

The Socio-Ecology of the African Elephant (*Loxodonta africana*)

by

George Wittemyer

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Committee in charge:

Professor Wayne M. Getz, Chair

Professor Steven R. Beissinger

Professor Justin S. Brashares

Professor Eileen A. Lacey

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Abstract

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A variety of challenges face the conservation of African elephants, stemming from the illegal poaching for ivory to habitat loss resulting in range restriction. Solutions to these challenges require information on the factors affecting population structure, movement and reproduction in this species. In this dissertation, I investigate the relationship between ecological variation and population processes in the wild elephant population inhabiting the Samburu and Buffalo Springs National Reserves in northern Kenya. Both empirical analyses and theoretical approaches are presented, motivated by fundamental questions regarding factors influencing population structure and by applied objectives concerning the management issues facing this species. In addition, this work

presents novel analytical techniques for defining and understanding population structure.

In Chapters 2 and 3, I focus on addressing specific management questions regarding the Samburu elephant population. This research describes the results of the initial individual identification project conducted on the elephants using the Samburu and Buffalo Springs National Reserves study area, and presents the results of a detailed assessment of the demographic status of the population and threats these elephants face. This work lay the foundation for all future research conducted on this elephant population. In Chapters 4-7, I focus on the socio-ecology of elephants. Specifically, Chapter 4 investigates the factors driving demographic variability common to elephant populations are investigated by assessing the relationship between elephant reproductive activity and climatic driven ecological variability. Chapter 5 provides the first quantitative assessment of a multi-leveled social organization and discusses some of the factors contributing to the evolution of such complex social relationships. In Chapter 6, a novel quantitative technique is presented that provides the most likely dominance ranks for a group of individuals in which agonistic interactions are rare, as is common in elephant populations. This method is then applied to data collected on the Samburu elephants in Chapter 7 to derive the most likely rank order across the studied individuals. The factors influencing spatial use and segregation are then investigated, during which the influence of rank on movement and range use is explored.

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Chapter One

Summary

George Wittemyer

Throughout Africa, wildlife faces increasing confinement to protected areas, over harvesting from the illegal trade in bushmeat or wildlife parts, and increasing levels of human-wildlife conflict largely in relation to accelerating rates of range compression. No species better exemplifies the current complexity of these issues than African elephants. With elephant populations increasing in some parts of Africa and declining in others, wildlife authorities face a range of conservation issues including human elephant conflict, ivory poaching, and growing habitat confinement that demand a variety of management solutions such as translocation, fencing and increased policing. The successful implementation of any of these management strategies and the long-term conservation of this species requires information on the factors influencing elephant demography, social structure and spatial organization.

This dissertation tackles both empirical and theoretical issues regarding population structuring of animals. The primary focus of the research presented here is the investigation of the socio-ecology of elephants, conducted through analyses of the relationship between ecological variation and population structure, movement, and reproduction. This work is conducted on the individually identified elephant population inhabiting the Samburu and Buffalo Springs National Reserves in northern Kenya. By exploring the socio-ecology of this population, we address management objectives specific to the Samburu population, such as assessment of causes of mortality and the dependence of these elephants on protected areas. In addition, we examine aspects of elephant ecology pertinent to population management issues across Africa, including the identification of cues elephants use to initiate reproductive bouts and factors influencing spatial properties of elephant populations. This work also makes

contributions to the advancement of socio-ecological theory through the exploration of factors influencing the evolution of multiple tiered social organizations and driving the formation of dominance hierarchies in species experiencing scramble competition. Tackling these various issues necessitated the development of novel analytical techniques. Specifically, methods are presented for quantitatively defining social delineations within a population from observations of pair-wise associations and solving the best dominance rank order for a group of individuals for which information on pair-wise agonistic interactions is sparse. Thus, this work provides novel techniques for analysis of population processes and advances socio-ecological theory by exploring the applicability and shortcomings of the socio-ecological framework to the social properties of a wild elephant population.

In Chapter 2, the results from an initial population assessment of the Samburu and Buffalo Springs National Reserves' elephant population, conducted between November 1997 and July 1999, are presented. This work was conducted in order to provide information about the status of this population to the Kenya Wildlife Service, the authority overseeing all wildlife in Kenya. This population is currently estimated to number over 900 individuals. The individual identification of the reserve elephants, following well established protocols described by Douglas-Hamilton (1972) and Moss (1996), serves as the foundation for my doctoral dissertation and all successive research conducted on the Samburu elephant population.

During the two-year identification project, the study elephants were found to be free ranging and relied heavily on areas outside the protected reserve boundaries. The numbers of elephants observed per day fluctuated but were greater during dry periods

then wet, indicating the reserves are important dry season holding grounds. However, the sizes of aggregations were greater during wet periods, as expected in relation to increased resource availability (explored in more detail in Chapter 5). The daily numbers of males and musth males, as expected in a polygynous species (Emling and Oring 1977), were correlated with numbers of females. Preliminary investigation suggested that female groups could be divided into two groups based on the proportion of a year the individuals were observed to use the parks. These groups, designated resident and non-resident family units, comprised approximately equal numbers of cows and calves, but demonstrated different temporal reserve-use patterns and calving peaks. Residents used the reserves all seasons across a year, while non-residents tended to use the reserves for only a single season. The reserves appeared to be a focal area for calving, indicating that the study area was of reproductive importance for the population. Demographic data indicated a female-biased population sex ratio, with over twice the number of mature females to males. The observed skew of the sex-ratio was greatest for older age classes, and the density of musth bulls in the study area was low. This demographic skew as well as observations of illegally killed individuals, demonstrated that the population was affected by poaching.

In chapter 3, I collated demographic data recorded on the study population between 1998 and 2003. This work provides a detailed assessment of the demographic change encountered by the Samburu elephant population, offering insight into the general well-being and risks faced by this population. The Samburu and Buffalo Springs National Reserves are part of the larger Samburu/Laikipia MIKE (Monitoring of Illegal Killing of Elephants) site. This area is one of 33 such sites designated in

Africa by the CITES (Convention on International Trade in Endangered Species) protectorate to monitor poaching levels in elephant populations at risk with regard to the trade in ivory. Individual based demographic records of the elephants utilizing Samburu and Buffalo Springs National Reserves indicate that this elephant population was increasing at an average rate of 4.6% per year. Although the majority of carcasses were not found, known sources of mortality include disease, injury, and predation by lions and humans. Poaching did occur during the study period. The population, however, is increasing and thus our findings indicate there is little impact from ivory poaching on the demographic status of these elephants. We conclude that this population is currently stable, although it continues to be at risk of human pressures. Thus, continued monitoring of the population demographic status is important for the conservation of these elephants.

