in savannah elephants, with individuals embedded in multi-tiered networks of relationships that encompass entire populations (Archie et al. 2008; Moss & Poole 1983; Wittemyer et al. 2005). Elephant relationships may persist for decades, and are therefore structured by repeated interactions between individuals. For elephants, valuable relationships with conspecifics have survival and reproductive value, and interact with ecological constraints to affect patterns of fission-fusion (Moss & Lee in press b). Although bais form a “minority habitat” and are therefore to some degree exceptional in the forest landscape (they are open, have few or no trees, and are not often used as areas for vegetation feeding; Chapter 3) they magnify social relationships by providing a focal area where elephants aggregate (Chapter 6). Levels of social interaction may be high in these areas and, while these should not be interpreted as being representative of social experiences in other parts of the landscape, they do provide excellent observation points to collect data on the quality, content and patterning of interactions between individuals and thereby afford insight into the social structure of a population (Hinde 1976).

In fission-fusion societies, the dynamics of association are a form of relationship manipulation and the nature of interactions vary according to the kinds of groups that form (Aureli et al. 2008). Examining social relationships, in particular for key features such as female-female agonism (Sterck et al. 1997) may reveal where and how forest elephants differ from their savannah counterparts. A fundamental difference in forest elephants is the apparent dispersal of both sexes from the natal group (Turkalo & Fay 1995); females may therefore be unable to rely on maternal knowledge in the same way as do savannah elephants, and might need to acquire social information in a similar fashion to males. If this is the case, females may actively seek social novelty, similar to savannah males (Lee 1986; Lee & Moss 1999), rather than restricting their interactions to the family group. The well-studied savannah elephant populations thus provide descriptions of behaviour that is characteristic of valuable relationships, which allows identification of homologous behaviour amongst forest elephants in bais.

Previously in this thesis I have shown that elephants use clearings as aggregation points, and that the social opportunities available in these areas form important attractants to individuals. With a short-term study such as this, quantification of individual relationships is virtually impossible, as repeated dyadic interactions are rarely observed (which has contributed to the limited exploration of forest elephant sociality to date, as discussed in previous chapters). Elephants themselves however do not share this “observer ignorance” and they exhibit behaviour that clearly shows their valuable relationships with conspecifics. This is behaviour that is not universally displayed within dyads, and therefore underlines the importance of individual identity in forest elephant society.

7.3 Chapter Aims

The previous chapter demonstrated elephants' preference to aggregate in clearings, and active, non-random choices of social partners structured by age and sex. To elaborate further on these themes, this chapter considers the nature of interactions among elephants in the clearing. This chapter therefore continues to explore age-sex differences during interactions within the bai context, and considers these in terms of life history strategies by comparing these with savannah elephant populations. Observations are discussed with reference to the social function of bais as mating arenas and areas for the exchange of female social knowledge.

7.3.1 Describe and explore elephant interactions at Maya Nord

I describe the nature, intensity and distribution of interactions amongst elephants at Maya Nord, and relate this to the rate of elephant visits. The distribution of interactions is described according to the behaviour types identified, the sex of initiators and recipients and the party types in which interactions occurred.

7.3.2 Explore how social behaviour is affected by aggregation rules

Social opportunities for elephants varied during the course of a year. To determine whether, and how, the changing social opportunities in the bai resulted in changing rates and types of interactions, I explore whether aggregation parameters, such as the number of individuals present, and the presence of mixed-sex parties, can be used to predict which behaviour are more likely to occur, given the occurrence of an interaction. Logistic regression models were used, making it possible to explore these parameters along with the effects of age and sex, which are known to be crucial in structuring elephant societies, relationships and interactions (Archie et al. 2006b; Moss & Poole 1983; Wittemyer & Getz 2007; Wittemyer et al. 2005).

7.3.3 Describe inter- and intra-sexual interactions and reproductive behaviour

To illustrate the nature of elephant relationships at Maya Nord, I describe the nature of inter- and intra-sexual interactions and describe observations of fundamental organising behaviour such as affiliation and allomothering. Previously in this thesis (Chapter 5) I have shown that the overall rarity of musth males makes it unlikely the Maya Nord functions solely as a mating arena; nonetheless behaviour associated with reproduction was observed, and this is also described and discussed.

7.4 Methods

Data were collected using functional descriptions of behaviour (see Ethogram in Appendix A). For analysis, behavioural categories were created, as outlined in Table 7.1. Interactions were assigned one/zero scores for the dyadic context in which they occurred; inter-family, inter-party or between individuals who entered the clearing together. Where dominance interactions involved multi-female groups or families, this was noted along with the age(s) of matriarch(s). Vocalisations were considered separately to the other categories, as they were associated with a number of behavioural contexts, and it was often difficult to assign vocalisations to specific individuals, or identify intended recipients. In addition, elephants responded to vocalisations from the surrounding forest.

Category	Example behaviour
Competition/Dominance	Supplants, blocking access to geophagy sites, non-aggressive competition (jostling for position at geophagy sites).
Submission/Avoidance	Submissive postures ("look back"), avoidance behaviour.
Aggression	Active aggression – charges, threats (e.g. ear folds), tusk pokes, slaps etc. Escalated contests (chases, fights).
Affiliation	Play, spar, co-ordinated movement (including waiting behaviour), touch, body contact.
Social monitoring	Social vigilance/arousal, monitoring conspecifics, approach, scent towards[1].
Maternal behaviour	Suckle, "discipline", guidance, comfort, allomothering[2].
Socio-sexual	Touch urogenital tract, chase, (attempted) mount.
Vocalisations	Including vocal distress, and vocalisation postures.

Table 7.1. Behavioural categories used in analyses.[1,2]See text for further explanation, and also Ethogram in Appendix A.

High intensity greeting "ceremonies" are well-documented among savannah elephants, and are indicative of close bonding: individuals become highly aroused and excited when meeting well-known associates and display chemo-sensory, acoustic, tactile and visual signalling through urinating, defecating, TGS, rumbles, body rubs and trunk-to-face/body contacts and body twirling (Moss & Poole 1983; Poole et al. 1988; Poole & Granli in press). Such high-intensity behaviour was not observed at Maya Nord, although greeting ceremonies have been reported among forest elephants at

Dzanga (Payne 2003; A. Turkalo pers. comm.). Trunk-to-mouth, or trunk-to-trunk contacts were frequently observed, but could serve both affiliative and dominance functions, and were categorised accordingly, or categorised as “scent towards”, a neutral social monitoring behaviour. Allomothering was defined as maternal behaviour directed to non-offspring (Lee 1987), and was restricted to guarding and suckling, to prevent confusion with other affiliative or friendly social interactions between females and calves. “Kidnapping”, where group members actively encouraged calves to leave their mothers, was considered a special tactic involved in group cohesion, and is described and discussed accordingly.

Oestrous behaviours were defined following Moss (1983) and all five cues (wariness, oestrous walk, chasing, mounting and consort behaviour) were detectable in the bai environment. Consortships were noted when a musth male and female remained in association (for which either animal may be responsible, Poole 1989b), whether or not the female displayed oestrous behaviours. Male testing of female reproductive status was a scored where males contacted the urogenital tract of females or tested their urine, along with whether or not the male subsequently performed flehmen behaviour, tasting the tip of his trunk. Vague trunk-scenting towards females or touching of other body parts was ignored, as these were not necessarily sexual in nature. Harassment of females, especially by younger males was captured through behaviour-dependent sampling of social interactions. Female reaction to testing was scored as neutral if there was no response or as avoidance behaviour when she moved away. Attempted testing of females was scored as socio-sexual even if she successfully avoided the male in question. It should be noted that these analyses underestimate the frequency of males' sexual interest in females, as in large clusters of elephants testing behaviour by males was difficult to observe. It should also be noted that female "avoidance" might act as a signal of oestrus, since "coy" responses indicate female attempts to initiate a consortship (Moss 1983). No proactive responses by females to males (backing into males, spinning etc.) were seen during the study period.

The distributions of interactions according to party type were assessed using chi-square tests. Party types were allocated according to the initiator (rather than recipient) party, and follow the same classifications as previous chapters; cow-calf (female with immature(s)); multi-female (at least two adult females present, with or without immatures); male (only adult males); mixed (both adult males and females); immature (all animals less than 10 years old), but with the addition of one (rare) party type; male*immature (at least one adult male, plus immature n=16 instances throughout the study period).

Logistic regressions were used to explore interactions according to the demographic class of the initiator (age, sex and an age*sex interaction) and "aggregation rules" that described the social situation (party size, party duration, sex of party members, whether or not the interaction occurred between family members, and between individuals in the same party). A forward stepwise method was used to assess the relative importance of predictors and these are reported in order of entry to the model (see Tables). Models were also run using a backward procedure to check for suppressor effects. All predictors were entered into each model unless otherwise stated. Predictors were continuous or binary categorical variables except for age which was categorical, the pairwise comparison values of which are included in Appendix E. Predictors were retained or dropped from logistic regression models due to their respective Wald values during the model fitting process; predictors dropped from the model (i.e. who did not contribute to the explanatory power of the model) are reported in table legends throughout. Party type could not be entered as a predictor due to the distribution of data, and so parties were classified as same-sex or mixed sex in order to explore potential changes in behaviour when adult males and females associated with one another. All models were run with males as baseline sex so that negative beta values indicated the behaviour was more likely amongst males. Prime reproductive adults aged 35-49 were selected as the baseline reference category to explore age effects. Where age classes were unknown, a general “adult” category was created. For socio-sexual behaviour, only elephants of known age classification over the age of 10 were used, and for maternal behaviour, only female initiators were included by definition.

To graphically represent chi-square and logistic regression statistics, a “proportion observed” measure was calculated by dividing the observed score by the sum of the observed and expected scores:

$$proportion\ observed\ measure = \frac{observed}{observed + expected}$$

If observed and expected values are equal, the exact value is 0.5. This measure varies between zero and one, and the variation indicates whether the observed values are greater than or less than expected. Thus the reported chi-square statistics refer to the overall analysis, but these graphs show in which categories (e.g. party type or age class) and in which direction the distribution of scores differ from expected. This allows direct comparison of the categories whilst correcting for unequal sample sizes. Expected scores were calculated by assuming that interaction scores should be equally distributed between party types or age classes. Chi-square statistics are reported in figure captions, and the 50% "observed=expected" line is indicated on all graphs.

7.5 Results: Interaction Types and Distributions

In total, 4224 dyadic interactions were recorded during the study period. 448 of these were scored in more than one behavioural category; e.g. an aggressive supplant was scored in both dominance and aggression categories. Interactions occurred at a high rate all year round (Figure 7.1), and the number of interactions recorded per month was strongly correlated to monthly elephant visit rate (r_S= 0.791, p= 0.004, n= 11). The results of this chapter should therefore be interpreted in light of the strong variation in social opportunities already discussed in earlier chapters.

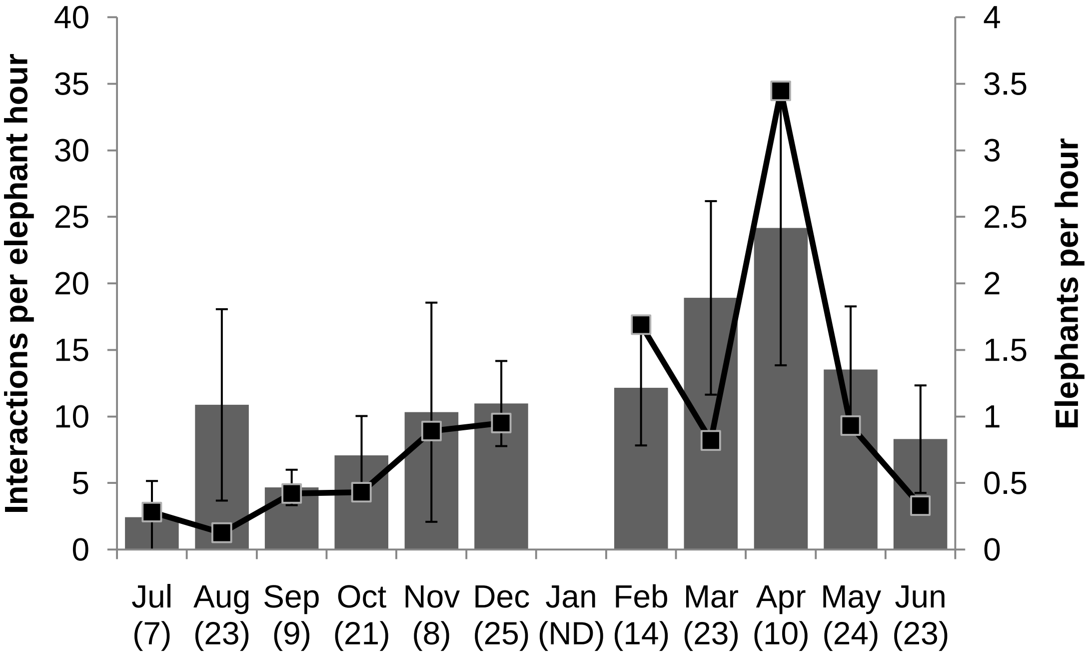

Figure 7.1. Mean interactions per hour of elephant presence, by month (bars) and elephant visit rate (line). N= 4224 interactions over all 1599 elephant visits observed over the study period, numbers in brackets indicate number of observation days per month. Error bars show 95% CI.

Interactions were fairly evenly distributed among the behavioural categories identified (Figure 7.2) although socio-sexual behaviour was rarest overall. Interactions were not equally distributed between party types (Figure 7.3), and appeared to be most common in mixed and multi-female parties. Females were most commonly involved in interactions overall, partly as a result of the observed sex ratio skew in the visiting population (see Chapter 5). Behaviour categories differed according to party type for competition/dominance behaviour, social monitoring, affiliation and socio-sexual behaviour (Figures 7.3 and 7.4 and associated chi-square statistics), but no overall differences by party type were detected for submission/avoidance, aggression, vocalisation or maternal behaviour, although all these occurred at reasonably high frequencies (Figure 7.2).

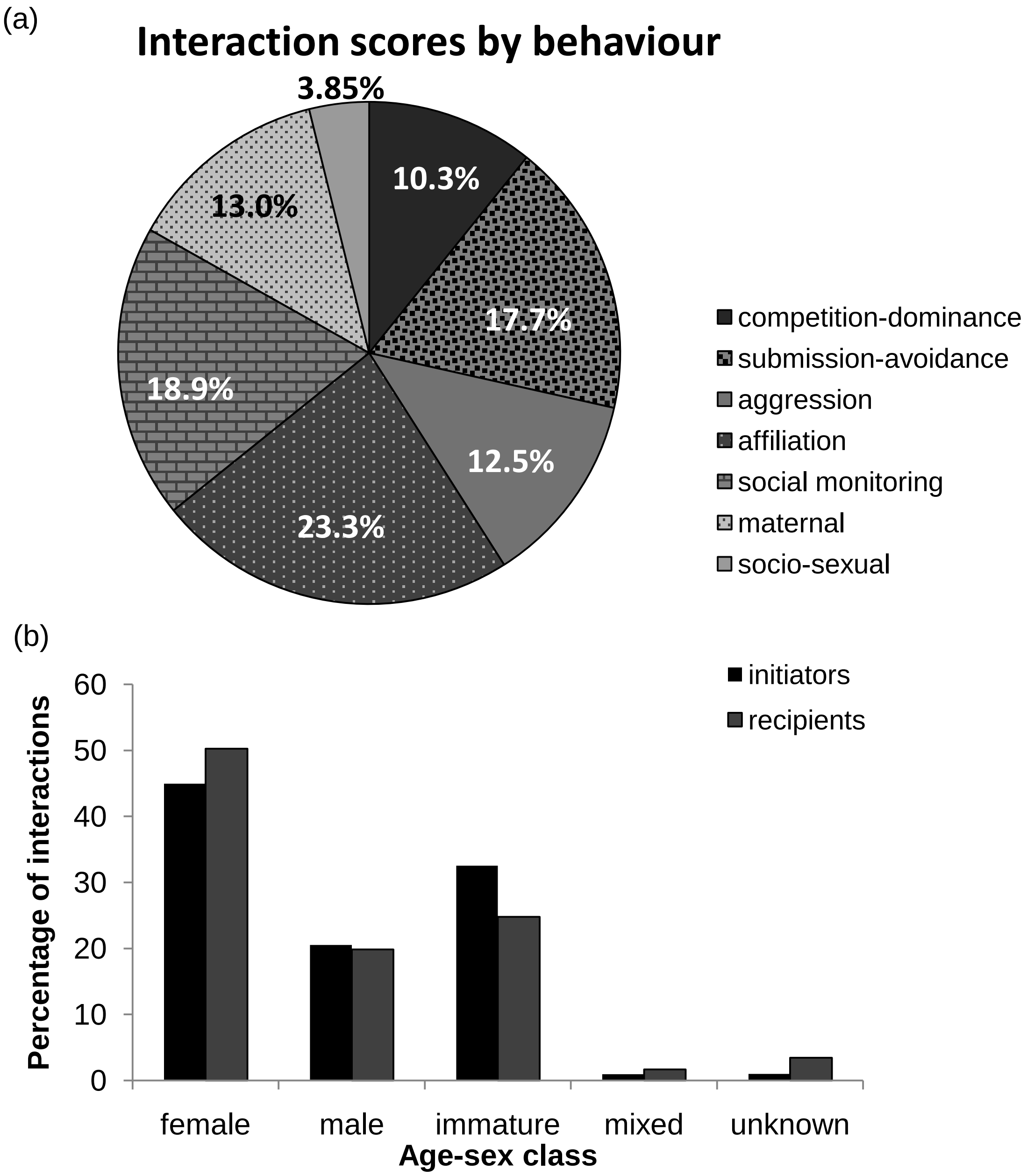

Figure 7.2. (a) Interaction scores classified according behaviour category and (a) age-sex class of initiators and recipients (where "mixed" indicates triadic or higher level interactions involving both adult males and females). N= 4224 interactions recorded over the study period, generating 4672 interaction scores, as some interactions were scored in more than one category.

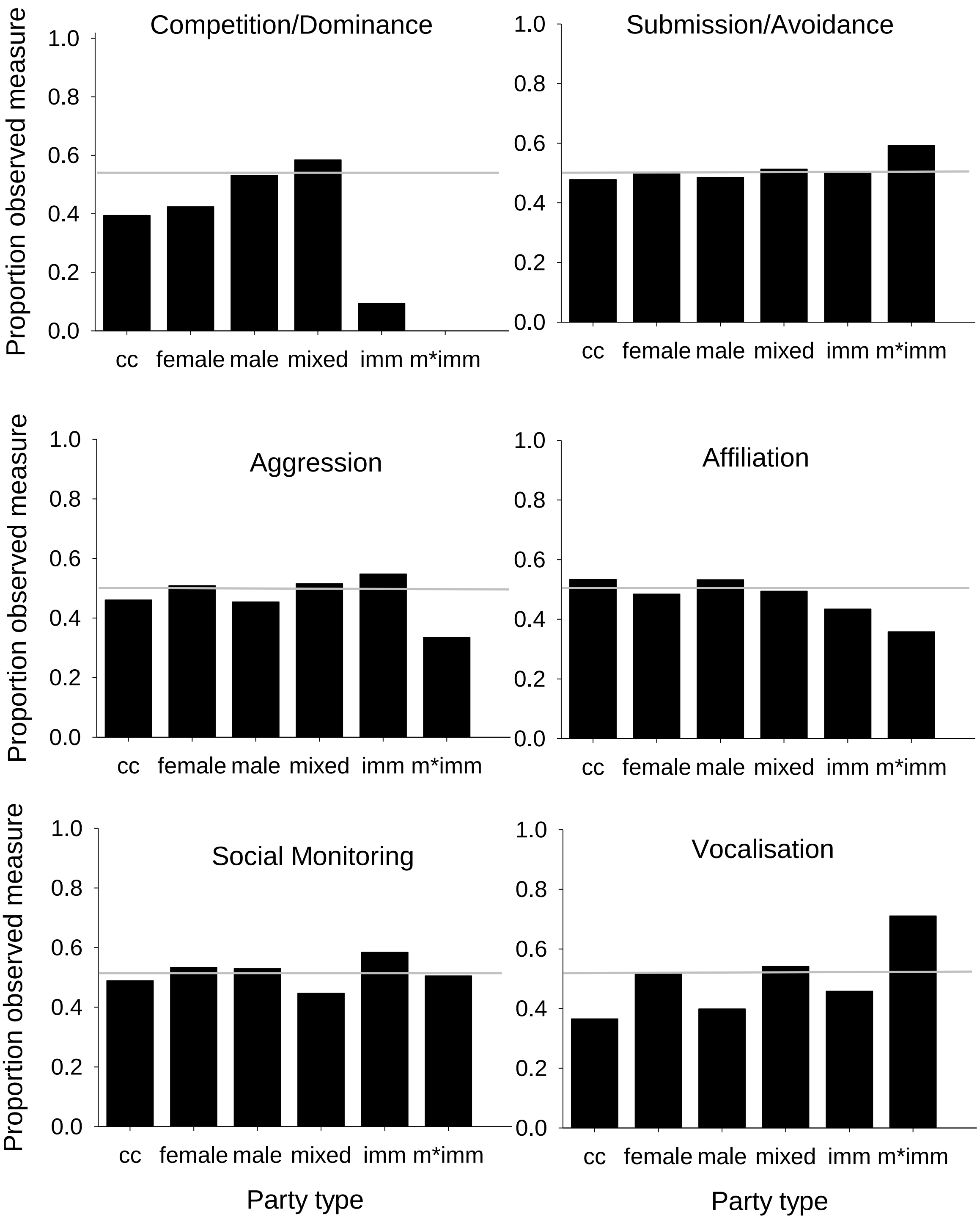

*Figure 7.3. Proportion observed measures for behaviour versus party type. cc= cow-calf; m*imm=male*immature party. Chi-square tests; df=5 for all categories. Competition-dominance X^2=59.09, p<0.001; affiliation X^2=10.05, p=0.074; social monitoring X^2=23.82, p<0.001; all other behaviour NS. Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.*

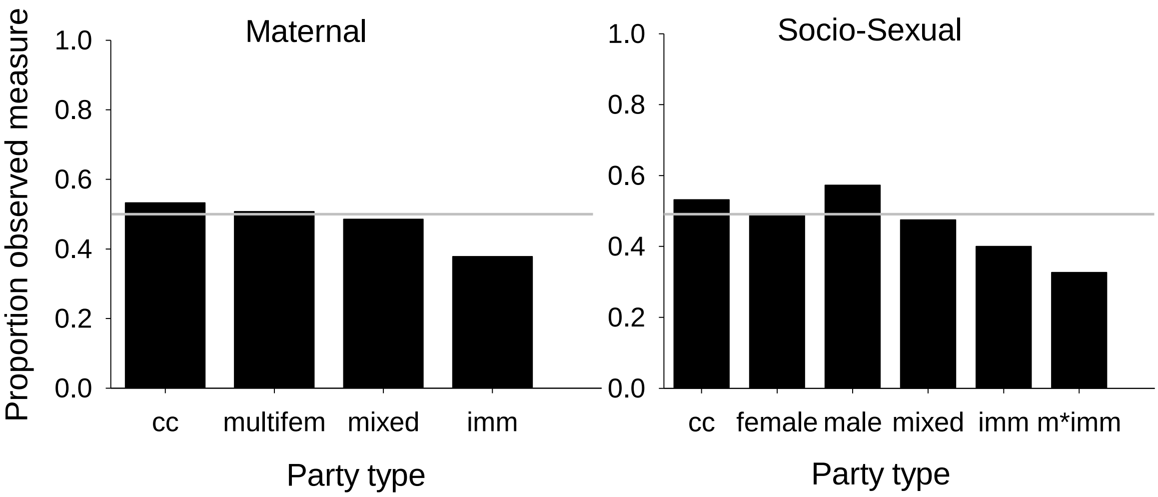

Figure 7.4. Proportion observed measures for maternal and reproductive behaviour according to party type. Maternal behaviour X^2 test NS. Socio-sexual behaviour X^2=14.17, df=5, p<0.01. Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.

