The influence of genetic relatedness on sociality and demography of female African elephants

By

Linus Kasian Munishi

Submitted In Fulfilment of the Requirements for the
Degree of

Doctor of Philosophy

at
The Nelson Mandela Metropolitan University

December 2011

Promoter: Professor Graham I.H. Kerley

Co-Promoter: Dr Charles A.H. Foley

ABSTRACT

Many elephant populations across Africa were or are being devastated by poaching and habitat loss, making population and range size for the species important issues of conservation concern in elephant ranging areas, including Tarangire National Park (TNP). Poaching and/or overhunting are known to have direct effects on the demography of elephant populations. The current understanding of the indirect effects of poaching on the sociality and demography of elephant populations is relatively poor, both at the group and an individual level. In this thesis the importance of genetic relatedness (as influenced by poaching) on sociality and demography of the female elephants was studied, using a combination of genetic, observation of behaviour and two decades of demography data collected from the northern subpopulation of TNP.

I investigated and characterized the relatedness categories within elephant groups. Using a conceptual model for group size analysis in aggregation economies, I hypothesized that elephant populations subject to social disruptions due to poaching would exhibit characteristics of the free entry model, whereas more stable, closed populations would better fit the group-controlled model. I present a rare quantitative analysis of genetic relatedness and group size patterns among groups of adult female elephants in two wild populations: one in Tarangire National Park (TNP), Tanzania, and another in Addo Elephant National Park (AENP), South Africa. I demonstrate that the group size in African elephant populations is governed by genetic relatedness, and that poaching/overhunting has a significant influence upon the apparent group formation and size in elephants.

I then focused on the effect of relatedness on agonistic interactions between adult females. I hypothesized that individual-based aggressive interactions among adult female African elephants would vary according to degree of kinship, with closely related dyads showing less aggression towards each other in resource-limited environments, thereby leading to indirect fitness benefits for individuals. As predicted, females did not show agonistic interactions to their close kin most often, and the frequency and intensity of aggressive interactions was inversely related to the degree of relatedness of the interactants. The effect of group relatedness and structure on reproductive success of individual female African elephant in TNP was also investigated. Adult female reproductive success was significantly influenced by within- group relatedness and structure. Higher reproductive success (with higher frequency of calf production and survival and more female calves produced) were more evident in the closely related groups than groups with low relatedness, suggesting that females from genetically disrupted groups are less likely to be reproductive than those in closely related groups.

The possibility of negative effects of poaching on the subsequent generation of poached adult females and the alternative of a positive demographic response through reduced density was assessed by analysing the demographic patterns of the first generation (F1) females of prime-aged adult female African elephants in TNP using within- group relatedness and size. I also compared vital rate (age of first birth and interbirth interval) responses of first generation (F1) cows from Tarangire (poached) elephants with other females from poached (Northern Luangwa National Park, Zambia) and unpoached (Amboseli National Park, Kenya and Addo Elephant National Park, South Africa) populations. Group relatedness had no significant effect on sex ratio of the F1 cows' calves. There was a significant difference between the mean age of first birth and interbirth interval of F1 cows from the two (poached, Tarangire and unpoached, Amboseli National Park) elephant populations, suggesting that elephant populations reduced by poaching to low levels show an increase vigour through release from density constraints.

Based on these results, the broader implications of secondary effects of poaching on elephant populations are critically evaluated. Also the importance of understanding the consequences of these effects is highlighted in light of other elephant conservation and management approaches. This understanding is useful in making conservation and management decisions for elephants and other biodiversity.

ACKNOWLEDGEMENTS

I would like to thank the Wildlife Conservation Society, Lincoln Park Zoo and Nelson Mandela Metropolitan University (NMMU) Office for International Education for funding this research. I thank the United Republic of Tanzania through Tanzania Wildlife Research Institute, the Commission for Science Technology and Tanzania National Parks for granting permission to me to live and conduct this study in Tarangire National Park. I would like to extend my special thanks to Professor Graham Kerley, thesis promoter, for his constant guidance, inspiration and support throughout. Through his constant support and inspiration during the entire period, as his student, I have been able to rekindle my career path. Like a wise teacher and academic mentor, he took me and led me progressively to new level. I have greatly enjoyed watching him as a role model and I thank him for playing such a pivotal role in this academic journey. A special thanks to Dr Charles Foley, who besides being my Co-promoter, has given me the opportunity to further develop and advance my career on the amazing population of Tarangire elephants. Lara Foley has been fantastic in providing logistical support during my field work in Tarangire. I thank the many field and camp assistants at Tarangire Elephant Project research camp for logistical support and assistance during my field work in Tarangire National Park, Tanzania. The professors, staffs and students, I have interacted with while at University of Washington, USA have provided me with an amazing scientific support and development. When I was looking for a lab space for genetic training and analysis, Professor Kerry Naish introduced me to Professor Sam Wasser who eventually provided invaluable support and advice on the genetic aspects of this thesis. I thank Professor Sam Wasser himself, his lab staff and students including, Celia Mailand, Rebecca Nelson Booth, Katherine Ayres and Sylvia Young. Dr Kathleen Gobush provided useful advice during DNA sampling and analysis. I am deeply grateful to Marietjie Landman for her very useful and invaluable statistical advice during the write-up of this thesis. I would also like to thank Dr Steve Henley for useful discussions during the write up of this thesis. My fiancé Neema, whose love, faith, dedication and support for me sustained my efforts and desire to achieve the goal of my career. She has been a wonderful mother for our beloved son, Lewis. My parents have also been extraordinary in providing support during my studies. I thank them for the bedrock-always there-they have provided me. Rev. Fr Gabriel Mmasi SJ. and Mathias Joseph Lyatuu have been supporting brothers especially during the tough times of my

life. Many colleagues have spent time sharing their own ideas and research with me; some have become close friends through the process. My thanks to Gosiame Neo-Mahupeleng, Shonisani Tshidino and Dr Douglas Okerio Onyancha for being great friends during my time at NMMU. Gosiame also has been a great colleague and has provided useful discussions during my time at NMMU. I look forward to continued friendship that we created amongst ourselves. Personally, I thank helpful students and staff at the Centre for African Conservation Ecology (ACE), and the Entire Zoo Department at NMMU who have provided assistance of various kinds. Pieter du Toit and Dr Shirley Parker-Nance have always been immensely supportive whenever I needed any assistance from them. All of these staff and students furthered, through their support, the cause of my learning something about conservation science while at NMMU. Last but not least, I am deeply indebted to all teachers and mentors who have in one way or another contributed in all levels of my career path.

CONTENTS

CHAPTER ONE

GENERAL INTRODUCTION

The effects of poaching on African elephants

Sufficient evidence exists in the literature that poaching and overhunting have direct negative effects on African elephant (*Loxodonta africana*) populations (Douglas-Hamilton 1987; Moss 1990; Whitehouse & Hall-Martin 2000; Whitehouse 2001; Foley 2002; Wittemyer 2005). However, poaching may have extensive indirect impacts on the genetic and social structure, as well as demographics and the adaptive value of elephant relationships (Gobush *et al*. 2009; Wittemyer *et al*. 2009; Archie & Chiyo 2011). Facilitated by modern molecular methods, genetic techniques have become increasingly valuable for generating the information on the population genetics which may be used to explain the causes and consequences of social behaviour, particularly in social species (Aviles *et al*. 2004; Archie & Chiyo 2011; Archie *et al*. 2011). African elephants provide an excellent case study to understand the relationships between social behaviour and population genetic structure in a conservation context (Archie & Chiyo 2011). This thesis sets out to explore how poaching and/or overhunting alter the genetic and social structure in female African elephants and the consequences of this on the breeding success of Tarangire female elephants.

The African elephant

The living elephants (*Elephas* and *Loxodonta*) are the only living remnants of a once highly successful mammalian order, the Proboscidea, which evolved in Africa as part of a unique group of mammals, the Afrotheria (Robinson & Seiffert 2003; Rohland *et al*. 2010). Their origin can be traced back to the earliest Eocene (*ca*. 55 million years ago) in Africa (Liu *et al*. 2008). Elephantidae and *Elephas* were the family and genus name, respectively, that Linnaeus assigned to the two elephant elephant species he recognized (*Elephas* and *Loxodonta*). These were separated into two genera in 1797 by Johann Blumenbach (Maglio 1973; Carruthers *et al*. 2008). Today, the taxonomic status of the African elephants of the genus *Loxodonta* are up for debate as to whether they should be classified into two species, based on evidence from genetic studies

(Roca *et al.* 2001; Rohland *et al*. 2007, 2010). Despite the evidence from these studies, the IUCN/SSC currently recognizes only one species on this continent, namely *Loxodonta africana* (IUCN 2011).

The African savanna elephant (*Loxodonta africana*) social structure is organised into multi-tiered, complex, matriarchal family groups, and independent mature males (Moss & Poole 1983; Moss 1988). This multi-tiered structure likely evolved to balance the costs and benefits of sociality (Wittemyer *et al*. 2005). The complex matriarchal society has potential benefits to females including the acquisition of resources, joint protection from predators, shared parenting duties (allo-parenting), and collective social and ecological knowledge, which may contribute to increased inclusive fitness (Foley 2002; Archie *et al*. 2006). Higher structures such as bond groups and clans might also enable the exchange of ecological information over relatively long distances (Foley 2002).

However, social living also has costs, including competition for resources such as food and water. The balance of the costs and benefits of associating at various tiers in the hierarchy differs temporally and seasonally, in response to resource variability (Poole 1996; Wittemyer *et al*. 2005; Wittemyer *et al*. 2007a), the number of individuals in each group, and the spatial distribution of groups (Foley 2002; Wittemyer *et al*. 2005) and the social and physiological status of the individual (Poole 1996; Foley 2002). Male elephants leave their natal families between 14 and 16 years of age (Hanks 1972; Poole 1996), associating temporarily with other males. The structure and size of male groups with which adult males associate, and the type of interactions he has with members of these groups are determined by his age, (and hence body size), season and sexual state (Moss 1988; Poole 1996).

Some newly independent males leave their natal groups and either feed alone or move in association with other older males (bulls) (Moss & Poole 1983). Among sexually mature males, older, high-ranking bulls spend more time in association with females and families when they are sexually active (in musth) and when they are sexually inactive they return to their bull areas where they move and forage with other males (Moss & Poole 1983; Poole 1996). Elephants are extremely adaptable, occupying a variety of habitats from desert to savanna to gallery forest (Poole 1996). Being water-dependent, they generally drink every 1-2 days and typically forage up to about 16 km from water, and in extreme cases this may extend up to 60 km (Kerley *et al*. 2008).

African elephants are mixed feeders, consuming a range of plants and plant parts from grasses to browse, bark, fruit and bulbs (Poole 1996; Kerley & Landman 2006; Kerley *et al*. 2008). The average estimates for daily food intake by elephants range from 4% to 7% of their body weight, with lactating females consuming proportionately higher quantities. They digest only 40% of what they consume (Poole 1996). The proportions of items consumed in their diet vary depending on region, vegetation cover, water availability, soil nutrient composition, and season (Kerley *et al*. 2008). For example, in savanna habitats grass may make up 70% of the elephants' diet in the wet season, with larger proportions of browse being consumed in the dry season when grass contributes only 2-40 percent of their diet (Poole 1996; Kerley *et al*. 2008). Thus, much as elephants need considerable diverse vegetation in the diet composition, their food consumption is subject to variation depending on the availability in their habitat.

Sociality and demographics

Predicting the sources of variation in the size of groups in populations and identifying factors causing fluctuations in species reproductive success are basic questions both in theoretical and applied ecology (Begon *et al*. 1987; Caughley & Sinclair 1994). Genetic relatedness among group members, in which individual kin are clustered together for generations, may be one of the most important factors that structures social organization in animal societies (Kapsalis 2004; Archie *et al*. 2006; Pomilla & Rosenbaum 2006).

Social organization and structure in mammals have been explained well by the genetic relatedness (Archie *et al*. 2006; Gero *et al*. 2008) and the relative importance of interactions between pairs of individuals in shaping behavioural processes (Pope 2000; Mitani *et al*. 2002; Kapsalis 2004); nevertheless, understanding the role of genetic relatedness in cooperative coalitions remains a basis for describing the dynamics and interactions of most animal social structures (Giraldeau & Caraco 2000; Pomilla & Rosenbaum 2006). Studies on primates and other mammals revealed the importance of genetic relatedness and kin evaluations in behavioural analyses (Mitani *et al*. 2002; Kapsalis 2004) and emphasize the need to investigate more on this phenomenon and how it influences other behavioural and reproductive patterns within- and between- populations.

Strong evidence exists for an association between genetic relatedness and demographic changes in social mammals such as primates (Pope 1998; Berman *et al*. 1997; Cheney & Seyfarth 2004), Belding's ground squirrel, *Spermophilus beldingi* (Sherman 1981) and African elephants (Archie *et al*. 2006). Furthermore, the degree of relatedness has been shown to influence reproductive success in mammals such as lions, *Panthera leo* (Packer *et al*. 1991) and red howler monkeys, *Alouatta seniculus* (Pope 2000).

While most studies on genetic relatedness have been concerned with the influence of relatedness on behaviour in particular animal societies (Archie *et al*. 2006), the mechanisms shaping social organization, the impact of these mechanisms on fitness-related behaviour and the way they vary between individuals within social groups are rarely determined, or poorly understood. This is probably due to incomplete knowledge of genetic relationships among the individuals (Kapsalis 2004). Evaluation of evolutionary mechanisms proposed to promote cooperative behaviour depends on the relative influence of the behaviour on the reproductive success of individuals within the group in which they interact behaviourally, and the degree of genetic relatedness among group members (Pope 2000). The current study therefore provided an opportunity to extend our understanding of the influence of genetic relatedness on behaviour, demography and reproductive success in elephants, and as such is important for management of both increasing and decreasing elephant populations.

Overview of altruism, Hamilton's rule and other forms of social behaviour

Altruism has been variously defined and from a collective explanation of different socioecologists, the term is generally understood to entail the behaviour that benefits others at a personal cost to the behaving individual (Hamilton 1964; Trivers 1971; Hamilton 1972; Kerr *et al*. 2004). In everyday life, animals are often faced with challenges and they need to make decisions on how to live and adapt in different environments (Conradt & Roper 2003). However, in many cases, decision making is probably shaped by the nature and relative magnitude of the benefits accrued to the decision makers. Various forms of behaviour have been explained on the basis of their contribution to fitness, i.e. whether they are beneficial (increase direct fitness) or costly (decrease direct fitness) for the individuals performing the behaviour. Using the Hamilton's classification of behaviour, behaviours that are beneficial to the actors and costly to the recipients (+/-) are selfish, whereas behaviours that are costly to the actors but beneficial to the recipients (-/+) are altruistic (Hamilton 1970).

In the well known and often cited example, one human being leaping into water, at some danger to himself, to save another distantly related human from drowning may be said to display altruistic behaviour. If he were to leap in to save his own child, the behaviour would not necessarily be an instance of "altruism"; he may merely be contributing to the survival of his own genes invested in the child (Trivers 1971). Those behaviours which have direct fitness benefits for both actors and recipients (+/+) are called mutually beneficial (West-Eberhard 1975; West *et al*. 2007a), while behaviours that have negative fitness consequences for both actor and recipient (-/-) are spiteful (Hamilton 1970).

According to Hamilton's (1964) inclusive fitness theory, the benefits and costs of the behaviour are measured in terms the lifetime consequences of the behaviour and the net fitness of that behaviour to the lifetime of the individual and can be summarized by the following mathematical formula:

$$r_{xy} \times b - c > 0$$

where: c, is the cost of direct fitness for the actor; b, the direct fitness benefit for the recipient of the altruistic behaviour; and r_{xy}, the degree of relatedness between the actor (x) and the recipient (y). According to this equation, altruistic behaviour should only evolve when the benefit to the recipient multiplied by its relatedness with the actor exceeds the cost to altruistic individual. Hamilton's inclusive fitness theory represents an important development in evolutionary biology. The theory has been applied in a variety of situations involving conflict or cooperation (Giraldeau & Caraco 1993, 2000; Smith *et al*. 2010) and in cooperative and non cooperative species (Komdeur & Hatchwell 1999; Dawkins 2006). In particular, the idea that individuals benefit from the reproduction of relatives (kin selection) has been extraordinarily successful in explaining a wide range of phenomena, especially cases of supposed altruism **(**Dawkins 2006; Griffin & West 2002; Clutton-Brock 2009; Bourke 2011)**.** In general, inclusive fitness theory remains a unifying framework for all possible explanations of social interactions, including altruism, cooperation, aggression, selfishness and spite (West *et al.* 2001; Bourke 2011). It has also become the central paradigm in social evolution theory (e.g. Sachs *et al*. 2004; Foster *et al*. 2006; Lehmann & Keller 2006; West *et al*. 2007b; Bourke 2011).

Although inclusive fitness theory is widely accepted as a leading theory that has transformed the study of behavioural ecology and evolutionary biology, a group of authors (e.g., Wilson 2005, 2008; Wilson & Wilson 2008; Nowak *et al*. 2010) have also offered criticisms on its conceptual robustness and empirical applications, particularly in eusocial insects. In response to this criticism, a comprehensive review by Bourke (2011), showed that decades-long empirical evidence of hard work by hundreds of field researchers who have provided a rich body of knowledge about the behavioural and evolutionary ecology using this theory. More generally, the review by Bourke (2011) argues that the critiques by opponents of the theory do not succeed because the inclusive fitness theory has added fundamental insights to natural selection theory. Bourke and other proponents of the inclusive fitness theory further argue that the theory allows the construction of a unified conceptual overview that can be applied across all taxa, and its evidence base is extensive and robust (Griffin & West 2002; Fletcher *et al*. 2006; Bourke 2007; West *et al*. 2008; Bourke 2011).

Despite this ongoing debate, it is evident that what remains unknown is the extent to which different answers are true for different species (Archie *et al*. 2011). In particular, measuring the correlation between social structure and population genetic structure (to know whether close social partners are also close relatives) remains an important focus of the research, providing more insights into which evolutionary mechanisms have been important in the origin and maintenance of social relationships (West *et al*. 2002; Clutton-Brock 2009; Archie *et al*. 2011; Bourke 2011). The findings from such works are important in revolutionizing the study of social behaviour. In this study, I use inclusive fitness theory (in its general sense as a conceptual tool) as it has been extraordinarily successful in explaining a wide range of phenomena **(**Griffin & West 2002; Bourke 2007; Clutton-Brock 2009; Bourke 2011), to explore the drivers of sociality in elephants, as well as the consequences of disrupting sociality (as potentially happens in a poached population).

Study site

The study site is Tarangire National Park (TNP), in northern Tanzania (Figure 1.1). The Park protects 2,600 km^2 of the larger 20,000 km^2 Tarangire ecosystem (Foley & Faust 2010), lying between 3°40' and 5°35'S and 35°45' and 37°00'E. The Tarangire ecosystem contains the largest populations of elephants in northern Tanzania, and the second-largest migratory ungulate populations in East Africa (TCP 1997). TNP was established in 1970 and borders Simanjiro Game Controlled Area (GCA) to the east. To the north-east the TNP borders Lolkisale GCA. To the north and northwest it borders Mto wa Mbu GCA, and Lake Manyara National Park and it borders Mkungunero Game Reserve to the south. The park is dominated by the Tarangire River, which provides the main source of water for migratory and resident animals during the dry season within the entire 20,000 km^2 ecosystem in which TNP lies (Van de Vijver *et al*. 1999).

The vegetation of TNP lies in the Somali-Masai regional centre of endemism and supports nine different vegetation sub-types or zones (Foley 2002). Two wooded savanna types dominate the park: (1) the microphyll savanna which can be found in the riverine area with dark alluvial, lacustrine soils and has *Acacia tortilis, Maerua triphylla*, *Grewia* spp. as the dominant tree species with scatterings of Baobab (*Adansonia digitata*) and sausage trees (*Kigelia africana*); (2) the deciduous savanna situated on the ridges and upper slopes with well-drained red loams of Pre-Cambrian origin and where *Combretum zeyheri, Commiphora* spp. and *Dalberghia melanoxylon*, the African ebony are the dominant trees (Van de Vijver *et al*. 1999). Tarangire National Park experiences two major seasons, the wet season (November-May) and the dry season (June-October), with average annual rainfall (based on 21 years of data) of 620 mm (Prins 1987; Van de Vijver *et al*. 1999).

Study population

During the past five decades, elephant numbers in the TNP have fluctuated markedly. Prior to being gazetted as a Game Reserve (GR) in 1958, the Tarangire area was used for wildlife hunting and elephants numbered *c.* 440 (Van de Vijver *et al*. 1999; Foley 2002). After the TNP obtained protected status, the elephant population number increased to *c.* 2900 in 1980 (Van de Vijver *et al*. 1999). With elephant population estimates of 440 in 1960 and 2900 in 1980 in TNP, the annual increase in elephant numbers during this period, resulting births and immigration, would be 9% (Van de Vijver *et al*. 1999).

Using this annual growth rate, and assuming a linear growth of the population, we can estimate that in 1971 there were about 1200 elephants. At the end of the 1970s and in early 1980s heavy poaching started in and around the park and elephant numbers declined dramatically (Ecosystem Ltd 1980). After the mid-1980s, poaching pressure was reduced and the number of elephants increased steadily with average annual growth rate of 7.1% from 1993 to the present (Foley & Faust 2010). The last full census in TNP was conducted in 2000 and provided a total population of 2,385 elephants (TWCM 2000).

During the wet season, there are significant movements of elephants and other large mammals out of the park to dispersal areas on village lands. In the dry season they return to the park because the Tarangire River is their major water source in the dry season (Foley & Faust 2010). The elephant population in TNP has been studied since 1993 (Foley 2002; Tarangire Elephant Project (TEP) long-term research). Based on a combination of ground sightings and radio-collar data, the elephant population in TNP has been divided into three distinct sub-populations (the northern, central and southern sub-populations) exhibiting different dry season range-use patterns (Foley & Faust 2010).

The northern subpopulation is the most studied of the Tarangire elephants: all animals have been well characterised and identified individually using combinations of unique ear features and tusk characteristics. In the study subpopulation, data on life histories and association patterns have been obtained for all individual elephants over the last 17 years by the Tarangire Elephant Project (TEP) long-term research (Figure 1.2). Demographic data are updated monthly. According to this, there are 29 elephant groups, with more than 800 adult females and juveniles in this sub-population (Figure 1.2). The 29 groups ranged in size from 3 to 14 adult females and their immature offspring in 1994. Observational records of the study elephants' social context were collected over the long-term study period beginning in 1993, as described in Foley (2002), focusing on all ‘core’ (family) groups as identified by 1994 in the northern subpopulation. At that time, the total population size in all the second-tier groups was 267, excluding independent adult (>12 years of age) males (Foley 2002).

Each individual’s core group was established and defined as any social group that was already formed at the time of the first census. Sighting of the group was recorded only once per day to avoid non-independence of observations and groups were sighted a minimum of every two months and, during the most intense years of monitoring, at least three times per month. Although the data given and analyses conducted in this thesis refer to the entire northern elephant subpopulation in TNP from November 1993 to October 2010, monitoring of this subpopulation is ongoing.