Using this demographic data set, we investigate the reproductive strategies of the Samburu elephants in Chapter 4. Reproductive phenology in wild mammal populations is often correlated with resource availability and hypothesized to be shaped by selective forces. African elephants are subject to distinct constraints, necessitating a long-term strategy of energy acquisition and reproductive expenditure to ensure successful offspring recruitment. The relationship between the reproductive phenology of the Samburu elephant population and resource availability is investigated using remotely sensed Normalized-Differential-Vegetation-Index (NDVI) data as a measure of time-specific variability in primary productivity and hence forage quality (Goward and Prince 1995). We found that the initiation of their 3-5 year reproductive bout is based on the quality of a season while parturition phenology relates to probable periods

of high primary productivity within a season. Thus, both the probability of conception and the phenology of parturition are related to variability in primary productivity, indicating elephants integrate information on known current and expected future conditions to increase the reproductive success. Extreme climatic events, such as those associated with the El-Niño Southern Oscillation (ENSO), can act to synchronize reproduction in populations, where reproductive phenology is closely related to variability in resources. I hypothesized that this relationship is the likely factor instigating fluctuations in recruitment observed in elephant populations, rather than the mortality-driven fluctuations observed in most ungulate populations (Gaillard *et al.*, 2000). This work extends our understanding of the factors influencing reproductive success in elephants, and as such is important for management of both increasing and decreasing wild elephant populations as well as captive breeding programs.

The influence of variation in resource quality and quantity has also been shown to impact social behavior. The socio-ecological framework was developed from research on the affect of ecological factors, particularly the distribution of resources, on social structure (Emling and Oring 1977, Clutton-brock and Harvey 1977, Wrangham 1980, Sterck *et al.* 1997, van Schaik 1989, Isbell 1991, Isbell and Truman 2002). Fission-fusion social organizations are of particular interest for the investigation of the relationship between ecology and social structure because such systems are well suited for comparing ecological variation with social changes. In Chapter 5, I investigate the formation and function of the multi-levelled, fission-fusion social structure in a free ranging African elephant population. Applying novel techniques, I quantitatively demonstrate the existence of four social tiers using cluster analysis on individual

association data. I assess the affect of season and study period on social structuring and levels of cohesion within and among social units. My results indicate that 2nd tier units, potentially the equivalent of the “family”, are stable across seasonal periods but the number of units increased as the study progressed and the population grew. It appears that these units are sufficiently small not to be influenced by ecologically related factors, such as resource competition, that might otherwise lead to them splitting. On the other hand, 3rd and 4th tier units are significantly affected by season in a way that suggests a trade-off between ecological costs (e.g. from resource competition) and different social and ecological benefits (e.g. from predator defence, territoriality, knowledge sharing and rearing of young). Age structure also appears to influence this multi-tiered social organization with the size of 2nd tier social units being significantly affected by the age of matriarchs: units led by matriarchs likely to be grandmothers (i.e. females 35 years and older) are significantly larger than those of younger matriarchs. A conceptual framework for understanding the emergence of multiple-tier social structure from interactions driven by socio-ecological processes is presented. This study is the first using rigorous quantitative methods to statistically demonstrate the existence of four hierarchical tiers of social organization in a non-human animal. Additionally, my results elucidate the role that ecological processes play in producing complex social structures.

Dominance relationships are an important construct of social interactions, and the development of quantitative methods to resolve dominance relations is an important challenge for behavioral ecologists. Previous approaches have addressed this issue by focusing on either solving the most linear the rank ordering possible of a group of

individuals or the calculation of a dominance strength metric on which to base the ordering of individuals. Both of these methods are challenged by sparse data that does not contain information on the relationships among all dyads. In Chapter 6, I present a “likely ranking interpolation” approach to address the sparse data problem. Our technique incorporates the advantages of both the optimisation and strength methods thereby simultaneously yielding the optimal ordinal rank and the cardinal strengths of individuals in the hierarchy. It provides insights beyond those offered by either method alone and is a more powerful method for ranking individuals when data is sparse.

In Chapter 7, I apply this method to observations of dominance interactions collected on the Samburu elephant population. My results demonstrate that elephants maintain a near-linear dominance hierarchy within as well as between social units. The maintenance of a hierarchical dominance order while experiencing scramble competition, found in African elephants, is a combination of traits not addressed by current models of the socio-ecological framework. As such, study of the relationship between dominance relationships and resource availability and use in this species offers important insight into the ecological factors influencing population structure and behavior. Agonistic interactions between social groups are analyzed, demonstrating elephants maintain between group near-linear dominance hierarchies. Differentiation in movement and spatial use in relation to rank is demonstrated through analysis of G.P.S. radio tracking data collected on 7 families of different rank. During the dry season, dominant groups moved significantly less, spend more time within the protected national reserves boundaries in the study area, used smaller home ranges as defined by MCP and kernel home range estimators, and spend a greater proportion of their time

within close proximity to permanent water than lower ranking groups. Such rank related distinctions in behavior and spatial use, however, are not found to occur during the wet season indicating spatial segregation of elephants is related to resource availability. My results provide evidence for resource partitioning in a species predominantly experiencing scramble competition. The predictions of the socio-ecological framework can be expanded to such scramble competitive systems but the degree to which scramble competition is driving spatial behavior will vary in relation to ecological constraints.

In summary, the work presented in this dissertation takes a multifaceted approach to understanding the socio-ecology of elephants. This research provides insight into the impact of ecological variability on population functions such as demographic processes and social behavior, puts forward novel quantitative techniques for analyzing behavioral data, and advances our understanding of the factors influencing spatial organization and movement behavior in elephants. The information derived from this research can assist management of wild and captive elephants in addition to furthering theoretical understanding of the relationship between resource variability and behavior.