7.6 Results: Aggregation Rules and Social Behaviour

7.6.1 Dominance, Submission and Aggression

As expected, dominance and competitive behaviour were structured by age, with 35-49 year olds showing the highest rates (Table 7.2, Figure 7.2). Males performed more competitive and dominance behaviour and the likelihood of such interactions occurring increased as they became older, whereas females showed a marked transition to increased competition and dominance only in the 35-49 year old or "adult" (age not classified) categories. This behaviour was also more likely in mixed-sex versus same-sex parties. Party count and duration also affected the likelihood of interactions being dominance-based. Dominance behaviour was more likely in larger parties and was more likely to occur early in the "lifetime" of a party, so that it became less likely to occur in a party as time went on.

Predictors added (in order)	B	S.E.	expB	Wald	Df	Sig.
initiator age^A				100.518	7	**<0.001**
mixed sex party	-0.275	0.115	0.759	5.688	1	0.17
initiator sex	-0.480	0.110	0.619	18.892	1	**<0.001**
party duration	-0.004	0.002	0.996	6.402	1	**0.011**
party count	0.023	0.011	1.023	4.126	1	**0.042**

*Table 7.2. Logistic Regression model for Competition/Dominance behaviour (n=3914 interactions). Model X^2=173.71, df=11, p<0.001. Nagelkerke's R^2=0.081. ^{A}Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: initiator age*sex. Interfamily was not tested as a predictor, as this flooded the model.*

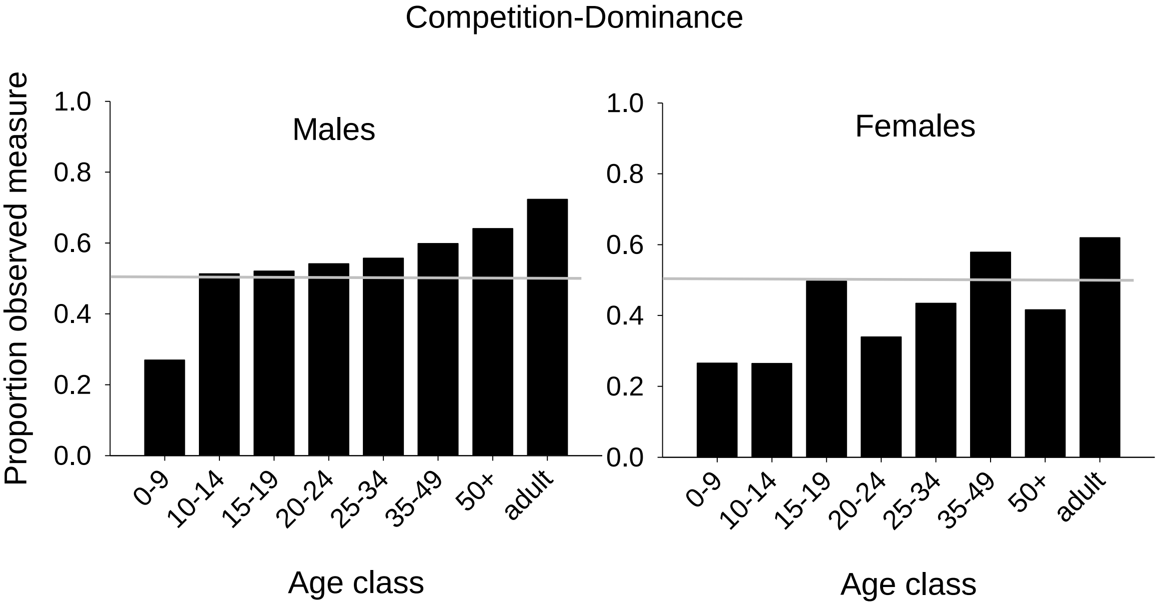

Figure 7.5. Proportional chi-square distribution of competition-dominance behaviour by age for males and females (n=3914 interactions). Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.

Submissive-avoidance behaviour and aggression were both more likely within, rather than between, families (Tables 7.3 and 7.4), but were otherwise influenced differently by aggregation rules. Submissive-avoidance behaviour was structured by the age and sex of initiators, and an age*sex interaction (Figure 7.6). Females were more likely to perform this behaviour, and younger animals of both sexes were more likely to show submission and avoidance, except amongst 10-14, 25-34 and 50+ year olds where the direction of the behaviour was sex dependent: Sub-adult females (10-14) were more likely to be submissive or avoid conspecifics than were similar aged males, 25-34 year old males were more likely to be submissive than similar-aged females, and the oldest males (aged 50+) were much less likely to be submissive than females in the same age class.

Predictors added (in order)	B	S.E.	expB	Wald	df	Sig.
interfamily interaction	1.790	0.132	5.99	183.027	1	**<0.001**
initiator age*sex^A				23.900	7	**0.001**
initiator sex	0.803	0.191	2.23	17.759	1	**<0.001**
initiator age^A				15.315	7	**.032**

Table 7.3. Logistic regression model for Submissive-Avoidance behaviour (n=3624 interactions). Model X^2=323.30, df=16, p<0.001. Nagelkerke's R^2=0.081. ^{A}Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: mixed sex party, party duration, party count.

Aggressive behaviour was structured by age, but not by sex, so that overall males and females were equally likely to be involved in aggressive interactions (Table 7.4). The likelihood of performing aggressive behaviour increased with age, with only animals aged 50 or more likely to be involved in aggression than 35-49 year olds, but this was not a strictly linear relationship (see Figure 7.6). Aggression was more likely between, rather than within-families, and became more likely as party size increased.

Predictors added (in order)	B	S.E.	expB	Wald	df	Sig.
interfamily interaction	.939	.142	2.558	43.936	1	**<0.001**
initiator age^A				66.782	7	**<0.001**
party count	.073	.012	1.075	39.384	1	**<0.001**

*Table 7.4. Logistic regression model for Aggressive behaviour (n=3624 interactions). Model X^2=230.98, df=9, p<0.001. Nagelkerke's R^2=0.116. ^{A}Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: mixed sex party, party duration, initiator sex, initiatory age*sex.*

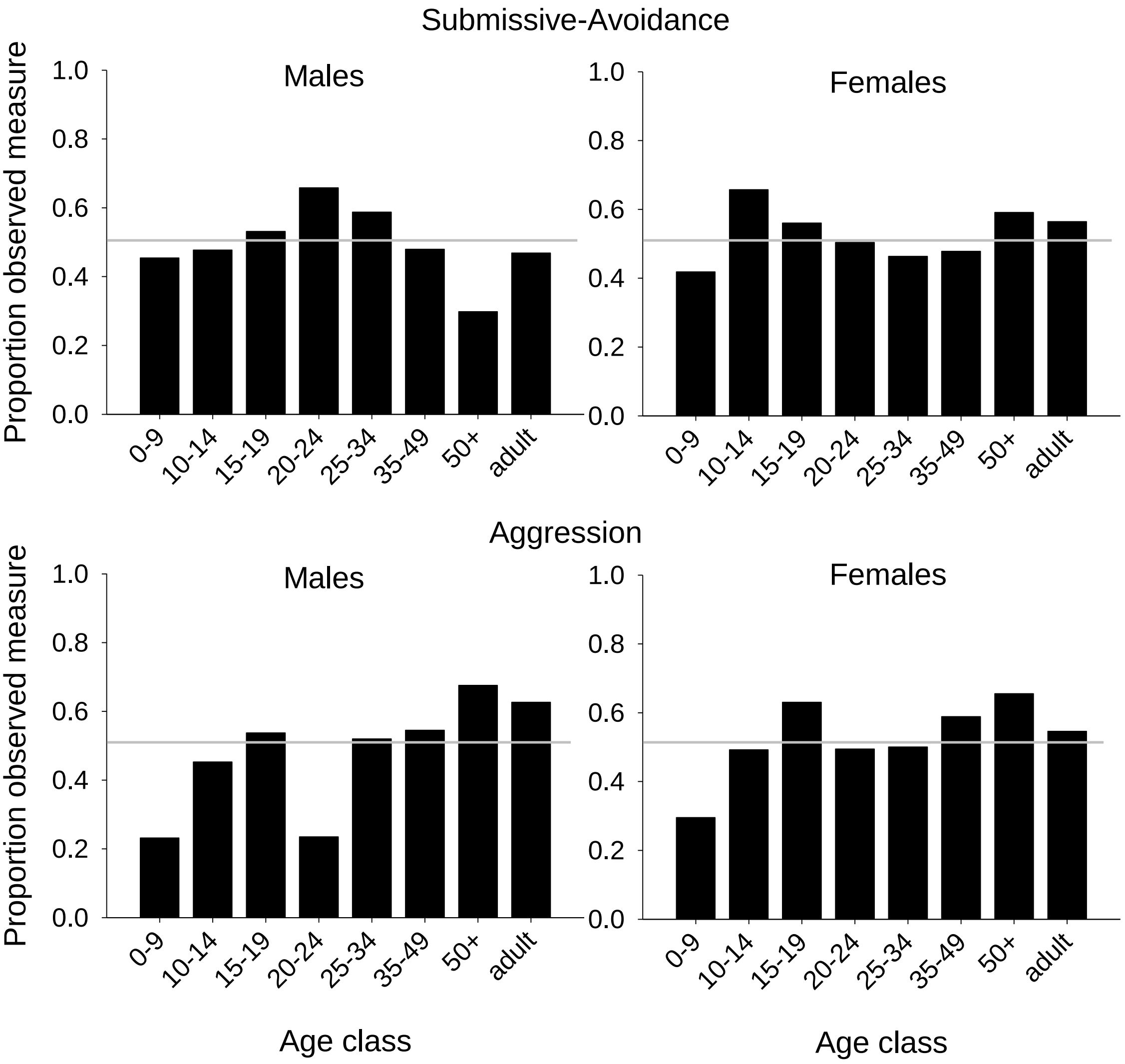

Figure 7.6. Proportional chi-square distribution of Submissive-Avoidance behaviour (top) and Aggression (bottom) by age for males and females. N= 3624 interactions in both cases. Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.

7.6.2 Affiliation & Social Monitoring

Affiliative behaviour was most strongly structured by age (Table 7.5), and an age-sex interaction (Figure 7.7). Immature and sub-adult animals were the most likely to perform affiliative behaviour, and old females were very unlikely instigate affiliative behaviour. Affiliative behaviour was also more likely to occur within families rather than between them.

Predictors added (in order)	B	S.E.	expB	Wald	df	Sig.
initiator age^A				91.883	7	**<0.001**
interfamily interaction	-0.957	0.087	0.384	120.873	1	**<0.001**
initiator age*sex^A				30.577	7	**<0.001**

Table 7.5. Logistic regression model for Affiliative behaviour (n=3624 interactions). Model $X^2=442.16$, *df=15,* $p<0.001$. *Nagelkerke's* $R^2=0.169$. ^{A}*Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: initiator sex, party duration, party count, mixed sex party*

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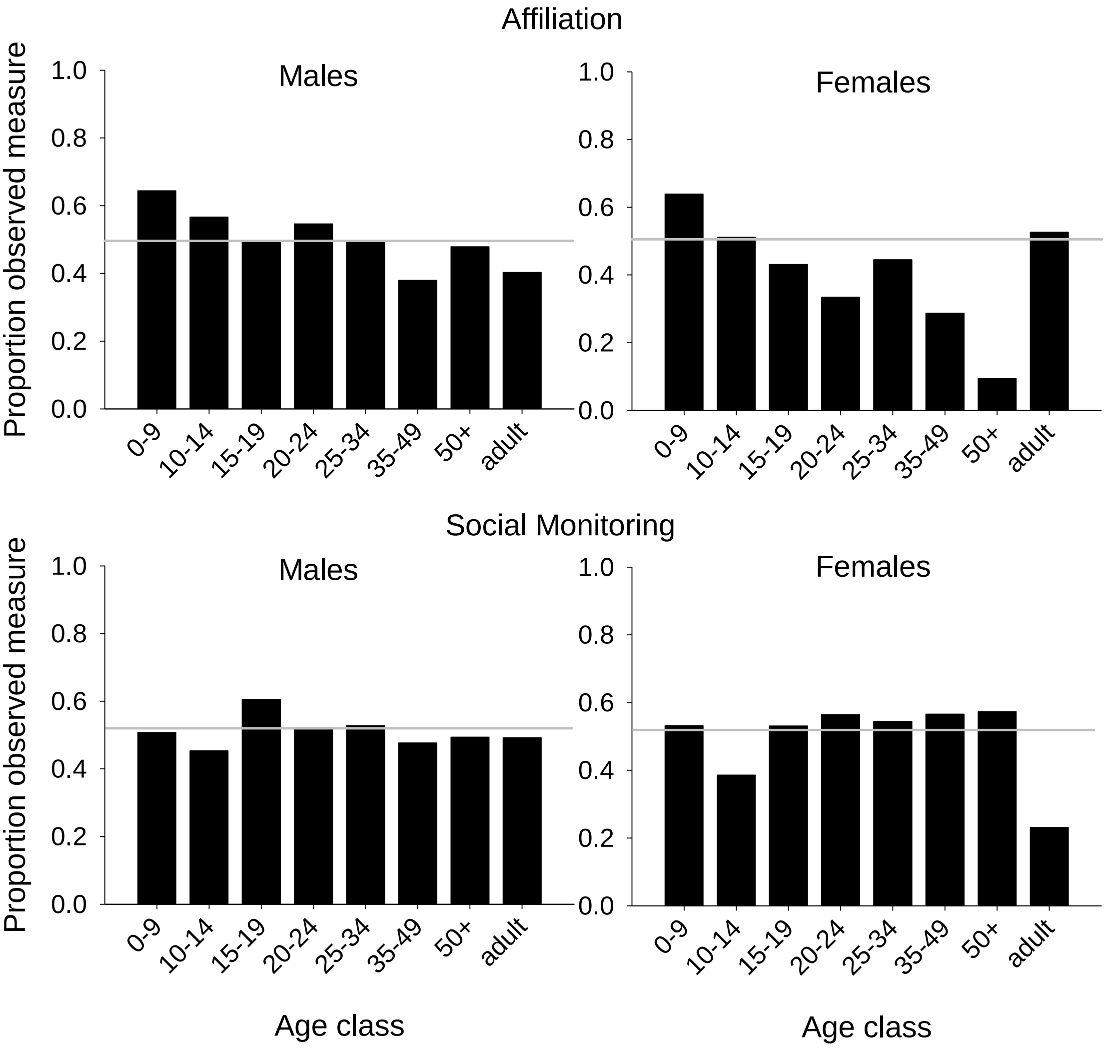

Figure 7.7. Proportional chi-square distribution of Affiliative and Social Monitoring behaviour by age for males and females. Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.

Social monitoring was more likely to occur between members of different families, in smaller parties, and was more likely in mixed-sex versus same-sex parties (Table 7.6, Figure 7.7). An age*sex interaction also structured the occurrence of social monitoring, where sub-adult animals (aged 10-14) and adult females (age not classified) were particularly unlikely to perform this behaviour.

Predictors added (in order)	B	S.E.	expB	Wald	df	Sig.
interfamily interaction	1.749	0.120	5.748	210.650	1	**<0.001**
party count	-0.068	0.014	.934	24.171	1	**<0.001**
initiator age*sex^{A}				15.777	7	0.027
mixed sex party	0.198	0.098	1.218	4.100	1	0.043

Table 7.6. Logistic regression model for Social Monitoring behaviour (n=3624 interactions). Model X^2=310.20 df=10, p<0.001. Nagelkerke's R^2=0.128. ^{A}Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: initiator age, initiator sex, party duration.

7.6.3 Maternal and Socio-Sexual Behaviour

Maternal behaviour was more likely in smaller parties and those of longer duration, presumably because mothers were not interacting with conspecifics (Table 7.7). The likelihood of exhibiting maternal behaviour increased with female age, with females aged 35-49 and old females of 50 or older being the most likely to show this behaviour. Females aged 20-24 performed less maternal behaviour than expected (Figure 7.8).

Predictors added (in order)	B	S.E.	expB	Wald	df	Sig.
party duration	0.010	0.002	0.885	37.757	1	**<0.001**
party count	-0.122	0.022	1.010	30.008	1	**<0.001**
initiator age[A]				26.672	7	**<0.001**

Table 7.7. Logistic regression model for Maternal behaviour (n=2395 interactions). Model X^2*=126.39, df=9, p<0.001. Nagelkerke's* R^2*=0.090.* [A]*Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: mixed sex party.*

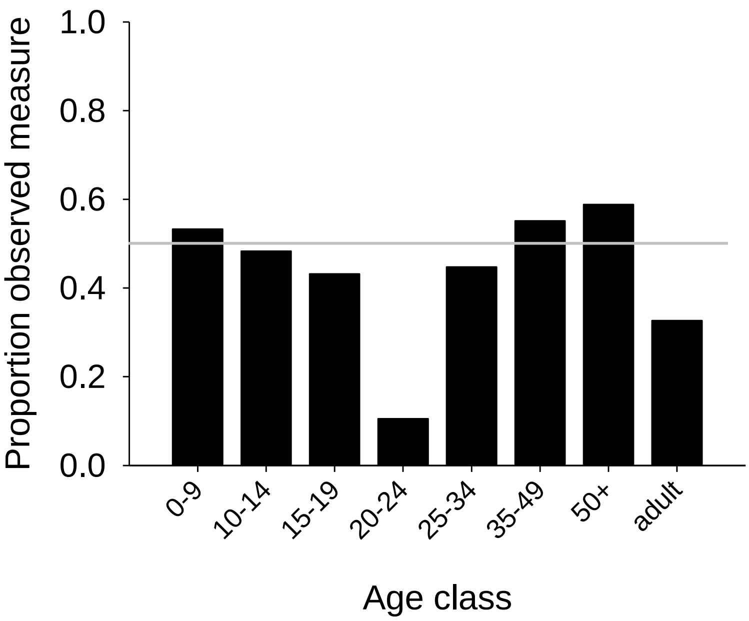

Figure 7.8. Proportional chi-square distribution of maternal behaviour by age (females only). N= 2395 interactions. Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.

Males were far more likely to perform socio-sexual behaviour than females (Table 7.9 and Figure 7.9), and this behaviour became less likely to occur as party duration increased. Age was also a significant predictor of the likelihood of interaction being socio-sexual in nature, with males aged 25-34 being the most likely to exhibit this behaviour. Females of all ages performed socio-sexual behaviour, mainly in avoiding male testing.

Predictors added (in order)	B	S.E.	expB	Wald	df	Sig.
initiator sex	-2.314	0.247	0.099	87.456	1	**<0.001**
initiator age^A				17.055	5	**0.004**
party duration	-0.023	0.006	0.978	15.187	1	**<0.001**

*Table 7.8. Logistic regression model for Socio-sexual behaviour (n=2640 interactions). Model X^2=197.02, df=7, p<0.001. Nagelkerke's R^2=0.213. ^{A}Categorical variable, pairwise comparison values of B & expB reported in Appendix E. Predictors dropped from the model: party count and initiator age*sex.*

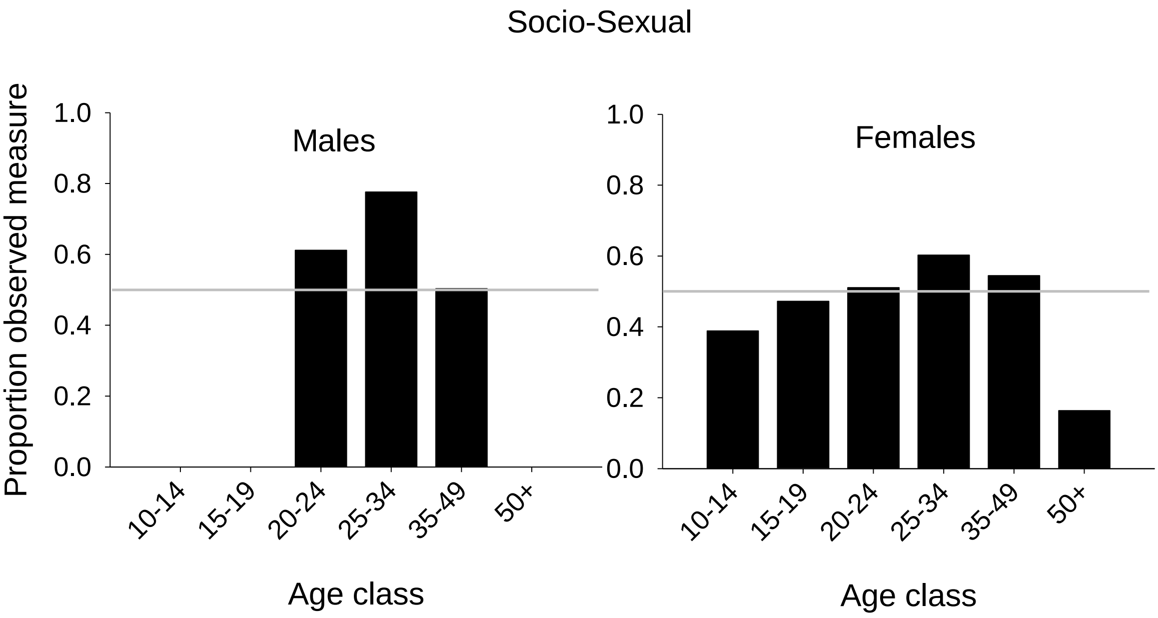

Figure 7.9. Proportional chi-square distribution of socio-sexual behaviour by age for males and females N= 2640 interactions. Grey line indicates 50% "observed = expected" line. See section 7.1 for measure definition.