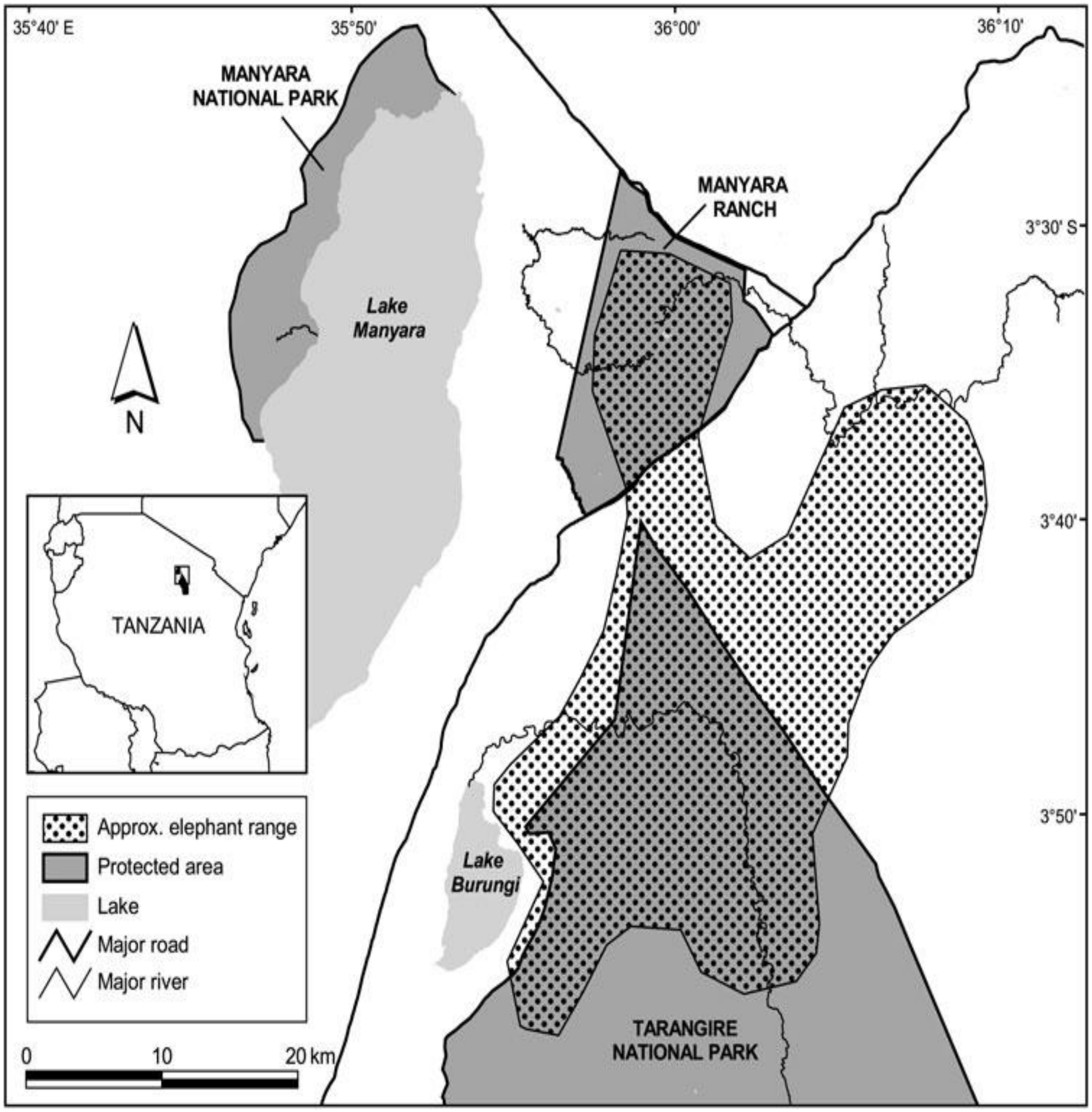

Figure 1.1 The location of the Tarangire National Park, in Tanzania and the approximate home range of the northern subpopulation of elephants (Foley & Faust 2010).

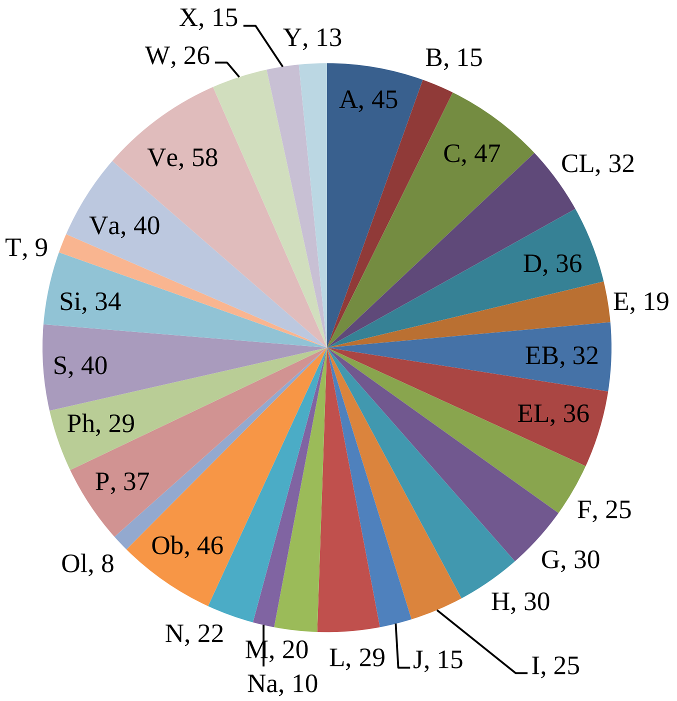

Figure 1.2 A pie chart showing the current distribution of the Tarangire northern subpopulation of elephants into its 29 groups. Group names are indicated by letter codes and sizes are expressed as numbers of total population size, excluding independent males (N = 823; Tarangire Elephant Project (TEP) long-term research unpublished data).

Thesis objectives and approach

The aim of this study is to use Hamilton's (1963, 1964) inclusive fitness theory and approximately two decades of the TEP data to investigate the effects of genetic relatedness on sociality, demography and reproductive success of Tarangire adult female elephants. The population of elephants in TNP has been studied for two decades and prior to that has also been exposed to extensive social disruption through poaching. To be able to understand how inclusive fitness (kin selection) theory applies to elephant social organization, I needed to establish the level of genetic relatedness among individual elephants in their social groups within the study subpopulation.

Thus **Chapter two** of the thesis gives the details of the microsatellite analysis of adult female elephants and how genetic relatedness within and among elephant (family) groups has been used to define kin and non-kin individuals in the northern subpopulation of Tarangire elephants. In addition, I investigated how genetic relatedness predicts elephant group size by comparing the empirical results from the two elephant populations in TNP and Addo Elephant National Park (AENP) with a conceptual genetic model (Giraldeau & Caraco 1993, 2000) for group size analysis.

Kin-selection theory can be applied in a situation involving either conflict or cooperation (Giraldeau & Caraco 1993; Smith *et al*. 2010; Bourke 2011) and using this theory, **Chapter three** addresses the question: **Does genetic relatedness predict competitive and conflict behaviour in adult female African elephants?** To answer this question, dyadic observations of individuals of different relatedness categories were made in the field in TNP. Agonistic data from these observations were used to test whether elephants show a lower frequency and intensity of aggression to their kin than unrelated individuals.

A species' social organization as well as its group size is usually seen as the result of an optimization process, which maximizes benefits while minimizing costs (Lehmann *et al*. 2007). According to natural theory, reproductive costs and benefits are expressed in terms of the number of weaned offspring contributed by an individual to the next generation in the absence of chance effects (Hamilton 1964; West-Eberhard 1975; Côté & Festa-Bianchet 2001). Because an elephant's life-span is one of the longest among mammalian (and all animal) species, short term (cross-sectional) studies on the species may give misleading results (Moss 1988; Whitehouse & Hall-Martin 2000; Whitehouse 2001).

Thus **Chapter four** addresses the question: **To what extent does group relatedness and structure influence individual reproductive success of female African elephants?** To answer this question, relatedness results from genotyped adult female elephants and individual-based demographic data from the TEP long-term (two decades) dataset were used. Individual reproductive success was calculated based on the number offspring per adult female per unit time to compare between individual reproductive success in relation to within the group relatedness and structure. Furthermore, the reproductive rate and success of an elephant population are influenced by the elephants' life history traits including; the age at first birth, inter-birth interval and reproductive senescence of adult cows (Moss 1994; Poole 1996; Moss 2001; Foley 2002). In general, elephant cows will tend to have higher reproductive rate (and hence faster population growth) when they have their first birth at much younger age and if the time that elapses between births of their calves (interbirth interval) is short.

Intensive studies have revealed that poaching affected the demography and life history producing a skewed reduced ratio of adult males to adult females, and increased age at first calving and interbirth interval (Moss 1990; Foley 2002). In addition, poaching reduced the elephant population substantially, presumably releasing food and other resources to surviving elephants. To assess how these effects (altered genetic and social structure and released resources) changes affect the reproductive success of the offspring of the poached cows, **Chapter five** addresses the question: **What are the effects of within- group relatedness and size on demographic patterns of the first generation (F1) females of prime-aged adult female African elephants in TNP?** This question was answered by using relatedness results and the TEP long-term demographic dataset. The life history variables (e.g., age at first birth, interbirth interval and calf survival to weaning) in all 24 elephant (family) groups were calculated and compared between groups in relation to within-group relatedness and size. Findings from the thesis were synthesized in **Chapter six** in order to provide a broad summary of the thesis and directions for further research.

CHAPTER TWO

DIFFERENCES IN THE EXPRESSION OF GROUP FORMATION, SIZE AND RELATEDNESS IN AFRICAN ELEPHANT POPULATIONS

INTRODUCTION

The social structure of the African elephant (*Loxodonta africana*) is organised into multi-tiered complex matriarchal groups, and independent mature males (Moss & Poole 1983; Moss 1988). This complex female social structure typically forms hierarchical relationships extending from mother-offspring unit to group (usually called “family”) units, bond groups and clans (Moss & Poole 1983; Poole 1996; Wittemyer *et al*. 2005), to sub-population and population (Wittemyer *et al*. 2005). A tight bond that results in identical association behaviour between a mother and her calf may be treated as a single entity and has been called a “mother-calf unit” (Wittemyer *et al*. 2005).

The basic social unit is the family which is composed of one to several related females and their immature offspring, and may range from two to 30 individuals (Poole 1996). Individual family units that spend significantly more time with certain other family units, and when together show particular spatial and affiliative behavioural patterns which indicate that they have close social relations, have been called a “bond group” (Moss & Poole 1983; Moss 1988). In many areas in savanna, there is a tendency for elephants to aggregate on a seasonal basis. The groups that use the same dry-season home range are called “clans”, which make a sub-population when they exceed one clan and occupy multiple overlapping home ranges ((Moss & Poole 1983; Wittemyer *et al*. 2005).

This multi-tiered structure likely evolved to balance the costs and benefits of sociality (Wittemyer 2005; Wittemyer *et al*. 2005). Potential benefits include the acquisition of resources, joint protection from predators, shared parenting duties (allo-parenting), collective social and ecological knowledge, all of which may contribute to increased inclusive fitness (Foley 2002; Archie *et al*. 2006). Higher tiered structures such as bond groups and clans might also enable the exchange of ecological information over relatively long distances (Foley 2002). However, social living also has costs including competition for resources such as food and water. The balance of the costs and benefits of associating at various tiers in the hierarchy differs temporarily and seasonally in response to resource variability (Wittemyer *et al*. 2005, 2007b), genetic relatedness (Archie *et al*. 2006, 2011; Archie & Chiyo 2011), the number of individuals in each group, the spatial distribution of groups and the social and physiological status of the individual (Poole 1996).

Female elephants remain near female relatives throughout their lives (Moss 1988) and show extensive affiliative and cooperative behaviour with female kin (Moss 1988; Archie *et al*. 2006). Thus, in African elephants, genetic relatedness appears to be an important predictor of the strength and quality of social bonds between individual elephants (Archie *et al*. 2011; Archie & Chiyo 2011). In this study, the group size and relatedness of two elephant populations (Tarangire National Park, [TNP], Tanzania and Addo Elephant National Park, [AENP], South Africa) are explored.

Elephants in TNP were severely poached for ivory during the 1970s and 1980s, eliminating the majority of the older male and female individuals from the population (Moss 1990; Foley 2002). In Tarangire, poaching presumably affected the demography, and the strong relationships among individuals, both within and between groups. Also, the poaching in TNP was more severe on some groups (groups that had individuals with the largest tusks) than others, resulting in a range of post-poaching group types and structures, from those with normal age structures, to others containing only very young individuals (Foley 2002). The elephant population in TNP is growing at an average annual rate of 7.1% (Foley & Faust 2010) and this population is thought to be the remnants of the originally resident, poached elephant groups (families) and immigrants from the neighbouring areas, which sought refuge in the park (Foley 2002).

In contrast, the AENP population originates from eleven individuals including five cows following the extensive hunting for ivory and culling in 1900s which had eradicated elephants from most of the Addo area (Whitehouse 2002). This population has not been subject to poaching for over 80 years now and it was fenced since 1954 (Whitehouse 2001); thus its social structure reflects the intrinsic dynamics of a stable group in this population.

The objective of the study was to assess the degree to which socially defined groups of adult female elephants in TNP could be detected based on genetic relatedness and kin group structure by testing the prediction that (i) adult females within the groups of elephants in TNP are significantly more related than random (ii) within-group adult female relatedness and kinship vary with group size. In addition, we investigated the variation in the genetic relatedness and group size patterns by comparing the empirical results from the two elephant populations in TNP and AENP with a conceptual genetic model for group formation (under free entry and group-controlled entry rules) in an aggregation economy (Giraldeau & Caraco 1993, 2000).

According to this model, increasing genetic relatedness decreases the equilibrium group size under *free entry*, while increasing the size under *group-controlled entry* (Giraldeau & Caraco 1993, 2000). Free entry assumes that solitary individuals enter any group at no cost and do so only if the fitness obtained in that group is greater than the fitness achieved by remaining alone; group size equilibrates when solitaries no longer choose to join groups. On the other hand, under group-controlled entry, group members regulate the size of the group, such that the predicted group size results from members' decision to accept or repel intruding solitaries when group sizes are below or equal to the optimum (Giraldeau & Caraco 1993, 2000).

The relationship between genetic relatedness among adult females and group size for both free entry and group-controlled rules (generated from the conceptual model) are illustrated by the graphs (Figure 2.1). Based on this conceptual model (Figure 2.1) and the characteristics of these two elephant populations, I predicted that the AENP population would have larger group sizes at any specific level of group relatedness than the TNP population.

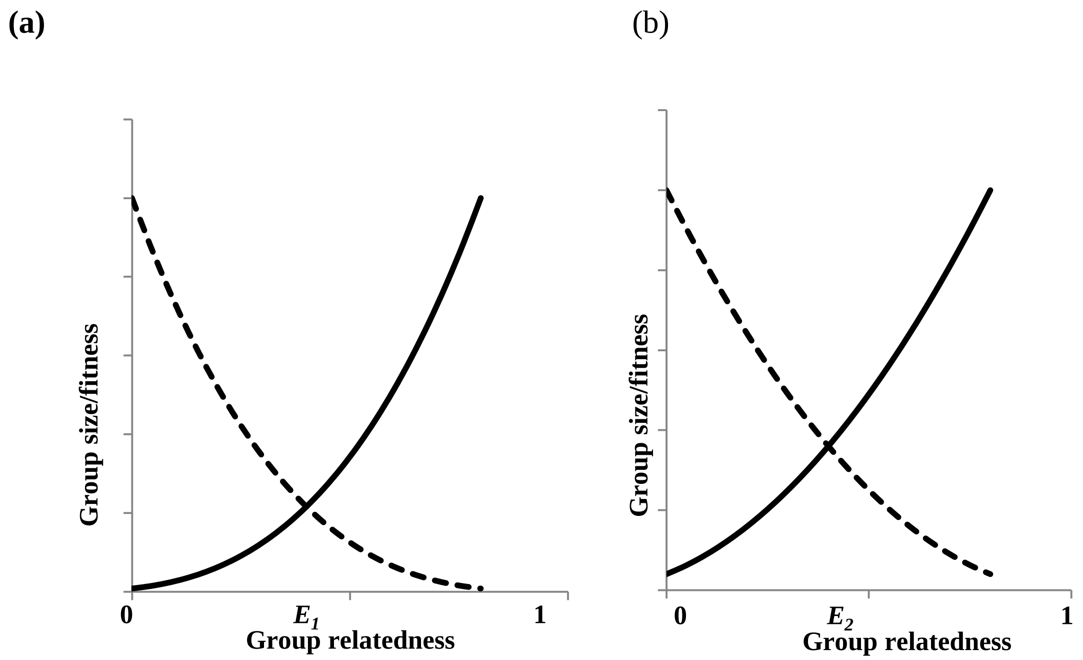

Figure 2.1 Group relatedness and size for models of two processes of group formation: designated free entry, *a* and group-controlled entry, *b* in constant environmental conditions. Group size ([broken line], and fitness [solid line], vertical axis), varies as the function of within group-relatedness and/or reproductive effort equilibrating group size and fitness at an intermediate of between 0 and 1 relatedness and reproductive effort (horizontal axis), such that the equilibrium point, E_1 is smaller than E_2, in the conceptual model developed by Giraldeau and Caraco (1993).

This conceptual model assumes that cooperative group living causes certain components of fitness to increase as a function of group size. This model therefore provides a robust framework to explore the drivers of sociality. As long as the group size that maximises each member's direct and indirect fitness always exceeds the group size where individual (i.e. direct) fitness attains a maximum, the prediction arising from this assumption remains valid (Rodman 1981; Aviles *et al*. 2004).

Direct fitness refers to the component of personal fitness gained from producing offspring due to one's own behaviour (West *et al*. 2007b). Indirect fitness follows from inclusive fitness theory that shows how altruistic cooperation can be favoured between relatives (West *et al*. 2007b; Bourke 2011). Direct and indirect fitnesses are summarized by Hamilton's rule which states that a gene/trait for any social behaviour can evolve by natural selection when $rb-c>0$, where c and b are the lifetime changes in the direct fitnesses (offspring numbers) brought about as the result of the behaviour being performed in, respectively, the performer (actor) and recipient of the behaviour and *r* is the genetic relatedness at the locus for the social behaviour (Bourke 2011).

Since *c* is the fitness cost to the actor, and *b* is the fitness benefit to the recipient, the inequality sign can be put into words and altruistic cooperation can therefore be favoured if the benefits to the recipient (*b*), weighted by the genetic relatedness of the recipient to the actor (*r*), outweigh the costs to the actor (*c*). Following Hamilton's rule (inclusive fitness theory), *c* represents the direct fitness consequences of a social behaviour and *rb* the indirect fitness when *r* is the genetic relatedness (West *et al*. 2007b).

I predicted that elephant groups in populations subject to social disruptions by poaching (TNP) to varying degree would exhibit characteristics of the free entry model, whereas more stable, closed populations (AENP) would better fit the group-controlled model. These two elephant populations (TNP and AENP) provide an excellent opportunity for studying genetic relatedness and its relationship with group size and how these populations compare with the rules of (free and group-controlled entry) inherent in the conceptual model for group formation.

It turns out that predicting stable group size can be a complicated matter; the solution will likely depend on behavioural details of group formation (rules of entry), demography, and the genetic relatedness between players (Giraldeau & Caraco 2000; Aviles *et al*. 2004). The criterion for group formation and size simply requires that two or more individuals concurrently influence each other's fitness gain and losses. However, this definition merits its ability to apply the two models in such a complex social structure of African elephants in order to understand how these models fit to different groups (called families) with varying degree of relatedness and environmental conditions.

I chose to analyse relatedness at group level because in elephants, groups are composed of a predictable set of individuals (Moss 1988; Archie *et al*. 2006). These groups, appear to be stable across seasons and most social interactions, both competitive and cooperative, indicating that most of the relevant forces shaping female relationships and hence their fitness, occur in these social units (Archie *et al*. 2006; Vance *et al*. 2009).

MATERIALS AND METHODS

Tarangire study site and population

Although the Tarangire elephants have been relatively unaffected by poaching in the past two decades, there has not been a regular full census in Tarangire National Park during this time period. The last full census in Tarangire National Park estimated the total population to consist of more than 2,300 individuals, composed of three subpopulations with distinct dry-season home ranges (Foley & Faust 2010; Figure 2.2). The northern subpopulation of the Tarangire elephants has been studied since 1993 [(Foley 2002), Tarangire Elephant Project (TEP)-long-term elephant research], documenting detailed and reliable demographic data in 29 different known groups in this population.

The elephant groups were identified at the start of the monitoring using the standard (behavioural observation) protocols that have been developed and applied in savanna elephant populations Moss 1988; Poole 1996; Archie *et al*. 2006). Eighteen of the 29 groups were identified by November 1993 and the rest by November 1994 (Foley & Faust 2010); because of this, all the analyses at group level used the end of 1994 as a baseline year and were adjusted appropriately to include the groups that were unknown at the time. Quantification of the elephant groups and the levels of association among adult females in the northern subpopulation were calculated for all known groups based on 2153 independent sightings (Foley 2002).

This study was motivated by a need to confirm the genetic relatedness among adult females in the elephant groups that were quantitatively defined from behavioural observations of approximately two decades of data. Genetic relationships among adult females that were born before the study were unknown, including that of their first-order relatives. Thus our study was the first to estimate genetic relatedness among adult females in all the 29 elephant groups in our study population.

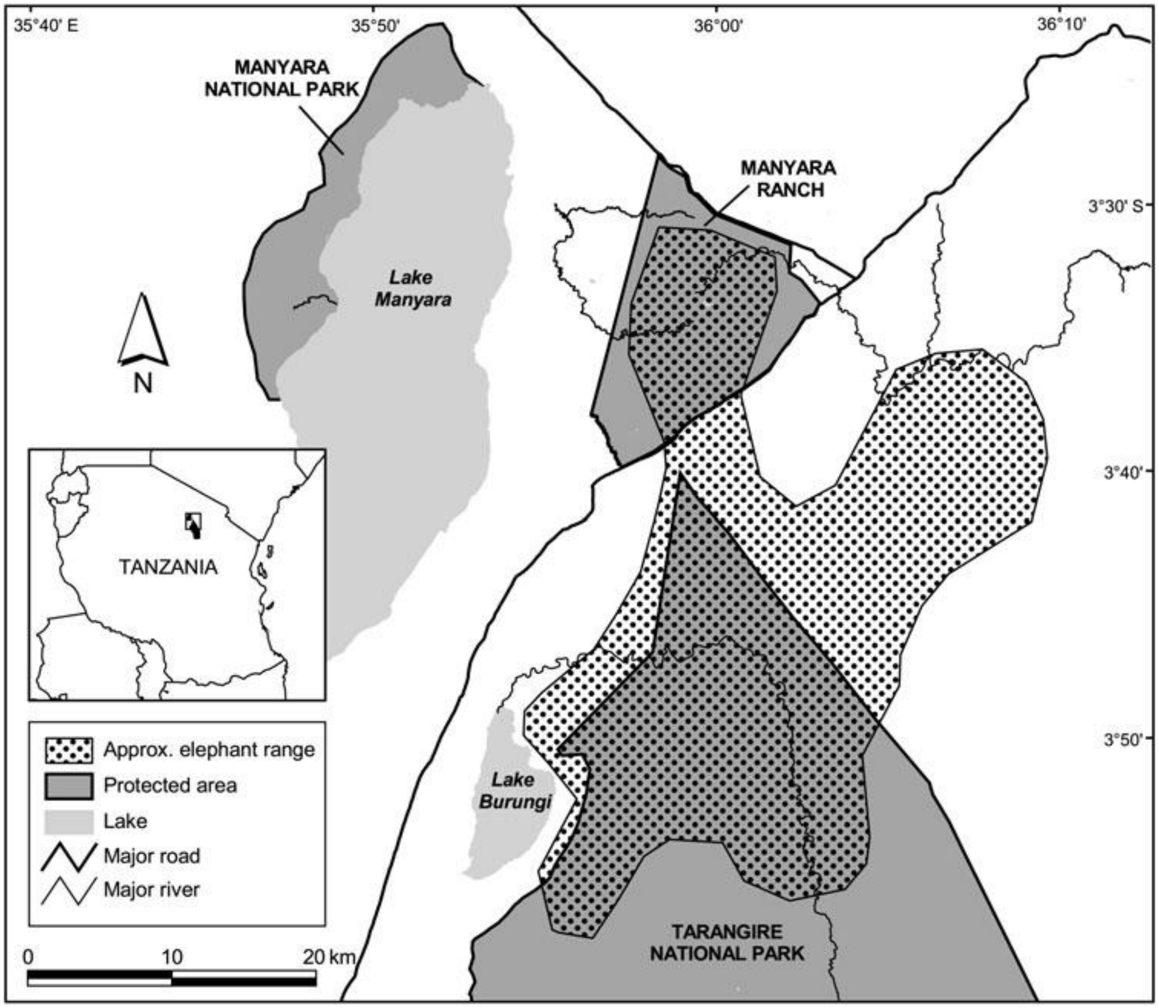

Figure 2.2 The location of the Tarangire National Park, in Tanzania and the approximate home range of the northern subpopulation of elephants (Foley & Faust 2010).

Addo study site and population

The Addo Elephant National Park (AENP), is situated *ca.* 60 km north-east (33°30'S, 25°45'E) of Port Elizabeth in the Eastern Cape Province, South Africa (Whitehouse 2001; Whitehouse & Kerley 2002). Although elephants were relatively abundant in the early 1900s in this area, conflicts with farmers resulted in an attempt to exterminate the entire population. However, this operation was aborted prior to completion, and 11 elephants survived to form AENP's founder population (Whitehouse & Hall-Martin 2000). Thus, the Park was established in 1931 to preserve the last remaining elephants in the region (Whitehouse 2001; Whitehouse & Kerley 2002). Elephants of AENP were fenced in 1954 when the population totaled 22 animals (Whitehouse 2001). The AENP elephants were intensively studied from 1976 to 1979 and from

1996 to 2001, allowing the reconstruction of the history of the population from detailed examination of long-term photographic records (Whitehouse 2001). Behavioural observations have revealed six matriarchal groups in this population ranging in size from 14 to 72 elephants (Whitehouse 2001). Since the AENP was fenced it has undergone expansions on six occasions, and the elephant population size has grown, and currently numbering over 440 individuals (Kerley & Landman 2006).