Chapter Two

The elephant population of Samburu and Buffalo Springs National Reserves, Kenya

G. Wittemyer

Introduction

The greater Laikipia-Samburu region has the largest population of elephants, *Loxodonta africana* (Blumenbach), primarily residing outside of protected areas in Kenya (Poole *et al.*, 1992). The Kenya Wildlife Service 1999 aerial census estimated the population at approximately 3,400 individuals (Kahumbu *et al.*, 1999). Extensive poaching occurred during the 1970s and 1980s in Kenya (Douglas-Hamilton, 1987). Although poaching still occurs in the region (King *et al.*, 1999), Samburu and Buffalo Springs National Reserves are safe havens for wildlife.

Wildlife tourism brings revenue and employment to the reserves and local communities. The elephants within the reserves are approachable making them ideal for tourism, research, and monitoring. A recent study on movement patterns suggested that the elephants using the reserves are part of a subpopulation, numbering around 800 individuals, of the greater Laikipia-Samburu population (Thouless, 1996). However, the status of the reserves' elephants was unclear as the study did not observe the subpopulation to enter the reserves, and detailed information on the use of the reserves was not undertaken (Thouless, 1993).

A twenty-one month individual identification study of the elephant population within these reserves was conducted between November 1997 and July 1999. Data on demography, social behavior, and ranging patterns were gathered. This chapter describes observed population fluctuations and social structure of the reserves' elephant population.

Materials and Methods

Study Area

The Samburu and Buffalo Springs National Reserves study area is approximately 330 square kilometers and located just north of the equator at a longitude of 37° E (Fig. 1). Topographically rugged hills and watercourses characterize the reserves, with an elevation range between 800-1200 metres.

The Ewaso Ngiro River, the largest semi-permanent river in this region, divides the reserves and is a focal area for wildlife. The river originates from tributaries on Mt. Kenya and the Aberdares Range, draining northward through the Laikipia District. Rainfall is localized and highly variable in the region, with the majority falling during the long rains in March-May and the short rains in October-December. The study area is dry and hot throughout much of the year, receiving 360 mm ± 170 mm (SD) of annual precipitation (Government of Kenya, 1997).

The distribution of vegetation in the study area largely depends upon the availability of water. The river acacia, *Acacia elatior*, and Duom palm, *Hyphaene coriacea*, dominate the riverine woodland along the banks of the Ewaso Ngiro. Salt bush, *Salsola droides*, a low growing shrub, is common on the saline soils of the low lying pans adjacent to the river. The two major vegetation communities in the study area are *Acacia-Commiphora* semi-arid scrub woodland and *Acacia* wooded grassland, typically found in dry regions further from the river. Most of the plant species inhabiting these regions are ephemeral or shed their leaves during the dry season.

Data Collection and Analysis

Observations were made within the demarcated boundaries of the two reserves. A general transect following the study area water courses was used during each sampling day (Douglas-Hamilton, 1996). However, the location and densities of elephants affected the route taken and time spent per study area region. It was not possible to cover the entire study area each day of the study, and areas with greater elephant densities were more heavily sampled as a result of the method employed. Daily effort was consistent the duration of the study though numbers of observation days varied across months (the mean number of observation days per month \pm SD was 18 ± 5). I conducted all identifications and successive data collection, excluding calving data after August 1999.

Each elephant within the study area was identified using sex, age, and features unique to the individual, such as ear patterns (Douglas-Hamilton, 1972; Moss, 1988, 1996). Photographs and drawings of these features were used in the development of an identification dossier. When an elephant was located, the date, time, and Global Positioning System (G.P.S.) location were recorded as well as the identities of conspecifics present. All individual associations and behavioral interactions were recorded. Elephants observed within one kilometer of each other were defined as “associating” (Douglas-Hamilton, 1972).

Family units consist of related breeding females (cows) and their offspring (Douglas-Hamilton, 1972; Moss, 1988). Family units were defined by quantifying association data of breeding females. Elephants associating at least $2/3^{\text{rds}}$ of the total number of observations for each female (median = 34, inter-quartile range 8-51

observations; N = 203) were categorized as a family unit. This was designed to avoid errors caused by incomplete censusing, which can occur in thick bush. Using this definition, 86% of the identified elephants were assigned to a family unit. No individual was assigned to more than one family unit. The monthly frequency of family unit presence was plotted to assess usage patterns. The emergent bimodal distribution was used to delineate the population into resident and non-resident family units (cf. Fig. 4).

Age estimates for individuals were conducted using shoulder height and physical appearance indices established through molar evaluation of culled individuals (Laws, 1966; Laws *et al.*, 1975) and the long term study of a known population (Lee & Moss, 1995; Moss, 1996). A preparatory training course on ageing elephants was completed in Amboseli National Park with known age elephants. Error in estimates may increase for older age groups as age related differences are more pronounced in the younger age groups (Jachmann, 1985; Moss, 1996). Therefore, age structure analysis was presented in 5 year age classes for elephants up to the age of 20 years and 15 year age classes for elephants over the age of 20 years (Moss, 1996). Data on surviving calves were from 26 months of known births in combination with age estimates of calves under three years at the onset of the study. Estimated calf ages were presented because calves under three are generally not weaned and in the early stages of tusk eruption (Moss, 1988), making them relatively easy to distinguish and age. Individuals of unknown age or sex were only included in analysis of family unit size.

Monthly rainfall data from 1957 to 1999 were provided by NRM³ (National Resource Monitoring, Management, and Modeling). Analyses across expected wet and

dry seasons were partitioned using the long-term average monthly rainfall, March-May and October-December being wet season months (averaging 54.1 ± 59.4 (SD) mm per month) and January-February and June-September being dry season months (averaging 7.0 ± 18.3 (SD) mm per month). Analysis was also conducted according to actual monthly rainfall during the study. Wet months were defined as receiving greater than twenty-five millimeters of precipitation (approximately one standard deviation more than the mean precipitation of dry season months) and dry months as receiving twenty-five millimeters or less.

Analysis of population fluctuations was conducted on actual numbers of elephants observed per day ($N = 327$ days). Repeated sightings of individuals were not included in daily totals. The number of associating individuals per observation was used to quantify group sizes for analysis. The first three months of data were spent identifying new elephants and becoming familiar with the study area. Therefore, they were not considered representative samples and excluded from analysis. Analyses were conducted using the SAS JMP IN statistical package. Nonparametric techniques were used for all tests.