7.6.4 Vocalisations

Over the study period 102 vocalisations were recorded, but their occurrence was not predicted by any aggregation parameters (model not shown). Vocalisation rates were certainly much higher than suggested by these data, since much of elephant communication is beyond the range of human hearing (e.g. McComb et al. 2003; Poole et al. 1988; Soltis et al. 2005). The most frequent vocalisations scored were rumbles (n=50) and vocal distress bellows (n=30). Rumbles were most often performed by adult females (n=19 of 26 cases where the caller was identified), and vocal distress was most common amongst immature animals (n=17 of 30 cases).

7.7 Results: Intra- and Inter-sexual Relationships

The patterning of interactions differed according to the sex of initiators and recipients (Figure 7.10), with inter-sex dyads showing the lowest rates of aggression, presumably partly due to a trade-off with engaging in the socio-sexual behaviour that were only possible in inter-sex dyads. Excluding sex-specific behaviour (maternal behaviour by females and socio-sexual behaviour in inter-sex dyads) all dyads exhibited all behaviour categories.

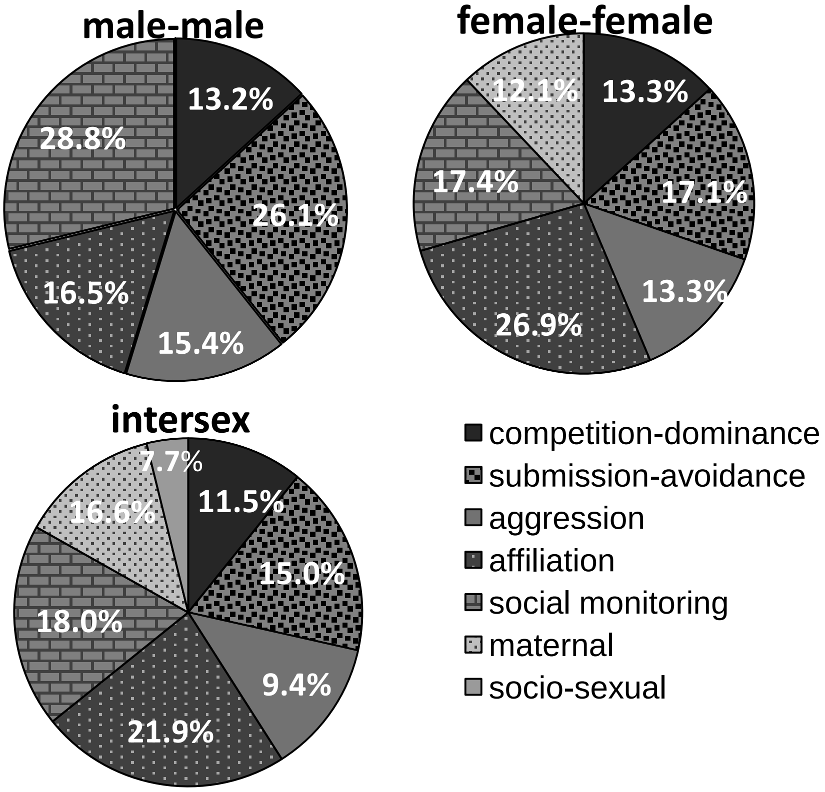

Figure 7.10. Interaction scores for male-male, inter-sex and female-female interactions. Scores are based on those assigned to n=519 male-male, n=1803 inter-sex and n=1509 female-female interactions recorded during the study period.

7.7.1 Male-Male Relationships

Male-male interactions were dominated by social monitoring and submission-avoidance behaviour (Figure 7.10). Highly affiliative behaviour was also observed between particular male dyads, where males entered and left the clearing together and performed friendly contacts including full body rubs and tail twining as well as lower-intensity trunk to face contacts (Figure 7.11).

Male-male aggression mostly consisted of threats (including ear folds, tusk pokes, chases and charges). Escalated interactions were rare, but fights occurred on two occasions; both cases involved prime non-musth males (aged 35-49) who were approximately matched for size (Figure 7.11). Both fights were brief, with a clear winner and both winners and losers remained in the clearing. Males did exhibit wounds indicative of other fights, consisting of grazes and abrasions to the head and buttocks (n= 4 males).

Males were also seen to engage in co-operative behaviour: in one instance Blake (35-49) and Elaki (25-34) had joined together in the clearing, and were vigilant to the approach of Albert (35-49). Elaki charged and supplanted Albert, who responded aggressively. Elaki initially avoided Albert by running away a short distance, before Blake and Elaki co-operated to supplant Albert, who responded submissively. After Blake's departure Elaki then aggressively approached another male, Ituri (35-49) but was forced to back down. Musth status had a role in this interaction: Elaki showed temporal gland secretion, but no enlargement or urine dribbling, whilst Ituri showed full temporal gland activity, and no urine dribbling.

Sparring behaviour was also relatively rare (n=4 instances), it being more common to see males “square up” to each other rather than actually physically engage with one another. Sparring occurred during friendly greetings (between 2 young adults 20-24 years old), rough play (Dezzie and Rita I, infant males, respectively aged 3-4 and 18mo-2 years old) and in more serious and unequal dominance contexts (Shukno 8-9 years initiated against Sebastian 10-14 years; Saul, 35-49 years initiated against an unknown male, 25-34 years).

Although associations did not show preferential age-sex partner choice amongst males (Chapter 6) some males did appear to be attracted to older males; on one occasion a group of four males was created by the successive joining by others. Arthur (35-49 years) and Galahad (25-34 years) showed affiliative behaviour, before being joined by a “tentative” Alvin (aged 20-24 years) and finally by the oldest male in the known population, Solomon (estimated 55+ years old) (Figure 7.11). Solomon was clearly dominant in this group, despite being in the presence of younger, fitter males, and was also dominant to Sabinyo, another old male. A further old male, Henry (50+ years), was also noted to be dominant to prime-age males, who were either deferential to, or supplanted by him. On another occasion, 2 immature males aged 5-9 years and 10-14 years looked to Alexander (35-49 years) for support having been alarmed by something invisible on the path as they went to exit the clearing.

Figure 7.11. Male-male interactions, left to right from top: Henry and George share sink-hole; Titus and Ezekial fight; Galahad and Arthur body rub and twine tails; mature multi-male group - Arthur, Galahad, Solomon and Alvin.

7.7.2 Male-Female Relationships

Inter-sex interactions primarily consisted of affiliative behaviour (Figure 7.10), 55% of which occurred within families (i.e. infants to mothers or between putative sibling pairs). Immature animals performed 59% of this affiliative behaviour, mainly to females or other immature animals. Inter-sex competition and dominance behaviour were distributed throughout age-sex classes, but most commonly performed by 35-49 year old adults (n= 60 of 208 interactions): males directed this behaviour to females of similar age, and females directed this behaviour to males less than 10 years old. Submission and avoidance behaviour was always directed to older animals and was generally shown by females to males (n= 188 of 270 interactions). Inter-sex aggression was rare, and was mainly directed by adult females towards males aged less than 19 years old (n= 60 of 170 aggressive interactions). Young non-family males (25 years or less) often made repeated approaches to females and their associates and were sometimes chased off by the largest females; once by a female coalition after repeated threats from a female did not stop the male's approach. Inter-sex sparring was rare (n= 6 dyads) and apart from one case involving play between animals of different families, sparring occurred in a range of contexts (n= 1 affiliative, n= 1 "neutral", n= 3 escalating dominance/aggression). Elephants nearly always monitored the approach of conspecifics, and this accounted for the relatively high proportion of social monitoring shown in inter-sex dyads.

Socio-sexual interactions were relatively rare (7.7% of inter-sex interactions, Figure 7.10) and were mainly testing and guarding behaviour performed by males to females. These sometimes had consequences for larger groups as females avoided unwanted attention. In one instance, old male Henry became intolerant of Philipp once he began testing a female, Kalli, and chased Philipp away. On the same visit, an unknown male chased and tried to mount Kalli, but there were no larger males present at the time. For further description of this behaviour, see Section 7.5.

7.7.3 Female-Female Relationships

A number of known females were clearly bonded to other adult females (see also Chapters 5 and 6). Females showed a higher level of intra-sexual affiliation compared to males and correspondingly less social monitoring. Competition-dominance and aggression levels were similar to males, but with less submission-avoidance. Co-operation between bonded females was observed, either for defence of calves (see Chapter 8) or in order to supplant conspecifics generally when larger females became involved in interactions in support of family members (as discussed above).

7.8 Results: Maternal and Socio-Sexual Behaviour

7.8.1 Suckling and Maternal Behaviour

Suckling bouts were recorded for 68 individual calves ranging in age from newborn (less than 1 month of age) up to 6-7 years old. Only 84 of the 170 recorded bouts were more than 1 minute in duration (mean= 2.36 mins, SD= 1.61 mins, max= 9 mins); more often bouts were brief (5-10 seconds). Of the observed suckling contacts, 95 were to male calves and 56 were to females (n=151 contacts where sex could be determined). This was significantly different from 50:50 (X^2= 10.07, df= 1, $p<0.02$) indicating that females invest differently in sons versus daughters. Weaning behaviour were also observed, where mothers terminated or refused suckling bouts, and these sometimes resulted in tantrums (bellows and blocking behaviour) or prolonged vocal and contact harassment of the mother by the calves. Maternal behaviour (e.g. suckling contacts, discipline, guidance and comfort; see Ethogram in Appendix A) was recorded on 519 occasions, and was most commonly directed to infants (calves < 2years old, n=379 instances), with 63% of these involving male infants. Maternal behaviour were also noted with older individuals; in the most extreme case, a young adult male Haithi (approximate 20 years old) was always seen in the company of his putative mother

Matkah (35-49 years; but a large, older female) and younger sister Mowgli (5-9 years). Their behaviour throughout their visits was highly cohesive and affiliative, with body rubs and trunk-face contacts throughout, and Matkah even made several attempts to discipline Haithi, tusking him in the head, despite him being larger than her.

7.8.2 Allomothering & "Kidnapping"

Allomothering behaviour was relatively commonly observed in the clearing. Mostly, this consisted of young females guarding or retrieving putative siblings, but on two occasions sub-adult females (5-9 years old) were seen to invite younger calves to suckle, despite the fact neither female was lactating. Suckling invitations consisted of a female touching the calf's face and head, and standing with one leg forward to facilitate access to the nipple. On one occasion the calf responded by simply touching the young female's breast and then rested, but on the other the calf did suckle in several bouts. On a third occasion, a sub-adult female Veena (5-9 years old) invited a newborn infant (<6mo old) from another family unit to suckle and then guarded the infant, despite the presence of a putative older sister (5-9 years old) in the infant's family unit. Finally, a non-lactating young adult female (15-19 years old) suckled the newborn (<1 month old) calf of her putative mother.

Allomothering behaviour was much rarer among adult females, but was nonetheless observed on two separate occasions. On the first of these, a well-known female (Naomi) approached and guarded the wounded juvenile daughter of another female (Serena), despite initial aggression from Serena when other elephants approached her calf. The calf, Sofia, was suffering from a severe head wound of unknown origin (see Figure 8.3). Naomi remained in the clearing guarding Sofia, even after the departure of her two female companions, with whom she was clearly bonded. On the second occasion an adult female who in late-stage pregnancy and lactating was seen to suckle the small infant of her female companion. None of these individuals were subsequently re-sighted to determine the level of relationship between these adult females.

“Kidnapping” was observed as a rare tactic employed to encourage females to leave the bai, when family members clearly wanted to move off (n= 3 instances). This was more active than “waiting” behaviour, where individuals would move to the periphery of the pool and stand around until the group moved off. In “kidnapping”, calves were actively encouraged to leave their mothers and follow other group members. These events often happened after waiting behaviour and were always performed by 10-14 year old females with their youngest putative siblings (all calves were around 2 years of age).

7.8.3 Oestrus

Oestrous behaviour was somewhat difficult to observe (oestrous walk, “coy” behaviour, solicitations, oestrous rumbles; Moss 1983), and was often diagnosed by male behaviour (e.g. consortships and mate guarding) rather than female behaviour *per se*. The difficulty in detecting oestrus from female behaviour alone was confounded by two females who were suspected to be pregnant but who approached and solicited attention from adult males who seemed unmotivated to respond to these advances. Only one female, Lindsay, was definitely observed in oestrus and she was accompanied in consortships by three musth males on different visits to the clearing. One of these was suspected to have resulted in copulation (see also below).

7.8.4 Males: Mating and Female Assessment

Socio-sexual interactions were relatively rare in the clearing. In total, 111 sexual contacts were observed within 68 dyads. Males most often tested females, rather than touching or following/chasing them (Figure 7.13) and when higher level interactions occurred, it was most often younger males who were responsible. On one occasion a young non-musth male (aged 20-24) chased and attempted to mount a female, Kalli, (Figure 7.12) creating a major disturbance to the other elephants using the clearing at the time. Such overt male harassment was rare, although male-female interactions were more often instigated by males and more often agonistic than affiliative (see Figure 7.10). Males rarely performed flehmen behaviour when testing females (Figure 7.13), emphasising the rarity of oestrous females: captive males perform flehmen more often when presented with urine from oestrous females than with urine from non-oestrous females (Sukumar 2003).

Figure 7.12. Unidentified male attempts to mount Kalli while her family members look on. See text for further details.

Three musth males were observed in consortships with Lindsay whilst she was in oestrus, each of these occurred on different days. The first consortship was highly active, in which the male, Maximus chased Lindsay repeatedly in and out of the clearing and attempted to mount her. Her two calves stayed very close, but the eldest was occasionally separated from Lindsay as she tried to avoid Maximus. Seconds after their last exit from the clearing, intense vocalisations from the forest edge indicated mating probably occurred. The second consortship was observed two days later, and the third nine days after this. Both these subsequent consortships were restricted to guarding behaviour. Guarding behaviour was only observed by these three 35-49 year old males during these consortships.

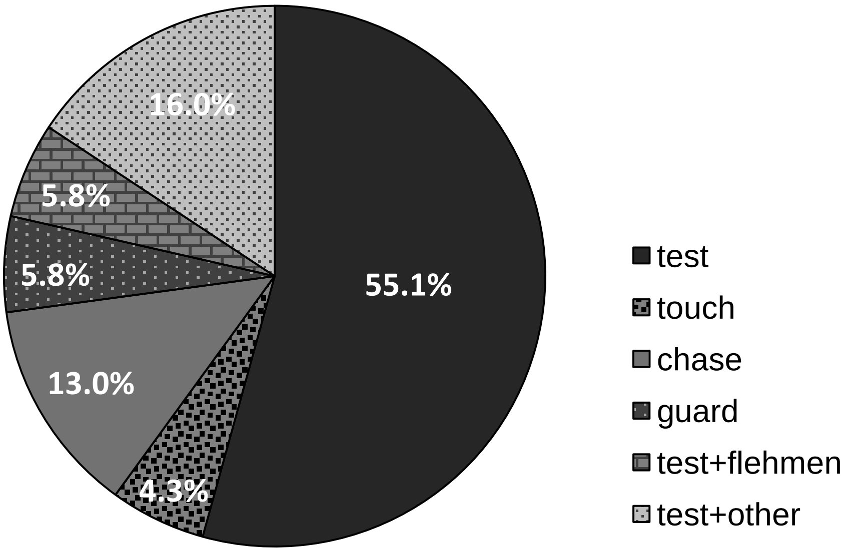

Figure 7.13. Nature of male sexual behaviour (n=69 dyads). "test+other" = more than one behaviour performed within the dyad.

7.9 Discussion

Elephants interacted with conspecifics at high rates (11.22 interactions per hour of elephant presence), having also made a decision to associate with available partners (see also Chapter 6). The social partners available affected the types of interactions, and age-, sex- and kin-structuring was an important determinant of interaction types for elephants in the clearing. Interactions were affected by aggregation rules that described the social situation, such as the number of individuals in a party, or the presence of mixed-sex parties, and were commonly related to party size and the presence of mixed-sex parties, but interactions were also strongly underpinned by the individual identities of the animals present. The regression models used here are limited in that they do not take account of the age or sex of recipients, as the data structure made it impossible to specifically model recipient characteristics. However, these models show that age-, sex- and kin-structuring of behaviour are all important for forest elephants. Play, a behaviour associated with stress-free, energy available contexts (Bekoff & Byers 1998), was notably rare and much rarer than at either the Mbeli or Dzanga clearings (VF pers. obs.). The low frequency of play is another indication of the risks and need for vigilance perceived by elephants when visiting Maya Nord, which are discussed in the next chapter.

Maya Nord does not appear to function as a mating or sexual arena, as shown by the rarity of musth males (Chapter 5), oestrous females or mating, and few escalated dominance interactions between males. Males performed competition-dominance and social monitoring behaviour above chance levels, consistent with the savannah male strategy of seeking of social novelty and maintaining a position within a dominance hierarchy. Young adults (aged 15-19) of both sexes showed developing aggression despite being relatively young; for males this is the developmental period at which males begin to compete with adult females as they approach and then surpass adult female body size (Lee & Moss 1995). These young males were in relatively good body condition, and probably use aggressive behaviour to facilitate access to resources to help them fuel this period of accelerated growth. This developmental stage precedes a drop in body condition amongst males aged 20-24 who may be suffering reduced foraging efficiency after dispersal from their natal area (see Chapter 5). Their aggressive behaviour may also be a function of their need to establish themselves within the male dominance hierarchy of their cohort when they are no longer reliant on maternal support to assist them in competitive interactions.

For females in this age group, these aggressive behaviours generally related to attempts to repel young males from approaching family groups.

Males were less frequently affiliative than were females but affiliative interactions were common between particular dyads, similar to savannah males. Some of the observed grouping behaviour and interactions suggest that older forest males may be both attractive to and function to suppress younger males (Evans 2006; Slotow et al. 2000; Poole 1982). Age was strongly related to dominance for males but was probably also underpinned by individual identity and social suppression as Solomon (the oldest known male in the population) was becoming very thin and aged, and yet was deferred to even by prime-age males.

Female-female relationships were characterised by a mixture of affiliation, competition-dominance and some aggression, suggesting that the tendency for females to aggregate promotes the exchange of social information and reinforces dominance and affiliative relationships. Younger adult females (aged 20-24) were particularly subordinate, although this did not seem to correlate with an increase in social monitoring. Their subordinate status presumably relates to their small body size, lack of maternal protection and the fact they are less aggressive than males. This female age-class was also interesting for showing remarkably little maternal behaviour: these females appear to constitute a transitional reproductive class with the highest pregnancy rate but no dependent calves (see Chapter 5). They may therefore be too preoccupied with their current (and novel) reproductive effort to participate in allomothering. These females also were more commonly seen alone than with family females. The clear effect of female age on maternal behaviour is consistent with the effects of maternal experience, which have been shown to be critical for calf survivorship in savannah elephants (Lee 1987; Lee & Moss in press a; McComb et al. 2001). The observed instances of allomothering suggest that young females may use visits to the clearing to add to their experience in dealing with young calves. Analyses of maternal behaviour suggests that forest elephant females may invest differently in male and female offspring, as is known for savannah elephants (Lee 1987; Lee & Moss 1986).

In conclusion, forest elephants at the Maya Nord clearing appear to show a suite of interactions which have direct parallels to those in savannah elephants, where individual identity and experience structure relationships both between- and within sexes. Coupled with how social opportunities affect elephant visit parameters and the elephant tendency to aggregate within the bai, this study shows how Maya Nord functions as a social as well as a nutritional resource base, especially for females.

Chapter Eight

Risk: Predators & People

Chapter 8 Risk: Predators & People

8.1 Abstract

PNOK elephants perceived bais as high-risk areas and were very sensitive to disturbance whilst in the clearing. The number of flight behaviours observed suggested that there were time and energy costs associated with the use of high-risk areas. These risks were inter- rather than intraspecific and were principally human-mediated, although hyenas do pose a predation risk for elephants in PNOK. Elephants showed no tolerance for, and were highly fearful of human observers, regardless of their age-sex class. No habituation was observed during the study period. Poaching continues in and around PNOK and socio-economic activities on the Park's periphery seem set to increase the threat to PNOK's elephants. The social and reproductive consequences of disruption remain unclear for PNOK elephants, but such disruption may affect individual ranging decisions and travel costs and may therefore have associated fitness consequences.

8.2 Introduction

This thesis has shown the importance of the Maya Nord clearing for forest elephants in PNOK as an ecological and a social resource. The north of PNOK contains many such clearings, and the relative importance of each of these is currently unclear. It seems likely that elephants use open clearings as social arenas; a place to aggregate and maintain relationships (see Chapters 6 and 7). However, these areas carry risks too, most notably from ivory poachers who have long targeted elephants at these sites.