Genetic sampling and DNA analysis

Fecal samples were collected from 138 individually identified adult female elephants in 29 groups of the TNP between January and February 2009. Female elephants were defined as adults (based on the age they were assigned in 1993) if they were older than 8 years - an age at which elephants are eligible for conception (sexually mature) in TNP and other areas (Foley 2002; Foley & Faust 2010; Owens & Owens 2009). Elephants range widely and unpredictably; therefore, during our sampling period it was not possible to collect fecal samples from eight adult females in three (**C**, **H** and **L** groups) of the elephant groups. In addition, two (**Na** and **Ol**) groups had only one adult female each, making it impossible to calculate within-group average pair-wise relatedness among adult females in those groups. Adult female within-group relatedness analyses were therefore confined to the remaining 24 elephant groups. Fresh dung samples were obtained soon after the identified animal defecated, minimizing potential misidentification of the target animal's dung and enabling collection of the mucosal layer of dung prior to desiccation (Okello *et al*. 2005).

All samples collected during this study were immediately preserved in labelled sample vials containing 98% ethanol, stored at room temperature in the field, and later shipped and stored at 4°C in the laboratory of the Center for Conservation Biology at the University of Washington for DNA extraction and analysis. PBS buffer solution (saturated with NaCl) was used to rehydrate the surface of the elephant fecal sample (Rutledge *et al*. 2009). This solution has been found to successfully yield undegraded DNA from amplified samples stored at room temperature for extended periods (Seutin *et al*. 1991). I used a sterile, cotton-tipped swab soaked with phosphate-buffered saline (PBS) buffer (pH 7.5) to swab the individual fecal matter (after drying off ethanol completely) for DNA extraction. The swab was firstly rinsed well in the sterile

PBS, and then it was used to repeatedly swab the entire surface of the sample in a horizontal, vertical and diagonal direction, targeting the mucosal layer from the elephant dung sample. The swab for every sample was immediately transferred to a separate 2 µL tube for DNA extraction.

Total genomic DNA was extracted from each adult female sample using the DNeasy protocol for animal tissues (Qiagen, Inc.), following the manufacturer's instructions. Risk of contamination was minimized and quality control ensured in the lab by extracting duplicate sub-samples of DNA in a separate laboratory area free of amplified DNA (Gobush *et al*. 2009). We included multiple negative controls during both extraction and amplification. The polymerase chain reaction (PCR) consisted of approximately 3 µL of total genomic DNA, 0.15 µL of 20µM 5'-end labeled forward primer, 0.15 µL of 20 µM of unlabelled reverse primer (Integrated DNA Technologies), 8.7 µL distilled water, 1.5µL 10x PCR buffer, 0.3 µL 10 mM dNTPs, 0.6 µL 25 mM $MgCl_2$, 0.375 µL 10mg/mL BSA, 0.225 µL of *Taq* DNA polymerase (5U/µL) (Promega) for a total volume of 15 µL.

In each primer pair (Integrated DNA Technologies), forward primers were fluorescently labeled on the 5'-end with HEX or FAM-6 dyes (Applied Biosystems Inc.). The cycling parameters for PCR cycles comprised of one cycle of denaturation at 94°C for four minutes, followed by 40 cycles of denaturing at 94°C for one minute, annealing at 58°C for one minute, extending at 72°C for one minute, followed by a final extension step at 72°C for two minutes in a 9600 ABI thermocycler (Comstock *et al*. 2000; Gobush *et al*. 2009). Twelve highly polymorphic nuclear microsatellite loci were used for genotyping individual elephants. These loci are: FH048, FH067, FH071, FH094, FH102, FH103 (Comstock *et al*. 2000); FH126, FH127, FH129, FH153 (Comstock *et al*. 2002); LAfMS03, LAfMS04 (Nyakaana & Arctander 1998).

All amplified PCR products (1 µL of each individual sample) were separated on an ABI PRISM 3100 Capillary Array Genetic Analyzer (Applied Biosystems) using GeneScan mode on ROX labelled ILS-600 as an internal standard. Allele frequency and sizes were analyzed and scored using the computer programs GENESCAN and GENOTYPER versions 3.7 (Applied Biosystems), respectively, and the categories were defined by the weighted average histogram plots for each allele size bin with tolerance of 0.5 base pairs (Comstock *et al*. 2000; Gobush *et al*. 2009). All heterozygote genotypes were replicated at least twice and all homozygote genotypes were replicated three times (Wasser *et al*. 2004). A given allele was assigned to an individual only if it amplified at least twice for heterozygous alleles and three times for homozygous alleles during all replicates (Wasser *et al*. 2004).

Data processing and statistical analyses

The genotyped data were examined for allele frequencies, observed and expected heterozygosities, using CERVUS version 3.0 (Kalinowski *et al*. 2007). Tests for loci linkage and Hardy-Weinberg equilibrium were also performed on CERVUS version 3.0. We used the *ML-Relate* (Kalinowski *et al*. 2006) to calculate maximum likelihood estimates of pair-wise relatedness (r) and relationship categories between individuals from GenePop files generated with CERVUS, using genotyped data. This method accommodates null alleles that have high frequency at particular loci and is considered to be more accurate than other estimators (Marshall *et al*. 1998; Milligan 2003).

During kin-structure analysis (used to separate related and unrelated individuals) in our study, individual adult females from the 24 elephant groups were separated based on ‘kin’ and ‘non-kin’ categories. The *ML-Relate* was used in this analysis and has been found very useful for discriminating among four common pedigree relationships: unrelated (U), half-siblings (HS), full-siblings (FS), and parent-offspring (PO) (Kalinowski *et al*. 2006). This way of analysis calculates the likelihood of four relationships (U, HS, FS, PO) for each pair of individuals as outputs in a matrix of the relationships that have the highest likelihood for each pair of individuals (Kalinowski *et al*. 2006).

Therefore, the ML-Relate software was used to calculate the likelihood of each of the above four relationships from our study animals. In every elephant group, individuals whose pedigree likelihood fell in three (PO, FS, HS) of the four relationship categories were categorized as ‘kin’; adult females categorized as unrelated (U) were classified as ‘non-kin’. According to the category estimation of ML-Relate, individuals would be classified as belonging to the ‘unrelated’ category if their coefficients of relatedness (r) values fell below the cut-off value of 0.25 (Kalinowski *et al*. 2006), i.e., less related than half-sibships (Queller & Goodnight 1989; Blouin *et al*. 1996). The accuracy of estimating and distinguishing between different categories of relatedness was achieved by running iterations using individuals' genotypes from all possible pairs of the studied population (Marshall *et al*. 1998; Kalinowski *et al*. 2006).

A total of 10 000 iterations were run to generate all the possible relatedness categories from adult female pairs and these iterations are sufficient enough to generate accurate relatedness estimates with reasonably high confidence (Blouin *et al*. 1996; Marshall *et al*. 1998). A two-tailed paired-sample *t* test (Zar 1999) was used to determine if the proportion of kin and non-kin was significant in all the 24 elephant groups. The age of matriarch was correlated with the proportion of non-kin individuals within the Tarangire elephant groups to determine whether the age of the matriarch in a group influenced the willingness to accept the non-kin members in the core elephant groups. Because proportions of non-kin within the elephant group were scaled between 0 and 100%, we used arcsine transformation to normalize the percentages of non-kin during our analysis (Zar 1999).

In order to understand how genetic relatedness predicts group size in African elephant under the two scenarios, a published conceptual model (Giraldeau & Caraco 1993) was used to compare the patterns of genetic relatedness and group size data collected from the two separate elephant populations: Tarangire National Park (TNP) and the Addo Elephant National Park (AENP). I generated the graphs following the modelled processes of group formation, size and relatedness from the conceptual model (Giraldeau & Caraco 1993). I compared the graphs generated from the theoretical model with the actual data from the two elephant populations (AENP and TNP) to see if the patterns we got from our empirical results fit the model.

In every group of Addo elephants, the individual adult female was identified and her relatedness compared against each adult individual separately based on the pedigree relationship across the group (Whitehouse 2001). The Addo elephant group sizes were taken as reported in the published reports (Whitehouse 2001) and within-group average relatedness analysis was estimated by averaging all pair-wise relatedness (r) values from a long-term pedigree data across the group. All the data given and analyses conducted for AENP elephants refer to the population up to the end of 1998 only (Whitehouse 2001). I compared group relatedness against group size for TNP and AENP elephant populations in R 2.13.0 (R Development Core Team 2011) using analysis of covariance (*ANCOVA*). Data were log transformed prior to analysis.

RESULTS

All samples from the Tarangire elephants were successfully genotyped at 12 microsatellite markers with 87.7% of the samples successfully amplified and confirmed at all 12 loci. All the microsatellite loci used in this analysis were checked and met Hardy-Weinberg's assumption and they were all unlinked. The mean observed heterozygosity for all loci was 0.62, with a range between 0.29 and 0.82 (Table 2.1).

Table 2.1 Results of allele frequencies and heterozygosity (with the test results after being checked for Hardy-Weinberg assumptions) measures for 24 elephant groups of Tarangire female elephants at the 12 microsatellite loci used in the study.

Locus	**Number of alleles**	**Allele size range (bp)**	**Observed heterozygosity (H_O)**	**Expected heterozygosity (H_E)**
LAfMSO3	5	137-147	0.473	0.526
LAfMSO4	5	150-160	0.29	0.306
FH048	8	156-178	0.641	0.666
FH067	7	81-105	0.742	0.761
FH071	3	60-64	0.545	0.576
FH094	3	223-229	0.555	0.546
FH102	7	173-189	0.562	0.602
FH103	5	145-153	0.618	0.618
FH126	9	92-114	0.824	0.818
FH127	13	157-287	0.748	0.798
FH129	8	150-164	0.712	0.756
FH153	13	155-183	0.771	0.779

The maximum likelihood estimates of pair-wise relatedness and relationship categories between adult females were calculated from genotypic data.

The likelihood of the four common relationships and their respective r-values were generated from the ML-Relate after entering all genotypes of the study animals. The average pair-wise relatedness (r-values) among adult female pairs in the four relatedness categories for TNP elephant groups varied from 0.5 to 0 and the summary of the results is shown in Table 2.2. The results show that eighty three percent (N = 24) of the Tarangire elephant groups had at least one pair of first-order (parent-offspring, or full siblings) adult female relatives in 1994. Fifty percent of the 24 groups had a matriarch older than 30 years, with the mean age ± S.E of 30.29 ± 1.29 years, ranging from 21 to 39 years.

Not all groups in the northern subpopulation (N = 24 groups) of the Tarangire elephants have the same within-group relatedness, and some groups are composed of completely unrelated adult females (Figure 2.3).

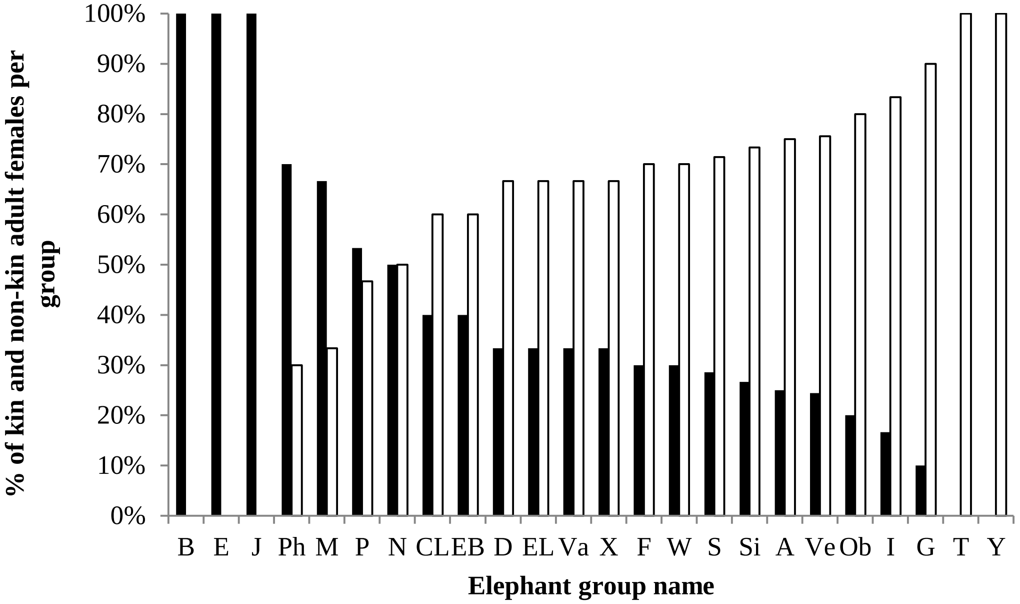

Figure 2.3 Distribution of kin (HS, FS and PO, solid bars) and non-kin (U, open bars) adult females within 24 elephant groups from Tarangire National Park. U=unrelated, HS= half-siblings, FS= full-siblings, PO= parent–offspring.

Table 2.2 Average pair-wise relatedness (r) values and relatedness categories for adult females in 24 elephant groups from Tarangire National Park.

Relatives	**Average r-value**	**Standard error**
Unrelated	0.040	0.004
Second-order: half-siblings	0.230	0.009
First-order: full-siblings	0.527	0.063
First-order: parent-offspring	0.512	0.008

Contrary to our prediction, there was no significant difference in the proportion of kin and non-kin adult females within all the 24 groups (two tailed paired-sample *t* test: $t = -1.68$, $df = 23$, $p > 0.05$) of TNP, so the results do not support the first prediction from this study that adult females within elephant groups in TNP are significantly more related than random. Although the proportion of non-kin members tended to decrease with increased age of the matriarch among the 24 groups of Tarangire females elephants, this relationship was not significant (Pearson's product moment correlation: = -0.29, *df =22, p* = 0.1758; Figure 2.4).

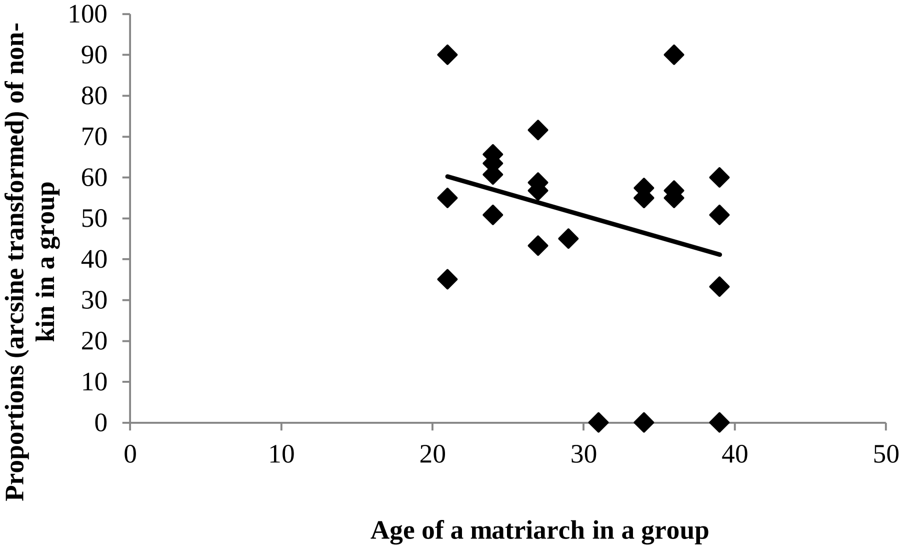

Figure 2.4 The proportion of non-kin in relation to the age of the matriarch within 24 elephant groups from Tarangire National Park, Tanzania.

As predicted, the TNP elephant population best fit the free entry model while the AENP population best fit the group-controlled model (Figures 2.1, 2.5). We found significant differences in the fit of the two population group size/relatedness curves (*ANCOVA*, group size: relatedness, $F_{3,\ 25} = 4.8$, $p = 0.0385$; Figure 2.5); TNP and AENP best fitting the free entry and group-controlled entry models, respectively.

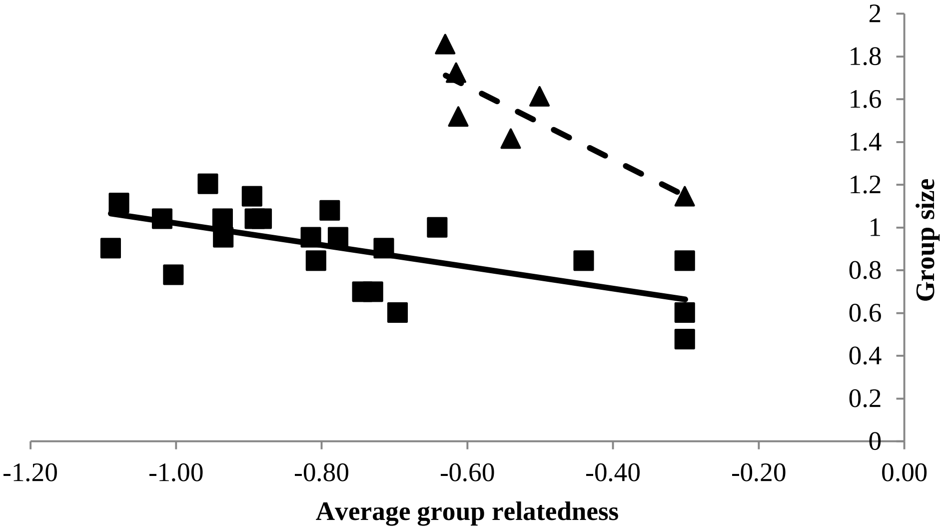

Figure 2.5 Average group relatedness in relation to group size (log transformed data) from twenty four elephant groups from Tarangire National Park (solid squares with solid line), Tanzania and six elephant groups from Addo Elephant National Park (solid triangles with broken line), South Africa.

Relatedness values dropped with larger group sizes for both TNP and AENP; however, the equilibrium group size that could be attained for Tarangire elephants would have been smaller (slope ± s.e, = -0.51 ± 1.85, intercept ± s.e, = 0.51 ± 0.60; log transformed data, Figure 2.5) than the equilibrium group size for AENP elephant population (slope ± s.e, = -1.71 ± 0.53, intercept ± s.e, = 0.63 ± 0.29; Figure 2.5) for a given average group relatedness value.

DISCUSSION

It is evident that genetic relatedness has a direct bearing on the group formation and size in African elephants. Hamilton’s rule predicts that the sharing of genes among the members of a group can facilitate the evolution of cooperative activities and the resulting inclusive fitness benefits could offset the costs associated with group living (Hamilton 1964). However, the optimal group size and fitness level achieved for a given value (or level) of relatedness will vary depending on the group membership and the environmental circumstances (such as food availability), the genetic relatedness of the individual joining the group, the effect that joining has on group member's relatives and the rules and assumptions concerning the free entry and group-controlled entry (Giraldeau & Caraco 1993).

When the group-controlled entry rules apply, related group members regulate their group size so that members enjoy the maximal benefit of group membership (Giraldeau & Caraco 2000). For example, when the social structure of elephants is disrupted, solitaries might prefer to join nonrelatives. The approach that adult female solitaries may apply to join a novel group is to form a membership where the solitary's direct and indirect (inclusive) fitness benefit is greater than that of foraging alone (Caraco & Wolf 1975; Giraldeau & Caraco 2000).

Since the effect of joining (or leaving) a group can be beneficial or costly (Clark & Mangel 1986; Packer *et al*. 1990; Giraldeau & Caraco 2000), the decision that an individual elephant makes when joining (or remaining) or leaving a group would be based on the benefit gain, which may consequently result in groups being composed of non-relatives. This would especially be true if joining a large group of related individuals by a solitary (single adult female and her immature offspring) would disproportionately reduce the fitness of that solitary (individual joining the group) as well as the fitness of its related (offspring) members. This has been indicated by a study in Amboseli National Park, Kenya whereby, when adult female elephants lose all the members of their natal core social group, they often immigrate to a new core social group (with few adult females) where they have no close kin (Archie *et al*. 2006).

An alternative explanation would be that, if the group of closely related individuals is large enough to collaborate and repel the solitary animals (i.e. adult female elephant with its offspring) from joining, then it is possible that this solitary individual would prefer to join a group of genetically non-related individuals or rather remain as an adult solitary individual with her immature offspring. This has been shown by the evidence from a study on Samburu elephants, where a single primiparous female that had lost all its core group affiliates remained solitary, never joining another group (Wittemyer *et al*. 2009). In another group from the same population, all three breeding females were unrelated and had distinct haplotypes, probably representing a situation where remnant single females from the different severely-poached groups joined together (Wittemyer *et al*. 2009). In a similar example from our study population in TNP, four of our elephant study groups (with matriarch age older than 30 years in 1994) were composed solely of a single breeding adult female and her offspring after many years of poaching in and around Tarangire and these groups have remained as independent units to date. The groups that have had only a single adult female were either able to exclude solitaries from joining their groups because of the ability of older matriarch to remain as group leader or alternatively, they were excluded from joining the large groups. This study has also indicated variation in relatedness among adult female group members, with two groups being composed of completely unrelated adult females.

The higher equilibrium group size of the AENP versus Tarangire population shown by our results supports the group-controlled entry assumption under high average group relatedness. By 1900, extensive elephant hunting for ivory had virtually eliminated elephants in South Africa leaving four small remnant populations (Whitehouse 2002). The AENP elephants in particular were reduced to eleven elephants in 1931, including five cows (of unknown relatedness), which formed the basis for the currently recognized family groups (Whitehouse 2001, 2002). The results from a detailed demographic data (spanning a period of 70 years- an elephant lifespan) and behavioural observations have revealed six main matriarchal core elephant groups within the entire AENP elephant population and 60 independent mature males (Whitehouse 2001).

Since they were originally identified, the six core social groups have grown in size ranging from 14 to 72 and their cohesiveness varies considerably; however, there is no evidence of permanent matriarchal group fission in this population (Whitehouse 2001). This strong cohesion associated with high genetic relatedness provides strong evidence supporting the assumptions held in the group-controlled entry model, implying that the equilibrium group size is higher in group-controlled model than in free entry rule when group members are closely related. It might be possible that under such circumstances within-group competition may be constrained by cohesive and cooperative strategies among group members since individuals are composed of kin (Giraldeau & Caraco 2000; West *et al*. 2007a&b), thereby increasing the direct and indirect contribution to member’s inclusive fitness.

Elephants of Tarangire on the other hand suffered poaching during the 1970s and 1980s and previous studies on this population concluded that poaching disrupted the demography and social structure in Tarangire elephant population (Moss 1990; Foley 2002).

The results from Tarangire elephants suggest that poaching disrupted the genetic basis of their social (group) structure, as we found that the groups are composed of both kin and non-kin adult individuals. The genetic differentiation between groups of Tarangire elephants is consistent with results from several other studies on the impact of poaching on elephants. For example, elephant populations in Queen Elizabeth National Park, Uganda (Nyakaana *et al*. 2001) and Mikumi National Park, Tanzania (Gobush *et al*. 2009) both experienced significant amounts of poaching and considerable variation in elephant group relatedness, with significant breakdown in female social structure.

Thus it is clear that poaching impacts extend beyond the death of elephants, but also includes social and genetic disruption of the surviving population. Although the TNP population has been growing at an average annual growth rate of 7.1% (Foley & Faust 2010), the disruption of the population's social (group) structure may require a long time to recover, probably in the order of the lifetime. The long-term recovery of AENP elephant population is a classical example of the consequences of disrupted social structure and the long-term costs required to recover the population, where the population was reduced drastically by overhunting (Whitehouse 2001, 2002).

Much as inclusive fitness benefits can play a potential role in influencing group size and stability (Hamilton 1964; Alexander 1974), direct fitness benefits alone may be an adequate reason for group formation (Alcock 1998; Lukas *et al*. 2005; Wittemyer *et al*. 2009). For example, a study on Samburu and Buffalo Springs elephants in Kenya (Wittemyer *et al*. 2009) showed that approximately 20 per cent of elephant family groups studied were not significantly related, demonstrating that kinship was not a prerequisite for social affiliation at the level of second-tier (family) group. The results from Samburu and Buffalo Springs study suggests that direct benefits can also structure strong bonding among elephants. Quantitative studies measuring the effects of genetic relatedness and group structure on fitness of female elephants may be the direction for further research.

In particular, research measuring differences in adult female reproductive success in relation to varying group relatedness and size can provide further understanding into various behavioural strategies employed by elephants that lead to formation of varying group structures. Explanations of cooperation between individuals in animal societies often suggest that direct benefits from mutualism play a more important role than kin selection for some cooperative actions, as has been shown by the studies on the evolution of cooperative breeding in other animal species (West *et al*. 2002; Aviles *et al*. 2004; Lukas *et al*. 2005; Pomilla & Rosenbaum 2006).