Results

Individual Identification

After twenty-one consecutive months of study, 744 elephants were identified. An additional twenty-three elephants were not fully identified. A minimum of 767 elephants used the study area during this period. New elephants, both cow/calf groups and males, entered and were identified in the study area throughout the project. No significant relationship was found between numbers of new elephants per month and

numbers of days spent observing per month (Spearman rank correlation: $r_s = -0.0195$, $N = 21$, $df = 19$, $p = 0.9519$). The monthly numbers of new elephants declined over the study period, with over half of the population being identified in the first five months of the study (Fig. 2). The majority of the population, 76%, was identified during the expected wet season months. The median number of new elephants seen was 20 individuals per month (inter-quartile range 10-37 individuals; $N = 21$). In April 1999 an unusual influx of 102 new elephants was observed, the greatest monthly number of elephants identified since the first month of the study.

Daily numbers of elephants recorded within the reserves fluctuated between 0 and 227 individuals, with a median of 49 individuals (inter-quartile range 24-76 individuals; $N = 327$). Daily numbers were significantly correlated with the observation day of the study ($r_s = 0.3708$, $N = 327$, $df = 325$, $p < 0.0001$). However, this correlation was not present during the last twelve months of the study, which were relatively dry ($r_s = 0.0742$, $N = 222$, $df = 220$, $p = 0.2710$). Daily numbers were negatively correlated with monthly rainfall ($r_s = -0.3597$, $N = 327$, $df = 325$, $p < 0.0001$), indicating fewer elephants were observed in the study area during months with higher rainfall (Fig. 3).

The average daily numbers during months with rainfall greater than twenty-five millimeters (median = 33.5, inter-quartile range 10.5-65.5; $N = 102$ days) were significantly less than numbers in months with rainfall twenty-five millimeters or less (median = 55, inter-quartile range 33-77; $Z = 4.142$, $n_1 = 102$, $n_2 = 225$, $p < 0.0001$). However, the group sizes during months with rainfall greater than twenty-five millimeters (median = 16, inter-quartile range 10-30; $N = 175$) were significantly greater than the group sizes during months with twenty-five millimeters or less of

rainfall (median = 14, inter-quartile range 8-25; $Z = 2.626$, $n_1 = 175$, $n_2 = 673$, $p = 0.0086$). The daily numbers of elephants observed within the study area during the expected wet season (median = 50, inter-quartile range 24-84 individuals; $N = 170$) were not significantly different from the expected dry season (median = 48, inter-quartile range 25-72; Normal Approximation Mann-Whitney Test: $Z = 1.135$, $n_1 = 170$, $n_2 = 157$, $p = 0.2565$). But group sizes during the expected wet season (median = 19, inter-quartile range 10-30; $N = 395$) were significantly greater than those recorded during the expected dry season (median = 12, inter-quartile range 7-20; $Z = 5.943$, $n_1 = 395$, $n_2 = 453$, $p < 0.0001$).

The daily numbers of elephants observed in the study area were more representative of cow/calf groups than independent males, because the numbers of cows observed per day (median = 18, inter-quartile range 9-28 individuals; $N = 327$ days) were significantly greater than the numbers of males (median = 2, inter-quartile range 1-4; $Z = 17.69$, $n_1 = 327$, $n_2 = 327$, $p < 0.0001$). The numbers of independent males per day were correlated with the numbers of cows ($r_s = 0.4897$, $N = 327$, $df = 325$, $p < 0.0001$). The numbers of musth males (Poole, 1987) per day (median = 0, range 0-3; $N = 327$) were also correlated with the numbers of cows ($r_s = 0.2039$, $N = 327$, $df = 325$, $p = 0.0002$), though the relationship was not as strong. This may be a result of the low density of musth males in the study area, as only nineteen individuals were observed in musth during the study period.

Social Structure

Identified cows and calves were grouped into 65 family units. Family unit monthly presence was bimodal, with modes of six family units present for 4 months and

eight family units present for 11 months (Fig. 4). This pattern was used to delineate the population into two categories. The 39 family units using the parks for 9 months or more are referred to as “resident” (56% of the identified cows and calves) and the 26 family units using the parks for 7 months or fewer are referred to as “non-resident” (44%). Although every family unit left the study area, durations of absence varied. Males were generally more transient, and lacked a bimodal frequency distribution (Fig. 4).

The median family unit size was 9 individuals (range 3-36; $N = 65$; Fig. 5). The numbers of individuals comprising resident family units (median = 8, range 3-36 individuals; $N = 39$) were not significantly different from non-resident family units (median = 9, range 3-25 individuals; $Z = 0.194$, $n_1 = 39$, $n_2 = 26$, $p > 0.25$). The elephant birth sex ratio is 1:1 (Poole, 1996). In undisturbed populations, males have slightly higher rates of mortality than females (Laws et. al., 1975; Lee & Moss, 1986; Poole, 1989a). The demographic section of the Samburu population under twenty years old did not significantly differ from the 1:1 ratio ($\chi^2 = 1.134$, $df = 1$, $p > 0.20$). However, the male:female sex ratio of elephants twenty years and older was 1:2.3, which significantly deviated from the expected sex ratio ($\chi^2 = 33.28$, $df = 1$, $p < 0.0001$; Table 1).

Birth and Mortality

The birthing cycles of the two social categories, estimated from numbers of surviving calves, appeared distinct across a five-year sample. The number of surviving calves born to resident family units peaked in 1999, while those born to nonresident family units peaked in 1998 (Fig. 6). The number of births in 1999 was exceptional

with 93 recorded in the population. Over 85% (N = 64) of the calves observed within one month of their birth were born during the wet seasons of that year.

Recorded mortality rates were low. Of the seven confirmed deaths within the reserves, four were calves less than two months of age. Because these elephants were free ranging, it was difficult to distinguish between absent and dead elephants. It is probable that more elephants died during the study period than were recorded.

Although no instances of poaching occurred within the study area, at least six elephants were illegally killed within a 20 km radius of the reserves in February (4) and May (1) 1998, and June (1) 1999. Other instances of poaching occurred in areas that were probably used by the study population.

Discussion

The elephant population of Samburu and Buffalo Springs National Reserves inhabits an unconfined semi-arid ecosystem. The number of elephants identified exceeded previous estimates of the reserves' population. As indicated by fluctuations in daily numbers, the population regularly used regions outside the protected area. The data presented in this paper represent minimum population figures, because not all individuals entering the reserves were observed.