The extension to PNOK officially granted in 2001 was designed to secure large areas of forest and savannah known to be important for large mammal populations, especially western lowland gorillas, lions (*Panthera leo*) and elephants. Policing such a large park is fraught with difficulty however, and as late as January 2008 poacher incursions were discovered 50km inside the Park north boundary (J. de Winter pers. comm.). This places poachers less than 20km from Maya Nord and at the heart of this vast protected area. Large swathes of PNOK are covered by dense Marantaceae forests, with a closed understory heavily invaded by *Haumania librechtsiana* (Lejoly 1996; Maisels 1996) which provides a refuge for elephants. The elephants' tendency to aggregate at clearings however makes them visible and therefore vulnerable. This chapter describes human- and non-human-mediated risks for elephants at Maya Nord, and discusses the potential social consequences of such disruption for forest elephants.

In addition, bais may pose non-human mediated risks for forest elephants: Leopards are suggested to pose a predation risk to forest elephants (Blake 2004). In addition the north of PNOK is highly unusual in supporting a permanent population of spotted hyaenas within the forest environment (but see also (Sillero-Zubiri & Gottelli 1992). Hyaenas have become an important predator of savannah elephant calves in Amboseli following the decline of the lion population (P.C. Lee pers. comm.). Hyaena dispersal from the savannah mosaic toward the south of the Park was probably facilitated by the carcasses left by large-scale ivory poaching at multiple elephant clearings. Hyaenas are not physically proficient in the forest environment (VF pers. obs.) which differs radically from the optimal habitat of open grasslands described by Kruuk (1972). Nonetheless they survive throughout the north sector of PNOK, far (>50km) from the savannah habitat and having traversed a major river (VF pers. obs.; Vanleeuwe et al. 1998).

8.3 Chapter Aims

8.3.1 Describe risk perception of elephants using Maya Nord

I describe vigilance and flight behaviour of elephants in the bai, along with the triggers for flight events. I explore the relationship between flight events and the number of elephants using the bai and discuss elephant reactions to observers.

8.3.2 Quantify the nature of the risks of bai use

Elephants clearly perceived risks associated with bai use. I discuss intra- and inter-specific risks for elephants, and how individual health status may affect elephant decisions to associate with conspecifics, presumably as a result of diminished competitive ability. Inter-specific risks are discussed in two sections – non-anthropogenic risks (predation and parasitism) and human-mediated risks, which were not anticipated before the study period, but which became an important feature of the observations made at Maya Nord.

8.3.3 Discuss the implications of risk and risk perception for elephants in clearings

Having demonstrated the importance of clearings as social arenas for forest elephants elsewhere in this thesis, the potential implications of using these high-risk areas are discussed, with reference to reproductive and social disruptions.

8.4 Methods

Vigilance behaviours were recorded using behaviour-dependent sampling (Chapter 2), and categorised as “listen”, “scent air” and “other” (see Ethogram Appendix A). Vigilance towards conspecifics was not included in these analyses. All instances of elephants fleeing the clearing were recorded, noting the time, direction of travel and cause (where this was known). All predator sign was noted, including direct observations at the clearing and tracks and vocalisations noted by the team in the forest and overnight. To assess the visit durations of animals that fled the clearing, the visits of 538 animals were compared according to whether or not they fled the clearing: 113 flee events and 425 non-flee events (these are the same data as were used to explore how social opportunity affects visit duration, Chapter 6). Predictors that were thought to influence the likelihood that elephants fled from the clearing were identified as sex, time of day and month, and these were entered into a forward stepwise logistic regression, which was also run backwards to check for suppressor effects.

8.5 Results: Vigilance and Flight Behaviours

Vigilance behaviours were common amongst the elephants that used Maya Nord (Figure 8.1) and these were not correlated to elephant visit rate (mean monthly vigilance versus total elephants per observation hour r_s= -0.042, p=0.907). All age-sex classes performed vigilance behaviours, and these most often consisted of scenting the air, with the trunk elevated above head height (77.9% of 3921 vigilance behaviours). Listening-only behaviours were relatively rare (10.2% of vigilance behaviours) and the remaining vigilance behaviours consisted of monitoring the clearing and other species (birds, buffalo *Syncerus caffer nanus*, sitatungas, red river hogs).

It was common for elephants to flee in the clearing, and flight events occurred on 66% of all days where elephants were present (94 of 142 elephant days). Flee rate was not correlated with elephant visit rate as shown in Section 4.2.2 (monthly total flight events per elephant hour versus total elephants per observation hour r_s = 0.382, p=0.247). All age-sex classes were observed to flee the clearing, including large musth males, and it was rare for any elephants in the clearing to remain once a flight event occurred.

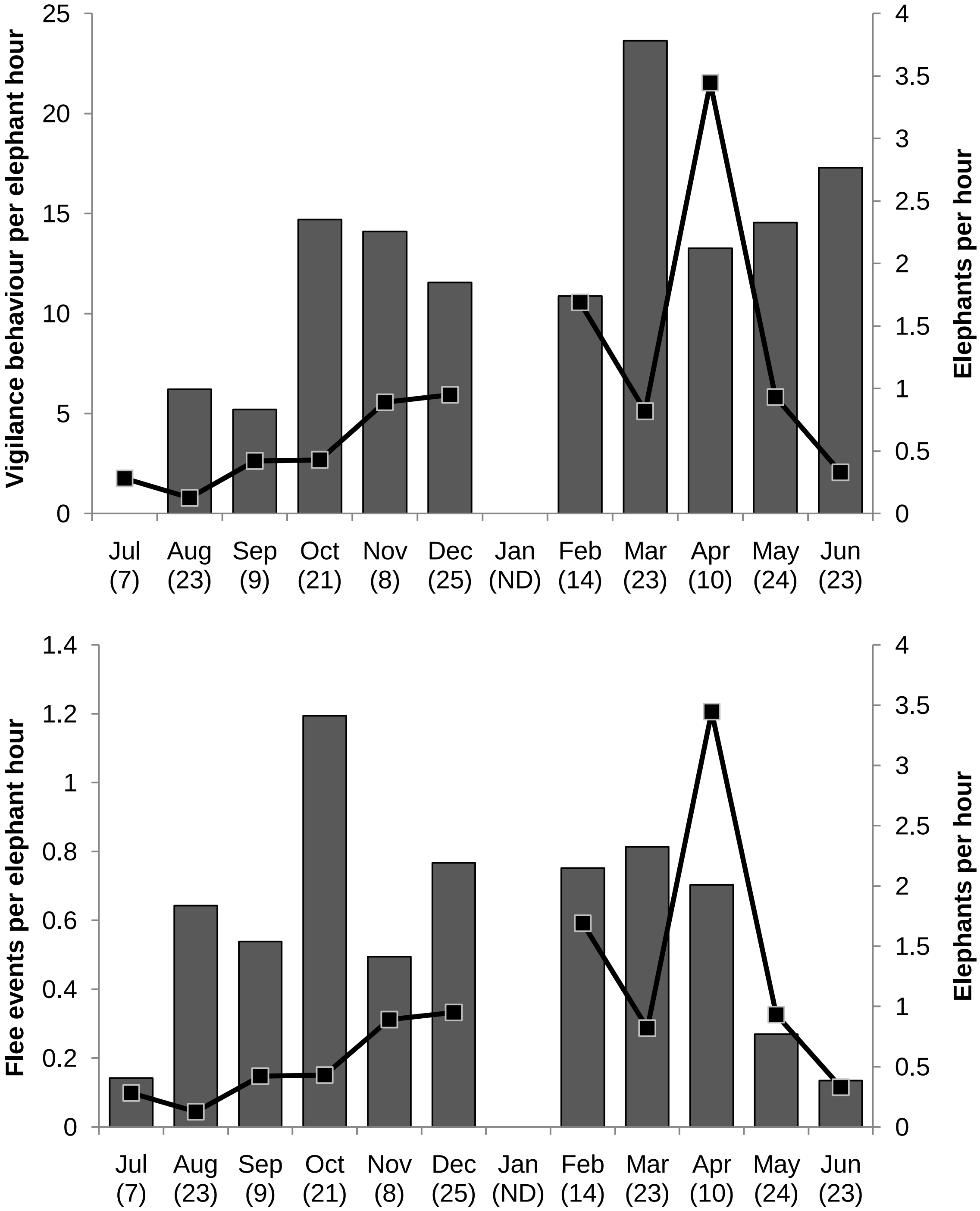

Figure 8.1. Rates of vigilance behaviour (top) and flight events (bottom) per hour of elephant presence (bars) against visit rate (line). N= 3920 instances of vigilance and n= 162 flight events.

Elephants rarely left the clearing calmly and if disturbed they always ran out of the pools. In fact, elephants were extremely sensitive to disturbance and responded to events such as interactions between buffalo groups and even the arrival of egret flocks (Figure 8.2), suggesting a heightened level of arousal while in the bai. The majority of responses were, however, either to observers or to other elephants. On one occasion an infant tripped in the pool and bumped into her mother's hind-leg, and the resulting commotion was enough to prompt an aggregation of more than 20 elephants to flee. Elephants always fled when they detected observers, and on days where wind direction was unfavourable observations were often terminated early. We attempted to minimise the effect of our presence on elephants by constructing a new observation platform in November 2007 and, while this reduced the rate at which elephants detected us, it by no means eliminated flight events (see Figure 8.1). We did not observe any habituation to our presence during the study period.

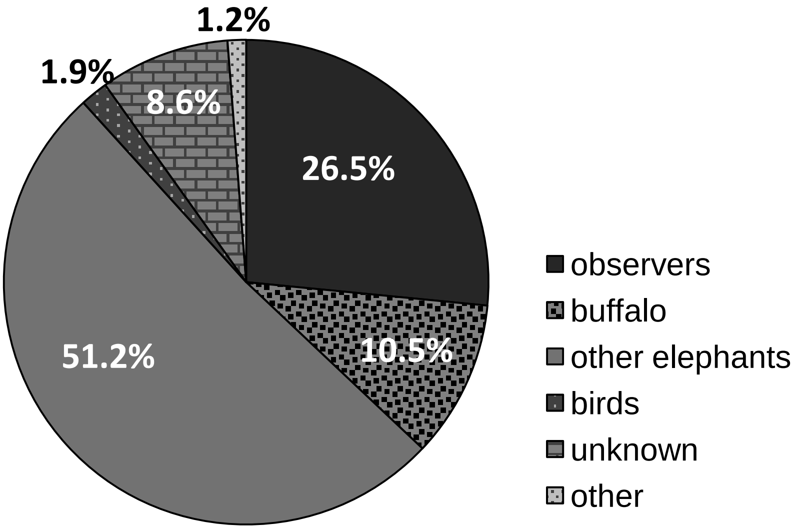

Figure 8.2. Causes of flight events from the clearing, n=162 parties.

Elephants that fled the clearing unsurprisingly tended to have shorter visits than animals who did not flee (Mann Whitney U= 21290, Z= -1.849, p= 0.064 r= -0.08). Once animals were disturbed, they left immediately and often very quickly (mean time to leave clearing 3.89 minutes, range 1-33 minutes). There was no difference in the speed to exit according to the disturbance type (categorised as observers, elephants or “other”: Kruskal Wallis test *H*= 1.830, df= 2, p= 0.401). Neither sex, nor month, nor time of day had any predictive power on the likelihood that elephants would flee the clearing (logistic regression, model not shown). Most animals who fled the clearing did not return during the observation day, and often where animals were re-sighted on subsequent visits they often appeared more nervous and showed higher rates of vigilance behaviours.

8.6 Results: Risks from Non-Humans

8.6.1 Intraspecific Risks

Competition between elephants can lead to aggressive interactions, and between males these occasionally prove fatal (Poole et al. in press). Previous researchers at Maya Nord had observed a fatal fight between two large males (H. Vanleeuwe pers. comm.) where the loser died in the clearing from his injuries. In this study levels of competition and aggression were low, and in fact elephants preferred to aggregate rather than avoid conspecifics (see Chapters 6 and 7). There were notable exceptions to this which involved sick or seriously injured individuals who actively avoided other elephants: one male, Enoch, had a tusk that had broken off at the base, exposing the pulp cavity. The tusk socket was swollen and he was clearly in pain and very poor physical condition. He was also very subordinate even to younger, smaller males and actively avoided a multi-male group. Interestingly, he was one of the few individuals who remained in the clearing when others fled, which may have been related to his poor state of health. However, it was not always the case that badly injured animals avoided others; adult male Akoa continued to associate with others after his wound was inflicted (although not immediately afterwards when he appeared to be in the most pain; see Section 8.4.2 for full details). Nicola made visits without her female companions after her injury occurred, but she continued to interact with other elephants, although like Akoa she made visits alone when she was first wounded (see also Section 8.4.2). Thus while elephants occasionally acted as a risk to each other, this was associated with specific kinds of interactions and not with general competitive pressure or presence.

8.6.2 Interspecific Risks

Although leopards were presumed to be common within the study area, sightings and traces of this highly cryptic species were rare. Sightings of them over the study period were much more common than I had observed at Mbeli however, probably because the site had been undisturbed for a considerable period (see Chapter 2). During the study seven visits by 2 individual leopards were recorded where they unsuccessfully attempted to hunt sitatunga. On no occasion did they interact with elephants.

In contrast, hyaena presence in the area was highly conspicuous. Hyaena tracks were observed weekly almost without fail on the path between the camp and the clearing, and hyenas frequently visited our camp. Contact calls (“whoops”) were often heard even when tracks were absent, and hyaenas were therefore considered to be permanent residents of the Maya zone. Hyaenas were seen during night observations, although it was hard to distinguish their exact movements in the clearing. They were seen eleven times during diurnal observations; the most dramatic of these occurring just after the study began. We arrived to discover five hyaenas feeding on the carcass of a young elephant in one of the main pools. The animal had certainly died overnight, as observers had been present until 17:30 on the previous evening. The carcass was left undisturbed for 3 days, during which time 3 elephant parties were observed to respond to it, scenting towards and once fleeing from the carcass. No physical contacts by elephants to the carcass were observed. We could not recover the lower jaw for ageing, as a hyaena carried it off into the forest on the third day of observations; however tusk development and overall body size suggest the individual was a juvenile aged 6-8 years old, and in good body condition.

Most of the remaining hyaena sightings were of resting or travelling animals, however on two other occasions, hyenas approached elephants: In the first of these, a hyaena approached a sick calf and was chased off by the calf's mother and another adult female. The calf in question, Ben (2-3 years old) had suffered a tail amputation that may itself have been attributable to a hyaena attack, and was very thin and unwell as a result. On the second occasion a hyaena approached a multi-female group which contained a very young infant and was chased off by the calf's mother. Although hyaenas appeared to target young elephants when they approached them, there was also evidence that they attacked older individuals. We observed a female, Maggie May in very poor body condition with serious wounds. She had sustained an enormous wound to her right flank, which was not fresh (for further observations on these kinds of wounds see section 8.4.2 and Table 8.1 below). However she also had fresh wounds on her hindquarters, several rips around her anal flap and a ragged and apparently chewed tail end: overall it appeared that hyaenas may have tried to capitalise on her weakened condition.

A surprising source of risk and irritation for elephants was the presence of yellow-billed oxpeckers (*Buphagus africanus*) in the clearing: these birds feed on large mammal ectoparasites and were permanently associated with the resident buffalo groups. Oxpeckers are not normally associated with elephants (but see Dale & Hustler 1991) and certainly for Maya Nord elephants the relationship appeared to be more parasitic than mutualistic, as birds re-opened wounds and fed on blood, as reported for other species (McElligott et al. 2004; Weeks 2000). This wound feeding behaviour slows healing time (Weeks 2000) and presumably also increases infection risks (e.g. for bacterial infections such as *Staphylococcus,* K. Cameron pers. comm.). Even without opening wounds, these birds caused a great deal of irritation to elephants who often performed contortions in attempting to blow the birds off their bodies. Families sometimes bunched together in response to oxpecker flocks and females were observed to blow them off family members. In extreme cases, animals even exited the clearing to escape the unwanted attention of these birds.

As noted above, elephants showed few responses to the presence of a fresh carcass. In one other case a recently dead elephant was also present in the bai; at the start of the study we discovered the presence of a skeleton next to one of the elephant pools.

Examination of the lower jaw suggested this belonged to a 50 year old female (based on Laws 1966 scale). No damage on the bones was apparent to suggest the cause of death and the teeth were not particularly worn. The skull was easily visible from the observation platform and was regularly observed in different positions, suggesting possible elephant contacts overnight. During our observations however, an interaction only happened once, where Yolande (25-34 years) patted the skull three times in quick succession as she passed, and then Yves (15-19 year old bond group male) also touched the skull and then continued using the sinkholes. The matriarch Yvonne (35-49 years) ignored the skull and Yolande's response to it.

8.7 Results: Human-Mediated Risks

Over the course of the study period a number of animals were seen with injuries (see also Section 5.3.2), of which 20.2% (n=24) were suspected, or definitely human–induced. All these injuries were considered to have had major health impacts at the time the injury occurred, although some elephants appeared to have completely recovered.

8.7.1 Snares

Thirteen identified elephants had sustained wounds to their trunks, most commonly as rips or slits to the trunk tip. However, four animals had partial amputations of the trunk; the most severe of these was Joseph (aged 5-9) who had lost almost half the length of his trunk, and although the wound was healed, he presumably suffered severe constraints on his capacity to use his trunk for feeding and drinking as a result.

All these were old wounds (see also Figure 2.3) and all animals were able to use their trunks. These injuries were suspected to be the result of the snares which are commonly used by hunters seeking duikers and other small forest game.

8.7.2 “Harpoons” and Bullets

Aggressive interactions between elephants can produce puncture wounds inflicted by tusks, but the resulting scars are generally concentrated on the buttocks and face, as animals gored in their flank often do not survive their injuries (P.C. Lee pers. comm.). Many elephants visiting Maya Nord showed large wounds or scars on their flanks, but the potential importance of this as a threat index was not recognised until a known male, Akoa (20-24 years old), appeared with serious injuries in December 2007. He had sustained a wound to his scrotum which had penetrated the urethra, and simultaneously amputated his tail (Figure 8.3). Over the remainder of the study period he continued to visit the clearing; both wounds were badly infected, and he suffered urine burns on his hind legs and the tail stump and extreme difficulty urinating. He became very thin over this period, and ultimately these wounds were expected to prove fatal. Originally, it appeared that this wound had been inflicted with a large machete; traditional magical practices amongst local ethnic groups make use of elephant body parts including the tail, although these are normally taken from dead animals (anonymous pers. comm.). Later, however, it became apparent that ivory poachers in PNOK use modified .12 calibre rifles to “harpoon” elephants (Figure 8.3), and this seems the most likely explanation for Akoa’s injuries.

Nicola (25-34 year old female) visited the clearing heavily pregnant but two weeks later was seen in the clearing without her usual female companions and with a fresh wound to her flank (Figure 8.3). Over subsequent visits it became apparent that she had also lost her calf, likely at the same time she sustained the injury. Unlike Akoa however, Nicola was seen to recover well. A sub-adult (10-14 year old) male, Jason, was observed with a fairly superficial laceration to his hip 7 days after he was identified and in perfectly good health. A further 12 animals showed large scars consistent with these harpoon injuries (Table 8.1). Bullet wounds were much harder to define, but were suspected from wounds or the style of scarring observed, especially on buttocks (Table 8.1).

Figure 8.3. Left to Right from Top. Akoa when first identified; Akoa post injury (wound infected and blackened skin showing urine burns to legs); Akoa urinating through scrotal wound; "Harpoons" recovered from poachers, displayed by PNOK staff; Nicola post-injury; Jonathan with scar covering nearly all of his right flank, Nicola in background with healing wound; Serena with her calf Sofia with head wound of unknown origin; Maggie May with large wound and amputated tail. See text for further details.

individual	sex	age class	affected body part	current health impact	human-inducted?	Notes
AF	F	adult	hip	low	bullet?	hugely deformed scar R hip
AF	F	adult	buttock	med	bullet?	hugely deformed and swollen L buttock
Akoa	M	20-24	scrotum & tail	high	harpoon	tail amputated at half length, underlying scrotal wound penetrated urethra
AM	M	adult	band	low	?	scar band across back and flanks
Anita	M	adult	flank	med	harpoon?	scar/wound R flank
Anya	F	20-24	buttock	low	?	large star-shaped scar R buttock
Arwen	F	35-49	flank	low	harpoon?	big scar L flank
Dexter	M	10-14	flank	low	harpoon?	scar R flank, still scabbed at centre
Elspeth	F	35-49	flank	high	harpoon?	large wound covers nearly all of L flank, necrosing tissue
Esther	F	35-49	buttock	med	bullet?	puncture R buttock - immediately think this is bullet wound
Gillian	F	25-34	flank	low	harpoon?	fairly large scar lower R belly/thigh
Isobel	F	50-64	lumbar	med	harpoon?	large scar over pelvic area; wound on R side which is infected and swollen beneath scar tissue. Also damaged trunk and scar L hip bone
Jason	M	10-14	flank	med	harpoon	fresh harpoon-like laceration L hip; looks q superficial
Jemima	F	20-24	trunk	low	snare?	amputated trunk tip; slice missing. old, healed wound
Jonathan	M	20-24	flank	low	harpoon	huge harpoon-style scar, totally healed
Joseph	M	5-9	trunk	med	snare?	has only 1/2 trunk
Maggie May	F	15-19	flank	high	harpoon?	huge wound across R flank; old. Also skin is ripped next to anus and tail end chewed
Matkah	F	35-49	flank	low	harpoon?	large scar R flank
Nicholas	M	35-49	trunk	low	snare?	trunk amputation - old wound
Nicola	F	35-49	flank	high	harpoon	wound R flank, tissues hanging from it. no longer pregnant. repeated SDBs at wound
Noah	M	15-19	flank	med	bullet?	bullet wound R flank/abdomen
Odette	F	25-34	flank	low	harpoon?	huge scar R flank
Olivia	F	35-49	band	low	harpoon?	scar band across back and flanks
Tessa	F	35-49	flank	low	harpoon?	large scar R flank
Vivian	F	35-49	flank	low	harpoon?	large scar L side
Zachary	M	25-34	buttock	low	bullet?	shiny round scar L buttock - ?bullet wound

Table 8.1. Individual details for 26 elephants with wounds suspected to be human-induced (past and current).