In some cases (e.g. when older female relates are removed from a group by poaching), group members may enhance their direct fitness by accepting (not repelling) a solitary when a group size is small. By accepting solitaries, the groups can be as large as optimal (Giraldeau & Caraco 1993, 2000) and the larger groups will likely increase the competitive ability over their potential competitors which may increase direct fitness their group members. In conclusion, despite our knowledge on the stability and hierarchical social structure in female African elephants, there is much that is not known or tested empirically on the group formation and size as a function of genetic relatedness.

Here I demonstrate that genetic relatedness has a significant influence upon the apparent group formation and size in elephant populations. The age of matriarch tended to have inverse relationship with the proportion of non-kin members within the group, suggesting that older adult females within a poached group influence the group members' decision to accept solitary (non-kin) joiners in a group. Studies of the relationships between genetic relatedness patterns and group size in African elephant populations are still rare. I have shown that the genetic patterns within groups in Tarangire elephants are consistent with the hypothesis that poaching leads to disruption of social structure in African elephants.

I provide empirical evidence supporting this. I argue that a failure to control poaching may have significant consequences for the elephant group relatedness and structure involving threats to population's future ability to increase. The long-term secondary effects of poaching on elephant social structure can be assessed using molecular (DNA) techniques and the information from such studies should be utilized alongside alternative conservation and management strategies that limit the disruption of social structure in African elephants.

CHAPTER THREE

GENETIC RELATEDNESS REFLECTS COMPETITIVE BEHAVIOUR IN FEMALE AFRICAN ELEPHANTS

INTRODUCTION

Individuals live among, compete with or sometimes cooperate with those around them (Dickamer & Vessey 1986; Alcock 1998; Reale *et al*. 2009). Together these individuals form populations, which are characterized by properties beyond those of individuals (Alcock 1998; Sober & Wilson 1998; Giraldeau & Caraco 2000). The properties include age and sex composition, social organization, habitat distribution and genetic structure. Socially living organisms differ in the degree to which different individuals are attracted to one another by identifiable mutual benefits (Emlen *et al*. 1995; Emlen 1996; Alcock 1998; Giraldeau & Caraco 2000). Social-grouping typically forms due to ecological constraints and/or when the costs of dispersal are higher than the costs of remaining philopatric (Wittemyer 2005; Schradin *et al*. 2010).

The type and structure of individual-based interactions within- and between-groups of social animals can be very dynamic and may vary depending on the degree of relatedness among individuals as well as the abundance and distribution of resources or predation (Emlen *et al*. 1995; Wittemyer 2005). Competition for critical resources (e.g., access to mating, limited food) and increased vulnerability to diseases and parasites among group-members can induce high costs and are thought to be the main reason for solitary living (Standen & Foley 1989; Giraldeau & Caraco 2000; Schradin *et al*. 2010).

Agonistic interactions resulting from competition among group members serve as a strong organizational feature of social groups (Wittemyer & Getz 2007). The evolution of fission-fusion societies in species such as African elephant (*Loxodonta africana*) regulates the effect of within- group competition through group splits when resources are scarce and enhances cooperative effects through group cohesion when resources are both plentiful and evenly distributed or benefits of sociality arise (Poole 1996; Wittemyer 2005). When sociality is favoured, animals may form groups that range from small pair-bonded units to huge aggregations (Drickamer & Vessey 1986; Alcock 1998; Silk 2007).

According to kin-selection theory (an evolutionary framework for sociality originally formulated by Hamilton 1964), the degree of kinship is predicted to influence the types of behaviour exhibited among competing individuals in a group (Emlen *et al*. 1995; Emlen 1996), leading to indirect fitness benefits for kin-selected individuals. Studies on African elephants have revealed multiple hierarchical social complexity and flexibility, with a great variety in associations between groups and individuals and this is maintained by fission-fusion processes (Moss 1988; Poole 1996; Wittemyer *et al*. 2005).

The elephant groups usually called “families” form the fundamental stable social units and are composed of predictable (in terms of their association pattern) sets of individuals (Moss & Poole 1983; Moss 1988; Archie *et al*. 2006). Also, evidence has shown that female elephants appear to have extensive social knowledge with which they are able to individually distinguish their relationships with other animals (up to 100) in their groups (McComb *et al*. 2001, 2011). In addition to this extensive social network, female elephant kin are clustered into their stable groups throughout their entire lifespan, thus providing the opportunity for kin-selection to act on the social behaviour among the individuals in the groups (Archie *et al*. 2006).

African elephants are mixed feeders, consuming a variety of plants and plant parts and reliant on widely distributed resources (Wittemyer 2005; Kerley *et al*. 2008). Elephants consume varying proportions of browse and grass depending on region, vegetation cover, water availability, soil nutrient composition, and season (Kerley *et al*. 2008). In elephants, diet switches occur between seasons with grasses being primarily consumed in wet season and browse in the dry season, although neither of these food sources appears to be monopolizable by individuals or groups (Wittemyer & Getz 2007; Kerley *et al*. 2008).

Aggressive competitive interactions among elephants, however, do occur in relation to infrequent use of point resources like fruiting trees and water holes (Wittemyer & Getz 2007; Wittemyer *et al*. 2007a). In a study of how the competitive interactions vary with degree of relatedness in a poached elephant population, Gobush & Wasser (2009) found that core groups of low genetic relatedness displayed a higher frequency of agonistic interactions with other unrelated core groups than did highly related core groups. While their findings were interpreted as the consequences of the removal of adult female kin in the group, that particular study did not focus on how relatedness affects aggression at an individual level.

Natural selection regularly occurs at individual level and selection acting on differences among variant individuals within a population will usually have a much stronger evolutionary effect than selection acting on differences among groups (Drickamer & Vessey 1986; Alcock 1998). In social groupings individuals can be used to represent group structure as a unit of interacting components, and also to quantify both the position of each individual versus group organization in dynamic social structure of a group (Alcock 1998; Hock *et al*. 2010). Such individual- based studies focusing explicitly on the frequency and intensity of individual-based competitive interactions in relation to degree of relatedness are lacking in African elephants. In contrast to Gobush and Wasser (2009) study, I characterize patterns of sociality, hypothesising that the benefits and costs of social foraging commonly depends on the dynamics of individuals and their interactions with other individuals within- and between-groups.

Assessment of individual-level competition both within- and between- groups, offers important insight into the proximate mechanisms for the evolution of African elephant sociality and their implications on the dynamics of this sociality, like fission-fusion processes. The objective of this study was to assess the effect of genetic relatedness and age on individual-based adult female competitive interactions within-and between-groups of a free-ranging African elephant population of Tarangire National Park (TNP), Tanzania. I addressed the question: to what extent do genetic relatedness and age predict the frequency and the intensity of aggression among competing individuals within and between groups of female African elephants in TNP? I predicted that the frequency and the level of dyadic individual competitive interactions would be higher among unrelated than related pairs of female African elephants.

MATERIALS AND METHODS

Study site

The study site is in Tarangire National Park (TNP), in northern Tanzania. The Park covers an area of 2,600 km^2, lying between 3°40' and 5°35'S and 35°45' and 37°00'E (Foley 2002; Figure 3.1). Tarangire National Park was established in 1970 and it borders Simanjiro Game Controlled Area (GCA) to the east and to the north-east the Park borders Lolkisale GCA. To the North it borders Mto wa Mbu GCA, and borders Mkungunero Game Reserve to the South.

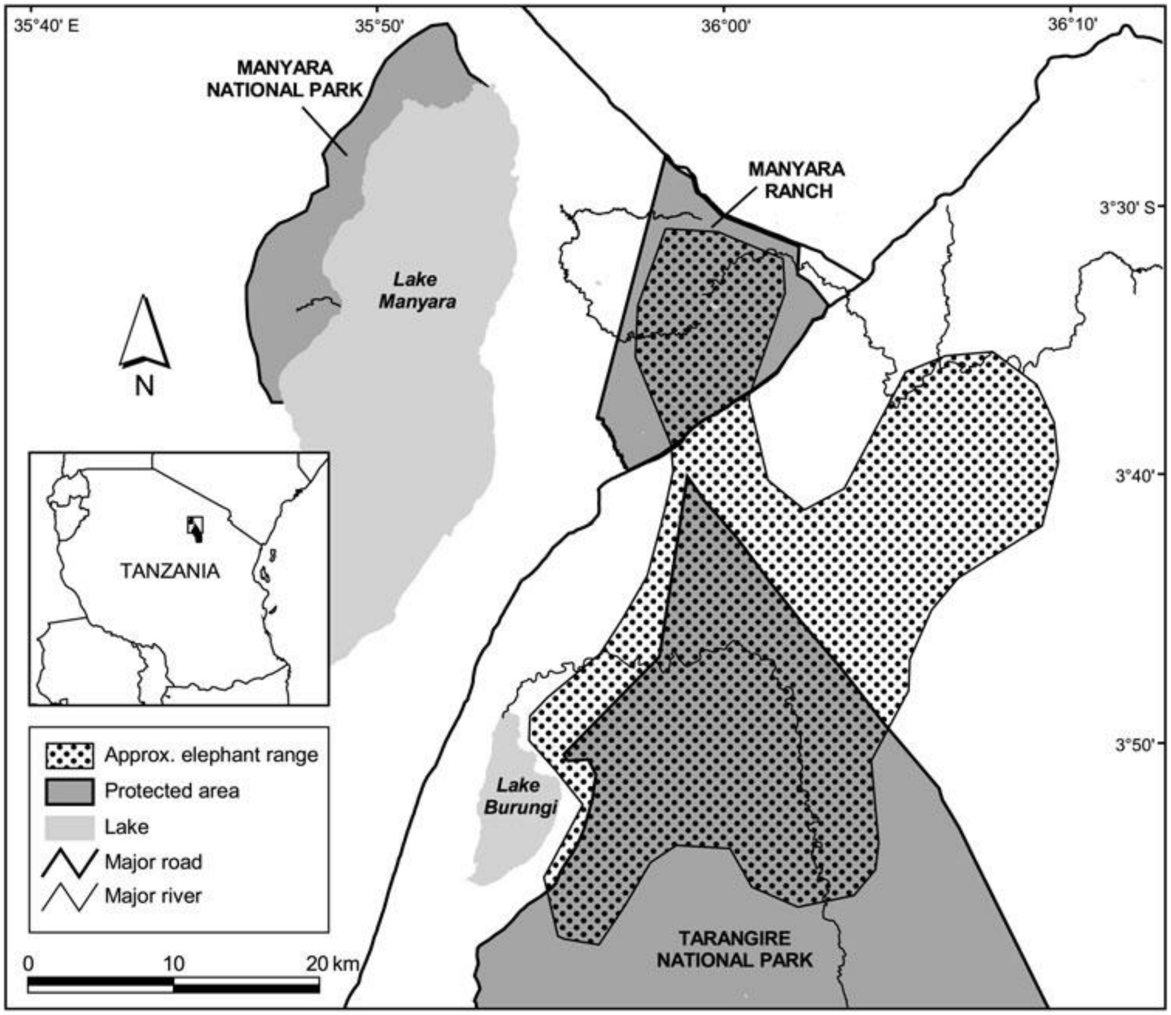

Figure 3.1 The location of the Tarangire National Park, in Tanzania and the approximate home range of the northern subpopulation of elephants (Foley & Faust 2010).

Seasons in the park can be subdivided into early rains (December-February), late rains (March-May), early dry (June-August) and the late dry which is between September-November (Foley 2002). The highest rainfall levels were recorded in 1979 and 1987, with 1337 and 1014 mm, respectively; lowest levels fell in 1983 and 1993, respectively.

Average annual rainfall in the park, based on 21 years of data, is 620 mm (Van de Vijver *et al*. 1999). The park is dominated by the Tarangire River, which provides the main source of water for migratory and resident animals during the dry season within the entire 35,000 km^2 Masai Ecosystem in which TNP lies (Prins 1987; Van de Vijver *et al*. 1999). As the dry season progresses, the Tarangire river disappears underground in some part of its course, making water availability for drinking by wildlife difficult (TCP 1997). As a result access to drinking water by elephants in the dry season is limited and therefore the adult individuals dig water holes along the Tarangire river banks and clear the holes to access the clean water. The Tarangire ecosystem contains the largest populations of elephants in northern Tanzania, and the second-largest migratory ungulate populations in East Africa (TCP 1997). During the wet season, there are significant movements of large mammals out of the park to dispersal areas on village lands, returning when ephemeral water in these areas disappears (Foley & Faust 2010).

Study population

The Tarangire elephants have been studied since 1993 (Foley 2002), documenting detailed and reliable demographic data in 29 different known groups in this population. Poaching for ivory in TNP during the 1970s and 1980s was responsible for eliminating the majority of the older male and female individuals in the population (Moss 1990; Foley 2002). The poaching in TNP was more severe on some groups than others, resulting in a range of surviving group types and structures, from those with normal age structures, to others containing only very young individuals (Foley 2002). Therefore, elephants in TNP provide an excellent opportunity for studying genetic relatedness and how this affects individual-based agonistic behaviour.

DNA sampling, extraction and analysis

See Chapter two for sampling protocol and analysis

Relatedness estimates

During kin-structure analysis (used to separate related from unrelated individuals) in our study, individual adult females from the elephant groups were separated among ‘Full-siblings, FS’, ‘Parent-offspring, PO’, ‘Half-siblings, HS’ and ‘Unrelated, U’ categories. The maximum likelihood estimate was used in this analysis and has been found very useful for discriminating among the four common pedigree relationships (Milligan 2003). This analysis calculates the likelihood of four relationships for each pair of individuals as outputs in a matrix of the relationships that have the highest likelihood for each pair of individuals (Kalinowski *et al*. 2006).

All first-order relatives (i.e. parent-offspring, PO or full-siblings, FS) were sorted out and pooled together and classified in one category of FS. This is because all pairwise coefficient of relatedness (r-values) generated between all adult female pairs in the two categories were approximately equal to theoretical r-values (~0.5) for first-order relatives (Queller & Goodnight 1989; Blouin *et al*. 1996; Kalinowski *et al*. 2006). The ‘unrelated’ female pairs were those individuals with which a given pair was categorized as being unrelated (U) from the likelihood calculations by the ML-Relate.

Behavioural data collection

Behavioural (agonistic interaction) data were collected on 117 individually known adult females from 29 known groups of Tarangire elephants. The agonistic interaction behaviour was defined as any form of aggressive (displacement) encounter exhibited toward another individual in a limited resource use (drinking at waterhole, mudbath, resting under the shade) environment. I used pairwise relatedness (r)-values and the four relationship categories (i.e. FS, PO, HS, U) generated by the ML-Relate from all possible pairings of adult female elephants and categorized the interacting individual pairs into 3 groups (FS, HS and U).

Behavioural data collection from the resultant pairs was opportunistic and data were collected during the day (between 0800 and 1700) between January 2009 and November 2010 using focal and *ad libitum* sampling (Altmann 1974; Lee 1996). Once an elephant group was encountered, a randomly selected female was observed for agonistic interactions (Altmann 1974;

Lee 1996). Sampling and focal observations were made to record agonistic encounters between adult females, within- and between- families (Côté & Festa-Bianchet 2001), together with the identities of the interactants (Foley 2002). During each observation period, samples were made at 20-minutes intervals to record the target's (aggression) behaviour (Foley 2002; Mitani *et al*. 2002), including initiators and the recipients of aggression.

Observations on focal individuals continued from the time the interactants started agonistic interaction to the time they stopped the interaction. I recorded all between adult female aggressive agonistic interactions among waterhole (drinking), mudbath (wallowing), resting in the shade and feeding groups. The intensity of agonistic interactions between adult females was scored using the aggression scales that ranged within the intensity of categories from mild to severe (Lee 1996; Foley 2002). These included: aggressor walking with ears spread out, raising head up, running, chasing or tusking, all this being directed to the recipient (Appendix 1).

The adult female was considered a winner of a dyadic interaction if she displaced the other female from her physical position or forcibly excluded her from the limited resources (waterhole, mudbath, shade). I separated "age class 1" and "age class 2" pairs of interacting females. The interacting female elephant dyads were in age class 1 if both were estimated to be older than 30 years (an age that the adult female was considered to potentially start gaining a social rank in a group hierarch, Poole 1996) otherwise those dyadic pairs with one of the interacting females aged between 20 and 30 years and the other being older than 30 years were categorized in age class 2.

Statistical analysis

Statistical analyses were conducted in the R package (R Development Core Team 2011) and SPSS (version 19, IBM, SPSS Inc., USA). I used generalized log linear models (GLLMs) to assess the effect of relatedness (as classified in three categories of FS, HS and U) and age (categorized in two classes) on the intensity of aggressive interactions among adult female elephants of TNP. I used a stepwise backward elimination procedure to test and choose the best model, firstly, by starting with the saturated model fitted with relatedness, age and intensity of aggression as factors. The intensity of aggressive interaction was categorized as a response variable whereas relatedness and age categories (as defined above) were considered as explanatory categorical variables during this analysis. Then, both the main effects of categorical variables (age and relatedness, and their interaction) were tested (Fienberg 1994; Agresti 2002) and the chi-square from the final model was tested and found to be significantly different from 0 (significance value, $p > 0.05$). Chi-square goodness-of-fit test was used to assess if there was a significant difference in the frequency of aggressive interactions in relation to relatedness and age classes among adult females.

RESULTS

I recorded 659 between- adult female agonistic interaction between 2009 and 2010. The frequency and intensity of aggressive competitive interactions displayed between adult females within elephant groups was inversely related to intra-group average relatedness (Figure 3.2).

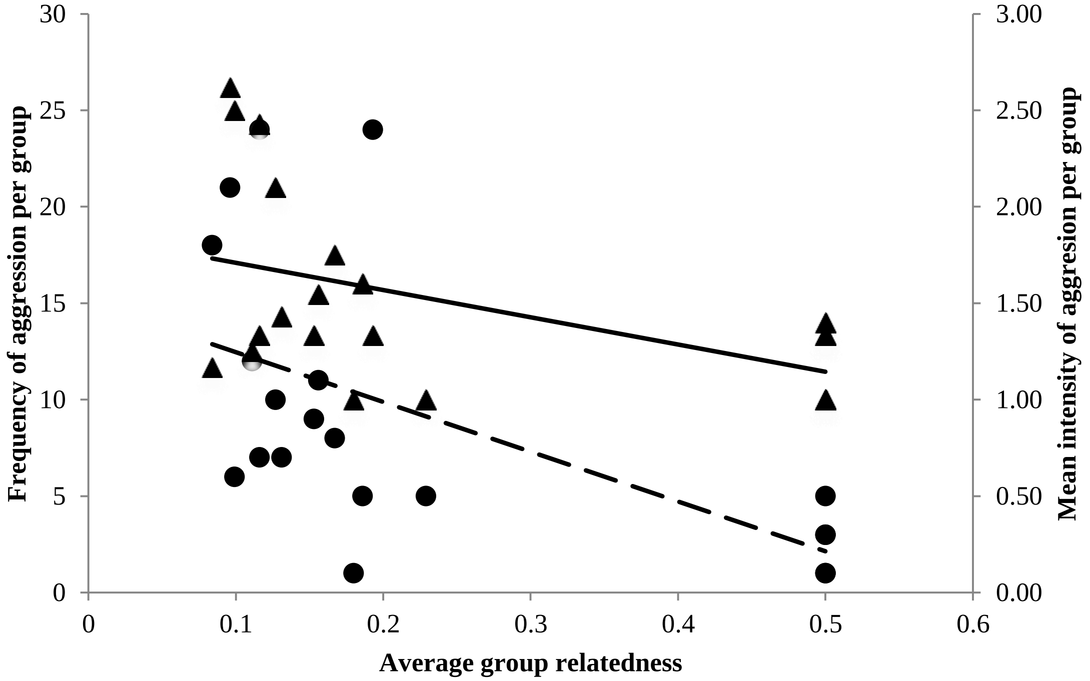

Figure 3.2 Intra-group frequency and mean intensity of aggression [using Foley's (2002) scales] between adult females in relation to average group relatedness in 21 elephant groups of Tarangire National Park, Tanzania. Solid circles and broken line are frequencies and solid triangles with solid line are between- adult female mean intensity of aggression per elephant group.

There was a significant negative correlation between the frequency of agonistic interactions and intra-group average relatedness (Pearson's product-moment correlation, = -0.57, *p*-value = 0.008; Figure 3.2). There was also a significant negative correlation between intra-group mean intensity of agonistic interactions and within-group average relatedness (Pearson's product-moment correlation, r_{18} = -0.46, *p*-value = 0.043, Figure 3.2). There was a significant difference in the frequency of aggressive interactions between adult females across the relatedness and age categories (χ^2 = 76.75, *p*-value < 0.000, Figure 3.3) as a whole, with that of age class 1 unrelated females being higher than that of other relatedness and age classes (Figure 3.3). Although there is a gap between r-values of 0.3 and 0.5, the frequency and intensity of aggression was higher among unrelated individuals than closely related dyads.

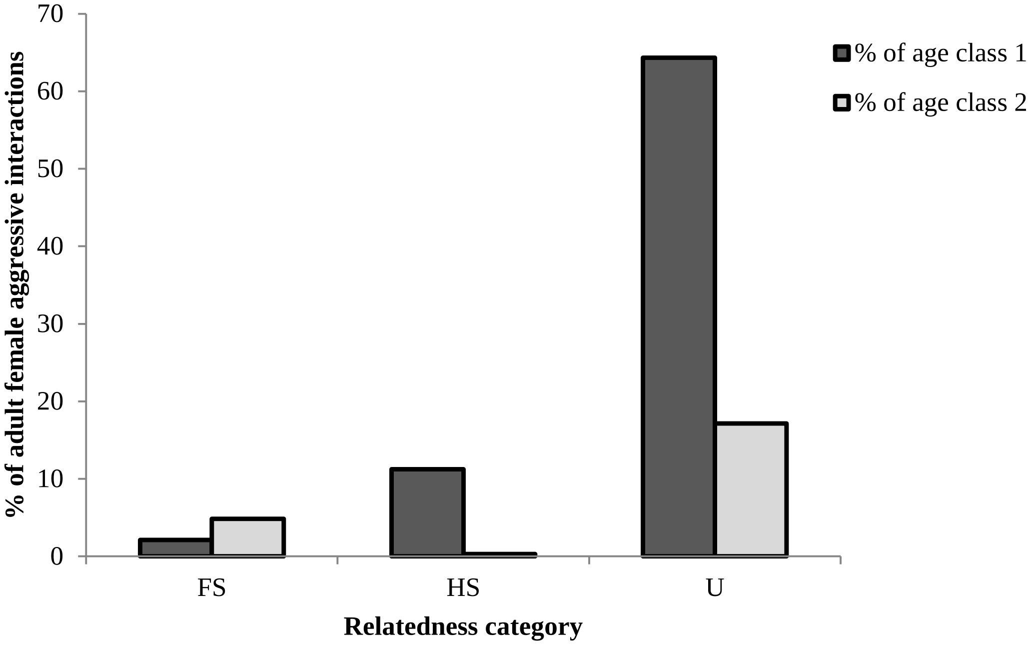

Figure 3.3 Proportions of dyadic aggressive interactions among Tarangire adult female elephants in relation to three relatedness categories [Full-siblings (FS), Half-siblings (HS), Unrelated females (U)].

The results showed that adult female elephant aggressive interactions (in a limited resource use) were a function of genetic relatedness and age of interacting female pairs. The intensity of aggression between adult females from within-and between-groups was predicted by relatedness and age (GLLM, Likelihood ratio test: χ^2 = 75.17, *p*-value < 0.000, Table 3.1). Thus, the final model (which included the main effects and the two-way interaction terms) was found to adequately fit the data well. The significant negative coefficients on FS and HS (Table 3.1) indicated the decrease in the likelihood of increased intensity of aggression among closely related adult female pairs both within-and between-elephant groups. After adding the interaction to the GLLM model, Age class 1 and its interaction with unrelated adult female pairs were significant predictors of intensity of aggression (Table 3.1).

Table 3.1 Summary of General Log Linear Models (GLLMs) showing the effects of genetic relatedness and age on the intensity of aggression (659 records) between adult female elephants of Tarangire National Park.

Parameter	β± S.E	Z-value	Pr(>|Z|)
Age class 1	1.3±0.09	13.3	0.000
Age class 2	0		
FS	-2.5±0.15	-16.00	0.000
HS	-1.95±0.12	-15.95	0.000
U	0		
Age class 1*FS	-1.75±0.55	-3.2	0.002
Age class 1*HS	1.31±0.86	1.52	0.128
Age class 1*U	0		

DISCUSSION

In this study I investigated how different relatedness and age categories between adult female elephants affect the frequency and intensity of aggression among group members. In all our analyses, we consistently found a higher frequency and intensity of aggression towards non-related (along the related-unrelated continuum) than related dyads in any limited resource (competing) environment. According to Hamilton's (1964) rule, all else being equal, closely related individuals are expected to engage in fewer actions that have detrimental fitness consequences for one another, and more actions with beneficial fitness consequences (Alexander 1974; Emlen *et al*. 1995; Bourke 2007).