The monthly number of elephants identified progressively decreased during the study. During the final three months, monthly identifications averaged 2.7 individuals. Follow up monitoring had not identified any new cow/calf groups through July 2000, although occasionally young, unidentified males (less than 25 years) were observed (Kahindi *pers. coms.*), indicating the majority of the population had been identified by July 1999.

The daily numbers of elephants observed were positively correlated with the observation day, though the correlation weakened as the study progressed. My monitoring capacity may have induced this trend. However, daily numbers were negatively correlated with monthly rainfall totals, indicating the population was increasingly outside the reserves during wet periods when they were less reliant on the river. The exceptional “El Nino” induced rainfall, which connected the short and long rains during the first year of the study (Fig. 3), may have depressed the numbers of elephants using the reserves through June 1998 by enhancing the ecological conditions in the region. As food and water surpluses outside the reserves gradually declined or became less accessible, portions of the population may have been pushed into the reserves where permanent water and little human competition occur. Daily numbers were not correlated with the observation day during the last twelve months, when monthly wet season rainfall was below average. Additionally, poor security during the initial twelve months of the study may have caused elephants to avoid the region.

Daily numbers were significantly lower in months with rainfall greater than twenty-five millimeters but aggregations tended to be larger during these intervals. Larger aggregations during wet periods have been observed in other ecosystems, where researchers suggested aggregations are ecologically dependent (Douglas-Hamilton, 1972; Moss & Poole, 1983; Moss, 1988). Ranges of daily numbers were wider during wet months, when the maximum daily numbers were observed within the study area (Fig. 3). Increased ranges reflect the mobility of the population, indicating greater daily variation in the numbers moving in and out of the reserves. Additionally, the majority of identification events occurred during the expected wet season months. During the

rains, normally dry regions contain temporary water sources, allowing dispersal that is water limited during the dry season. The observed population fluctuations and increase in identification events may have been related to this “opening” of dry regions, inducing elephant migrations (Western & Lindsay, 1984; Thouless, 1995). Additionally, aggregations were greater during expected wet season months, although daily numbers did not differ across season, indicating elephants may have amassed in anticipation of the rains. This may have been related to social factors such as seasonal peaks in reproduction, as signified by monthly numbers of births.

The 1:2.3 (male:female) sex ratio of elephants twenty years and older is relevant to the management of this population, as it may affect population dynamics (Lewis, 1984; Poole, 1989a; Barnes & Kapela, 1991). The strength of sex ratio skew increased exponentially across age classes. The sex ratio may have been caused by study area biases, such that areas of high cow/calf concentrations were sampled more heavily than areas with equal or higher concentrations of male densities. However, there was no evidence of sexually distinct areas (e.g. Moss & Poole, 1983). In contrast to undisturbed populations that have only slightly skewed sex ratios, similar degrees of skew to that of the Samburu population were observed in elephant populations that have experienced high levels of poaching (Poole, 1989a). The skewed sex ratio was most probably caused by selective poaching, as mature males are more likely than females to be killed for ivory due to their larger tusks (Pilgram & Western, 1986; Poole, 1989a). The observed sex ratio indicated that the population had not recovered from past poaching pressures and may be subject to a current level of poaching sufficient to maintain the skew. Daily numbers were more representative of breeding females than

males as a result of the population differences and the number of musth males, which are the oldest males in a population (Poole, 1987; Poole, 1989b), was low.

The reserves are a focal area for calving, which peaked during the wet season months of 1999. This peak occurred two years after the exceptional rains of 1997, signifying increased breeding activity during that wet year. Additionally, the daily numbers of males, both total and musth individuals, were correlated with the numbers of cows indicating male density may have been partially motivated by cow presence. It is likely musth males excluded other competitors from the study area during their periods of dominance (Poole, 1989b) resulting in little variation in the number of musth males present during the study. The low number of mature males in the population probably also contributed to this trend.

Preliminary analysis was indicative of two distinct social sets, categorized into resident and non-resident families. These groups utilized the reserves differently, which may reflect distinct movement patterns and ranges. Additionally, their breeding cycles varied, indicated by ages of surviving calves, and calving peaks occurred during different years. The two groups may have been affected by different stimuli in relation to fecundity, such as reaction to localized ecological conditions, mobility of the family unit, or insecurity. The age structures of both groups were indicative of high levels of recruitment and the family unit structure was similar across groups. Mature males were largely independent as has been found in other studies (Douglas-Hamilton, 1972; Moss, 1988).

In April 1999 a major influx of unidentified elephants into the reserves was observed. The number of new elephants identified this month was in the 95th percentile

of the identification numbers' range, second only to the initial month of the study. Though not analyzed, these elephants were behaviorally distinct from other elephants in the study area, tending to be more nervous and, in some cases, highly aggressive. Range shifts may be related to ecological, social, or security factors. This unusual influx occurred during the wet season and may have been in response to seasonal variations in range use. However, this month's numbers exceeded any prior seasonal peak and the behavioral abnormalities of these individuals were rarely experienced in the study area. Considering the security situation in the region and the behavior of these elephants, it is likely human disturbance caused this influx.

This study was set up with the aim of providing information on the elephant population and creating an "early warning system" for wildlife authorities regarding marked changes in poaching levels or elephant population shifts. Ecological conditions appeared to be a driving factor of the Samburu population's social behavior and movements. It was clear the population was dependent on areas exterior to the reserves' boundaries. Although the study area was physically unconfined, it may have been constricted by security factors. Ground observations and calving events suggested elephants identified the reserves as a "safe haven". If human pressures reduce the elephant range, the numbers using the reserves may increase. This could have negative ecological effects. Additionally, if stresses on the population increase, the viability of the population may be affected.