8.8 Results: Disruptions to Reproductive & Social Behaviour

As previously noted, orphans were very rare at Maya Nord (n=1, Chapter 5). It was difficult to identify the disruptions to family groups that result from the loss of key females since the structure of forest elephant groups remains poorly quantified. In the absence of longitudinal or genetic data on known individuals, it was sometimes impossible to assess if sub-adult animals “belonged” to the female-calf units that they were ranging with, as they were not always permanently associated with these groups. For many cow-calf parties, sub-adult (10-14 year old) females were often peripheral, but without re-sighting individuals it was not possible to determine whether this formed a developmental stage prior to dispersal or if these young females were associating with females who were not their mothers. Where young animals were seen alone it was often unclear if they had lost their mothers or were simply ranging independently. Only one identified family unit clearly had a “missing” female; adult female Louise (35-49 years old) was sighted with six immature offspring, ranging up to 20 years old. The youngest of these, Louis (2-3 years old) was her own suckling calf and Lola (15-17 years old) and Lucien (17-18 years old) were probably also her offspring: Lolly (4-5 years old), Leah (15-16 years old) and Lucas (19-20 years old) were more peripheral within the group and likely belonged to a “missing” female. It seems that Louise tolerated these young elephants ranging with her own offspring, as they were always together, except for Lucas, who made one visit without the family and Lucien who was absent on one visit where the rest of the family was seen.

PNOK females younger than 20 years apparently do not successfully rear calves (see also Chapter 5), although there were relatively few females in this age category and it is possible their calves had already dispersed. With a small sample size and a short-term data set it is not possible to determine whether this apparent lack of success the result of demographic stochasticity (Lee et al. in press a), or is a genuine feature of female reproduction in PNOK.

Disruptions to social structure remain to be teased apart for these elephants, but the behavioural disruption seen during flight suggests that there were energy and time costs associated with the use of this environment. Did these risks therefore reduce the likelihood of elephants revisiting this bai? Or was the low revisit rate a function of the generally high availability of bais (all associated with some poaching risk) throughout the elephants' range? Such questions remain to be addressed in subsequent studies.

8.9 Discussion

Intraspecific risks appear to be negligible for forest elephants using clearings; competition and aggression rates are low, and interspecific risks pose much greater threats. Hyenas present a clear predation risk for elephants in PNOK. Leopards are probably a lesser risk, although they are ambush predators and therefore range more widely where elephants roam. Hyenas require a degree of open ground to make a kill and use the major elephant paths linking clearings to move between them: they thus pose risks to elephants using clearings, particularly females and young calves. This raises the question of why calves still range "alone" from a young age: Even if these youngsters are moving in co-ordination with family members, they are certainly not protected by them when using clearings alone. Young animals were also observed to engage in risky approaches to adult buffalo within the clearing, despite having no familial support; other sites have reported that young elephants have died after provoking aggression from buffalo (A. Turkalo pers. comm.). Encounters with oxpeckers may also pose some health risks for elephants since elephant skin is prone to severe infections (Moss 1988).

Elephants at Maya Nord perceive bais as high-risk areas and are highly responsive to the smallest stimuli. They show no tolerance for, and are extremely fearful of humans. Since Maya Nord has not been a poaching target in recent years, these rules must be learned elsewhere during the course of elephants' ranging. The intensity of this response is not matched by other study populations in Central Africa; elephants at Dzanga for instance are under intense human pressure and yet have enough non-threatening encounters with humans that enable them to learn that particular sites or areas are secure (A. Turkalo pers. comm.). In Lopé, Gabon, elephants react to all humans as predators through both flight and aggression (P. Henschel pers. comm.). Odzala elephants apparently do not have the opportunity to learn that not all humans pose risks. Forest elephants are highly risk-averse, and adopt "siege" rather than "skirmish" strategies when faced with the dangers of crossing roads (Blake et al. 2008), preferring to allow roads to limit their ranging rather than crossing roads quickly and minimising their time in these zones. Their continued use of bais suggests a strong motivation to use these areas: since the mineral salts available at bais are available elsewhere in the forest, and since elephants stay longer at bais when aggregating with conspecifics, the opportunity to maintain social relationships appears to provide a strong driver for elephants to continue visiting clearings. The strength of this motivation is underlined by the fact that elephants continue to visit clearings even when they contain hundreds of carcasses left by poachers (Vanleeuwe et al. 1997). Large adult males at Maya Nord already follow strong risk avoidance strategies, and more commonly aggregate during the hours of darkness rather than daylight (VF pers. obs., Chapter 4).

Based on the distribution of calves to females in the youngest reproductive age group, females below the age of 20 appeared to experience difficulties successfully rearing calves suggesting that early reproductive efforts may be high-risk investments for PNOK elephants (see Chapter 5), although sample sizes were small and the short study period limits certainty regarding these data. Small-bodied and still growing females may be less able to support the lactational demands of calves or may be unable to defend them against predators. However, if lactational costs were the cause it might be expected that this study would have observed at least some young females in poor body condition with similarly weak calves and this was not observed during the study. Maternal experience strongly influences calf survival for savannah elephants, along with the number of allomothers available (Lee 1987; Lee & Moss in press). It is possible that forest females forego the benefits of allomothers in response to foraging constraints for high quality fruit resources.

The heart of PNOK may be geographically remote from human activities and habitation but elephants here show clear evidence of behavioural trauma. The social consequences of this kind of disturbance are not yet clear. Elsewhere, social disruption in elephants has had profound impacts on individual welfare and the reproductive output of populations (Bradshaw et al. 2005; Gobush et al. 2008; Slotow et al. 2000). Human pressure on PNOK can only continue to increase: a Gabonese logging concession bordering the Park's Western edge is shortly to become active, bringing people, firearms and transport to facilitate further ivory and bushmeat poaching (Wilkie et al. 2000). This is especially worrying given that PNOK elephants range into Gabon: in fact, one of the large elephant paths leading from Maya Nord travels directly across the border (Vanleeuwe et al. 1997). Elephants are targeted for bushmeat in Congo, and more generally, Central Africa's elephants are threatened by a burgeoning demand for ivory (Wasser et al. 2008, 2010). Congo's elephants are at risk through the presence of unregulated markets in Congo and neighbouring countries, and high corruption levels (Lumieux & Clarke 2009). CITES maintains a current ivory trade ban, but political concerns forced the withdrawal of proposal for a 20 year trade moratorium at the most recent Conference of the Parties in March 2010 (Earth Negotiations Bulletin 2010). Meanwhile, demand in new Chinese markets continues to grow, and ivory sources from seizures in Hong Kong show clear links to Central African sources centred on Gabon and Congo (Wasser et al. 2008). Without effective protection Central Africa's elephants become increasingly threatened each year and the likelihood increases that Congo's forests may be emptied in a repeat of what has happened recently in the Democratic Republic of Congo (Wasser et al. 2010).

Chapter Nine

Discussion

Chapter 9 Discussion

9.1 Introduction

African savannah elephants use a fission-fusion social system in order to maximise social opportunities while balancing resource limitations or individual reductions in intake associated with intraspecific competition (Archie et al. 2006b; Moss & Lee in press b; Wittemyer et al. 2005, 2009). This fission-fusion strategy generates a complex series of social relationships that persist over decades and which are structured by age-, sex- and individual experience. Individual experience and social relationships have long-term implications for fitness and reproductive success (Evans 2006; Evans & Harris 2008; McComb et al. 2001; Moss & Lee in press a.; Lee et al. in press b; Poole et al. in press). In contrast to the well-studied populations of East and Southern Africa (e.g. Douglas-Hamilton 1972; Moss et al in press; Whitehouse & Hall-Martin 2000; Wittemyer et al. 2009), forest elephant sociality has remained little-quantified, partly as a result of the difficulties of making direct observations of animals in dense forest habitats. Forest elephants range alone or in small groups, with a basic unit of a female and her dependent offspring. They tend to aggregate at open areas, often to perform geophagy behaviours (Fishlock et al. 2008; Morgan & Lee 2007; Turkalo & Fay 1995, 2001). This tendency to aggregate, particularly at natural forest clearings, has led to suggestions that elephants may use these areas to maintain social relationships with conspecifics with whom they do not forage.

The purpose of this thesis was to examine the role of forest clearings as social arenas for forest elephants, and to begin an empirical exploration of forest elephant sociality. To approach this problem, elephant use of Maya Nord was examined according to three main themes; ecology, sociality and risk.

The resources available in and around the clearing were broadly categorised and temporal changes in elephant visiting to the clearing were described. Elephants used the Maya Nord clearing at a variable rate throughout the year, but this was unrelated to the resources available in the immediate locality as far as could be determined through monitoring local forest productivity and elephant diet through examination of dung-piles (Chapters 3 and 4). It seems therefore that peak visiting at Maya Nord does not coincide with a proliferation of local resources. Rather, elephants appear to range widely over Odzala's Marantaceae forests in response to changes in the availability of high-quality fruit resources, and use the Maya Nord clearing when they are present in the area. Geochemical analyses of the mineral resources available in bais confirmed that geophagy was related to the acquisition of minerals, as reported from other sites (Klaus et al. 1998). Sodium appetite has widely been reported as a stimulus for geophagy behaviour among generalist herbivores, whose diets tend to be deficient as relatively few plants provide a good source of this metabolically important mineral. Although the sampling techniques used in this study were relatively unsophisticated, it appeared that elephants were accessing sodium whilst avoiding elevated potassium levels. However elephants rarely consumed herbaceous vegetation in the bai, despite this being higher in sodium and calcium compared to the dominant species found in the surrounding Marantaceae forest (Chapter 4; Magliocca & Gautier-Hion 2002). The study failed to detect significant proportions of clay in the samples, despite the fact that clay content has been suggested to be a stimulus for geophagy behaviours (Chapter 3; Klaus et al. 1998).

Amongst the proposed functions for bai use outlined in Chapter 1, Maya Nord is best described as a nutritional resource that facilitates social behaviour and this social function provided a strong motivation for individuals to visit, over and above the nutritional resources available. Levels of contest competition were minimal, as escalated interactions were rare and even in high visiting periods elephants did not minimise competition either through queuing behaviours (waiting at the forest or pool edge before approaching geophagy sites) or by evenly spacing their visits throughout the day (Chapter 4). The net effect of this was larger parties and larger aggregations during high visiting periods. Elephants showed strong preferences to aggregate rather than disperse across the available resource access points and stayed longer in the clearing when they contacted conspecifics (Chapter 6). Decisions to aggregate were strongly structured by age and sex, and represented non-random choices by the individuals concerned. Elephants showed active preference for certain age-sex companions and active avoidance of others, indicating that whilst age-sex rules play a role in social decisions many of these decisions were also underpinned by individual identity (Chapter 6). Age- and sex- structuring of behaviour was also apparent in interactions and suggests that the motivation to aggregate with conspecifics may vary according to age, sex and reproductive status (Chapter 7). Clearings can thus provide elephants with rich social environments and opportunities for social learning.

The analyses in this thesis are based on diurnal observations of elephants at Maya Nord. Much elephant activity at bais occurs during the hours of darkness, and so aggregations tend to be larger during the night. However, as far as could be observed, elephant behaviour was not qualitatively different during night-time aggregations: elephants did now show queuing behaviour, and they continued to focus their activity on elephant pools, rather than dispersing across the clearing and feeding on herbaceous vegetation. Although I could not quantify this statistically, it seems unlikely that an elephants' social experience during night-time aggregations differs qualitatively from that experienced in similar-sized aggregations (of similar composition) during daylight hours.

9.2 Social Arenas

9.2.1 Classifying arena function

The function of a social arena may change over time, through ecological or demographic shifts or through anthropogenic changes in the landscape. Although our understanding of the creation of different types of bais and their "lifecycles" is limited (Blake 2002), it seems unlikely that great changes have occurred recently at Maya Nord. The topography of the clearing has changed very little since the early 1990s, and observations at Dzanga Bai have been ongoing for 20 years without documenting site shifts or abandonment (A. Turkalo pers. comm.). Anthropogenic pressures on Central

African forests certainly have changed over the past two decades at both sites, and these need to be considered when interpreting the results of this study (see below).

Maya Nord does not function as a bull retirement area or purely as a mating arena for PNOK elephants. Males are significantly under-represented in the population that uses the clearing during daylight hours and although males often associated with females, musth bulls were rarely observed (Chapter 5). Network analyses of association showed females were more strongly embedded in social relationships than males; thus it appears that the clearing functions as an area for female social exchange, and that although males also maintain social relationships during clearing visits they do so at lower rates than females (Chapter 6) and they also use the clearing to monitor female reproductive status (Chapter 7). Old matriarchs emerged as an attractive, central and structuring force in the social network, and 10-14 year old elephants of both sexes were socially explorative, presumably as a development stage during the process of dispersal (Chapter 6). Strong sex differences were identified in both associations and social interactions (Chapters 6 and 7). Forest elephants appear to show very similar social organisation and behaviour to savannah populations, and use open areas in order to maintain this organisation, despite perceiving risks in doing so (Chapter 8).

9.2.2 Social functions and opportunities for social learning in bais

Fission-fusion dynamics create variable and to a degree unpredictable social environments, with associated cognitive demands (Aureli et al. 2008; Lee 1991; Lee & Moss 1999). Elephants clearly demonstrate tendencies for social learning, as evidenced by their adoption of elephant role models during the capture and "taming" of wild elephants amongst the mahout tradition in Asia, in the role that human caretakers and older elephants play for orphaned animals in Africa and in their demonstration of empathetic behaviours relating to dead or ill conspecifics (Bates et al. 2008a; Douglas-Hamilton et al. 2006; McComb et al. 2005; Merte et al. 2008). They exhibit excellent spatial-temporal and social memory (e.g. Bates et al. 2008a; Hart et al. 2008; McComb et al. 2000) and complex communication systems that may have to be learned (Poole & Moss 1989; Poole et al. 1988, 2005; McComb et al. 2000, 2003). The social environment is vital for elephant development (Evans 2006; Evans & Harris 2008; Lee 1991; McComb et al. 2001) and can have long-term fitness consequences e.g. through the availability of allomothers (Lee 1987; Moss & Lee in press a). Social disruptions can have catastrophic effects on individual behaviour, welfare and reproductive success (Abe 1994; Bradshaw et al. 2005; Gobush et al. 2008; Nyakaana et al. 2001; Slotow & van Dyk 2001a).

This study has confirmed that forest elephants use a fission-fusion system of social organisation. Their social and ecological learning requirements are probably thus very similar to those of savannah elephants; early evidence also suggests that their communication system is highly homologous to that of savannah elephants (Payne 2003; Payne et al. 2003; Thompson 2009). Similar to savannah elephants, this thesis suggests that the "pull" of sociality underpins forest elephant behaviour, even in the context of the "push" of risk, competition and social dominance. Aggregations in clearings provide rich social experiences for forest elephants and opportunities for social contacts out with the mother-calf unit. These may facilitate learning both via individual learning and social eavesdropping routes: individual learning as a direct outcome of interactions with conspecifics (e.g. in dominance interactions, an individual learns that bigger animals are stronger) and social eavesdropping that occurs through the extraction of information when witnessing interactions between conspecifics (Bonnie & Earley 2007). Young animals probably learn the rules of elephant sociality (such as transitive dominance relationships) in clearings and later use them to maintain social relationships with individuals that they do not forage with. They can also potentially minimise the social costs of dispersal (Isbell & van Vuren 1996) by using aggregations to begin establishing social relationships before they leave their natal unit: This study found young elephants of both sexes to be social explorative in a manner similar to young males in savannah elephant families who actively seek social novelty in preparation for their departure from the natal group (Lee 1986).

9.2.3 Social arenas and reproduction

The use of forest clearings impacts forest elephant reproduction both directly and indirectly. Firstly, open habitats are the only places where elephants can perform the visual signalling associated with reproduction (i.e. musth and oestrous walks, Moss 1983; Poole & Moss 1981), which form part of the behavioural repertoire of forest elephants (VF pers. obs.). Males can use chemosensory cues on major trails leading into clearings in order to locate oestrous females and monitor musth bulls. The presence of females in clearings is undoubtedly attractive to males, who approach females to test their reproductive status. Indirectly, males can also maintain relationships with other males and assess their place in the dominance hierarchy. Bais might offer attractive arenas for males to escalate contests, offering an open area and stable substrate where they can spar, signal and be observed by conspecifics. Despite this, escalated interactions between were rare at Maya Nord, and most commonly occurred between females and young males (aged 15-19) who were particularly aggressive (although not dominant). This low incidence of escalated male-male interactions may have been exaggerated by male risk avoidance strategies (i.e. large, old males avoid clearings during daylight hours, see also below). Males at Maya Nord generally maintained a dominance hierarchy through competitive-dominance behaviours such as supplanting individuals from geophagy sites, and avoided potentially costly fights. Males also used clearing visits to maintain their affiliative relationships, albeit at a lower rate than females.

Bai visits and the social experiences during these visits provide a mechanism by which females can adjust or minimise some the additional costs of reproduction. Agonistic and competitive interactions were common amongst females, and may not have been attributable to contest competition for these point resources, since females rarely successfully prevented others from using any of the resource access points available. Contests generally only excluded individuals from preferred geophagy sites, and whilst recipients of agonistic behaviour avoided the initiator, they did not often leave the party. Wittemyer & Getz (2007) speculate that such contests in low-gain or no-gain situations might serve to reinforce dominance relationships through winner/loser effects, thereby avoiding later escalation (and the associated costs) over more beneficial resources. They further speculate that the cognitive abilities of elephants may further reinforce these winner/loser effects, and thereby reinforce the transitivity of relationships (Wittemyer & Getz 2007).

Indirect effects for female reproduction may also accrue through social learning opportunities in aggregations. Matriarch age is a significant predictor of the number of calves produced per family unit per female reproductive year at Amboseli (Moss & Lee in press a). Although calf survival is influenced by the number of available allomothers young females apparently cannot increase the success of their first reproductive effort through allomothering experience (Lee 1987; Lee & Moss in press). Nonetheless calves appeared to be an attractant for young females and since forest elephant foraging groups are small, females without younger siblings may acquire their first experiences of calf care in the bai environment. Aggregating at bais may also reduce predation pressures for forest elephants facing predation by lions (historically present in PNOK; Henschel 2008) and hyaenas (a relatively recent risk in evolutionary terms).

9.3 Sociality and Social Structure

The analyses of forest elephant social structure presented in this thesis bear close similarities to savannah elephant systems, where multi-level organisation is structured by age- and sex and underpinned by individual identity and knowledge. Although large multi-female groups are absent in a forest foraging context, forest elephant females use clearings to aggregate and maintain their social relationships. These females thus fission in response to reproductive energetic demands (access to high-quality and patchily distributed fruit resources), in contrast to savannah elephants who can more often solve resource acquisition problems through co-ordinated group movement and group consensus over travel direction. Aureli et al. (2008) have urged a shift in the use of the term “fission-fusion” as a label, and towards the idea that this term represents an area of social “space” where taxa (or populations) may vary in spatial cohesion and group membership. African elephants provide a clear demonstration of this kind of variation, as elephant populations across Africa use very similar and flexible social systems, and this behavioural plasticity probably underlies their successful exploitation of a wide range of habitats.

Forest and savannah elephants are thus suggested to lie on the same social continuum, balancing social “pulls” to aggregate against the ecological “pushes” that force groups to fission (Figure 9.1). Aggregating with conspecifics is vital for normal social development in elephants (Bradshaw et al. 2001), and since conspecifics are both attractive and rewarding to elephants, they constitute a social “pull”. Less straightforward perhaps is the categorisation of ecological effects as “pushes” in sociality. Environmental heterogeneity can of course lead to decisions to fusion: Groups numbering hundreds of individuals are seen during wet seasons in Amboseli as primary productivity peaks, meaning forage is abundant and evenly distributed and energetic balances permit large group sizes (Croze & Moss, in press; Lindsay, in press). However these groupings are facilitated by the resource availability, rather than caused by it; individuals could choose to exploit the available resources without necessarily interacting with other elephants, much as forest elephants could use bais in the presence of conspecifics without using the bai as a social arena. The fact that these large groupings in savannah elephants also bring reproductive opportunities enriches the social experience for group members, even for those who are not directly involved in the mating opportunities that arise. It is therefore suggested that ecological factors generally provides “pushes” rather than “pulls” for elephants, as an inevitable outcome of competition for limited resources.

This kind of categorisation places resource competition as a key driving force for the evolution of elephant social systems. Predation risk and co-operation also shape animal societies, and both these are pertinent to elephants: protection of vulnerable calves favours groupings for savannah females even when these are costly (Moss & Lee in press b), and this promotes female co-operation and the evolution of gregariousness. The number of allomothers available to share calf care positively correlates with calf survival (Lee 1987). However, elephant families themselves fission and fusion over the course of hours or days, and the extent of this is variable both between families and within the same families over time, depending in part on resource availability (Moss & Lee in press b). The mothers of the youngest calves (less than 12 months old) who are most vulnerable to predation and the most reliant on their mothers for nutrition, may themselves be most affected by intra-unit competition, resulting in lower cohesion between these females and other family members (Wittemyer et al. 2005): fission-fusion thus becomes a trade-off that individuals must assess and manage over the course of their lives (Moss & Lee in press b).