The results show that the costs and benefits of within-group cooperation and affiliation to each other in female African elephants lie in the degree to which group members are related to one another (Figure 3.2). The evolution of grouping is nearly invariably explained by enumeration of its advantages to individuals (Alexander 1974; Alcock 1998), and the assumption in this case is that individuals gain fitness advantage from group membership (Giraldeau & Caraco 2000; Clutton-Brock 2009). Evolutionary biologists have documented consistent increased in cooperation and intra-group mutualism among kin individuals (Giraldeau & Caraco 2000; Clutton-Brock 2009) and more so in African elephants (Archie *et al*. 2006, Archie & Chiyo 2011).

In their study in Amboseli elephants (in Kenya), Archie *et al.* (2006) found that individual adult female differences in the tendency to fission and/or stay close to others (within the group) was predicted by genetic relatedness, with core groups being more likely to fuse with each other when adult females in the group were genetic relatives. In general, the fission-fusion process in social grouping has been shown to be an optimization strategy for coping with ecological constraints (Poole 1996; van Schaik 1999; Wittemyer 2005). Kin-selection theory predicts that relatedness may reduce the level of aggression among competing group members and accepting (failing to repel) a relative when group size is at least as large as the optimum constitutes kin-directed altruism (Giraldeau & Caraco 2000; Aviles *et al*. 2004). Intra-group aggression may occur in large groups as an indicator of increased competition among the group members in resource-limited environments (van Schaik 1999).

However, aggression (restricting or forcibly displacing individuals from a resource) is more likely to occur between unrelated individuals or groups (Giraldeau & Caraco 1993, 2000; Gobush & Wasser 2009). The significant negative correlation between the frequency/intensity of agonistic interactions in relation to the degree of relatedness as shown by this study highlights the potential benefit that adult female elephants can accrue from living in closely related groups. Thus, there are clear direct and indirect fitness benefits for closely related individuals to engage more in cooperative and affiliative actions (Emlen *et al*. 1995; Emlen 1996; West *et al*. 2007b; Bourke 2007). Grouping with kin is believed to provide a means of mitigating some of the costs of exploitation by non-group members, and provides individuals with the better opportunity to locate and access limited resources (Dublin 1983; Rieucau & Giraldeau 2009; Bates *et al*. 2010).

The group normally should repel an intruder where the average individual fitness (both direct and indirect) fitness to group size starts to decline, unless the intruder is so closely related that the joiner increases the inclusive fitness benefits of the group members via the effects on the fitness of relatives (Giraldeau & Caraco 1993; Aviles *et al*. 2004; Bourke 2007). If such social mechanisms were in place among individuals who tend to share a more recent common ancestor, then genetic relatedness may present a proximate mechanism for explaining patterns and stability of sociality in female African elephants. Whether or not genetic relatedness is a mechanism for maintaining sociality in social species, this study does not address the question of whether relatedness represents the short or long term mechanism for maintaining sociality in African elephants.

Elephants have well developed complex social structure with unusually long lifespan and broadly overlapping generations. The nature and the relative magnitude of aggressive interactions among individual adult females are determined by age and kinship lines (Dublin 1983). These results suggest that elephant populations that have been disrupted through poaching will have long-term and persistent negative effects on the adaptive value of elephant relationships even decades after the poaching has stopped. The results also show that age of interactants increased the likelihood of the individuals engaging in more frequent and intensive aggression between adult female elephants across all the relatedness categories (Figure 3.3; Table 3.1).

Adult females (within and between the group) were more likely to show aggressive interactions with females closer to their age possibly because aggression may facilitate the development and maintenance of dominance rank. Among elephants, where individual females may be associated for decades, group integrity clearly requires a delicate balance of cooperation and competition (Dublin 1983) and this balance is probably maintained by dominance hierarchies among individuals (Dublin 1983; Moss 1988; Poole 1996). Being social mammals that live in groups, their longevity has created individual-based interactions among group members that are moulded by the formation of transitive dominance hierarchies both within and between the group (Wittemyer & Getz 2007; Wittemyer *et al*. 2007a).

This social dominance is one such mechanism that governs coordination, cooperation and competition among group members in social mammals (Dublin 1983; Sober & Wilson 1998; van Schaik 1999; Côté & Festa-Bianchet 2001). Despite being infrequently engaged among related individuals (Wittemyer & Getz 2007), agonistic interactions (and thus dominance rank) can be of immediate benefits in providing access to limited resources, protection from harassment against competing (unrelated) individuals and socialization of infants so that all group members can be more productive (Sober & Wilson 1998; van Schaik 1999; Wittemyer *et al*. 2007a).

Thus, these results suggest that removal of related adult individuals from a group by poaching (or the entry of non-related individuals into the group) lowers intra-group relatedness (Gobush & Wasser 2009; Chapter two), with increased frequency and intensity of aggression between adult females and possible disruption of dominance hierarchies among (unrelated) groups. Although evidence has shown unrelated adult females joining together to form a novel group after the loss of their core group members (Archie *et al*. 2006; Wittemyer *et al*. 2009; Chapter two), frequent aggressive encounters between them can be observed because individuals are unlikely to accrue direct and indirect fitness benefits from these unrelated associations.

Such aggressive interactions have been observed in Tarangire elephants when immigration events occurred into the population after poaching in 1980s. Previous studies (Moss 1990; Foley 2002) on Tarangire elephants have indicated that poaching severely affected this population. Foley’s (2002) study also indicated that during the first four years of the long-term behavioural monitoring work on Tarangire elephants, the oldest matriarchs from immigrant groups were regularly supplanted by younger matriarchs from resident groups.

In addition, high frequency and levels of aggression from resident elephants would be directed towards individuals of groups that had recently immigrated into the population (Foley 2002). Studies on Mikumi elephants (Gobush & Wasser 2009; Gobush *et al*. 2009) also showed that poaching removed adult female elephants from the population, altering their social and genetic structures. Their studies showed tolerance was the most frequent response between closely related core groups and that core groups that lacked closely related individuals displayed less cohesion and a higher frequency of agonism with other unrelated core groups than did highly related core groups.

CONCLUSION

Much as group size may be used to assess the effects of group relatedness on competitive behaviour between the groups, between-individual characteristics may be the fundamental approach to assess the effects of different hierarchies of relatedness and age categories in shaping elephants' competitive behaviour and its importance both at the individual and group level. The results from this study give an alternative explanation for the importance of between-adult female genetic relatedness and age in shaping and maintaining female African elephant society. Genetic relatedness, however, may be a proximate mechanism shaping elephant sociality both within-and between-group at the level of individual, as demonstrated by this study.

African elephants are facing more threats from poaching and habitat loss (destruction and fragmentation) with growing contact with humans and livestock and increased human wildlife conflict (Archie & Chiyo 2011; Wittemyer *et al*. 2011). The results from this study demonstrate the importance of individual variation in genetic relatedness on the frequency and intensity of aggression at the level of the group and provide the illustrative examples of the possible impact of poaching on the collective network of elephant social structure. Thus, understanding how elephant social behaviour shapes and is shaped by genetic structure, and how human activities such as poaching are changing those relationships, is necessary to conserve African elephants (Archie & Chiyo 2011).

CHAPTER FOUR

THE INFLUENCE OF GROUP RELATEDNESS AND STRUCTURE ON REPRODUCTIVE SUCCESS OF TARANGIRE FEMALE ELEPHANTS

INTRODUCTION

Long-term studies of African elephant (*Loxodonta africana*) at several sites (Amboseli National Park, Kenya: Moss & Poole 1983; Moss 1988, 2001; Addo Elephant National Park, South Africa: Whitehouse 2001; Tarangire National Park (TNP), Tanzania: Foley 2002; Samburu and Buffalo Springs National Reserves in Northern Kenya: Wittemyer 2005) have revealed complex matriarchal societies for this long-lived, large brained, largest terrestrial mammal. Along with unusually long lifespan and broadly overlapping generations (Dublin 1983; Moss 2001; Wittemyer *et al*. 2007b), elephants are also characterized by extensive maternal investment (Lee & Moss 1986). Yet factors affecting variation in individual female reproductive success remain largely unexplored.

Wherever they have been studied, female elephants live in a fission-fusion society where individuals join and leave the groups on a fluid basis, with associations lasting minutes to years (e.g., Archie *et al*. 2006; Vance *et al*. 2009; Archie *et al*. 2011). Grouping patterns within this flexible system likely reflect sex-specific survival and reproductive strategies (Alexander 1974; Clark & Mangel 1986). Associations of female elephants within the elephant groups are strong and stable and persist for decades even after the original maternal kin have died (Archie *et al*. 2006). Whereas male elephant reproductive strategies clearly focus on gaining and maintaining access to cycling females, female reproductive strategies are likely to centre on calf production and protection (Moss 1983; Bates *et al*. 2010).

An important aspect of social grouping behaviour that until recently has largely been unexplored in many species concerns the costs and benefits of cooperative breeding between individual group members. Cooperative, or communal, breeding occurs when more than a pair of individuals exhibit parent-like ("helping") behaviour toward young of another parent within the same social unit (Lee 1987; Koenig *et al*. 1992). Female elephants would seem to be ideal subjects for such grouping studies because they live in predictable matriarchal social groups that allow within group related members to live in these groups for decades of their lives (Moss 1988; Archie *et al*. 2006). The results from Chapter three have shown increased agonistic interaction in less related groups, thus, less affiliative and cooperative behaviour among adult females. I tested the prediction that reproductive success would decline as a function of within-group relatedness.

Assessing the relatedness, and structure of individual groups that have higher or lower per capita reproduction rates is fundamental to our understanding of the evolutionary role of group formation on fitness and its long-term consequences to population dynamics if we are to manage and conserve the species successfully. As such, it is not surprising that fitness of many social species is closely related to variation in group relatedness and structure. Demonstrating the effects of group relatedness and structure on fitness requires data over appropriate temporal and spatial scales, and for long-lived animals this necessitates years of study (Moss 1988; Whitehouse & Hall-Martin 2000; Durant *et al*. 2004). In this study, I investigated the influence of group relatedness within core elephant groups (usually called family groups) and structure on reproductive success (RS) of individual adult female African elephants.

MATERIALS AND METHODS

Study population

Elephants in TNP have been studied continuously since 1993 [Tarangire Elephant Project (TEP)-long-term elephant research]. The Tarangire elephants are one of the populations that suffered heavy poaching in 1970s and 1980s so the groups were socially and demographically altered (Moss 1990; Foley 2002). Also, the poaching in TNP was more severe on some groups (presumably groups that had individuals with the largest tusks and which spent more time outside the national park) than others, resulting in a range of group types, from those with normal age structures, to others containing only very young individuals (Foley 2002). Thus, the founders of population are thought to be the remnants of the originally resident poached elephant groups (families) and immigrants from the neighbourhood, which sought refuge in the park (Foley 2002). Since the longitudinal fieldwork began in 1993 in this population the demographic records for all 29 known elephant groups are available as individual level records and these records are updated monthly. Eighteen of the 29 groups were identified by November 1993 and the rest by November 1994 (Foley & Faust 2010); because of this, all the analyses at group level used the end of 1994 as a baseline year to include the groups that were unknown in 1993.

The elephant groups were identified at the start of the long-term (1993) study on the basis of well-defined criteria that are accepted as standard (behavioural observation) protocols in studies of African elephants (Moss & Poole 1983; Moss 1988; Poole 1996; Moss 2001). Quantification of the elephant groups and the levels of association among adult females in the northern subpopulation were calculated for all known groups based on 2153 independent sightings (Foley 2002). Given the multilevelled, fission-fusion nature of elephant social structure (Wittemyer *et al*. 2005), the elephant groups, equivalent of the 'family group' was chosen as the social level at which our analysis was based.

I chose to analyse relatedness at group level because in elephant populations, groups are composed of a predictable set of individuals (Moss 1988; Archie *et al*. 2006). These groups appear to be stable across seasonal periods. Also, most of the relevant forces shaping female relationships, both competitive and cooperative, and hence their fitness, occur in these social units (Vance *et al*. 2009; Archie & Chiyo 2011).

DNA sampling, extraction and analysis

See Chapter two for sampling protocol and analysis

Reproductive success data and statistical analysis

I calculated the reproductive success of the individually known adult females (N = 66) from 24 elephant groups of Tarangire National Park (TNP). Adult females here are defined as those breeding females that remained in the 24 groups after heavy poaching that happened in TNP in 1970s and 1980s. These females ranged in age from 27 to 56 years old at the end of 2010. I used the sex ratio at birth (proportion of males) and the number of weaned (juvenile) offspring surviving to the individual adult female across the breeding (study) period to assess the variation in the RS among individual adult females.

Juvenile elephants were defined as those weaned calves older than four (and younger than eight) years, the estimated age around which elephant calves are most susceptible to mortality during harsh conditions (Dudley *et al*. 2001; Foley 2002; Young & van Aarde 2010).

To standardise reproductive effort by individual adult females (i.e. number of years of breeding observations), I only measured reproductive success of the cows that had an infant at the onset of the monitoring study in 1993 and continued breeding throughout the course of this observation period (1993-2010). Reproductive effort is a key parameter of life history because it measures the resources allocated to reproduction at the expense of growth and maintenance (Brown & Sibly 2006; Galimbert *et al*. 2007). This standardization approach, controls for the number of reproductive years available to females of different ages in the family group and also allows identifying the pattern of reproduction that produces an optimal individual female reproductive success (McComb *et al*. 2001; Galimbert *et al*. 2007), given a range of group relatedness and structure.

The sex ratio at birth and total offspring surviving to more four years per adult female old were examined using data recorded over a 17 year period (1993-2010). Demography data were used to find out if there was variation in breeding success among adult females as a function of within group relatedness and structure in Tarangire elephants. All the analyses at group level used the end of 1994 as a baseline year to determine the consequences of various group structure and relatedness on individual adult female reproductive success. Multiple linear regression models were used to assess the effects of elephant group relatedness and structure on the calf production rate in R 2.13.

RESULTS

There were 305 juveniles that survived older than four years produced by the 66 studied individual adult females from 24 elephant groups. Adult female elephants' calf production and survival ranged from 3 to 6 juveniles (mean ± S.E, 4.62 ± 0.11) during the period between 1994 and 2010. The mean group size (number of adult females and their immature offspring) in 1994 ranged between 3 and 14 with the mean ± S.E of 9.0 ± 0.65. Within-group average relatedness among adult females in 24 elephant groups of TNP varied from 0.5 to 0 (Figure 4.1).

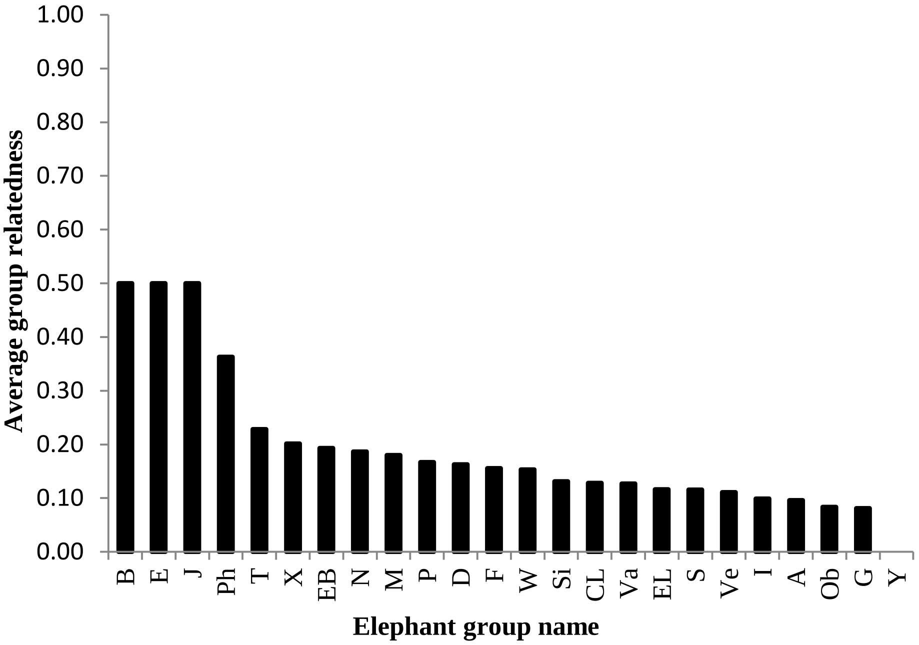

Figure 4.1 Within- group average relatedness in 24 elephant groups from Tarangire National Park.

Within-group difference between kin and non-kin individuals in the 24 elephant groups had consistent impacts on adult female RS. Individual adult female RS (surviving juvenile offspring) differed significantly between smaller (group size ≤ mean group size) and larger (group size > mean group size) group size ($\chi^2 = 27.15$, $p = 0.0000$, with Yates correction applied, Zar 1999), with females in closely related (both large and small) groups consistently having higher reproductive success than unrelated/non-kin groups throughout the study period. The results strongly support the hypothesis that kin-group structure influences adult female RS. There was a significant negative correlation between group relatedness and the offspring sex ratio of the individual adult females (Pearson's product moment correlation: = -0.28, $df = 64$, $p = 0.02$). Adult females in closely related groups had a higher proportion of female calves than those in less related/non-kin groups.

Multiple regression analysis showed a significant effect of group relatedness and structure on individual adult female RS ($R^2 = 0.23$, $F_{4, 61} = 5.87$, $p = 0.00046$; Table 4.1). The age of the female had a significant positive effect on the juvenile offspring surviving to adult females (Table 4). Other potentially confounding variables- the group size and the number of females (other than breeding cows) in the group were included in the model because their effects were found to be statistically significant.

Table 4.1 Summary of the multiple regression models showing the effects on individual adult female reproductive success (surviving juvenile offspring per female over the course of the study) of the variation in the average group relatedness and structure of Tarangire elephants in Tanzania.

Variable§	**Coefficient**	***t*-value**	**Significance**
Group relatedness	-3.15	-2.83	$p = 0.00623$*
Age of female	0.05	3.52	$p = 0.00082$*
Group size	0.11	1.77	$p = 0.08265$
Number of adult females in a group	-0.28	-2.72	$p = 0.00859$*

§All the four variables were included in the final model and interactions between these variables and the group relatedness were dropped because they not significant. *Significant values are $p < 0.05$.

DISCUSSION

Effects of group relatedness and structure on calf production and survival

Group relatedness and structure had significant effect on individual adult female RS, supporting the prediction of this study. Kin-selection theory (Hamilton 1964) predicts that, in social grouping system (as in female elephants), high degree of relatedness between group members should promote the expression of communal care when cooperation for defence and protection of infants is a major contribution to female reproductive success. Helping increases the survival of the breeders (who are assumed to be kin), thereby increasing the likelihood of their being alive to reproduce later in the same or in future seasons (Emlen *et al*. 1991, 1995). Thus, such help should ultimately result in higher reproductive success of the recipient.

Also, helping in cooperatively breeding animals attracts and raises new group members even if these are unrelated (Kokko *et al*. 2001). This helps group members to survive and reproduce better not only because individuals gain greater protection from predators but also they cope more effectively with unfamiliar situations through faster innovations of novel solutions by some new group members (Liker & Bókony 2009).

One situation in which (new) individuals may gain from other group members is when resource acquisition involves familiarity with natal area as well as complex interactions with the environment (McComb *et al*. 2001; Foley 2002; Radespiel & Zimmermann 2003; Foley *et al*. 2008) and if older leaders in a group possess some form of superior knowledge enabling better decisions in response to environmental or social triggers (Foley 2002; Foley *et al*. 2008; McComb *et al*. 2011). For example, in Tarangire National Park, elephant groups exhibited distinctly different spatial patterns during the drought years of 1993-94 and the reason for this was probably due to disproportionate variation in spatial knowledge among the groups (Foley 2002). Some groups migrated outside the Park while others remained within the Park throughout the main drought period and calves belonging to groups that migrated out of the National Park suffered lower mortality than calves whose groups remained in the Park (Foley 2002; Foley *et al*. 2008). Groups that left the Park during the drought presumably were knowledgeable of areas that had permanent water supply and higher forage availability than inside the Park (Foley 2002).

Life history theory predicts that reproductive success should increase with age as parental experience, familiarity with physical environment and social status increases (Côté & Festa-Bianchet, 2001; Radespiel & Zimmermann 2003). The results from this study indicated the positive significant effect of age on female reproductive success. Age and hence body size of adult female elephants may provide individuals with the ability to defend their young from predators, enhance their ability to locate scarce resources, their ability to lead other group members to resources such as breeding opportunities, food and water (Dublin 1983; Wittemyer *et al*. 2007a; McComb *et al*. 2011).

Phenotypic factors such as body size also have important effect on breeding success of females (Clutton-Brock 1988). If the body size of female African elephants affect birth weight of their offspring as it has been found in other mammalian fauna such as red deer, *Cervus elaphus* (Clutton-Brock *et al*. 1988), northern elephant seals, *Mirounga angustirostris* (Le Boeuf & Raiter 1988), and greater kudu, *Tragelaphus strepsiceros* (Owen-Smith 1993), then older, larger females will produce offspring with bigger body size. This will enhance the offspring's early growth, survival and ultimately increase their potential future reproductive success (Emlen *et al*. 1991; Owen-Smith 1993; Côté & Festa-Bianchet 2001). Age also determines dominance, leadership and calf-survival among females (McComb *et al*. 2001; Foley 2002) and as a result, high-ranking or large females may have a greater capacity to provide maternal care, thus increasing the probability of offspring survival (Côté & Festa-Bianchet 2001; McComb *et al*. 2001).

Effects of group relatedness and size on sex ratio, calf production and survival

Studies using limited-dispersal and genetic relatedness models have helped to confirm that biased sex-ratio is widespread among animals (including cooperative breeding vertebrates) and varies widely in direction and intensity (Hamilton 1967; Taylor 1992; Queller 1994; Emlen 1997a&b; West *et al*. 2001, 2002). In particular, it has been shown that limited dispersal favours female-biased sex ratios in cooperative breeding animals (Hamilton 1967; Emlen 1997a&b; West *et al*. 2002). These studies further suggested that, the specific cases of the evolution of the female-biased Hamiltonian ratios in cooperative species is important in promoting kin-based altruism through the maintenance of a positive association of closely related individuals (Nunney 1985; Emlen *et al.* 1995; Emlen 1997a; West *et al*. 2002). The results from this study confirmed this is the case with female African elephants. Adult females in closely related groups showed a strong positive association with the proportion of female offspring in their natal group thereby, promoting philopatry, which may lead to increased inclusive fitness benefits.

In cooperative breeding species such as African elephants, the type and the level of fitness-related benefits to individuals may vary depending on the abundance and distribution of food or predation, the pattern of dispersal and the scale at which competition occurs (Giraldeau & Caraco 2000; West *et al*. 2001, 2002; Aviles *et al.* 2004; Wittemyer *et al*. 2005). These benefits of sociality, whether direct or indirect, may accrue to all social partners, for instance, when cooperative members in kin groups prevent unrelated competitors joining the group or defend and utilize patchily distributed and scarce resources (Giraldeau & Caraco 2000; Rieucau & Giraldeau 2009; Archie *et al*. 2011). Accepting (failing to repel) a relative particularly when group size is at least as large as the optimum size, constitutes kin-directed altruism (Giraldeau & Caraco 2000; Aviles *et al.* 2004). An altruistic kin may have fewer offspring than a nonaltruist within its own group, but groups of altruists will have more offspring than groups of nonaltruists (Sober & Wilson 1998; Thain & Hickman 2004).

This study further presents the evidence that smaller and larger groups with more kin had consistently higher reproductive success than unrelated groups of any given size. However, since living in groups confers a wide variety of costs and benefits, changes in group size have conflicting effects, and an individual's decision to join or leave a group of a particular size must weigh up different factors (Packer *et al*. 1990; Giraldeau & Caraco 2000). For example, when sociality is favoured, animals will prefer larger groups than smaller groups (Silk 2007). However, if feeding efficiency is maximized by solitary foraging but each individual's risk of predation is reduced by dilution effect, the group size that maximizes individual fitness may be larger than one (Packer *et al*. 1990).

Thus, much as group size may provide a variety of benefits in female elephants, competition for resources and the reproductive costs among group members may increase as group size increases. The results from chapter three showed increased frequency and intensity of agonistic interactions in unrelated female pairs both within- and between-groups in limited resources. Much as they occur infrequently and are associated with patchy resources, agonistic interactions potentially can reduce energetic costs of maternal effort and hence, calf survival (Dublin 1983; Lee & Moss 1986; Lee 1987; Wittemyer *et al*. 2007a). Such costs and competition may have probably contributed to the decline in individual reproductive success in groups with few or no kin.