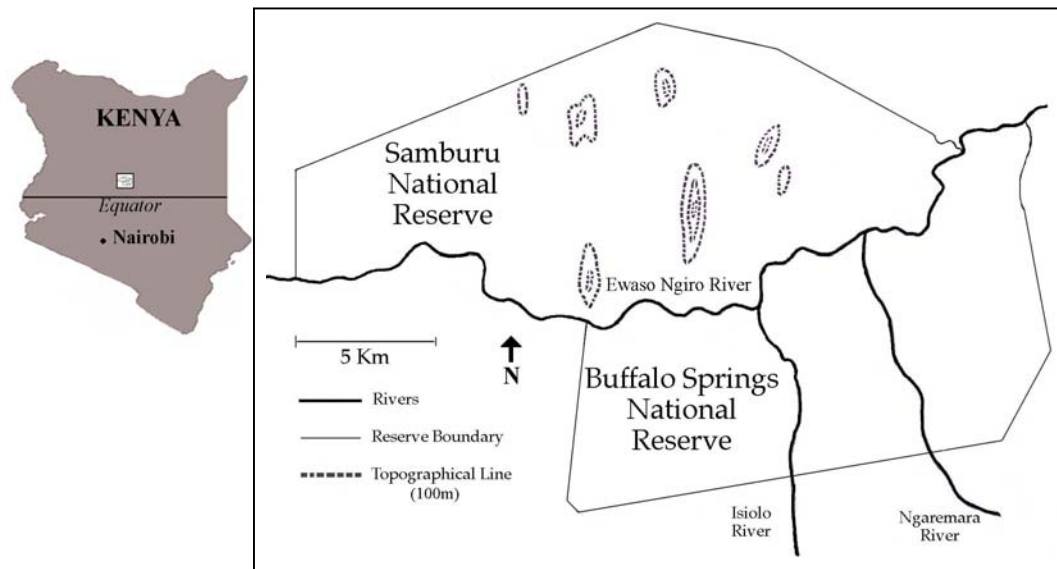


Fig. 1. Map of the Samburu and Buffalo Springs National Reserves study area. The study area, 330 km², is located just north of the equator and centered on the Ewaso N'giro River, the major water source in the region.

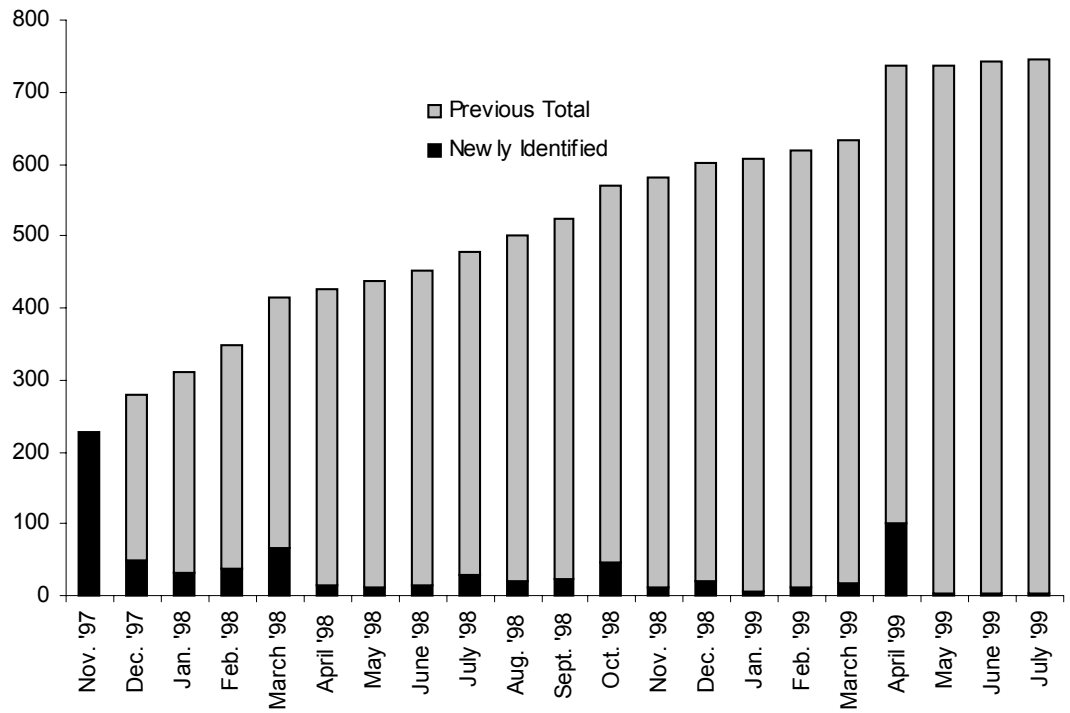


Fig. 2. The number of elephants identified per month varied during the study. The combination of gray and black columns represents the total number of elephants identified in the population during that month. The greatest number of new individuals since the first month of the study was identified in April 1999. Few elephants were identified during the last three months of the study.

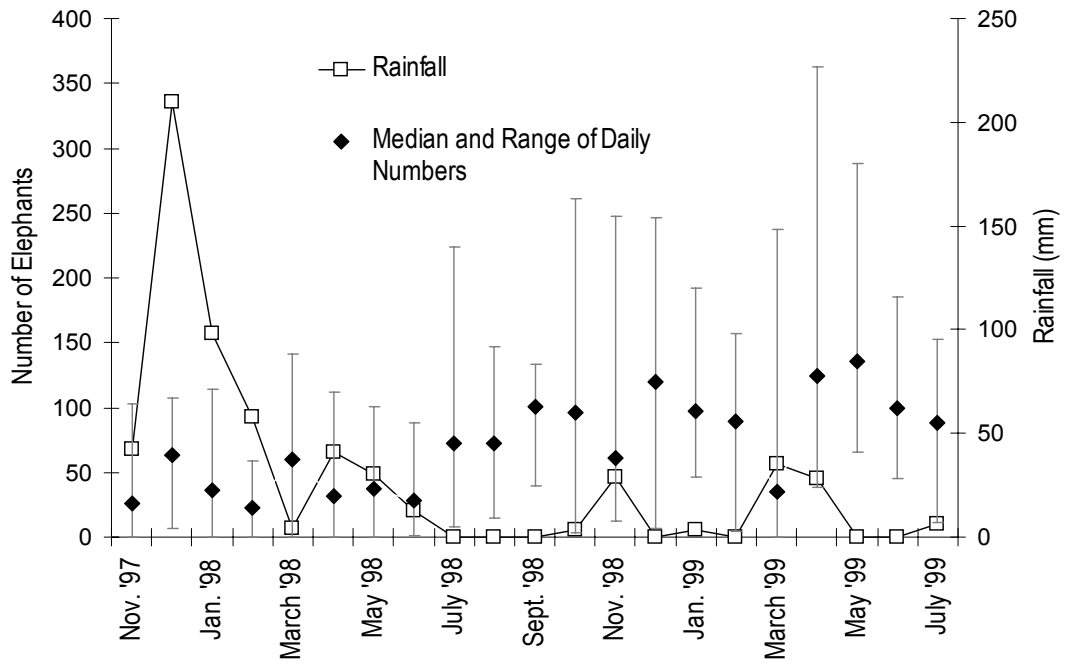


Fig. 3. Monthly rainfall measurements (white squares) were negatively correlated with daily numbers of individual elephants observed in the study area ($r_s = -0.3597$, $N = 327$, $df = 325$, $p < 0.0001$). Black diamonds signify the median number of elephants observed per day. Error bars represent the total range of the daily numbers for that month.