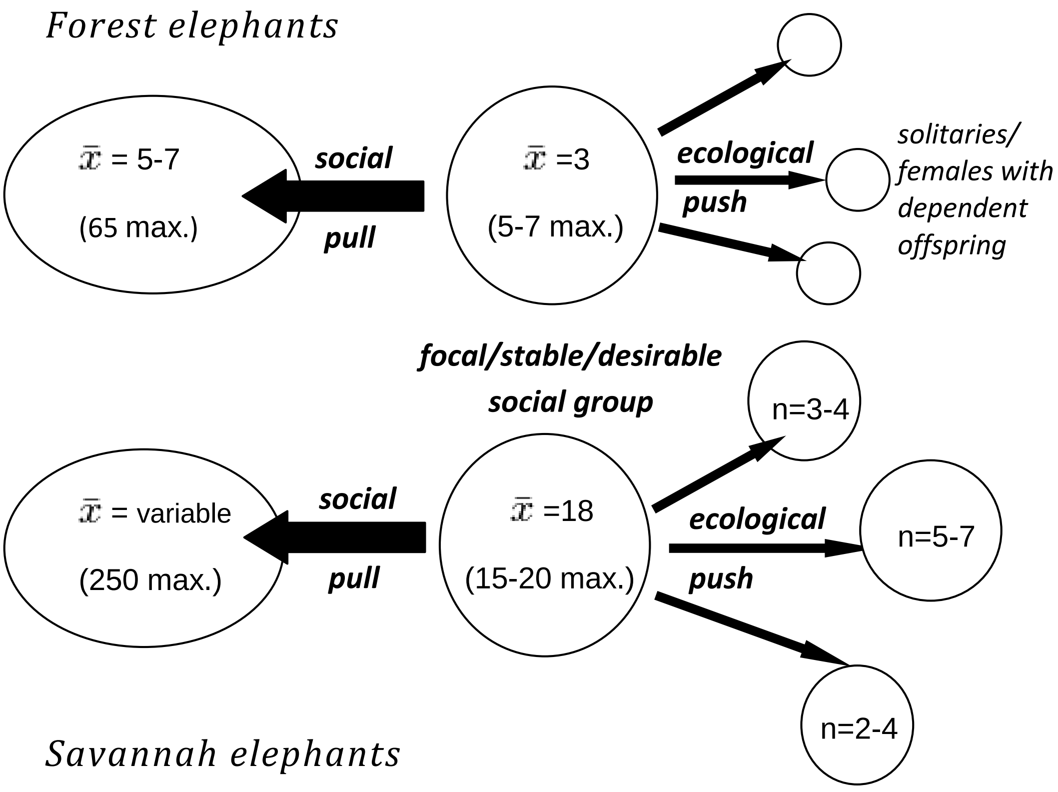

Figure 9.1. Schematic of the suggested equilibrium of female elephant social dynamics, where similar processes govern decisions to fission and fusion, and the principle difference between forest and savannah elephant sociality lies in the size of groupings. Individuals may incur foraging costs in order to maintain groupings with their most preferred associates, but resource availability generates a set of ecological pushes which force groups to fission.

Previous models of savannah elephant sociality construct levels of association and social complexity upwards from the basic mother-calf unit (e.g. Wittemyer & Getz 2007). My results suggest that it may be more appropriate to consider elephant sociality and associations as in dynamic equilibrium between social and ecological influences acting at all levels of grouping, and to explicitly test how these underlie the opportunity costs that elephants are willing to pay in order to maintain social groupings.

Forest elephant sociality still presents a number of interesting questions regarding the intensity of and variation in female relationships. Clearly not all females dispersed from their natal group and some females are observed with fully adult “daughters”. It is tempting (and parsimonious) to assume that reproductive status might constrain females relationships by preventing them from foraging together and that bais may allow them to maintain relationships with female kin. However, high intensity greetings were not part of the behavioural repertoire observed at Maya Nord; although individuals did greet and vocalise when other females arrived in the pools, this never escalated into the intense and excited greeting ceremonies documented during family-unit and bond group reunions in savannah elephants (Moss & Poole 1983; Poole et al. 1988). It may be that the maternal kinship patterns which are so essential for reproductive success amongst savannah elephant females are somehow “dampened” amongst forest elephant females, who have, in evolutionary terms, faced lower predation pressure. Monitoring depletion of resources by conspecifics has also been suggested to be vital for the evolution of female kin groups (Isbell 2004), but forest elephants may achieve this through infrasonic communication (e.g. Leighty et al. 2008; McComb et al. 2003; Poole et al. 1988), and point resource depletion at geophagy sites seems to be a negligible factor, since the topography (and the foci of elephant activity) of Maya Nord has remained unchanged for well over a decade.

Similar to forest elephants, Asian elephant sociality remains relatively poorly understood (Vidya & Sukumar 2005) and studying elephants in Asia is further complicated by traditions of domestication and high levels of human-elephant interaction (Choudhury 1999; Sukumar 2003). Studies of Asian elephants have indicated low rates of association among relatives, and a suggestion that these elephants do not show multi-level organisation above the family level (Fernando & Lande 2000; McKay 1973; Vidya & Sukumar 2005). However, Asian elephants also show tendencies to aggregate and classification of Asian elephant call types has indicated that they too possess a series of distinct call types which are individually distinct (de Silva 2010). It may be that quantifying ecological pushes for Asian elephants assists in our understanding of the trade-offs possible between these pushes and the social pulls that elephants clearly experience.

9.4 Risk and Social Perturbation

The tendency for forest elephants to aggregate is not in itself a response to anthropogenic stress (cf. Abe 1994 for elephants Queen Elizabeth National Park, Uganda), but this tendency does render them vulnerable to targeting by poachers, and these risks seem to far outweigh the non-anthropogenic risks identified. This thesis has demonstrated that PNOK elephants are sentient of these risks and extremely sensitive to disturbance, and suffer time and energy costs associated with flight behaviours as a result. In the course of this study, elephants were observed to suffer reproductive loss and sustain serious (in some cases, probably fatal) wounds through human conflict. The precise social consequences of such disturbance are unclear, but seem likely to affect individual ranging decisions as forest elephants are highly risk averse, and adopt "siege" rather than "skirmish" strategies when faced with other anthropogenic contacts such as with roads and people: elephants tend not to cross roads and therefore allow roads to limit their ranging (a siege), rather than quickly crossing them and moving into "safer" areas on the other side of a road (a skirmish) (Barnes et al. 1991; Blake et al. 2008).

Old females are often the first targets after males in poached populations. This study has shown that, similar to savannah elephants, old females hold key social roles amongst forest elephants. Removal of these individuals has been demonstrated to impair social function over decades in savannah elephant populations by increasing physiological stress and reducing reproductive function amongst surviving females; (Gobush et al. 2008; McComb et al. 2001).

Bais play a clear role in the maintenance of forest elephant society and social disruptions elsewhere have resulted in abnormal, aggressive and maladaptive behaviours (Bradshaw et al. 2005; Slotow et al. 2000; see also Payne 2003 for a forest elephant case). These kinds of effects remain unclear for PNOK elephants, but they clearly show behavioural stress in response to anthropogenic threats. It seems inevitable these threats can only increase as (legal) human activities on the periphery of PNOK increase. Unregulated markets in Congo and neighbouring countries facilitate smuggling to satisfy ivory demands in China, and these demands continue to grow (Blake et al. 2007; Lumieux & Clarke 2009; Wasser et al. 2010), threatening further elephant populations in PNOK and across Central Africa.

9.5 Applications, Management, Future Research

Forest clearings have been long identified as key observation points for megafauna in the Central African forests (Turkalo 1995; Turkalo & Fay 1997, 2001). Bais make it possible to monitor large mammal populations in forest environments in terms of numbers, health, reproductive status and behaviour (Breuer et al. in prep; Fishlock et al. in prep.). They represent a specialised habitat for the animals that visit them, but with carefully designed research questions they can yield rich datasets over short periods, which can prove highly informative for managers and researchers alike. Wildlife declines in protected areas across Africa render such studies invaluable e.g. (Craigie et al. 2010). Behavioural studies require basic biological information on population demography and health in order to properly interpret the behaviours observed, however this information is also immediately valuable to wildlife management authorities; data collected during this study on the rates of wounding to elephants were used to secure the release of additional funding for immediate park protection by ECOFAC and the Congolese authorities.

For elephants, as with other long-lived highly social species, managing and mitigating threats to population persistence can be most effective when the linked social and demographic consequences of environmental or social disturbance are understood and behavioural studies can contribute invaluable information for the conservation of endangered or threatened taxa (e.g. Sutherland 1998). Social structure and dynamics influence how and when individuals use habitats and social behaviour interacts with population demography and dynamics (Dunbar 1985; Lehmann et al. 2007; Tuyttens &

Macdonald 2000; Wrangham 1980). Elephants require large home ranges and have "suitably elephantine scale" effects on their habitats (Blake 2002). This makes them a keystone species in the Central African rainforest as they create large scale trail systems used by other animals and disperse fruits across vast distances (e.g. Blake & Inkamba-Nkulu 2004; Cochrane 2003).

From this study, two research directions emerge regarding forest elephant sociality, ranging and dispersal. Firstly, the dispersal of females is clearly not universal, as this study and others have documented multi-female groups e.g. (Momont 2007; Payne 2003; A. Turkalo pers. comm.). Longitudinal research at bai studies might assess how this is tied to reproductive status and reproductive success, and the extent to which females use bais to maintain relationships with kin. These data can probably only be assessed through long-term behavioural observations, perhaps coupled with the deployment of GPS collars to assess ranging: Genetic studies have not successfully addressed these questions in forest environments, as clearings are water-filled, effectively ruining the quality of dung samples for genetic analysis. In addition, for highly risk-averse populations such as the elephants of PNOK, simply acquiring enough samples without disturbing bai visiting patterns could prove highly problematic, especially when coupled with the kind of seasonal variation in visiting documented in this study.

Secondly, forest elephant ranging patterns are affected by strong individual differences and clear anthropogenic effects (Beyers 2008; Blake 2002; Blake et al. 2008; Momont 2007). An intriguing part of ranging decisions for forest elephants are questions regarding the use of multiple bais (Inkamba-Nkulu 2007) and the possibility that elephants may use differentiated or distributed social arenas. Certainly not all bais are equivalent; this study has demonstrated stronger seasonal effects in the use of a clearing than known elsewhere and other studies have documented male-dominated visiting (e.g. Momont 2007). This raises fascinating possibilities of cultural fidelity in bai use patterns, and whether bais are learned, or simply exploited as point resources, discovered by individuals following trails. These questions relate to locational dispersal strategies which are currently unknown for forest elephants.

This thesis has shown how elephants across Africa ultimately use a similar system of sociality and flexibility. They are further united in their increasingly desperate need for effective protection in an increasingly anthropogenically dominated and hostile world. Without this protection, the research directions outlined above become obsolete as we face the real possibility of losing some of the most charismatic and fascinating animals that share our planet.

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APPENDIX A: Ethogram

Behaviour	**Description**	**Category**
Supplant	Individual approaches conspecific and causes them to move away from activity/location. In bai, usually related to displacing individuals from sinkholes, though also used as a tactic to move individuals away from parties.	Dominance
Block access	Individual positions themselves between conspecific and conspecific's point of interest, which may be other elephants, or a sinkhole. May be coupled with looks or *social monitoring*. May escalate into *head high*.	Dominance
Head high posture	Individual stands tall with head elevated, sometimes with neck extended, watching conspecifics. May be coupled with *ear fold* and precede aggression.	Dominance
Parallel walk	Is effectively a moving block, or continual supplant, where individual positions themselves between conspecific and conspecific's point of interest, and forces conspecific to move away in order to maintain distance.	Dominance
Ear fold	Horizontal fold across pinna of ear, sometimes coupled with *head high* posture.	Aggression
Chase	Individual runs after conspecific, generally *ear fold/ trunk crunch*, and attempting to *tusk poke* or *slap* conspecific.	Aggression
Slap	Smack trunk to body part of conspecific.	Aggression
Tusk poke	Tusk jabbed into body part of conspecific.	Aggression
Trunk poke	End of trunk jabbed into body part of conspecific.	Aggression
Trunk crunch	Portion of trunk directly above mouth hardens as muscles tense. Usually coupled with an *ear fold* and generally precedes active aggression, such as a *slap* or *tusk poke.*	Aggression
Kick	Foot contact directed to or making contact with conspecific body part.	Aggression
Square up/ engage	Individuals face each other, heads high and watch. Becomes "engage" event once they touch each other, and engage weight into the contest with twined trunks, pushing. As disengage, loser generally flees, and is pursued by winner, who is often ear fold and may try to tusk poke.	Aggression
Discipline	Any light slap, kick or tusk poke by mother to offspring. Generally delivered either when calves try to access sinkholes or engage in suckling requests.	Maternal
Guidance	Mother touches trunk to back, buttocks or tail or calf while travelling to indicate direction to calf.	Maternal

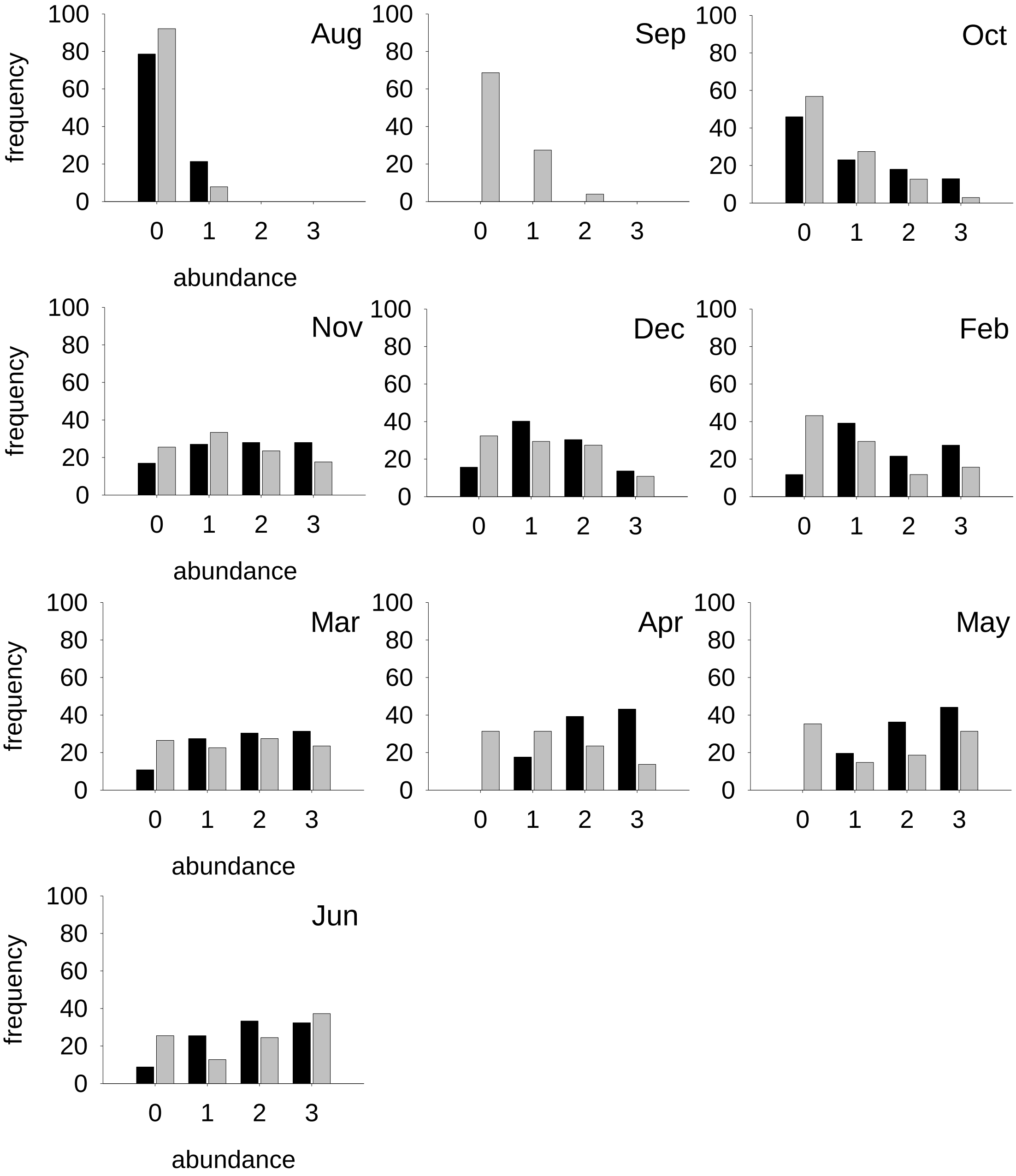
Behaviour	**Description**	**Category**
Comfort	Any *friendly touching*, stroking or body contact delivered to distressed conspecific.	Maternal or affiliative
Allomothering	*Suckling*, *suckling invites*, *guarding* or *retrieval* of calves directed to non-offspring.	Maternal
Suckle	Calf engages with nipple.	Maternal
Guarding	Female moves into close proximity with calf.	Maternal
Retrieval	Female moves towards calf, encourages calf to follow her back to rest of party, to sinkhole, or to leave bai.	Maternal
Suck request	Any attention seeking contact where calf moves to access nipple, often touches trunk to breast, may pull on or touch nipple. May involve trunk to face contacts, body rubs, or touching vulva if calf does not gain suckling bout or is not satisfied by the bouts gained. Can escalate to weaning tantrum if mother does not respond.	Maternal
Suck invite	Female stands with leg forward to facilitate access to nipple, may also touch trunk calf's face or head	Maternal
Weaning	Female refuses suckling bout and uses foreleg to block access to the nipple, or terminates bout.	Maternal
Weaning tantrum	After refusal or termination of suckling bout by mother, calf pushes against mother, vocalises, may tusk poke mother's flank, buttock, or leg. Sometimes calf may place themselves in order to try and block maternal behaviour, either by standing in the sinkhole, or repeatedly placing their trunk in mother's mouth, ear or eye.	Maternal
Scent towards	Reach trunk towards conspecific	Social Monitoring
Monitoring	Watching conspecifics, sometimes with ears raised	Social Monitoring
Listening	Ears raised and attentive	Social Monitoring/ Vigilance
Intention signals	Foot wave, trunk swing, looks; indicates indecision	Social monitoring/ Affiliation
Scent air	Trunk raised either to head height, or above head.	Vigilance
Avoid	Move away from conspecific	Submission
Look back	Individual stands with back to conspecific, watching over shoulder	Submission
Friendly approach	Slow travel towards a conspecific, relaxed carriage, often coupled with intention movements	Submission / Affiliation

Behaviour	**Description**	**Category**
Friendly contact	All trunk to face/body contacts, body rubs, resting in body contact, tail twining Relaxed and calm interactions	Affiliation
Co-ordinated movement	Follow party or family members, or change direction of travel to incorporate their movements	Affiliation
Waiting ("Let's Go" [Moss 1981])	Individual moves away from party, stands facing away from conspecifics. May walk back to party and away again several times, attempting to elicit movement from other party members.	Affiliation
Play	Social play; includes gentle wrestling in the "engage" posture, chasing, exaggerated approaches to conspecifics, mounting (no sexual or dominance context). (NB "object" play e.g. with water, vegetation, charging birds etc. is not included in Chapter 7 analyses).	Affiliation (social play)
Spar	Engage and wrestle, but no aggressive component	Affiliation/ Dominance
Scent vulva	Male touch trunk to female uro-genital tract. May be followed by flehmen behaviour (tasting trunk tip).	Affiliation/ Socio-sexual
Consortship	Male guarding female; co-ordinated movement and association between male and female, either of whom may be responsible for maintenance of proximity.	Socio-sexual
Oestrous walk	"Coy" exaggerated walk, rolling gait, frequent "look back" over shoulder to monitor any following males [Moss 1983]	Socio-sexual
Musth walk	"Head high, chin-in, ears tense posture" [Poole 1987a; Poole & Granli in press]	Socio-sexual
Chase & Mount	Male chases female (may be elicited by female avoidance or running from the male), often with full- or semi-erection, attempts to lay trunk along back of female prior to mounting attempt.	Socio-sexual
Vocalisation	Any vocalisation or vocalisation posture (standing with mouth open); includes rumbles, bellows, trumpets, audible vocal distress	Aggression /Submission

APPENDIX B: Forest Productivity Data

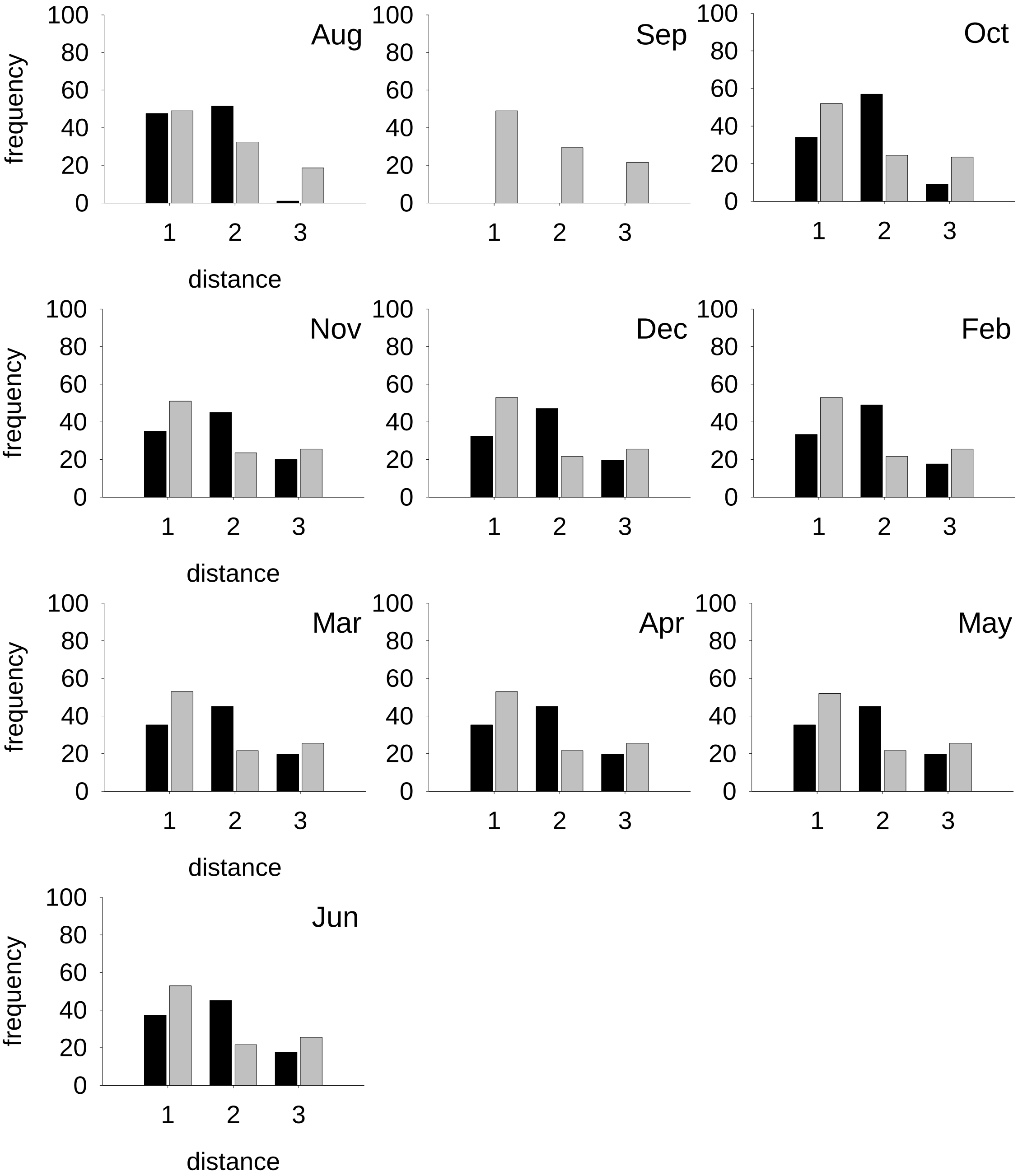
Appendix B1 – New Leaf Scores by Month

Distributions are presented as percentage of total score by category along path length. Bar colouration indicates path (black = Maya Nord, grey = Maya Centre). Categories are 0; absent, 1; rare, 2; common, 3; abundant.