However, despite the costs to individual (i.e. direct) fitness, a large group may evolve because under certain circumstances, direct and indirect fitness increase through increased total relatedness (Rodman 1981; Giraldeau & Caraco 1993). If individual fitness reaches a maximum at some group size, then inclusive fitness (of which individual fitness is a component: Hamilton 1964) will always peak at larger group size at which individual fitness is no longer maximized (Rodman 1981; Aviles *et al*. 2004). It might be possible that individual adult females can still tolerate and remain in large groups (although they experience reduced reproductive success in large groups), only when costs and benefits to solitaries versus (unrelated) joiners are highly asymmetrical (Smith 1985; Giraldeau & Caraco 1993, 2000). This would occur, for example, in situations where elephants are vulnerable to poaching or predation pressure.

For example, studies on Botswana's Savuti lions have shown that lions switch to preying on elephants during the late dry season, and the frequency of this has increased in the last two decades (1985 - 2005) (Joubert 2006; Power & Compion 2009). Another study by Loveridge *et al*. (2006) in Hwange National Park, Zimbabwe, indicated that elephant juvenile calves made up an unusually large proportion of lion prey during the study period (23% of kills recorded). This occurred during the dry season when elephant herds were forced by drought to split up and travel large distances in search of water and forage (Loveridge *et al*. 2006). During the dry season elephant groups may travel large distances between water and forage (Dudley *et al*. 2001; Loveridge *et al*. 2006; Chamaille´-Jammes *et al*. 2008; Foley *et al*. 2008) because of their regular drinking requirements and selective feeding behaviour (Stokke 2000).

CONCLUSION

This study provides rare, quantitative evidence that group relatedness and structure have significant effects on individual adult female reproductive success. Two main findings are clearly demonstrated by our study. One is that adult female RS was significantly influenced by within- group relatedness and structure. The second is that elephant group relatedness showed significant inverse relationship between offspring sex ratio of adult females and group relatedness, with closely related groups having more female calves than males.

Female African elephants live in flexible, multitiered, fission- fusion societies (Wittemyer *et al*. 2005; Archie *et al*. 2011). In fact, this combination of social traits, i.e., close and enduring female social relationships and fission-fusion sociality in addition to males breeding randomly across the population, structure opportunities for kin selection thereby limiting inbreeding in the population (Archie *et al*. 2008, 2011). Because poaching tends to eliminate the oldest elephants from populations, illegal hunting and poaching are likely to alter the opportunity for kin-selection to act on elephant population genetic structure with important potential consequences for both evolutionary processes and reproductive success in female elephants (Whitehouse 2001; Archie *et al*. 2006, 2008, 2011).

The significant negative correlation between the proportion of male offspring and intragroup relatedness shown by this study implies that unrelated females in disrupted groups (through poaching) will tend to have fewer female offspring translating into low female reproductive success. This may have consequences for conservation and evolutionary biology (May 1991; Caughley 1994; Breck *et al*. 2008; Hayward *et al*. 2011), particularly for small/endangered populations of complex social mammals such as elephants and whales (McComb *et al*. 2001; Whitehouse 2001).

CHAPTER FIVE

RESPONSES TO POACHING IMPACTS ON THE POST POACHING GENERATION OF FEMALE AFRICAN ELEPHANTS

INTRODUCTION

Demographic disruption associated with poaching or culling can be sufficient to regulate population dynamics in African elephant (*Loxodonta africana*) populations (Douglas-Hamilton 1987; Moss 1990; Foley 2002; Wittemyer 2005; Gobush *et al*. 2008). This type of population regulation, however, can also be an important component of the resource release in tropical environments where both food and water are limiting resources (Sukumar 1989; Bradshaw 2008; Chamaille-James *et al*. 2008).

African savanna elephants (*Loxodonta africana*) have life history traits that resemble most large ungulates in that they are strongly iteroparous, have low annual fecundity and high annual adult survivorship, produce only one offspring per reproductive bout, and have long generation times (Wittemyer *et al*. 2007b). Like many other populations of large mammals, African elephants have a relatively low growth rate (Gaillard *et al*. 1998, 2001) with wide overlap between generations, resulting in a slow turnover of reproducing individuals. In elephant populations that are not hunted, matrilineally related kin are clustered into social groups that are stable from one generation to the next (Moss 1988; Poole 1996; Archie *et al*. 2006). One of the most obvious (and quantifiable) sources of demographic and genetic variation among social groups in elephants is poaching and/or overhunting.

Widespread poaching in and around Tarangire National Park (TNP), Tanzania in 1970s and 1980s had fragmented and severely reduced elephant populations in the area (Foley 2002). Evidence shows that the heaviest poaching in Tarangire occurred between 1974-1977 when aerial survey in 1978 estimated 1342 ± s.e 484 live elephants and 554 ± s.e 66 elephant carcasses (Foley 2002), an equivalent of 29% mortality and an indication of reduced population size by poaching during this period.

In addition to causing a significant disruption of the female social structure, heavy poaching severely reduces the ratio of adult males to adult females, and eliminates the majority of older animals in the population thereby creating a highly skewed sex and age structure (Moss 1990; Foley 2002).

Poaching also reduces the group size and lowers relatedness with negative consequences on the reproductive success of female elephants (Chapter four). As much as the effects of poaching on many aspects of elephant social systems have been studied, the impacts on demographic patterns between generations are not yet understood. Poaching directly removes older animals from the population and evidence suggests that the removal of kin (as a social partner) from a group has negative consequences on the demographic vigour and reproductive success of elephants (Archie & Chiyo 2011; Chapter four). Fecundity in a poached population is considered to be low because of disrupted genetic and social environment for breeding (Gobush *et al*. 2008, 2009; Archie & Chiyo 2011, Chapter four). In a heavily poached population with few older males and females, reproductive rates may be significantly lower at least for some elephants than in an unpoached population (Archie & Chiyo 2011; Chapter four) and this may be due to delayed age of first reproduction and lengthening of interbirth interval (Foley 2002).

Alternative evidence shows that elephant population regulation is driven by spatial response to food and water availability and by density (Chamaille-James *et al*. 2008; Young & van Aarde 2010) and this is particularly true in tropical environments where both food and water are limiting resources (Sukumar 1989; Caughley & Sinclair 1994; Chamaille-James *et al*. 2008). Since poaching decreases the number of elephants in the population, then the population released from poaching will tend to have more access to resources (food and water) because of reduced elephant abundance below a certain (carrying capacity) level. Such a response could lead to increased reproductive success by females through decreased age at first birth and shortening of interbirth interval.

Specifically, I test the hypothesis that since poaching reduces group relatedness and therefore female reproductive success (Chapter two & four), then the disrupted group relatedness should have an effect on the F1 females of the original breeding cows within the elephant groups through their influence on vital rates e.g., sex ratio age at first birth, inter-birth interval, and infant production rates. The alternative hypothesis is that the F1 female elephants will show increased demographic vigour (decreased age of first birth, shorter interbirth interval, reduced infant mortality) in response to resource release due to decreased elephant density.

In addition, I compare the two vital rates (age of first birth and interbirth interval) from Tarangire elephant population with those from a relatively unpoached elephants from Amboseli National Park (ANP), Kenya (Moss 1994, 2001) and discuss these results in relation with other elephant populations that were heavily impacted by poaching in the 1970s and 1980s. With continued increase in poaching in other elephant populations (Wittemyer *et al*. 2011), comparisons of the social consequences of these disparate forms of population alterations in elephants could have important management benefits.

MATERIALS AND METHODS

Tarangire study population

Although the Tarangire elephants have been relatively unaffected by poaching in the past two decades, there has not been regular full census in TNP during this time period. The last full census in TNP was in 2000 and estimated the total population to be more than 2,300 elephants, which includes three subpopulations with distinct dry-season home ranges (Foley & Faust 2010). The northern subpopulation, which is the focus of my study has been continuously monitored since 1993 and supports approximately 1200 elephants [Tarangire Elephant Project (TEP)-long-term elephant research].

I used individual - based data from 24 of the 29 different known groups collected from this subpopulation between 1994 and 2010 for this study. Eighteen of the 29 groups were identified by November 1993 and the rest by November 1994 (Foley & Faust 2010); because of this, all the analyses at group level used the end of 1994 as a baseline year. All data were collected on adult female elephants of known or estimated age. Female elephants were defined as adults (based on the age they were assigned in 1993) if they were older than 8 years - an age at which elephants are eligible for conception (sexually mature) in TNP and other areas (Foley 2002; Owens & Owens 2009; Foley & Faust 2010). The data given here comes from the offspring of F1 females (N = 96) of the original breeding cows (N = 109) in 24 elephant groups.

The F1 analyses conducted throughout this study refer to adult females that were born between end of 1989 and 2001 to the female survivors of Tarangire elephants that remained in those groups after the poaching era- the post-poaching generation.

All analyses used the group sizes of 1994 as a baseline to allow comparison between the effects/consequences that poaching may have on the F1 females of the original breeding cows that remained in those groups after the heaviest poaching in the late 1970s and 1980s ceased.

DNA sampling, extraction and analysis

See Chapter two for sampling protocol and analysis

Amboseli study area and population

The Amboseli ecosystem in southern Kenya (with an area of approximately 3500 km^2) is semi-arid mixed savanna and woodland in which Amboseli National Park (ANP) covers an area of 392 km^2 (Moss 2001; Archie *et al*. 2006). ANP was established in 1974 and the Park has permanent springs and is associated with fertile (eutrophic volcanic ash and alluvial) soils that support higher primary production than in other savanna habitats (Coe *et al*. 1976; Moss 2001). Rain falls mainly during two seasons: the ‘long rains’ of March to May and the ‘short rains’ of November to December which averages 341 mm per year (Moss 2001). The dry seasons are January to March and then June to October (Moss 2001). The adult females in ANP live in 55 groups (called ‘families’) that range in size from 1 to 17 mother-calf units with mean ± s.d of 6.73 ± 3.92 (Archie *et al*. 2006). These groups were identified at the start of the long-term Amboseli Elephant Research Project between 1972 and 1978 (Moss 2001; Archie *et al*. 2006). The Amboseli elephant research project maintains this long-term demography data set for each individual and the population currently consists of approximately 1400 elephants (Chiyo *et al*. 2011).

Statistical analysis

The demography of F1 cows is presented for the period between 1994 until the end of 2010. The length of a generation was measured as the mean time elapsed between the birth of the parents and the birth of the offspring (Beeby 1993). The sex ratio at birth was expressed as a proportion (number of females/total males and female calves), where 0.5 reflects an equal sex ratio, higher values are female biased, and lower values are male biased (Gough & Kerley 2006). Age of first birth (AFB) was taken as the age at which the individual female gave birth to the first calf. The inter-birth interval (I-I) was calculated as the interval between the estimated birth dates of a female's two consecutive calves (Foley & Faust 2010). The age of first calving and the inter-calf interval analyses were limited to individuals (N = 60) that had a birth date estimated ≤ to one month.

A two-tailed paired sample t-test was used to test for differences between the number of male and female calves at birth within the group. Both the mean AFB and I-I from the F1 females of Tarangire elephants were compared to the mean values from Amboseli (unpoached) elephants using the Neu method (Neu *et al*. 1974). The objective was to test whether difference in the mean AFB and I-I between poached (TNP) and unpoached (ANP) elephant populations differed significantly. This test (for comparing two independent population means) was employed by constructing a 95% confidence interval (C.I.) from the Tarangire dataset in order to determine whether the mean values (from published study, Moss 2001) for ANP elephant population lay within the magnitude of the significant effects (Neu *et al*. 1974; Mendenhall & Sincich 2003).

RESULTS

The mean group size (number of adult females and their dependant offspring) for Tarangire elephants at the end of 1994 ranged between 3 and 14 with the mean ± S.E of 9.0 ± 0.65. Within-group average relatedness among adult females in the elephant groups of TNP varied from 0.5 to 0 (Figure 4.1, Chapter four). There were 172 calves (males = 73 and females = 99) born to the F1 females (N = 96) of original breeding cows in all (N = 24) studied elephant groups. Sixty nine percent of the F1 cows had given birth to at least one calf during the study period. Calf production and survival for the F1 females within elephant groups ranged from 2 to 15 juveniles (mean ± S.E, 7.0 ± 0.60) during the period between 1994 and 2010. Although many female calves were born to the F1 cows within the groups, the observed difference in sex ratio at birth between male and female calves did not differ significantly within the group (two-tailed paired-sample *t* test: *t* = -1.696, *df* = 23, *p* = 0.103). Group relatedness had no significant effect on sex ratio of the F1 cows' calves (Pearson's product moment correlation: = -0.09, *df* = 22, *p* = 0.67). Mean calf sex ratio at birth for F1 cows in the 24 elephant groups was 0.58 ± S.E 0.04 (range 0.20 - 1.0).

The mean AFB among F1 cows of Tarangire elephants tended to decline with group relatedness, however, this relationship was not significant (Pearson's product moment correlation: = -0.24, *df* = 58, *p* = 0.32). The AFB for the F1 cows from Tarangire ranged between 8.7 and 14.4 years with the mean ± S.E of 10.9 ± 0.15. The mean I-I for the F1 females of Tarangire elephants was (mean ± S.E) 3.8 ± 0.1 with a range 1.9 - 6.8 years. The 95% confidence limits for the mean AFB and I-I for F1 females ranged from 10.7 to 11.2 and 3.8 to 4.0 years, respectively (Table 5.1). The mean AFB and I-I for female elephants from Amboseli National Park were 14.1 and 4.5 years respectively (Moss 2001; Table 5.1).

Table 5.1 Comparison of vital rates of F1 cows from the northern subpopulation of Tarangire elephants with females from other (poached and unpoached) elephant populations

Location	Population status	Mean age of first birth (years)	Lower C.L.	Upper C.L.	Mean interbirth interval (years)	Lower C.L.	Upper C.L.	Source
TNP, Tanzania	Poached§	10.9	10.7	11.2	3.8	3.6	4.0	This study
ANP, Kenya	Unpoached	14.1	-	-	4.5	-	-	Moss 2001
NLNP, Zambia	Poached	11.3	-	-	-	-	-	Owens & Owens 2009
AENP, South Africa	Unpoached	12.3	-	-	3.3	-	-	Gough & Kerley 2006

TNP = Tarangire National Park, ANP = Amboseli National Park, NLNP = Northern Luangwa National Park, AENP = Addo Elephant National Park, C.L. = Confidence limit.

§All the vital rates were calculated from only F1 cows of prime-aged female from Tarangire elephants. The vital rate values on the above table from other (ANP, NLNP, AENP) areas are computed for all adult females in the respective populations.

Using a 95% prediction interval (Neu *et al*. 1974; Mendenhall & Sincich 2003), the mean AFB and I-I for ANP elephants did not fall within the prediction limits (the computed lower and upper confidence limit) of Tarangire results. Thus, we reject the null hypothesis and accept the alternative hypothesis that there is sufficient evidence (at $p < 0.05$) suggesting there is significant difference between the mean AFB and I-I from the two (poached, TNP and unpoached, ANP) elephant populations. The results therefore support the second hypothesis of this study that elephant populations reduced by poaching to low levels would show an increase vigour through reduced AFB and shorter I-I.

DISCUSSION

Group relatedness of Tarangire elephants did not provide significant effects on the (analysed) demographic variations of F1 cows in response to poaching. The demographic results indicated that F1 cows tend to have their first calves at an average age of 10.9 years, an age that is much younger than elsewhere (Moss 2001; Gough & Kerley 2006) with thirteen percent of the F1 (N = 60) cows giving birth to their first calf at an age less than 9 years, which is the lowest age previously recorded for the African elephants (Foley 2002). Fifty-two per cent of F1 cows gave birth of their first calf aged between 8.7 - 11 years. Additionally, the mean length of calving intervals for F1 cows was 3.8 years which is shorter than the estimated mean value (5.1 years) for the original breeding cows from the same population (Foley 2002).

Studies on demography of poached elephant populations have shown evidence of the direct effects that poaching has on the adult age and sex ratio (Douglas-Hamilton 1987; Moss 1990; Foley 2002; Foley & Faust 2010). For example, Moss' (1990) study indicated that the sex ratio of breeding females to breeding males in Tarangire was 28:1 or 97% females and 3% males. Only six males over 25 were seen during the Tarangire survey and none of these was over 30. In an unpoached population in ANP, the corresponding sex ratio of breeding adults was 3.1:1 or 75% females and 25 % males (Moss 1990). Because poaching tends to create a skewed sex ratio of the oldest elephants from populations, we would predict the offspring of poached population to favour investment in the sex ratio of the negatively skewed sex in the population. Poaching also removes adult females from elephant societies, thereby creating a disrupted social and genetic structure (Gobush & Wasser 2009; Gobush *et al*. 2009; Archie & Chiyo 2011).

Given this, female cows from the disrupted group relatedness and size are predicted to invest in female over male calves particularly when to do so increases inclusive fitness of the breeding individual female elephants.

However, there was no evidence showing the significant deviation of offspring sex ratio from 1:1 for the F1 cows from Tarangire elephants**.** The mean calf sex ratio at birth for F1 cows within the 24 elephant groups did not differ significantly from 0.5. These demographic results suggest two things: either that the genetic relatedness has no direct relationship with the demographic dynamics (patterns) in African elephant populations or that elephants respond to poaching (top-down population regulation) through fast reproduction when the population is released from stresses of poaching. This rapid reproduction is primarily achieved through the sexual maturation of females at much younger than average age at first reproduction and shortening of the length of calving intervals.

These results imply that when resources such as food and water are not limiting (allowing for rapid growth), there may be less effect of other factors (such as variation in relatedness) on the demography of F1 cows from a poached population. Those factors (such as social rank and genetics) are likely to play a much greater role under conditions of hardship. The results support another demographic study on elephants by Owens & Owens (2009) which showed that severe poaching during 1970s and 1980s led to reduced age of reproduction among the remaining female elephants in Zambia's North Luangwa National Park (NLNP). In NLNP, fifty-eight per cent of births were delivered by cows aged 8.5 - 14 years, an age at which elephants were reported to be sexually immature in nearby South Luangwa National Park before poaching (Owens & Owens 2009).

The mean age of first calving for females at NLNP (1993, 1994) was 11.3 years while prior to poaching, the mean age of first calving in South Luangwa National Park was 16 years (Owens & Owens 2009). The findings from Owen & Owens (2009) study mirror other studies on other elephant populations that suffered poaching in the 1970s and 1980s. A 12-years study in Tarangire National Park (TNP), Tanzania revealed that the age of first calving in Tarangire elephants was very low after poaching (Foley 2002; Foley & Faust 2010). The mean age of first calving for the northern subpopulation of Tarangire elephants was 11.1 years. Twenty-five percent of females had given birth by age 10 and 75% by 12.2 years (Foley & Faust 2010).

The findings from these two (TNP and NLNP) poached populations also indicate that the mean and range of estimates of age at first calving tend to be narrower than relatively unpoached elephant populations elsewhere. One of the predictions tested by this study is that the mean AFB and I-I differ significantly between poached (TNP, Tanzania) and unpoached cows (ANP, Kenya). The results from this prediction provided evidence to support this prediction and both the mean AFB and I-I for ANP cows were found to be significantly higher than the respective values from the poached (F1 cows of TNP) elephant population (Table 4.1). The mean AFB for females from the Addo Elephant National Park (AENP) elephants (a population that has been unpoached for over 80 years) is 12.3 years for (Gough & Kerley 2006; Table 4.1).

Why would cows in poached populations mature earlier than elsewhere? It is evident that, for mammals, resource quality affects fecundity (Sukumar 1989; Wittemyer *et al*. 2007b; Chamaille´-Jammes *et al*. 2008) and the age at sexual maturity, hence, the age when they may have their first calves (Sukumar 1989; Owen-Smith 1990). The evidence from this study suggests that elephant (poached) populations that have declined through poaching may therefore be less constrained by resources and this could be one of the reasons why elephant cows in these areas have their first calves at a relatively young age.

In Amboseli area, there are permanent springs associated with fertile soils that support higher primary production than in other savanna habitats (Coe *et al*. 1976; Moss 2001), suggesting that the biomasses of these areas are also above the long term carrying capacities of the ecosystem (Coe *et al*. 1976). The elephants of Addo Elephant National Park have year round access to drinking water and drought resistant, succulent thicket vegetation in an environment that receives year-round rainfall, suggesting that the elephant resources are not seasonally limited this area (Gough & Kerley 2006; Kerley & Landman 2006).

However, even after accounting for access to additional resources, elephants in unpoached (both ANP and AENP) populations have their first calves at older ages than those from poached populations. This suggests that in the event of good resource availability, elephant populations subject to reduced population numbers (through demographic manipulations by predation) are able to alter life history through reduction in age at sexual maturity and reduced calving interval, because they experience changes in growth and reproduction after the removal (reductions) of individuals from the population.

It is possible that recruitment in African elephants can indeed be fairly high when there are resources adequate enough to allow for rapid reproduction and higher survival of individuals resulting in fast population growth. I interpret this effect, seen clearly in the decrease in age at first birth and interbirth interval, as a resource release. An additional explanation that is probably supportive with resource release hypothesis in an altered population can be provided by study Foley & Faust (2010) also on Tarangire elephants. Foley & Faust (2010) found that rapid growth was aided by high rainfall, low population density and release from the stresses of poaching. Although their study period included a severe drought (1993 - 1994), with consequent low conception rate (9% in 1993), for most of the study, rainfall was near or above average. In these years of good rainfall, Tarangire elephants fed year-round on perennial grasses rather than switching to browse as is typical during the dry season (Foley 2002). This allowed them to maintain body condition and allocate energy to rapid reproduction, by females having the mean AFB of 11.1 years during the study period, with the conception rates of 76% in 1998 (Foley & Faust 2010).

In high elephant density populations, nutritional limitations occur and individuals may face a serious trade-off between survival and reproduction (Trimble *et al*. 2009; Young & van Aarde 2010). Also females in poached populations may have unusual social, physiological, and reproductive disadvantages over females in unpoached populations because unpoached females are more likely to have an old, experienced related matriarch in their group (Gobush *et al*. 2008; Archie & Chiyo 2011). Although Tarangire elephants have experienced social and demographic disruption caused by poaching, it is possible that the impact on genetic relatedness might not have been too extreme to have a negative impact on the F1 generation of the original breeding cows.

CHAPTER SIX

THESIS SYNTHESIS AND CONCLUSION

Previous studies on Tarangire elephants have focused on direct effects of poaching on elephant demography and social structure (Foley 2002; Foley & Faust 2010). With the rapid increase in modern genetic tools, it is becoming possible to generate genetic information from natural wildlife populations that can contribute to the understanding of animal socio-biology and the species conservation (Archie & Chiyo 2011). This thesis is about the influence of genetic relatedness on demography and sociality in female African elephants.

The thesis is the first study to investigate the secondary effects of poaching on Tarangire female elephants, whose output aimed to generate information on these secondary effects of poaching on elephant sociality and breeding success and how this compares with other poached elephant populations. The information from this work is expected to enable elephant conservation and management strategies/authorities to make more scientifically informed decisions in the future (Whitehouse & Kerley 2002). The genetic analysis from this study has generated detailed data on the genetic relatedness between individual adult females both within-and-between-groups of the northern subpopulation of Tarangire elephants. The data provide information that contributes to enhancing our understanding of the possible effects of poaching on the social structure of this complex species and the potential consequences of this on the reproductive success at the level of individuals.

The thesis centred its objectives around the (i) impact of poaching on group relatedness/size patterns and how these patterns compare with the robust and reliable conceptual genetic model for group size analysis (ii) the effect of genetic relatedness on competitive behaviour among adult female elephants. (iii) the influence of within group relatedness on the RS of individual adult female elephants as influenced by poaching, and (iv) the effects of group relatedness on demography of subsequent generation of the prime-aged cows that remained in those groups after poaching. In the pursuit of these objectives, particular attention is given to those influences and effects which are either within/between groups or between individual adult females and which affect the overall individual fitness.

Chapter two of the thesis has investigated the relatedness at the level of individual within elephant groups. For this, I have provided a novel mechanism that explains the common size pattern in elephant groups. I demonstrate that poaching and overhunting have a significant influence upon the group formation and size in elephants. I extend the predictions to suggest when individuals should prefer kin versus non-kin as within-group members in African elephant populations.

Differences in intraspecific competitive and cooperative strategies have been documented between related and unrelated individuals on cooperative group living species (Packer *et al*. 1991; Mitani *et al*. 2000; Lukas *et al*. 2005; Smith *et al*. 2010). This study found that the degree of relatedness between adult females (both within and between the elephant groups) and age predict competitive and conflict behaviour in African elephants. Elephants maintain a related and tightly knit, fission-fusion society where despotic behaviour among individuals within the group can be avoided through group fissions (Poole 1996; Archie *et al*. 2006; Wittemyer & Getz 2007). Genetic relatedness between individuals seems to provide the mechanism shaping within- group cooperation, as demonstrated by within- group aggressive interactions in relation to group relatedness from this study.