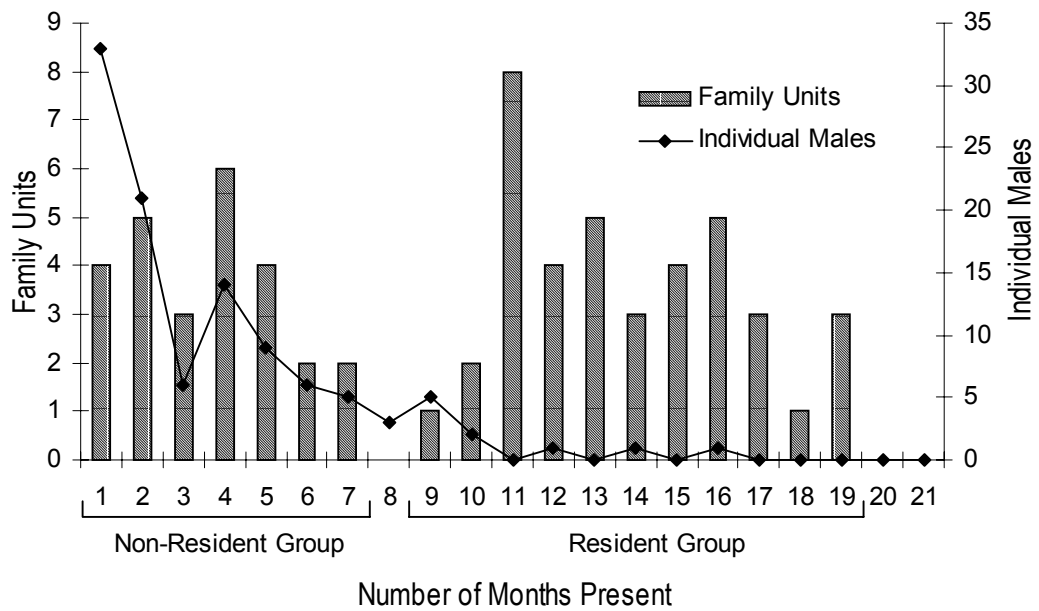


Fig. 4. Columns represent the family unit monthly presence and diamonds represent male monthly presence. The bimodal distribution of family unit presence was used to delineate resident and non-resident family units. The distribution of males was not representative of distinct groups.

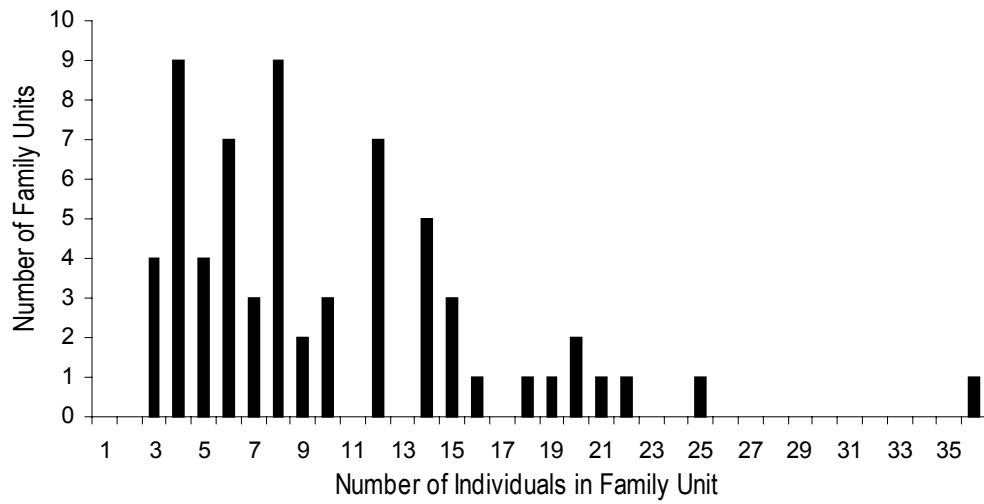


Fig. 5. Distribution of core family unit size consisting of associating cows and their offspring. Breeding females associating greater than $2/3^{\text{rds}}$ of the total number of observations were categorized as a family unit.

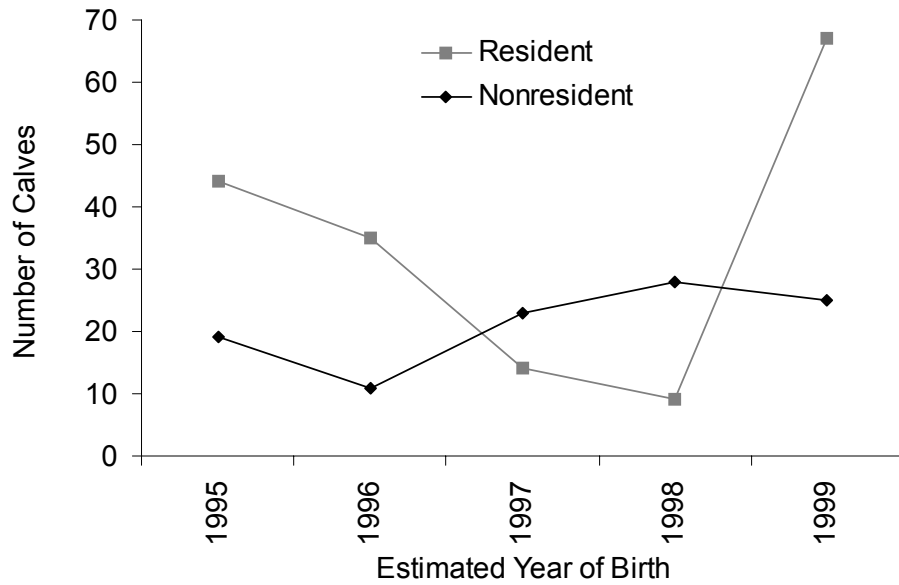


Fig. 6. The number of surviving calves was indicative of a staggered calving interval between resident and nonresident family units. Ages were estimated for calves born in 1995, 1996, and early 1997.