Aug
Sep
Oct
Nov
Dec
Feb
Mar
Apr
May
Jun
frequency
100
80
60
40
20
0
0
1
2
3
abundance

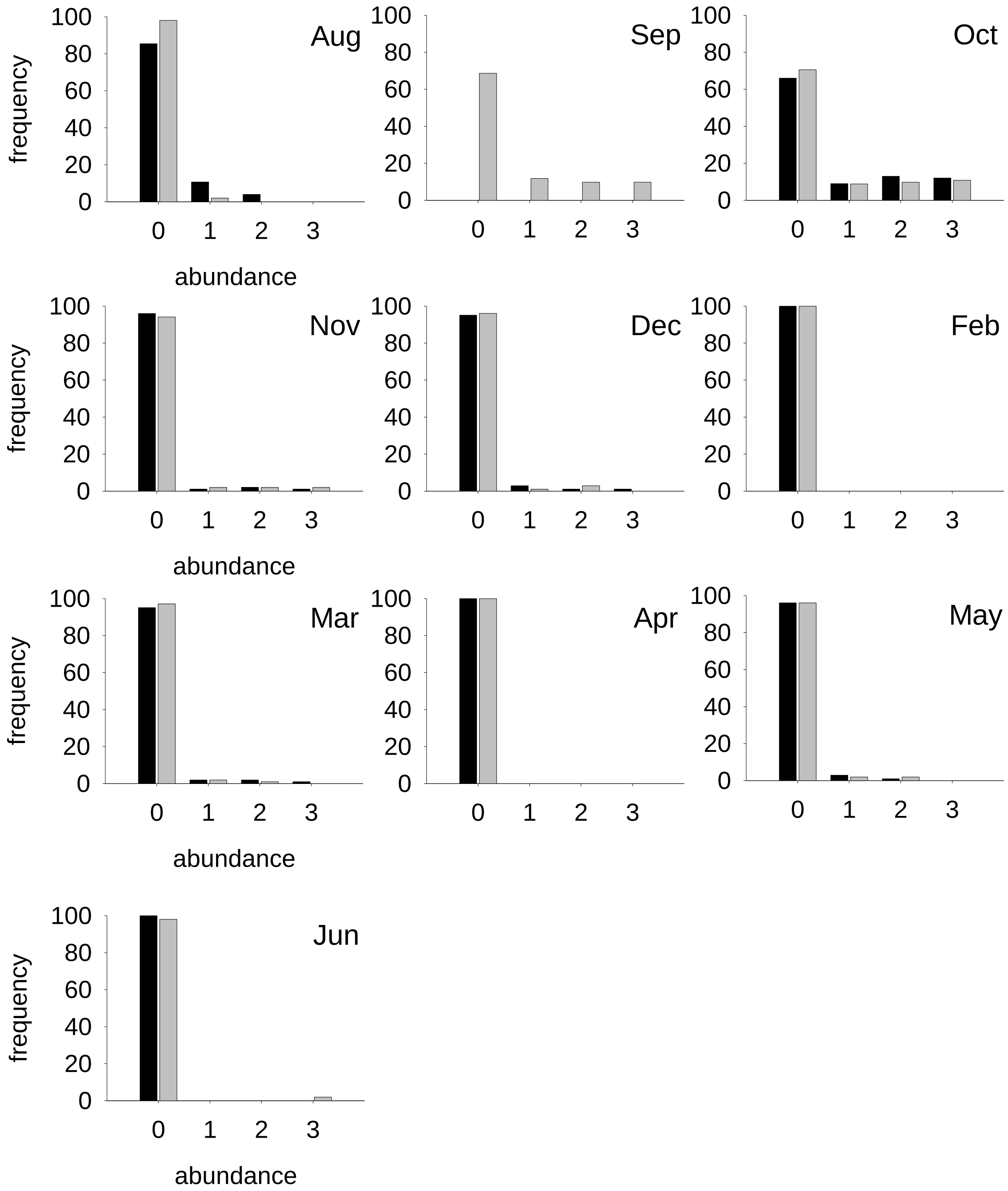
Appendix B2 – Visibility Scores by Month.

Distributions are presented as percentage of total score by category along path length. Bar colouration indicates path (black = Maya Nord, grey = Maya Centre). Categories are 1; <5m, 2; 5-10m, 3; 10-15m.



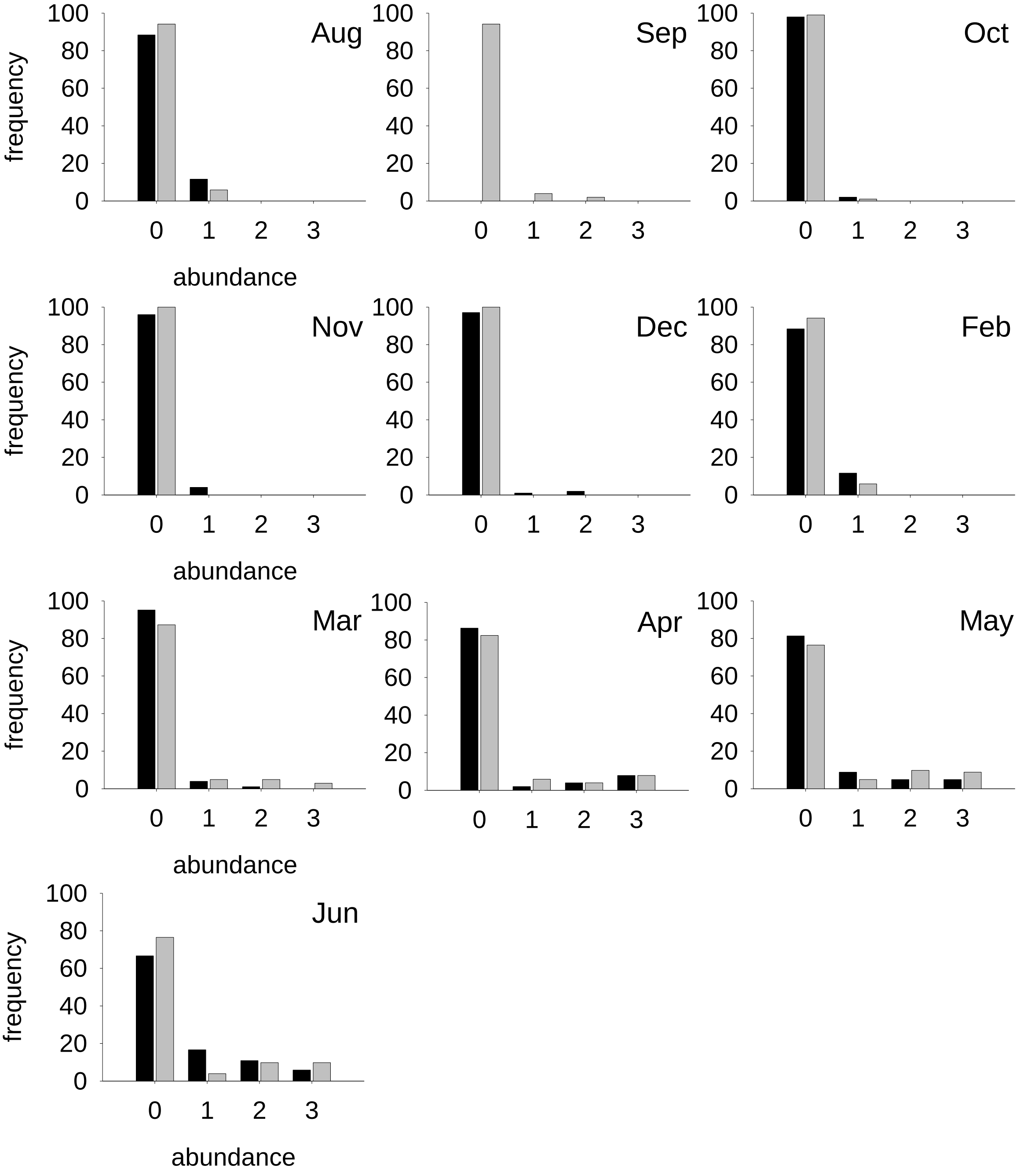
Appendix B3 – Ripe Fruit Scores by Month.

Distributions are presented as percentage of total score by category along path length. Bar colouration indicates path (black = Maya Nord, grey = Maya Centre). Categories are 0; absent, 1; rare, 2; common, 3; abundant.



Appendix B4 – Unripe Fruit Scores by Month.

Distributions are presented as percentage of total score by category along path length. Bar colouration indicates path (black = Maya Nord, grey = Maya Centre). Categories are 0; absent, 1; rare, 2; common, 3; abundant.



APPENDIX C: Population Demography and Health

Appendix C1 Data & Tests Used

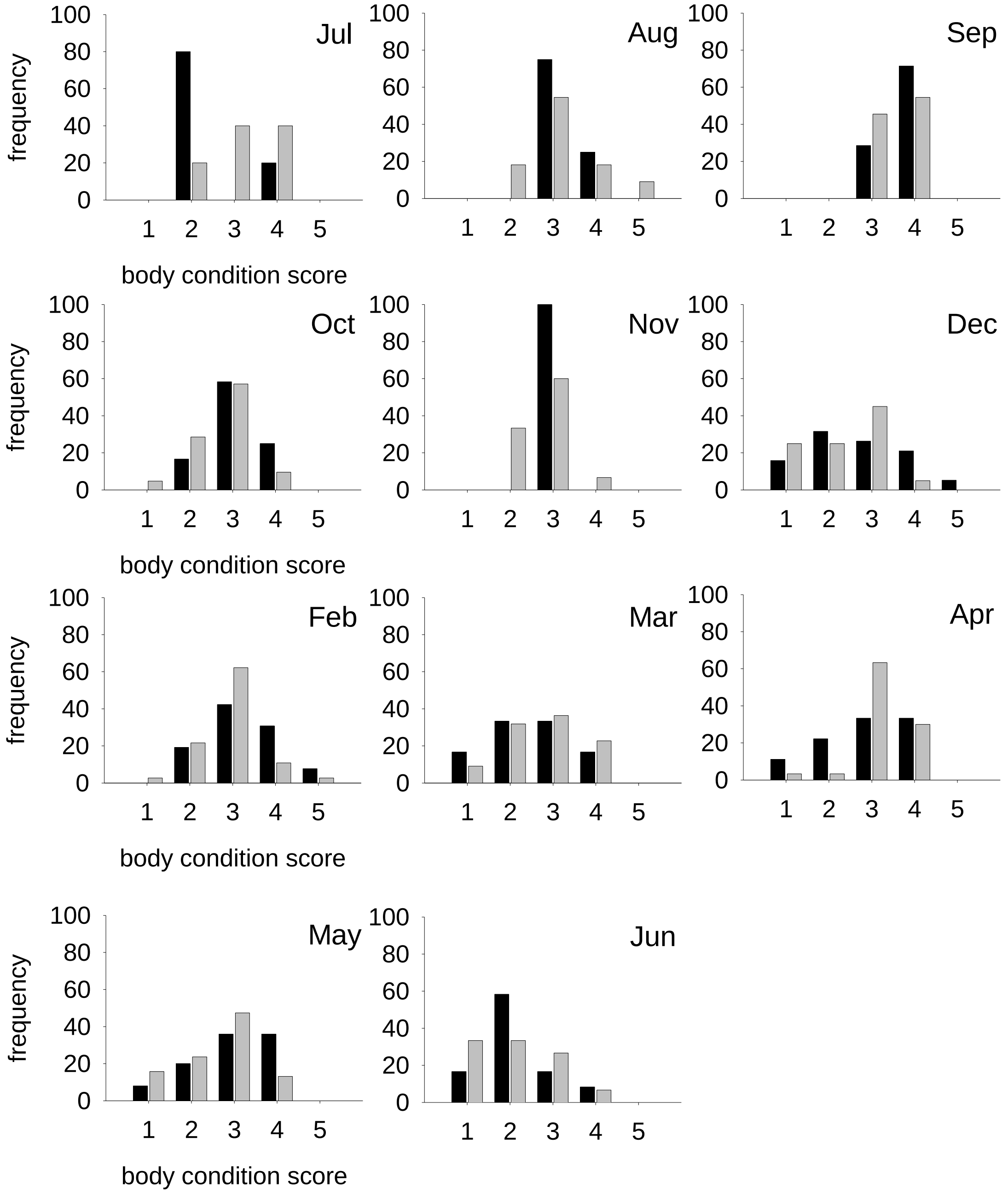
Section		Measure	Manipulation/test	Data used	n=
Population age-sex structure		differences in age-sex distribution identified vs. non-identified individuals	Kolmogorov-Smirnov 2 sample tests	all age estimates; males and females separately	404 IDs; 151 non-identified
		comparison to Querouil et al. 1999 study	descriptive statistics		n=555 this study vs. 629 their study
		Identification rates	descriptive statistics; % animals identified	all observations	all observations
		Population estimates		all observations	
Health	Body Condition Scores	temporal changes	one-way ANOVA	no newborns (<6mo) or animals with injuries. All animals only contribute one score per month	633 scores made on 100 M; 160 F
		lowered scores in June	Wilcoxon signed-ranks test	known individuals seen in June vs. other months	11
		age effects	one-way ANOVA	both sexes together	100M; 160F

	Wounds	incidence, age-sex class, body part affected, welfare implications	descriptive statistics	all observations	all observations

Section		**Measure**	**Manipulation/test**	**Data used**	**n=**
Female reproduction	Female reproductive status	reproductive parameters: parity, pregnancy, calves <2, no current reproductive effort annual fecundity inter-birth interval	descriptive statistics	females >10, split by age class	169
	Calf survival	observed deaths	descriptive statistics	known calves < 5 years old	84
		age-sex structure	sex ratios		
			calf survival calculation	known deaths and surviving calves seen more than once, all <5yrs	32
	Female temporal gland activity	all observations	descriptive statistics	all observations	all observations
Musth		co-occurrence of temporal gland enlargement, temporal gland secretion and urine dribbling	descriptive statistics (percentages)	males >10 (including multiple sightings of known males)	223
		proportion males >35 showing musth signs	descriptive statistics	known males >35yrs	46

Appendix C2 –Body Condition Scores by Month.

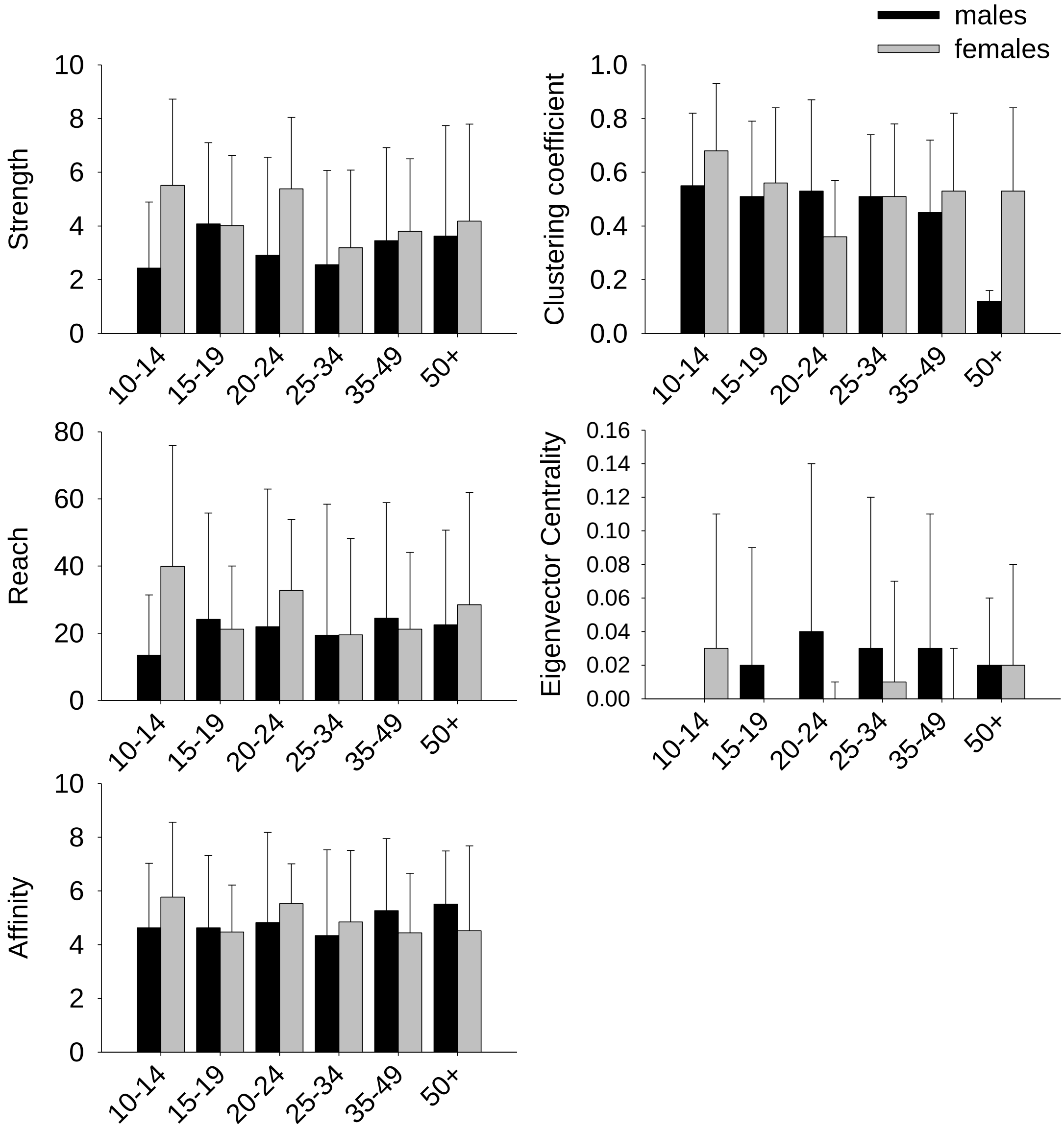
Distributions are presented as percentage of total score by sex for each month. Black bars = males (n=141), grey bars = females (n=225). For score definitions see Table 5.1. Monthly sample sizes are tabulated below.



Month (n=)	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Apr	May	Jun
Males	5	8	7	12	6	19	26	12	9	25	12
Females	5	11	11	21	15	20	37	22	30	38	15

APPENDIX D: Social Networks

APPENDIX D1: Observed network measures for an aggregation-based network for males and females together. Error bars show SE. N= 292 identified individuals aged 10 years or older.