Thus, this study draws attention to the possibility of poaching altering natural behavioural patterns in African elephants with important conservation and management implications. Most relevant to conservation is that it is possible for cooperative and affiliative relationships to be lost from within poached elephant groups (Gobush & Wasser 2009; Archie & Chiyo 2011). The benefits of such relationships are likely to include cooperative defence of calves against predators, allo-parenting assistance from other group members, resource defence and shared social and ecological knowledge from older and more experienced group members (Lee 1987; Foley 2002; Archie *et al*. 2006, 2011).

When an old matriarch is removed from her family, her influence on other elephants and groups is also removed. For example, more effective leadership, between group competitive behaviours as well as defence behaviours against perceived danger occur if the oldest matriarchs (who are likely to have accumulated the most experience) are in the group, generating important insights into selection for survival (longevity) and reproductive success (McComb *et al*. 2001, 2011). Also, if the offspring's present and future behaviour and social status are influenced by her mother and other group members, then the increase in aggression seen in unrelated females has implications for health and development of the (dependent) offspring within the group in elephant societies. The degree of sociality and the circumstances under which social knowledge and behaviour are acquired during different stages of an animal's life are particularly important not only to increase our understanding of basic biology and sociality of the species but also form an integral part of management and conservation strategies (May 1991; Lee 1996; Breck *et al*. 2008; Evans & Harris 2008).

The African elephant is one of a few species of mammals that moderate behaviour of the offspring (Lee 1996; Evans & Harris 2008). This is when individuals acquire skills and develop relationships that are of both immediate and long-term benefit to their survival and reproductive success (Moss, 1988; Poole 1996; Croze & Reader 2000; Evans & Harris 2008). For example, in unpoached wild populations, elephant calves in the groups learn and acquire different aspects of behaviour during developmental stages including the changes from suckling to independent feeding, play fighting as opposed to aggression and conflict (Lee 1987; Moss 1988; Lee 1996).

In addition, more effective fitness related behaviours (against perceived dangers) are acquired by sub adult members of the group if an old matriarch is in the group, conferring better decisions in response to environmental or social triggers in their life (McComb *et al*. 2011). Since poaching selectively removes older individuals from these groups and reduces the strength of the bonds between older cows and the other members of their family (including calves), then elephant calves raised in unrelated groups may consequently develop anomalous behaviour that may have important repercussions along the animal's different life stages (Whitehouse 2001; Archie & Chiyo 2011).

Although no obvious anomalous behaviour were observed in Tarangire elephants, altered genetic and social structure of a population (through poaching) may sufficiently alter conditions to significantly increase the frequency and the intensity of aggression among unrelated adult females. The effect of poaching on competitive behaviour among adult females may provide additional evidence of the importance of conserving natural behavioural patterns in African elephants (Whitehouse 2001). Moreover, the results provide additional awareness of the poaching problem and its long-term consequences on the elephant populations. Conservation and management authorities play an important role in the continued survival of several threatened species (Whitehouse 2001; Okello *et al*. 2008; Archie & Chiyo 2011).

However, conservationists and managers of animals in their natural habitat have previously paid little attention to behavioural issues, although behavioural enrichment is increasingly recognised as a necessary part of the management of captive populations (May 1991; Whitehouse 2001; Whitehouse & Kerley 2002). For example, in the planning of the translocation of elephants, there is also a question of behavioural patterns, and this is particularly important among social animals (individuals) since the significant parts of the behavioural repertoire depend on genetic relatedness and learning in an appropriate setting (May 1991; Lee 1996; Whitehouse 2001; Evans & Harris 2008). Several translocations and introductions of ‘stray” elephants have taken place in South Africa in the past, and evidence shows that such management actions may have unpredictable asocial behaviour with potential consequences on biodiversity (Slotow *et al*. 2000; Slotow & van Dyk 2001).

In the face of habitat loss and range restrictions, elephant populations are being confined in smaller areas and the conservation and management authorities are being challenged on the types of decisions that can be made with the minimum possible negative impact to the population. As the 21st century progresses, the diversity of life on earth will be under increasing pressure from the direct and indirect effects of explosive human population growth with wildlife habitat diminishing and becoming increasingly fragmented (Whitehouse 2001; Klug & Cummings 2005; Pinter-Wollman *et al.* 2009a), calling for alternative elephant population management in the affected habitats.

Being social animals where individuals within the group are composed of kin, the decisions to move the elephants should consider genetic relationship among the individuals involved as well as social cohesion (intact units) ((May 1991; Whitehouse & Kerley 2002; Okello *et al*. 2008). This will help to minimize conflict/stress, control possible occurrence of deviant behaviour and facilitate reproduction. Elephants are also strong competitors, with group dominance status being of greatest benefit when defending discrete, high quality resources (Moss & Poole 1983; Foley 2002; Wittemyer *et al*. 2007a). In light of the current rate of loss of global biodiversity, it could be argued that a fully integrated approach to conservation should seek not only to conserve individuals and species, but also to conserve natural behavioural patterns in the natural environment (May 1991; Whitehouse 2001; Klug & Cummings 2005). The results from this study also need to be reflected in relation to the selective feeding behaviour of female elephants (Stokke 2000), the variations in the nutritional requirements according physiological demands as well as the life-history stage of other group members (Lee & Moss 1986; Stokke 2000; Harris *et al*. 2008; Woolley *et al*. 2011). In general, elephants prefer to move little, drink easily and regularly, eat well, and avoid people (Poole 1996; Harris *et al*. 2008).

Differences in diet and landscape choices of African elephants have been shown to vary according to sex and herd structure particularly during the dry in savanna habitats. For example, a study by Stokke (2000) in northern Botswana showed that female elephants with dependent young fed more selectively than the very large adult males. This intraspecific age-and sex-variation in diet quality can also possibly imply difference in nutritional requirements by individuals, with a more selective approach by reproductive (lactating, pregnant) females and their growing calves trading-off quality against quantity (Lee & Moss 1986; Stokke 2000; Woolley *et al*. 2011). Despite being mixed feeders, and consuming a variety of plant and plant parts (Kerley *et al*. 2008), when unrestricted by availability, adult female elephants forage on phosphorus-rich food, while weaned calves select more consistently for nitrogen (Woolley *et al*. 2011). To surmount issues of scale and availability, if one makes more areas available, elephant groups with calves will probably prefer areas near water and seek out diverse pasture with high nutritious (mineral) ingredients and multivitamin vegetative cover (Croze & Reader 2000; Harris *et al*. 2008; Woolley *et al*. 2011).

This presumes that elephants optimize tradeoffs between benefiting from high-quality resources and costs to find them (Harris *et al*. 2008). In savanna habitats, large groupings of elephants near water sources, particularly during the dry season, can deplete local food resources (Chamaille´-Jammes *et al*. 2008). Therefore, at high densities, during the dry season, unrelated individuals and groups with juveniles may be displaced from local (near food and water) resources and travel large distances between water and forage (Loveridge *et al*. 2006; Chamaille´-Jammes *et al*. 2008) because of their regular (often daily) drinking demands and selective feeding behaviour (Stokke 2000).

If the daily distances moved by individuals and family groups increase as a function of relatedness hierarchies in response to (nearby) resource depletion, calves may dehydrate, be abandoned and even risk predation (Loveridge *et al*. 2006; Power & Compion 2009). Weaned calves in particular may be more susceptible to abandonment and dehydration because of a weakened bond with their mother and lack of milk for hydration (Dublin 1983; Lee & Moss 1986). Thus, an understanding of what governs animals' competitive (fitness) behaviour in this constantly changing world (with drought-prolonged by climate change impacts) is highly important because of the fitness consequences of the species and for improvement of wildlife conservation and management strategies (Pinter-Wollman 2009; Pinter-Wollman *et al*. 2009a&b).

The study also investigated the effect on individual adult female RS of group relatedness and structure. The results show that both group structure and relatedness had significant effect on adult female RS. Under natural conditions, females form beneficial social relationships with relatives and older, experienced animals where cooperatively helping behaviour is largely mediated by their kin composition (Archie & Chiyo 2011; Archie *et al*. 2011). The results from this study provide strong evidence of the importance of inclusive fitness benefits in shaping elephant social structure, fitness behaviour and reproductive success.

Indeed, this is one of the few studies of large mammals that demonstrate that genetic relatedness between individuals (in group living), which is accompanied by group structure, can influence the individual fitness costs and benefits with the far reaching implications on the growth rate in the population. The genetic relatedness of individuals within the group in elephants facilitates the cooperative affilliative behaviour, allowing the benefits of between group competition to be shared among individuals within the group (Giraldeau & Caraco 2000; Wittemyer & Getz 2007).

The results of the study demonstrate that such benefits can be greatly reduced or eliminated by poaching should adult female kin be removed from the elephant groups, causing increased mortality and decreased reproductive rate (Foley 2002; Archie & Chiyo 2011). Poaching disrupts kin-based association patterns, decreases the quality of elephant social relationships, and decreases both the group size and relatedness with potential (long-term) consequences on elephant reproductive success. These consequences may be experienced by different populations to varying degrees depending on the local environmental conditions and the magnitude of poaching in that population.

The Tarangire elephants seem to show the signs of rapid population growth after release from poaching (Foley 2002; Foley & Faust 2010). Furthermore, the findings from this study suggest that although long-term negative impacts from poaching of older individuals may persist for decades among the poached population, these effects do not seem to negatively affect the vital rates of the subsequent (F1) generation of the prime-aged cows in Tarangire elephants. Instead the results showed that F1 cows from a poached population significantly increase the probability of breeding faster than adult females in unpoached elephant populations.

The results from this study have wider implications particularly for applied management (such as culling) on elephant populations due to the observed variations in the vital rate responses by poached elephants when compared with other unpoached populations. Most relevant to our results is that since culling involves the removal of animals (top-down regulation) from the population, evidence from this study now suggests that this may not be a good option for managing elephant numbers. Instead, the removal of individuals from elephant population through culling to a certain level will result in a population growing faster than the population in the absence of culling with undesirable consequences to elephant management and biodiversity conservation. For example a study on one of the world’s largest elephant populations in Hwange National Park (HNP), Zimbabwe demonstrated that population that was released from culling more than doubled since culling stopped (Chamaille-James *et al*. 2008).

The HNP elephant population was subjected to culling between 1983 and 1987, during which approximately 10,000 elephants were killed (Dudley *et al*. 2001). The HNP population then increased rapidly during the first 6 years after culling after which it began to fluctuate widely at about 30,000 individuals in response to variable annual rainfall (Bradshaw 2008; Chamaille-James *et al*. 2008). The HNP study empirically supports the resource release hypothesis and that incorporating culling as a management tool for reducing elephant numbers may not be a sustainable option and can result in increased elephant population even over short time scales (Bradshaw 2008). The Tarangire elephants are growing rapidly despite the poaching they experienced in the 1970s (Moss 1990; Foley & Faust 2010).

While the key to this growth lies primarily with the high rainfall, low density and the lessening of poaching pressure (Foley 2002; Foley & Faust 2010), RS of the Tarangire elephants is probably driven by the reduced AFB and I-I among adult females in their core groups. By restricting the potential reproductive lifespan, and by reducing the likelihood of reaching reproductive senescence age, individuals are able to have more offspring in their reproductive lifespan (Owen-Smith 1993; Foley 2002). The fitness benefits in terms of enhanced fecundity or survival once sexual maturity is attained must more than outweigh these costs (Owen-Smith 1993).

However, evidence shows that, when nutritional limitations occur in unstable, unpredictable systems (habitats), a syndrome of delayed maturity, smaller reproductive effort and greater longevity should evolve (Sukumar 1989; Seydack & Bigalke 1992; Brown & Sibly 2006). If production nutrients in the nutrient-rich habitats are surplus relative to maintenance nutrients, the adaptive strategy is to maximise current reproduction even at the risk of reduced survival (Seydack & Bigalke 1992; Brown & Sibly 2006). This pattern has been shown by evidence from nutrient-poor habitats (in southern Cape, South Africa) in which bushpig and elephants had large body size (high somatic investment) but low reproductive rates (Koen *et al*. 1988; Seydack & Bigalke 1992).

In contrast, in nutrient-rich succulent vegetation in Eastern Cape (Addo Elephant National Park), elephants are relatively lean with relatively small body size and high reproductive rate (Seydack & Bigalke 1992; Gough & Kerley 2006). Once poaching has severely altered social and genetic patterns in some habitats, there may be low and delayed recruitment and fecundity (Gobush *et al*. 2008). For example the Mikumi elephant population experienced severe poaching during the 1980s when it was reduced by approximately seventy five percent (Gobush *et al*. 2009). The observed decline in reproductive output and the prolonged delay in growth rate of Mikumi elephants after poaching allow us to predict that if in a nutrient-poor environments, disrupted social and genetic basis of elephant groups can have an apparently negative feedback process on elephant population that once initiated, it may be delayed until the reproductive success is unlikely**.** This may be the case in the Mikumi elephants and thus conservation management authorities need to be aware that a heavily poached elephant population from a low quality and limited resource environments may carry a high risk of recovery.

Further research

This thesis thus represents the culmination of an extended period of field research (from approximately two decades of data), and that there is still much not known and much research to be done is clear. It is hoped that the ordering of existing knowledge in these chapters will stimulate interest and further research in this important area of elephant socio-biology, and will provide a sound basis for development of further research as well as for various management strategies.

i. Research on the differences in dominance hierarchy structure and stability between adult females both within-and between-elephant groups in relation to degree of relatedness can provide further understanding into the nature and form of competition that occurs within and between groups as well as their associated mechanisms.
ii. With the Tarangire elephant population growing at a rate of 7% per year, there is no information on how this rapid growth is impacting the resource use and reproductive success at the individual level, thus predicting the effect of density-dependent on the growth of this population can be the direction for further research.
iii. The relationship between genetic relatedness and distances moved by individuals as determined by patchily limited resources may help understand the nature and mechanisms of intra-specific competition in African elephants.
iv. Levels of genetic relatedness and group structure in relation to seasonal group fission-fusion should be assessed in order to identify how this influences the reproductive success of female elephants.
v. The relationship between genetic relatedness and levels of allomothering by group members to individual offspring would provide more understanding of whether care giving (helping) in African elephants is allocated according to potential trade-offs between direct and indirect fitness benefits.

The information from this study comes at the moment when Tarangire elephants are experiencing a rapid growth with increased human-elephant conflict and this is becoming a serious problem across Tanzania. With rapid population growth of elephants in Tarangire there may be a considerable pressure to the management authority to ‘do something’ about the problem and many local people are asking for elephant population to be fenced or numbers to be controlled. It is therefore deemed necessary for the conservation and management authorities to consider management strategies and decisions which embrace and keep natural elephant social organization intact (Couzin 2006; Archie *et al*. 2008), if long-term viability of the population is to be achieved. The natural social and ecological settings in elephant sociality are important and they should further receive considerable attention because of their consequences on the survival and persistence of the species. Successful long-term conservation and management of Tarangire elephants should be based on the understanding which is influenced by and reflects the history of elephant poaching as well as its consequences on the genetic and social structure of this population.

REFERENCES

VAN AARDE, R.J. & JACKSON, T.P. 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation* **134**: 289-297.

AGRESTI, A. 2002. *Categorical data analysis.* Second edition. John Wiley and Sons, New York.

ALCOCK, J. 1998. *Animal behavior: An evolutionary approach*. Sixth edition. Sinauer Associates, Inc. Sunderland, MA. USA.

ALEXANDER, R.D. 1974. The evolution of social behaviour. *Annual Review of Ecology and Systematics* **5**: 325-383.

ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour* **49**: 227-267.

ARCHIE, E.A., MOSS, C.J. & ALBERTS, S.C. 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B* **273**: 513-522.

ARCHIE, E.A., MALDONADO, J.E., HOLLISTER-SMITH, J.A., POOLE, J.H., MOSS, C.J., FLEISCHER, R.C. & ALBERTS, S.C. 2008. Fine-scale population genetic structure in a fission-fusion society. *Molecular Ecology* **17**: 2666-2679.

ARCHIE, E.A. & CHIYO, P.I. 2011. Elephant behaviour and conservation: social relationships, the effects of poaching, and genetic tools for management. *Molecular Ecology* doi: 10.1111/j.1365-294X.2011.05237.x

ARCHIE, E.A., MOSS, C.J. & ALBERTS, S.C. 2011. Friends and relations: kinship and the nature of female elephant social relationships. In: *Amboseli Elephants: A long-term perspective on a long-lived mammal,* (eds.) C.J. Moss & H. Croze. University of Chicago Press, Chicago.

AVILÉS, L., FLETCHER, J.A., & CUTTER, A.D. 2004. The kin composition of social groups: Trading group size for degree of altruism. *American Naturalist* **164**: 132-144.

BATES, L.A., HANDFORD, R., LEE, P.C., NJIRAINI, N., POOLE, J.H. *et al*. 2010. Why do African elephants (*Loxodonta africana*) simulate oestrus? An analysis of longitudinal data. *PLoS ONE 5(4*): e10052. doi:10.1371/journal.pone.0010052.

BEEBY, A. 1993. *Applying ecology*. Chapman and Hall, London, UK.

BERGON, M., HARPES, J.L. & TOWNSEND, C.L. 1987. Ecology: individual population and community. Blackwell Scientific Publications.

BERMAN, C.M., RASMUSSEN, K.L.R. & SUOMI, S.J. 1997. Group size, infant development and social networks in free-ranging rhesus monkeys**.** *Animal Behavior* **53**: 405-421.

BLOUIN, M.S., PARSONS, M., LACAILLE, V. & LOTZ, S. 1996. Use of microsatellite loci to classify individuals by relatedness. *Molecular Ecology* **5**: 393-401.

BOURKE, A.F.G. 2007. Kin selection and the evolutionary theory of aging. *Annual Review of Ecology, Evolution, and Systematics* **38**:103-28.

BOURKE, A.F.G. 2011. The validity and value of inclusive fitness theory. *Proceedings of the Royal Society B* doi: 10.1098/rspb.2011.1465.

BRADSHAW, C.J.A. 2008. Having your water and drinking it too: resource limitation modifies density regulation. *Journal of Animal Ecology* **77**: 1-4.

BRECK, S.W., WILLIAMS, C.L., BECKMANN, J.P., MATTHEWS, S.M., LACKEY, C.W. & BEECHAM, J.J. 2008. Using genetic relatedness to investigate the development of conflict behaviour in black bears. *Journal of Mammalogy* **89**: 428-434.

BROWN, J.H. & SIBLY, R.M. 2006. Life-history evolution under a production constraint. *Proceedings of the National Academy of the Sciences of USA* **103**: 17595 -17599.

CARACO, T. & WOLF, L.L. 1975. Ecological determinants of group sizes of foraging lions. *American Naturalist* **109**: 343-352.

CARRUTHERS, J., BOSHOFF, A., SLOTOW, R., BIGGS, H.C., AVERY, G. & MATTHEWS, W. 2008. The elephant in South Africa: History and distribution. In: *Assessment of South African Elephant Management,* (eds.) K.G. Mennell & R.J. Scholes. Witwatersrand University Press, Johannesburg.

CAUGHLEY, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* **63**: 215-244.

CAUGHLEY, G. & SINCLAIR, A.R.E. 1994. Wildlife ecology and management. Blackwell Science, Oxford, UK.

CHAMAILLE´-JAMMES, S., FRITZ, H., VALEIX, M., MURINDAGOMO, F. & COLBERT, J. 2008. Resource variability, aggregation and direct density dependence in an open context. The local regulation of an elephant population. *Journal of Animal Ecology* **77**: 135-144.

CHENEY, D.L. & SEYFARTH, R.M. 2004. The recognition of other individuals' kinship relationships. In: *Kinship and Behaviour in Primates*, (eds.) B. Chapais & C.M. Berman. Oxford University Press, New York.

CHIYO, P.I., ARCHIE, E.A., HOLLISTER-SMITH, J.A., LEE, P.C., POOLE, J.H., MOSS, C.J. & ALBERTS, S.C. 2011. Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. *Animal Behaviour* **81**: 1193-1199.

CLARK, C.W. & MANGEL, M. 1986. The evolutionary advantages of group foraging. *Theoretical Population Biology* **30**: 45-75.

CLUTTON-BROCK, T.H. 1988. Reproductive success. *Studies of Individual Variation in Contrasting Breeding Systems.* University of Chicago Press, Chicago, USA.

CLUTTON-BROCK, T.H., ALBORN, S.D. & GUINNESS, F.E. 1988. Reproductive success in Male and Female Red Deer. In: *Reproductive success*. *Studies of Individual Variation in Contrasting Breeding Systems,* (ed.) T.H. Clutton-Brock. University of Chicago Press, Chicago, USA.

CLUTTON-BROCK, T.H. 2009. Cooperation between non-kin in animal societies. *Nature* **462**: 51-57.

COE, M.J., CUMMING, D.H. & PHILLIPSON, J. 1976. Biomass and production of large african herbivores in relation to rainfall and primary production. *Oecologia* **22**: 341-354.

COMSTOCK, K.E., WASSER, S.K. & OSTRANDER, E.A. 2000. Polymorphic microsatellite DNA loci identified in the African elephant (*Loxodonta africana*). *Molecular Ecology* **9**: 1004-1006.

COMSTOCK, K.E., GEORGIADIS, N., PECON-SLATTERY, J., ROCA, A.L., OSTRANDER, E. A., O'BRIEN, S.J. & WASSER, S.K. 2002. Patterns of molecular genetic variation among African elephant populations. *Molecular Ecology* **11:** 2489-2498.

CONRADT, L. & ROPER, T.J. 2003. Group decision-making in animals. *Nature* **421**: 155-158.

CÔTÉ, S.D. & FESTA-BIANCHET, M. 2001. Reproductive success in female mountain goats: the influence of age and social rank. *Animal Behaviour* **62**: 173-181.

COUZIN, I.D. 2006. Behavioral Ecology: Social organization in fission-fusion societies. *Current Biology* **16**: 169-171.

CROZE, H. & READER, J. 2000. *Pyramids of life. Patterns of life and death in the ecosystem*. The Harvill Press, London.

DAWKINS, R. 2006. *The selfish gene. 30th Anniversary edition*. Oxford University Press, UK.

VAN DE VIJVER, C.A.D.M., FOLEY, C.A. & OLFF, H. 1999. Changes in the woody component of an East African savanna during 25 years. *Journal of Tropical Ecology* **15**: 545-564.

DOUGLAS-HAMILTON I. 1987. African elephants: population trends and their causes. *Oryx* **21**: 11-24.

DRICKAMER, L.C. & VESSEY, S.H. 1986. Animal behavior: Concepts, processes, and methods. Second edition. Prindle, Weber and Schmidt, Boston, USA.

DUBLIN, H.T. 1983. Cooperation and reproductive competition among female African elephants. In: *Social Behavior of Female Vertebrates,* (ed.) S.K. Wasser. Academic Press, Inc. New York.

DUDLEY, J.P., CRAIG, G.C., GIBSON, D.S.C., HAYNES, G. & KLIMOWICZ, J. 2001. Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology* **39**: 187-194.

DURANT, S.M., KELLY, M. & CARO, T.M. 2004. Factors affecting life and death in Serengeti cheetahs: environment, age, and sociality. *Behavioural Ecology* **15**: 11-22.

ECOSYSTEMS LTD 1980. *The status and utilization of wildlife in Arusha Region, Tanzania*. Unpublished Report. Ecosystems Ltd, Nairobi, Kenya.

EMLEN, S., REEVE, H.K., SHERMAN, P.W., WREGE, P.H., RATNIEKS, F.L.W. & SHELLMAN-REEVE, J. 1991. Adaptive versus nonadaptive explanations of behavior: The case of alloparental helping. *American Naturalist* **138**: 259-270.

EMLEN, S.T., WREGE, P.H. & DEMONG, N.J. 1995. Making decisions in the family: an evolutionary perspective. *American Scientist* **83**: 148-157.

EMLEN, S.T. 1996. Reproductive sharing in different types of kin associations. *American Naturalist* **148**: 756-763.

EMLEN, S.T. 1997a. Predicting family dynamics in social vertebrates. In: *Behavioural ecology: An evolutionary approach, 4th Edition*. (eds.) J.R. Krebs & N.B. Davies. Blackwell Scientific, Oxford, UK.

EMLEN, S.T. 1997b. When mothers prefer daughters over sons. *Trends in Ecology and Evolution* **12**: 291-292.

EVANS, K.E. & HARRIS, S. 2008. Adolescence in male African elephants, *Loxodonta africana,* and the importance of sociality. *Animal Behaviour* **76**: 779-787.

FIENBERG, S.E. 1994. *The analysis of cross-classified categorical data*. Second edition. MIT Press, Cambridge, MA.

FLETCHER, J.A., ZWICK, M., DOEBELI, M. & WILSON, D.S. 2006. What’s wrong with inclusive fitness? *Trends in Ecology and Evolution* **21**: 597-598.