APPENDIX D2 Inter-sex Network of Party Associates (n= 292 identified individuals aged 10 or older)

Strength			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	1.44	1.57	1.39	1.54	0.82	0.73	0.33
15-19	M	2.2	1.29	2.24	1.36	0.26	0.1	0.21
20-24	M	1.31	1.61	1.37	1.66	0.05	0.23	0.81
25-34	M	1.14	1.61	1.19	1.54	0.19	0.78	0.96
35-49	M	1.47	1.58	1.49	1.56	0.25	0.68	0.89
50+	M	1.54	1.93	1.52	1.9	0.87	0.93	0.72
10-14	F	2.58	1.6	2.45	1.61	0.99	0.42	0.09
15-19	F	2.28	1.83	2.29	1.95	0.42	0	0.03
20-24	F	2.82	1.48	2.83	1.56	0.42	0.16	0.18
25-34	F	1.6	1.55	1.55	1.52	0.85	0.66	0.29
35-49	F	1.88	1.55	1.83	1.55	1	0.49	0.04
50+	F	2.22	2.45	2.14	2.35	0.94	0.94	0.61

Eigenvector Centrality			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0.03	0.1	0.01	0.03	0.74	0.77	1
15-19	M	0	0	0	0	0.02	0.22	0.69
20-24	M	0	0	0.02	0.07	0	0	0
25-34	M	0	0	0	0	0.97	1	1
35-49	M	0	0	0.01	0.05	0.16	0.23	0.27
50+	M	0	0	0	0	0.02	0.05	0.37
10-14	F	0.02	0.1	0.01	0.03	0.73	0.77	1
15-19	F	0	0	0	0	0.99	1	1
20-24	F	0.05	0.14	0.02	0.04	0.72	0.92	1
25-34	F	0	0	0.01	0.06	0	0	0
35-49	F	0.01	0.06	0.01	0.07	0.12	0.28	0.92
50+	F	0.05	0.14	0.01	0.04	0.74	0.77	1

Reach			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	5.63	7.79	5.36	7.19	0.95	1	0.83
15-19	M	7.55	6.26	7.65	6.82	0.35	0	0
20-24	M	4.72	8.07	4.98	7.8	0.11	0.75	1
25-34	M	3.29	6.54	3.77	6.13	0.01	0.81	1
35-49	M	4.76	6.14	4.64	5.82	0.86	0.98	0.94

50+	M	4.45	6.57	4.53	6.24	0.33	0.91	0.99
10-14	F	8.8	9.37	7.9	7.91	1	1	0.98
15-19	F	7.55	8.21	7.94	8.1	0.02	0.75	1
20-24	F	9.72	8.4	9.95	7.84	0.23	0.88	0.93
25-34	F	5.08	7.48	4.75	6.57	0.97	1	0.99
35-49	F	5.73	7.63	5.67	7.05	0.83	1	1
50+	F	9.11	12.2	8.18	10.95	1	1	0.52
Clustering coefficient			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0.6	0.32	0.43	0.39	1	0	0
15-19	M	0.63	0.28	0.35	0.35	1	0	0
20-24	M	0.5	0.36	0.38	0.36	1	0.44	0
25-34	M	0.46	0.18	0.26	0.27	1	0	0
35-49	M	0.4	0.26	0.25	0.29	1	0	0
50+	M	0.13	0.04	0.1	0.07	1	0	0
10-14	F	0.72	0.26	0.35	0.34	1	0	0
15-19	F	0.53	0.27	0.37	0.35	1	0	0
20-24	F	0.44	0.23	0.24	0.27	1	0.17	0
25-34	F	0.47	0.33	0.28	0.32	1	0.71	0
35-49	F	0.53	0.32	0.35	0.35	1	0	0
50+	F	0.63	0.31	0.41	0.46	1	0	0
Affinity			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	3.42	1.38	3.57	1.14	0.11	0.97	0.96
15-19	M	2.98	1.55	2.93	1.55	0.69	0.52	0.41
20-24	M	2.74	1.53	2.86	1.56	0.1	0.4	0.76
25-34	M	2.24	1.31	2.43	1.37	0.07	0.3	0.69
35-49	M	2.82	1.2	2.81	1.21	0.54	0.47	0.47
50+	M	2.38	1.09	2.55	1.17	0.08	0.24	0.56
10-14	F	2.6	1.46	2.86	1.2	0.02	1	1
15-19	F	2.67	1.32	3.21	1.29	0	0.63	1
20-24	F	2.88	1.32	3.11	12	0.02	0.92	0.98
25-34	F	2.45	1.3	2.56	1.11	0.11	1	1
35-49	F	2.33	1.32	2.67	1.26	0	0.95	1
50+	F	3.34	1.65	3.13	1.6	0.96	0.67	0.32

APPENDIX D3 Inter-Sex Network of Aggregation Associates (n= 292 identified individuals aged 10 or older)

Strength			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	2.43	2.46	2.33	2.43	0.97	0.71	0.17
15-19	M	4.08	3.02	4.06	3.04	0.59	0.41	0.35
20-24	M	2.91	3.65	2.93	3.65	0.17	0.4	0.86
25-34	M	2.56	3.51	2.59	3.55	0.33	0.09	0.42
35-49	M	3.45	3.47	3.46	3.45	0.38	0.75	0.77
50+	M	3.62	4.12	3.6	4.1	0.75	0.73	0.63
10-14	F	5.51	3.21	5.47	3.19	0.75	0.7	0.52
15-19	F	4.01	2.61	4.07	2.63	0.18	0.29	0.59
20-24	F	5.38	2.66	5.43	2.71	0.24	0.23	0.24
25-34	F	3.19	2.89	3.2	2.87	0.36	0.79	0.87
35-49	F	3.8	2.7	3.78	2.68	0.87	0.8	0.52
50+	F	4.18	3.61	4.14	3.51	0.81	0.97	0.94

Eigenvector Centrality			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0	0	0	0	0	0.14	1
15-19	M	0.02	0.07	0.02	0.07	1	0	0
20-24	M	0.04	0.1	0.04	0.1	0.72	0	0
25-34	M	0.03	0.09	0.03	0.09	0.15	0.01	0.47
35-49	M	0.03	0.08	0.03	0.08	0	0.01	0.99
50+	M	0.02	0.04	0.02	0.04	0.01	0.78	0.99
10-14	F	0.03	0.08	0.03	0.08	0.97	1	0.57
15-19	F	0	0	0	0	0.09	0.84	1
20-24	F	0	0.01	0	0.01	0.5	1	0.83
25-34	F	0.01	0.06	0.01	0.06	0.45	0	0.44
35-49	F	0	0.03	0	0.03	0	0.02	1
50+	F	0.02	0.06	0.02	0.06	0.98	1	1

Reach			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	13.41	18	13.09	16.81	0.88	1	0.98
15-19	M	24.14	31.63	24.12	31.19	0.53	0.99	0.88
20-24	M	21.92	40.99	21.8	41	0.9	0.41	0.1
25-34	M	19.4	38.99	19.72	38.75	0.07	0.99	0.98
35-49	M	24.48	34.4	24.1	34.06	0.99	1	0.19
50+	M	22.5	28.19	21.94	27.62	0.96	0.88	0.13

10-14	F	39.89	35.99	39.36	35.01	0.88	1	0.81
15-19	F	21.22	18.79	22.22	18.18	0	0.97	1
20-24	F	32.69	21.13	31.94	20.68	0.98	0.91	0.4
25-34	F	19.52	28.69	19.69	28.25	0.28	1	0.95
35-49	F	21.18	22.89	21.14	22.05	0.63	1	1
50+	F	28.5	33.39	27.53	32.31	1	1	0.44
Clustering coefficient			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0.55	0.27	0.41	0.33	1	0	0
15-19	M	0.51	0.28	0.36	0.29	1	0.22	0
20-24	M	0.53	0.34	0.49	0.31	1	1	0.41
25-34	M	0.51	0.23	0.41	0.29	1	0	0
35-49	M	0.45	0.27	0.41	0.29	0.99	0	0
50+	M	0.12	0.04	0.11	0.04	1	0.98	0.7
10-14	F	0.68	0.25	0.58	0.28	1	0.05	0
15-19	F	0.56	0.28	0.45	0.28	1	0.62	0
20-24	F	0.36	0.21	0.33	0.23	1	0	0
25-34	F	0.51	0.27	0.42	0.27	1	0.31	0
35-49	F	0.53	0.29	0.46	0.3	1	0	0
50+	F	0.53	0.31	0.5	0.33	1	0	0
Affinity			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	4.63	2.4	5.29	1.7	0	1	1
15-19	M	4.63	2.69	4.68	2.64	0.37	0.77	0.74
20-24	M	4.82	3.36	4.72	3.36	0.96	0.83	0.05
25-34	M	4.34	3.19	4.72	3.04	0	0.98	1
35-49	M	5.27	2.68	5.18	2.65	0.92	0.91	0.46
50+	M	5.51	1.98	5.4	1.94	0.94	0.68	0.51
10-14	F	5.77	2.79	6.03	2.6	0.01	1	1
15-19	F	4.47	1.75	4.79	1.8	0	0.25	0.92
20-24	F	5.53	1.48	5.39	1.42	0.99	0.96	0.82
25-34	F	4.85	2.66	4.96	2.64	0.04	0.75	0.99
35-49	F	4.44	2.22	4.69	2.1	0	1	1
50+	F	4.52	3.16	4.51	3.03	0.49	1	0.94

Appendix D4a Male Network of Party Associates (n= 115 identified males aged 10 or over)

Strength			SE	E	SE(E)	P	SE(P)	CV test P
10-14	M	0.24	0.4	0.25	0.42	0.27	0.27	0.23
15-19	M	0.99	1.01	1	1.03	0.45	0.38	0.29
20-24	M	0.47	0.58	0.49	0.67	0.23	0.15	0.02
25-34	M	0.67	0.94	0.68	0.92	0.42	0.61	0.74
35-49	M	0.65	0.83	0.64	0.81	0.88	0.69	0.39
50+	M	0.64	0.63	0.64	0.63	0.49	0.53	0.69

Eigenvector Centrality			SE	E	SE(E)	P	SE(P)	CV test P
10-14	M	0	0	0	0	0	0	1
15-19	M	0.03	0.12	0.02	0.09	0.76	0.92	1
20-24	M	0.01	0.05	0.03	0.1	0.02	0.04	1
25-34	M	0.03	0.12	0.04	0.13	0.01	0.24	1
35-49	M	0.02	0.1	0.02	0.08	0.28	0.96	0.99
50+	M	0	0	0.02	0.04	0	0	0.28

Reach			SE	E	SE(E)	P	SE(P)	CV test P
10-14	M	0.29	0.55	0.29	0.59	0.07	0.07	0.92
15-19	M	1.88	2.36	1.75	2.13	0.88	0.87	0.81
20-24	M	0.76	1.16	0.82	1.53	0.23	0.11	0.06
25-34	M	1.04	1.87	1.21	2.09	0.06	0.21	0.74
35-49	M	1.11	1.8	1.06	1.62	0.84	0.96	0.95
50+	M	0.79	0.98	0.84	1.04	0.19	0.25	0.46

Clustering coefficient			SE	E	SE(E)	P	SE(P)	CV test P
10-14	M	0.14	0.14	0.16	0.18	0.38	0.38	0
15-19	M	0.37	0.23	0.22	0.16	1	1	0.21
20-24	M	0.45	0.38	0.33	0.4	0.93	0.26	0.1
25-34	M	0.36	0.12	0.22	0.14	0.97	0.28	0.08
35-49	M	0.31	0.28	0.19	0.16	1	1	0.71
50+	M	0.17	0.18	0.07	0.4	1	1	0.82

Affinity			SE	E	SE(E)	P	SE(P)	CV test P
10-14	M	1.17	0.56	1.21	0.54	0.14	0.84	0.98
15-19	M	1.58	0.76	1.5	0.68	0.96	0.89	0.8
20-24	M	1.56	0.96	1.49	0.76	0.79	0.92	0.94
25-34	M	1.24	0.55	1.43	0.75	0	0	0.01
35-49	M	1.44	0.7	1.47	0.66	0.18	0.72	0.91
50+	M	1.18	0.71	1.24	0.72	0.23	0.39	0.53

Appendix D4b Female Network of Party Associates (n= 117 identified females aged 10 or over)

Strength			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	1.93	1.09	1.8	1.11	1	0.3	0.06
15-19	F	1.54	1.21	1.53	1.27	0.56	0.04	0.11
20-24	F	2.14	1.13	2.12	1.09	0.67	0.72	0.62
25-34	F	0.98	0.95	0.92	0.93	0.98	0.78	0.11
35-49	F	1.36	1.16	1.33	1.15	0.99	0.92	0.28
50+	F	1.79	1.82	1.75	1.75	0.87	0.93	0.77

Eigenvector Centrality			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	0.03	0.11	0.03	0.11	0.29	0.3	1
15-19	F	0	0	0	0	0.71	0.91	0.99
20-24	F	0.05	0.16	0.06	0.15	0	0.49	1
25-34	F	0	0	0	0	0	0	0.01
35-49	F	0.01	0.06	0.01	0.06	0.18	0.81	0.96
50+	F	0.05	0.16	0.05	0.15	0.31	0.31	1

Reach			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	4.73	5.08	4.35	4.49	1	1	0.82
15-19	F	3.7	4.5	3.77	4.19	0.26	1	1
20-24	F	5.81	5.4	5.67	4.88	0.75	0.85	0.8
25-34	F	1.89	2.54	1.86	2.47	0.68	0.89	0.67
35-49	F	3.2	4.18	3.1	3.78	1	1	1
50+	F	5.81	7.33	5.17	6.54	1	1	0.38

Clustering coefficient			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	0.75	0.24	0.34	0.33	1	0	0
15-19	F	0.63	0.29	0.23	0.24	1	0.96	0
20-24	F	0.52	0.19	0.27	0.28	1	0	0
25-34	F	0.59	0.35	0.37	0.41	1	0.02	0
35-49	F	0.57	0.32	0.35	0.36	1	0	0
50+	F	0.65	0.27	0.44	0.41	1	0	0

Affinity			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	1.93	1.01	2.1	0.83	0.01	1	1
15-19	F	1.9	0.98	2.09	0.9	0.01	0.95	1
20-24	F	2.3	1	2.37	0.88	0.21	0.94	0.93
25-34	F	1.61	0.71	1.78	0.71	0	0.56	0.97
35-49	F	1.9	0.95	2.02	0.8	0	1	1
50+	F	2.77	1.23	2.55	1.13	1	0.8	0.41

Appendix D5a Male Network of Aggregation Associates (n= 115 identified males aged ≥10)

Strength			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0.47	0.52	0.45	0.52	0.64	0.41	0.11
15-19	M	1.78	1.92	1.79	1.93	0.36	0.34	0.47
20-24	M	1.42	2.38	1.42	2.38	0.5	0.5	0
25-34	M	1.46	2.25	1.46	2.23	0.51	0.13	0.35
35-49	M	1.43	2.04	1.43	2.04	0.41	0.47	0.55
50+	M	1.49	1.9	1.49	1.9	0.71	0.69	0

Eigenvector Centrality			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0	0	0	0	0.78	0.88	0.32
15-19	M	0.02	0.05	0.02	0.08	0.99	0.01	0.01
20-24	M	0.04	0.12	0.04	0.12	0.94	0	0
25-34	M	0.04	0.11	0.04	0.11	0.51	0.46	0.49
35-49	M	0.03	0.09	0.03	0.09	0.36	0.6	0.63
50+	M	0.02	0.05	0.02	0.05	0.69	0.96	0.71

Reach			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0.71	0.9	0.67	0.85	0.53	0.61	0.46
15-19	M	6.2	13	6.16	13	0.47	0.33	0.45
20-24	M	7.37	17.81	7.38	17.81	0.4	0.49	0.58
25-34	M	6.91	16.5	7	16.48	0.12	0.83	0.91
35-49	M	6.2	14.33	6.27	14.3	0.06	0.95	0.95
50+	M	5.18	9.13	5.14	9.06	0.53	0.46	0.69

Clustering coefficient			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	0.21	0.18	0.22	0.2	0.38	0.38	0
15-19	M	0.35	0.25	0.31	0.24	1	0.73	0.05
20-24	M	0.39	0.32	0.39	0.32	0.53	0.47	0.15
25-34	M	0.46	0.26	0.4	0.3	1	0.03	0.01
35-49	M	0.31	0.28	0.3	0.29	0.95	0.06	0.05
50+	M	0.19	0.09	0.18	0.1	1	0.18	0.13

Affinity			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	M	1.54	0.71	1.52	0.64	0.57	0.99	0.98
15-19	M	2.29	1.7	2.26	1.69	0.69	0.6	0.12
20-24	M	2.76	2.49	2.76	2.49	0.4	0.59	0.58
25-34	M	2.52	2.13	2.71	2.11	0.01	0.84	0.99
35-49	M	2.32	2.11	2.44	2.1	0	0.77	1
50+	M	2.65	1.78	2.64	1.75	0.53	0.61	0.71

Appendix D5b Female Network of Aggregation Associates (n=117 identified females aged ≥10)

Strength			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	3.95	2.48	3.95	2.42	0.56	0.97	0.87
15-19	F	2.88	2.11	2.93	2.15	0.11	0.11	0.44
20-24	F	3.7	1.77	3.69	1.76	0.53	0.61	0.61
25-34	F	1.9	1.64	1.89	1.62	0.76	0.79	0.7
35-49	F	2.74	2.13	2.72	2.1	0.89	1	0.87
50+	F	2.81	2.37	2.75	2.3	0.98	0.99	0.97

Eigenvector Centrality			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	0.06	0.13	0.06	0.13	0.58	0.58	0.13
15-19	F	0.02	0.08	0.02	0.08	0.24	0.24	0.22
20-24	F	0	0	0	0	0.21	0.4	0.77
25-34	F	0	0	0	0	0.21	0.5	0.88
35-49	F	0.02	0.07	0.02	0.07	0	0.27	0.99
50+	F	0	0	0	0	0.37	0.41	0.54

Reach			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	21.11	22.53	20.88	21.49	0.74	1	0.99
15-19	F	12.56	15.29	12.91	14.84	0.08	0.98	1
20-24	F	15.98	9.83	15.34	9.57	1	0.99	0.12
25-34	F	6.81	7.74	6.73	7.05	0.71	1	0.99
35-49	F	11.99	14.83	11.84	14.18	0.98	1	1
50+	F	11.88	12.6	11.34	11.79	1	1	1

Clustering coefficient			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	0.69	0.25	0.59	0.3	1	0.01	0
15-19	F	0.52	0.27	0.43	0.3	1	0.04	0
20-24	F	0.43	0.19	0.38	0.22	1	0	0
25-34	F	0.52	0.32	0.43	0.32	1	0.65	0
35-49	F	0.57	0.3	0.5	0.31	1	0	0
50+	F	0.52	0.29	0.49	0.31	1	0	0

Affinity			**SE**	**E**	**SE(E)**	**P**	**SE(P)**	**CV test P**
10-14	F	4.07	2.21	4.3	2.01	0.01	1	1
15-19	F	3.29	1.8	3.5	1.66	0.01	1	1
20-24	F	4.09	0.79	3.95	0.79	1	0.49	0.24
25-34	F	3.18	1.51	3.25	1.33	0.09	1	1
35-49	F	3.53	1.77	3.68	1.74	0	0.94	1
50+	F	3.64	1.46	3.57	1.38	1	1	1

APPENDIX E: Aggregation Rules and Social Behaviour

Categorical variable pairwise comparisons for Logistic Regression Models

Competition/Dominance Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age (baseline 35-49)				100.518	7	.000
<10 vs. 35-49	-1.535	.167	.215	84.153	1	.000
10-14 vs. 35-49	-.858	.243	.424	12.443	1	.000
15-19 vs. 35-49	-.480	.173	.619	7.681	1	.006
20-24 vs. 35-49	-.550	.197	.577	7.817	1	.005
25-34 vs. 35-49	-.509	.179	.601	8.066	1	.005
50+ vs. 35-49	.029	.238	1.030	.015	1	.902
adult vs. 35-49	.128	.185	1.136	.473	1	.492

Aggressive Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age (baseline 35-49)				66.782	7	.000
<10 vs. 35-49	-1.287	.183	.276	49.583	1	.000
10-14 vs. 35-49	-.515	.239	.598	4.646	1	.031
15-19 vs. 35-49	-.046	.162	.955	.079	1	.778
20-24 vs. 35-49	-.639	.236	.528	7.353	1	.007
25-34 vs. 35-49	-.211	.182	.810	1.334	1	.248
50+ vs. 35-49	.451	.227	1.570	3.947	1	.047
adult vs. 35-49	-.041	.213	.960	.037	1	.847

Submission/Avoidance Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age by sex (baseline 35-49 M)				23.900	7	.001
<10 by sex vs. 35-49 M	-.335	.279	.715	1.448	1	.229
10-14 by sex vs. 35-49 M	-.805	.408	.447	3.890	1	.049
15-19 by sex vs. 35-49M	-.266	.334	.766	.636	1	.425
20-24 by sex vs. 35-49M	.516	.367	1.676	1.976	1	.160
25-34 by sex vs. 35-49M	.740	.357	2.095	4.282	1	.039
50+ by sex vs. 35-49M	-1.610	.626	.200	6.615	1	.010
adult by sex vs. 35-49M	-.413	.699	.662	.349	1	.555
Age (baseline 35-49)				15.315	7	.032
<10 vs. 35-49	.382	.233	1.466	2.692	1	.101
10-14 vs. 35-49	.946	.273	2.574	11.966	1	.001
15-19 vs. 35-49	.424	.277	1.528	2.341	1	.126
20-24 vs. 35-49	.360	.276	1.433	1.698	1	.193
25-34 vs. 35-49	-.077	.305	.926	.064	1	.801
50+ vs. 35-49	.516	.323	1.675	2.552	1	.110
adult vs. 35-49	.361	.665	1.434	.294	1	.588

(M= male)

Affiliative Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age (baseline 35-49)				91.883	7	.000
<10 vs. 35-49	1.101	.126	3.006	75.970	1	.000
10-14 vs. 35-49	.956	.238	2.602	16.163	1	.000
15-19 vs. 35-49	.422	.242	1.525	3.033	1	.082
20-24 vs. 35-49	.196	.263	1.216	.553	1	.457
25-34 vs. 35-49	.689	.237	1.992	8.467	1	.004
50+ vs. 35-49	-1.522	.722	.218	4.438	1	.035
adult vs. 35-49	.953	.588	2.592	2.624	1	.105
Age by sex (baseline 35-49 M)				30.577	7	.000
<10 by sex vs. 35-49 M	.428	.133	1.534	10.354	1	.001
10-14 by sex vs. 35-49 M	-.084	.324	.919	.068	1	.794
15-19 by sex vs. 35-49M	.179	.278	1.196	.415	1	.519
20-24 by sex vs. 35-49M	1.089	.331	2.972	10.799	1	.001

25-34 by sex vs. 35-49M	.009	.278	1.009	.001	1	.973
50+ by sex vs. 35-49M	2.217	.800	9.177	7.682	1	.006
adult by sex vs. 35-49M	-.655	.616	.520	1.129	1	.288

Social Monitoring Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age by sex (baseline 35-49 M)				15.777	7	.027
<10 by sex vs. 35-49 M	.073	.141	1.075	.267	1	.605
10-14 by sex vs. 35-49 M	.936	.255	2.550	13.510	1	.000
15-19 by sex vs. 35-49M	.183	.179	1.201	1.052	1	.305
20-24 by sex vs. 35-49M	.139	.258	1.149	.290	1	.590
25-34 by sex vs. 35-49M	-.161	.202	.851	.635	1	.425
50+ by sex vs. 35-49M	.039	.390	1.040	.010	1	.921
adult by sex vs. 35-49M	.187	.199	1.206	.885	1	.347

(M= male)

Maternal Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age (baseline 35-49)				26.762	7	.000
<10 vs. 35-49	-.087	.146	.917	.351	1	.553
10-14 vs. 35-49	-.380	.316	.684	1.444	1	.229
15-19 vs. 35-49	-.423	.228	.655	3.443	1	.064
20-24 vs. 35-49	-2.735	.724	.065	14.257	1	.000
25-34 vs. 35-49	-.482	.234	.618	4.227	1	.040
50+ vs. 35-49	.396	.377	1.486	1.100	1	.294
adult vs. 35-49	-.652	.279	.521	5.448	1	.020

Socio-Sexual Behaviour:

Categorical predictor	B	S.E.	expB	Wald	Df	Sig.
Age (baseline 35-49)				17.055	5	.004
10-14 vs. 35-49	-.752	.378	.471	3.950	1	.047
15-19 vs. 35-49	-.473	.308	.623	2.359	1	.125
20-24 vs. 35-49	.090	.268	1.095	.114	1	.735
25-34 vs. 35-49	.388	.240	1.474	2.614	1	.106
50+ vs. 35-49	-1.630	.735	.196	4.923	1	.026