FOLEY, C.A.H. 2002. The effects of poaching on elephant social systems. PhD thesis, Princeton University.

FOLEY, C., PETTORELLI, N. & FOLEY, L. 2008. Severe drought and calf survival in elephants. *Biology Letters* **4**: 541-544.

FOLEY, C.A.H. & FAUST, L.J. 2010. Rapid population growth in an elephant *Loxodonta africana* population recovering from poaching in Tarangire National Park, Tanzania. *Oryx* **44**: 205-212.

FOSTER, K.R., WENSELEERS, T. & RATNIEKS, F.L.W. 2006. Kin selection is the key to altruism. *Trends in Ecology and Evolution* **21**: 57-60.

GAILLARD, J.M., FESTA-BIANCHET, M. & YOCCOZ, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* **13**: 58-63.

GAILLARD, J.M., FESTA-BIANCHET, M. & YOCCOZ, N.G. 2001. Not All Sheep Are Equal. *Science* **292**: 1499-1500.

GALIMBERTI, F., SANVITO, S., BRASCHI, C. & BOITANI, L. 2007. The Cost of success: Reproductive Effort in Male Southern Elephant Seals (*Mirounga leonina*). *Behavioral Ecology and Sociobiology* **62**: 159-171.

GERO, S., ENGELHAUPT, D. & WHITEHEAD, H. 2008. Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology* **63**: 143-151.

GIRALDEAU, L-A. & CARACO, T. 1993. Genetic relatedness and group size in an aggregation economy. *Evolutionary Ecology* **7**: 429-438.

GIRALDEAU, L-A & CARACO, T. 2000. Social foraging theory. *Monographs in behaviour and ecology*. Princeton University Press, Princeton, N.J.

GOBUSH, K.S., MUTAYOBA, B. & WASSER, S.K. 2008. Long-term impacts of poaching on relatedness, stress physiology and reproductive output of adult female African elephants. *Conservation Biology* **22**: 1590-1599.

GOBUSH, K.S. & WASSER, S.K. 2009. Behavioural correlates of low relatedness in African elephant core groups of a poached population. *Animal Behaviour* **78**: 1079-1086.

GOBUSH, K.S., KERR, B. & WASSER, S.K. 2009. Genetic relatedness and disrupted social structure in a poached population of African elephants. *Molecular Ecology* **18**: 722-734.

GOUGH, K.F. & KERLEY, G.I.H. 2006. Demography and population dynamics in the elephants Loxodonta africana of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? *Oryx* **40**: 434-441.

GRIFFIN, A.S. & WEST, S.A. 2002. Kin selection: fact and fiction. *Trends in Ecology and Evolution* **17**: 15-21.

HAMILTON, W.D. 1963. The Evolution of Altruistic Behavior. *American Naturalist* **97**: 354-356.

HAMILTON, W.D. 1964. Genetical evolution of social behaviour I and II. *Journal of Theoretical Biology* **7**: 1-52.

HAMILTON, W.D. 1967. Extraordinary sex ratios. *Science* **156**: 477-488.

HAMILTON, W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* **228**: 1218-1220.

HAMILTON, W.D. 1972. Altruism and related phenomena, mainly in the social insects. *Annual Review of Ecology and Systematics* **3**: 193-232.

HANKS, J. 1972. Reproduction of Elephant, *Loxodonta africana*, in The Luangwa Valley, Zambia. *Journal of Reproductive Fertility* **30**: 13-26.

HARRIS, G.M., RUSSELL, G.J., VAN AARDE, R.I. & PIMM, S.L. 2008. Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* **42**: 66-75.

HAYWARD, M.W., KOWALCZYK, R., KRASINSKI, Z.A. *et al*. 2011. Restoration and intensive management have no effect on evolutionary strategies. *Endangered Species Research* **15**: 53-61.

HOCK, K., NG, K.L. & FEFFERMAN, N.H. 2010. Systems approach to studying animal sociality: Individual position versus group organization in dynamic social network models. *PLoS ONE* 5(12): e15789. doi:10.1371/journal.pone.0015789

IUCN 2011. IUCN red list of threatened species. Version 2011.1. <www.iucnredlist.org>.

JOUBERT, D. 2006. Hunting behaviour of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park, Botswana. *African Journal of Ecology* **44**: 279-28.

KALINOWSKI, S.T., TAPER, M.L. & MARSHALL, T.C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**: 1099-1106.

KALINOWSKI, S.T. WAGNER, A.P. & TAPER, M.L. 2006. *ML-Relate*: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes* **6**: 576-579.

KAPSALIS, E. 2004. Matrilineal kinship and primate behaviour. In: *Kinship and Behavior in Primates,* (eds.) B. Chapais & C. M. Berman. Oxford University Press, New York.

KERR, B., GODFREY-SMITH, P. & FELDMAN, M.W. 2004. What is altruism? *Trends in Ecology and Evolution* **19**: 135-140.

KERLEY, G.I.H. & LANDMAN, M. 2006. The impacts of elephants on biodiversity in the Eastern Cape subtropical Thickets. *South African Journal of Science* **102**: 395-402.

KERLEY, G.I.H., LANDMAN, M., KRUGER, L., OWEN-SMITH, N. *et al.* 2008. Effects of elephant on ecosystems and biodiversity. In: *Assessment of South African Elephant Management,* (eds.) K.G. Mennell & R.J. Scholes. Witwatersrand University Press, Johannesburg.

KLUG, W.S. & CUMMINGS, R. 2005. Essentials of genetics. *Fifth edition*. Pearson Prentice Hall. New Jersey.

KOEN J.H., HALL-MARTIN, A.J., ERASMUS, T. 1988. Macronutrients in plants available to the Knysna, Addo and Kruger National Park Elephants. *South African Journal of Wildlife Research* **18**: 69-71.

KOENIG, W.D., PITELKA, F.A., CARMEN, W.J., MUMME, R.L. & STANBACK, M.T. 1992. The Evolution of Delayed Dispersal in Cooperative Breeders. *Quarterly Review of Biology* **67**: 111-150.

KOKKO, H., JOHNSTONE, R.A. & CLUTTON-BROCK, T.H. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society B* **268**: 187-196.

KOMDEUR, J. & HATCHWELL, B.J. 1999. Kin recognition: function and mechanism in avian societies. *Trends in Ecology and Evolution* **14**: 237-241.

Le BOEUF, B.J. & REITER, J. 1988. Lifetime reproductive success in northern elephant seals. In: *Reproductive success*. *Studies of individual variation in contrasting breeding systems*, (ed.) T.H. Clutton-Brock. University of Chicago Press, Chicago, USA.

LEE, P.C. & MOSS, C.J. 1986. Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology* **18**: 353-361.

LEE, P.C. 1987. Allomothering among African elephants. *Animal Behaviour* **35**: 278-291.

LEE, P.C. 1996. Studying the behaviour of elephants. In: *Studying elephants,* (ed.) K. Kangwana. African Wildlife Foundation, Nairobi.

LEHMANN, L. & KELLER, L. 2006. The evolution of cooperation and altruism - a general framework and a classification of models. *Journal of Evolutionary Biology* **19**: 1365-1376.

LEHMANN, J., KORSTJENS, A.H. & DUNBAR, R.I.M. 2007. Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology* **21**: 613-634.

LIKER, A. & BOKONY, V. 2009. Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of the Sciences of USA* **106**: 7893-7898.

LIU, G.S.C.A., SEIFFERT, E.R. & SIMONS, E.L. 2008. Stable isotope evidence for an amphibious phase in early proboscidean evolution. *Proceedings of the National Academy of the Sciences of USA* **105**: 5786-5791.

LOVERIDGE, A.J., HUNT, J.E., MURINDAGOMO, F. & MACDONALD, D.. 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *Journal of Zoology* **270**: 523-530.

LUKAS, D., REYNOLDS, V., BOESCH, C. & VIGILANT, L. 2005. To what extent does living in a group mean living with kin? *Molecular Ecology* **4**: 2181-2196.

MAGLIO, V.J. 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* **63**: 1-149.

MARSHALL, T.C., SLATE, J., KRUUK, L.E.B. & PERMBERTON, J.M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**: 639-655.

MAY, R.M. 1991. The role of ecological theory in planning the reintroduction of endangered species. *Symp. Zool. Soc. Lond.* **62**:145-163.

MAYNARD-SMITH, J. 1964. Kin selection and group selection. *Nature* **201**: 1145-1147.

McCOMB, K., MOSS, C., DURANT, S.M., BAKER, L. & SAYIALEL, S. 2001 Matriarchs as repositories of social knowledge in African elephants. *Science* **292**: 491-494.

McCOMB, K., SHANNON, G., DURANT, S.M., SAYIALEL, K., SLOTOW, R., POOLE, J. & MOSS, C.J. 2011. Leadership in elephants: the adaptive value of age. *Proceedings of the Royal Society B* doi:10.1098/rspb.2011.0168.

MENDENHALL, W. & SINCICH, T. 2003. *A second course in statistics: regression analysis*. Sixth edition. Pearson education, Inc. New Jersey, USA.

MILLIGAN, B.G. 2003. Maximum-likelihood estimation of relatedness. *Genetics* **163**: 1153-1167.

MITANI, J.C., MERRIWETHER, D.A. & ZHANG, C. 2000. Male affiliation, cooperation, and kinship in wild chimpanzees. *Animal Behaviour* **59**: 885-893.

MITANI, J.C., WATTS, D.P., PEPPER, J.W. & MERRIWETHER, D.A. 2002. Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour* **64**: 727-737.

MOSS, C. 1983. Oestrus behaviour and female choice in the African elephant. *Behaviour* **86**: 167-196.

MOSS, C.J. & POOLE, J.H. 1983. Relationships and social structure of African elephants. In: *Primate Social Relationships,* (ed.) R.A. Hinde. Sunderland, MA: Sinauer.

MOSS, C.J. 1988. *Elephant memories*. University of Chicago Press, Chicago.

MOSS, C. 1990. Elephants in Tarangire. *Pachyderm* **13**: 28-32.

MOSS, C.J. 1994. Some reproductive parameters in a population of African elephants, *Loxodonta africana*. In: *Proceedings of the second international NCRR conference*, (ed.) C.H. Bambra. Institute of Primate Research, Nairobi.

MOSS, C. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology* **255**: 145-156.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. Technique for analysis of utilization-availability data. *Journal of Wildlife Management* **38**: 541-545.

NOWAK, M.A., TARNITA, C.E. & WILSON, E.O. 2010. The evolution of eusociality. *Nature* **466**: 1057-1062.

NUNNEY, L. 1985. Female-biased sex ratios: Individual or group selection? *Evolution* **39**: 349-361.

NYAKAANA, S. & ARCTANDER, P. 1998. Isolation and characterisation of microsatellite loci in the African elephant (*Loxodonta africana*). *Molecular Ecology* **7**: 1436-1437.

NYAKAANA, S., ABE, E.L., ARCTANDER, P. & SIEGISMUND, H.R. 2001. DNA evidence for elephant social behaviour breakdown in Queen Elizabeth National Park, Uganda. *Animal Conservation* **4**: 231-237.

OKELLO, J.B.A., WITTEMYER, G., RASMUSSEN, H.B., DOUGLAS-HAMILTON, I., NYAKAANA, S., ARCHTANDER, P. & SIEGISMUND, H.R. 2005. Noninvasive genotyping and mendelian analysis of microsatellites in African savannah elephants. *Journal of Heredity* **96**: 679-687.

OKELLO, J.B.A., MASEMBE, C., RASMUSSEN, H.B., WITTEMYER, G., OMONDI, P., KAHINDI, O., MUWANIKA, V.B., ARCHTANDER, P., DOUGLAS-HAMILTON, I., NYAKAANA, S. & SIEGISMUND, H.R. 2008. Population genetic structure of savannah elephants in Kenya: Conservation and management implications. *Journal of Heredity* doi:10.1093/jhered/esn028.

OWENS, M.J. & OWENS, D. 2009. Early age reproduction in female savanna elephants (*Loxodonta africana*) after severe poaching. *African Journal of Ecology* **47**: 214-222.

OWEN-SMITH, N. 1990. Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology* **59**: 893-913.

OWEN-SMITH, N. 1993. Age, size, dominance and reproduction among male kudus: Mating enhancement by attrition of rivals. *Behavioral Ecology and Sociobiology* **32**: 177-184.

PACKER, C., SCHEEL, D., & PUSEY, A.E. 1990. Why lions form groups: food is not enough. *American Naturalist* **136**: 1-19.

PACKER, C., GILBERT, D.A., PUSEY, A.E. & OBRIEN, S.J. 1991. A molecular genetic-analysis of kinship and cooperation in African lions. *Nature* **351**: 562-565.

PINTER-WOLLMAN, N. 2009. Spatial behaviour of translocated African elephants (*Loxodonta africana*) in a novel environment: using behaviour to inform conservation actions. *Behaviour* **146**: 1171-1192.

PINTER-WOLLMAN, N., ISBELL, L.A. & HART, L.A. 2009a. The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*). *Proceedings of the Royal Society B* **276**: 1009-1014.

PINTER-WOLLMAN, N., ISBELL, L.A. & HART, L.A. 2009b. Assessing translocation outcome: Comparing behavioral and physiological aspects of translocated and resident African elephants (*Loxodonta africana*). *Biological Conservation* **142**: 1116-1124.

POMILLA, C. & ROSENBAUM, H.C. 2006. Estimates of relatedness in groups of humpback whales (*Megaptera novaeangliae*) on two wintering grounds of the Southern Hemisphere. *Molecular Ecology* **15**: 2541-2555.

POOLE, J. 1996. The African elephant. In: *Studying Elephants*, (ed.) K. Kangwana. African Wildlife Foundation, Nairobi.

POPE, T.R. 1998. Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. *Journal of Mammalogy* **79**: 692-712.

POPE, T. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology* **48**: 253-267.

POWER, R.J. & COMPION, S. 2009. Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *African Zoology* **44:** 36-44.

PRINS, H.H.T. 1987. Nature conservation as an integral part of optimal land use in East Africa: the case of the Masai ecosystem of northern Tanzania. *Biological Conservation* **40:** 141-161.

QUELLER, D.C. & GOODNIGHT, K.F. 1989. Estimating relatedness using genetic markers. *Evolution* **43**: 258-275.

QUELLER, D.C. 1994. Genetic relatedness in viscous populations. *Evolutionary Ecology* **8**: 70-73.

R DEVELOPMENT CORE TEAM. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

RADESPIEL, U. & ZIMMERMANN, E. 2003. The Influence of familiarity, age, experience and female mate choice on pregnancies in captive grey mouse lemurs. *Behaviour* **140**: 301-318.

RASMUSSEN, H.B., OKELLO, J.B.A., WITTEMYER, G., SIEGISMUND, H.R., ARCTANDER, P., VOLLRATH, R. & DOUGLAS-HAMILTON, I. 2007. Age- and tactic-related paternity success in male African elephants. *Behavioral Ecology* doi:10.1093/beheco/arm093.

REALE, D., MARTIN, J., COLTMAN, D.W., POISSANT, J. & FESTA-BIANCHET, M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology* **22**: 1599-1607.

RIEUCAU, G. & GIRALDEAU, L-A. 2009. Group size effect caused by food competition in nutmeg mannikins (*Lonchura punctulata*). *Behavioral Ecology* **20**: 421-425.

ROBINSON, T.J. & SEIFFERT, E.R. 2003. Afrotherian origins and interrelationships: new views and future prospects. *Current Topics in Development Biology* **63**: 37-60.

ROCA, A.L., GEORGIADIS, N., PECON-SLATTERRY, J. & OBRIEN, S.J. 2001. Genetic evidence for two species of elephant in Africa. *Science* **293**: 1473-1477.

RODMAN, P.S. 1981. Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. *American Naturalist* **118**: 275-283.

ROHLAND, N., MALASPINAS, A.S., POLLACK, J.L., SLATKIN, M., MATHEUS, P. *et al.* 2007. Proboscidean mitogenomics: Chronology and mode of elephant evolution using mastodon as outgroup. *PLoS Biol 5(8)*: e207. doi:10.1371/journal.pbio.0050207.

ROHLAND, N., REICH, D., MALLICK, S., MEYER, M., *et al*. 2010. Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. PloS Biol 8 (12): e1000564.doi:10.1371/journal.pbio.1000564.

RUTLEDGE, L.Y., HOLLOWAY, J.J., PATTERSON, B.R. & WHITE, B.N. 2009. An improved field method to obtain DNA for individual identification from wolf scat. *Journal of Wildlife Management* **73**: 1430-1435.

SACHS, J.L., MUELLER, U.G., WILCOX, T.P. & BULL, J.J. 2004. The evolution of cooperation. *Quarterly Review of Biology* **79**: 135-160.

SCHRADIN, C., KONIG, B. & PILLAY, N. 2010. Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology* **79**: 515-521.

SEUTIN, G., WHITE, B.N. & BOAG, P.T. 1991. Preservation of avian blood and tissue samples for DNA analysis. *Canadian Journal of Zoology* **69**: 82-90.

SEYDACK, A.H.W. & BIGALKE, R.C. 1992. Nutritional ecology and life history tactics in the bushpig (*Potamochoerus porcus*): Development of an interactive model. *Oecologia* **90**: 102-112.

SHERMAN, P.W. 1981. Kinship, demography and belding's ground squirrel nepotism. *Behavioral Ecology and Sociobiology* **8**: 251-259.

SILK, J.B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B* **362**: 539-559.

SLOTOW, R., VAN DYK, G., POOLE, J.H., PAGE, B. & KLOCKE, A. 2000. Older bull elephants control young males. *Nature* **408**: 425-426.

SLOTOW, R. & VAN DYK, G. 2001. Role of delinquent young "orphan" male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. *Koedoe* **44**: 85-94.

SMITH, E.A. 1985. Inuit foraging groups: Some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethology and Sociobiology* **6**: 27-47.

SMITH, J.E., VAN HORN, R.C., POWNING, K.S., COLE, A.R., GRAHAM, K.E., MEMENIS, S.K. & HOLEKAMP, K.E. 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology* **21**: 284-303.

SOBER, E. & WILSON, D.S. 1998. *Unto others. The evolution and psychology of unselfish behaviour*. Harvard University Press, Massachusets, USA.

STANDEN, R. & FOLEY, R.A. 1989. Comparative socioecology. *The behavioural ecology of humans and other mammals.* Blackwell Scientific Publications.

STOKKE, S. 2000. Sex differences in feeding-patch choice in megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology* **77**: 1723-1732.

SUKUMAR, R. 1989. *The Asian Elephant: Ecology and Management*. (Cambridge Studies in Applied Ecology and Resource Management). Cambridge University Press, Cambridge, U.K.

TARANGIRE CONSERVATION PROJECT (TCP). 1997. *Analysis of migratory movements of large mammals and their interaction with human activities in the Tarangire area in Tanzania as a contribution to a conservation and sustainable development strategy*. Final report: Explanatory section, Arusha.

TAYLOR, P.D. 1992. Altruism in viscous populations- an inclusive fitness approach. *Evolutionary Ecology* **6**: 352-356.

THAIN, M. & HICKMAN, M. 2004. Dictionary of biology. Eleventh edition. Penguin Group Inc., USA.

TRIMBLE, M.J., FERREIRA, S.M. & VAN AARDE, R.J. 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. *Journal of Zoology* **279**: 18-26.

TRIVERS, R.L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* **46**: 35-57.

TWCM (TANZANIA WILDLIFE CONSERVATION MONITORING). 2000. Total count of elephant and buffalo in the Tarangire ecosystem, March 2000. Unpublished Report. Tanzania Wildlife Conservation Monitoring, Arusha, Tanzania.

VANCE, E.R., ARCHIE, E.A. & MOSS, C.J. 2009. Social networks in African elephants. *Computational and Mathematical Organization Theory* **15**: 273-293.

VAN SCHAIK, C.P. 1999. The socioecology of fission-fusion sociality in orangutans. *Primates* **40:** 69-86.

WASSER, S.K., SHEDLOCK, A.M., COMSTOCK, K., OSTRANDER, E.A., MUTAYOBA, B. & STEPHENS, M. 2004. Assigning African elephant DNA to geographic region of origin: Applications to the ivory trade. *Proceedings of the National Academy of the Sciences of USA* **101**: 14847-14852.

WEST, S.A., MURRAY, M.G., MACHADO, C.A., GRIFFIN, A.S. & HERRE, E.A. 2001. Testing Hamilton's rule with competition between relatives. *Nature* **409**: 510-513.

WEST, S.A., PEN, I. & GRIFFIN, A.S. 2002. Cooperation and competition between relatives. *Science* **296**: 72-75.

WEST, S.A., GRIFFIN, A.S. & GARDNER, A. 2007a. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology* **20**: 415-432.

WEST, S.A., GRIFFIN, A.S. & GARDNER, A. 2007b. Evolutionary explanations for cooperation. *Current Biology* **17**: R661-R672.

WEST, S.A., GRIFFIN, A.S. & GARDNER, A. 2008. Social semantics: how useful has group selection been? *Journal of Evolutionary Biology* **21**: 374-385.

WEST-EBERHARD, M.J. 1975. The Evolution of Social Behavior by Kin Selection. *Quarterly Review of Biology* **50**: 1-33.

WHITEHOUSE, A.M. & HALL-MARTIN, A.J. 2000. Elephants in Addo Elephant National Park, South Africa: reconstruction of the population’s history. *Oryx* **34**: 46-55.

WHITEHOUSE, A.M. 2001. The Addo elephants: Conservation biology of a small, closed population. PhD thesis. University of Port Elizabeth.

WHITEHOUSE, A.M. 2002. Tusklessness in the elephant population of the Addo Elephant National Park, South Africa. *Journal of Zoology* **257**: 249-254.

WILSON, E.O. 2005. Kin selection as the key to altruism: its rise and fall. *Social Research* **72**: 159-166.

WILSON, E.O. 2008. One giant leap: how insects achieved altruism and colonial life. *Bioscience* **58**: 17-25.

WILSON, D.S. & WILSON, E.O. 2008. Evolution ‘for the good of the group’. *American Scientist* **96**: 380-389.

WHITEHOUSE, A.M. & KERLEY, G.I.H. 2002. Retrospective assessment of long-term conservation management: recovery from near extinction of the elephants in Addo Elephant National Park, South Africa. *Oryx* **36**: 243-248.

WITTEMYER, G. 2005. The Socio-ecology of the African elephant (*Loxodonta africana*). PhD thesis, University of California, Berkeley, CA.

WITTEMYER, G., DOUGLAS-HAMILTON, I. & GETZ, W.M. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* **69**: 1357-1371.

WITTEMYER, G. & GETZ, W.M. 2007. Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Animal Behaviour* **73**: 671-681.

WITTEMYER, G., GETZ, W.M., VOLLRATH, F. & DOUGLAS-HAMILTON, I. 2007a. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology* **61**: 1919-1931.

WITTEMYER, G., RASMUSSEN, H.B. & DOUGLAS-HAMILTON, I. 2007b. Breeding phenology in relation to NDVI variability in free-ranging African elephant. *Ecography* **30**: 42-50.

WITTEMYER, G., OKELLO, J.B. A., RASMUSSEN, H.B. ARCTANDER, P., NYAKAANA, S., DOUGLAS-HAMILTON, I. & SIEGISMUND, H.R. 2009. Where sociality and relatedness diverge: the genetic basis for hierarchical social organization in African elephants. *Proceedings of the Royal Society B* **276**: 3513-3521.

WITTEMYER, G., DABALLEN, D. & DOUGLAS-HAMILTON, I. 2011. Rising ivory prices threaten elephants. *Nature* **476**: 282-283.

WOOLLEY, L-A., PAGE, B. & SLOTOW, R. 2011. Foraging strategy within African elephant family units: Why body size matters. *Biotropica* **43**: 489-495.

YOUNG, K.M. & VAN AARDE, R.J. 2010. Density as an explanatory variable of movements and calf survival in savanna elephants across southern Africa. *Journal of Animal Ecology* **79**: 662-673.

ZAR, J.H. 1999. *Biostatistical Analysis*. Fourth edition. Upper Saddle River, New Jersey.

APPENDIX 1 A list of aggression scales [adopted from Foley's (2002) study] for agonistic behaviours measured in this study, ranging from mild (1) to severe (7).

1. Aggressor walks toward recipient
2. Aggressor walks with ears spread out or flaps ear outward toward the recipient or gives a headshake toward the recipient.
3. Aggressor raises her head and spreads her ears out toward the recipient.
4. Aggressor raises her head to the recipient, spreads ears out, and folds them horizontally across the centre.
5. Aggressor walks fast with head up and ears spread out and folded; lunges at or hits recipient.
6. Aggressor runs toward and chases recipient.
7. Aggressor chases and tusks recipient, or fights recipient.