Age Groups (Years)	Males •	Females •	Sex Ratio of Aggregated Ages • : •	Group Population Percentage
0- 4.9	129	121		34%
5- 9.9	77	89	258:279	22%
10-14.9	25	37	(1:1.1)	8%
15-19.9	27	32		8%
20-34.9	47	80	62:145	17%
35-49.9	14	59	(1:2.3)	10%
50+	1	6		1%
Total	320	424		

Table 1: The age and sex structure of the Samburu and Buffalo Springs National Reserve's elephant population

Chapter Three

Demographic Status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya

**G. Wittemyer, D. K. Daballen, H. B. Rasmussen, O. Kahindi, and I.
Douglas-Hamilton**

Introduction

Long term monitoring of known individuals offers the most comprehensive method for recording the demography of an animal population. Our study of individual elephants in the Samburu and Buffalo Springs National Reserves in Northern Kenya began in 1997 with the intention of recording elephant social behavior and demography (Wittemyer, 2001). More recently, our study site was incorporated within Kenya's system for Monitoring the Illegal Killing of Elephants (MIKE), instituted under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In consequence our data assumed a wider relevance within the framework of this international treaty.

This paper presents information on the elephant demography of a core area within the Samburu/Laikipia MIKE Site (Fig. 1) where we have identified over 900 elephants as users of these reserves since September 1997. Although identified in one sub-area, these free-ranging elephants constitute 18% of the approximately 5400 elephants counted in the aerial census of 2002 within the Samburu and Laikipia Districts (Omondi *et al.*, 2002). The Samburu and Buffalo Springs National Reserves cover an area of approximately 320 km². Elephants using the area are free ranging and Global Positioning System (G.P.S.) radio tracking data collected from 14 elephants collared within the study area demonstrate that over 90% of their range lies outside the two reserve boundaries and covers in total approximately 27% of the Laikipia/Samburu MIKE Site (Fig. 1). Our demographic method of monitoring individuals (Douglas-Hamilton, 1972; Moss, 1996) supplements standard MIKE methodologies for measuring elephant mortality, and contributes independent data to the wider ongoing

MIKE studies of the Kenya Wildlife Service within this MIKE site. When carried out over extended periods this method has been shown to be an effective way of monitoring birth and mortality and detecting outbreaks of disease, starvation and human predation (Douglas-Hamilton, 1972; Weyerhauser, 1981; Moss, 1996).

Methods

The Save the Elephants research team has comprehensively monitored demographic changes in the population using the Samburu and Buffalo Springs National Reserves from 1998 to 2003 and every elephant is individually identified (Wittemyer, 2001). Established routes were patrolled weekly, and all individuals encountered were recorded along with new births. Elephants missing from their family units (excluding sub-adult males) or absent from the study area for more than two years were recorded as dead.

Because births and deaths can go undetected among infrequently observed elephants, the demographic data presented in this paper have been estimated by using a subset of the total known population. This subset includes individuals observed in at least three months of every year, amounting to 59% of the known cows and calves and 57% of the known bulls. Male elephants between the ages of 15 and 20 years were particularly infrequent visitors to the reserves; accordingly, the majority of these individuals were excluded from the analysis. This age class appears to be highly migratory, rarely staying within the study area for more than a few months.

Results

The reserves' population increased each year, averaging a 4.6% growth rate per annum over the 6 year study. The number of births fluctuated greatly between years,

varying from 19 in 1998 to 75 in 2003 (Fig. 2). Such fluctuation in births is typical of elephant populations (Laws, 1969; Douglas-Hamilton, 1972; Moss, 2001). The greatest growth rate occurred in 1999 two years after the high rainfall associated with the “El Nino” phenomena (coinciding with elephants’ 22 month gestation period), and the lowest occurred in 2002 in relation to a severe drought in 2000. Recorded births are also seasonal, correlated with monthly rainfall ($R^2=0.578$, $p=0.0041$), as has been recorded in other savannah populations (Laws *et al.*, 1975; Hall-Martin, 1987).

Births exceeded deaths throughout the study period (Fig. 2). The average annual mortality was 2.6%. The greatest number of individual deaths occurred in the youngest (0-5 years) age class, but the oldest age class (over 30 years) had the greatest average annual mortality of 3.4% over six years (Table 1). The greatest mortality recorded over the six-year study coincided with the short but severe drought of 2000 (Fig. 2). Known causes of death were disease, predation by lions and humans, and injury, but the majority of deaths were unspecified as the carcasses were not found (Table 2).

Discussion

By monitoring births and deaths of known individuals we show that the Samburu elephant population is increasing (Fig. 2). Our results are consistent with aerial census data (Omondi *et al.*, 2002), and similar upward trends are reported in most elephant populations in Kenya and Tanzania (Blanc *et al.*, 2003) occurring since the ivory trade ban of 1989. The relatively high rate of increase may relate to climatic conditions during the study, particularly the “El Nino” weather phenomena of 1997 that produced the greatest rainfall since 1961 in the study area. However, a short, severe

drought also occurred during the study period. Because the study area is in a semi-arid ecosystem, elephant reproduction is seasonal and correlated with rainfall.

Average mortality, at 2.6% per annum, was generally low (Table 1). However, over 11% of males older than 30 years in Samburu were lost in one year, and 24.4% (n = 10) died during the study. Since few males are thought to be over 45 years of age, these deaths are unlikely to result from old age. Older females experienced similar rates of loss at 18.8% over the study period. Matriarchs of family units seemed particularly vulnerable accounting for 47.8% (n = 11) of breeding female mortalities. The death of a family unit's matriarch is likely to have important social and fitness impacts on survivors (Moss, 1988; McComb *et al.*, 2000). Calf deaths were often associated with times of nutritional stress (dry seasons). Lions killed 23.8% (n = 10) of recorded calf mortalities, four of which were observed alone prior to their death (Table 2).

Out of 95 recorded deaths (Table 2), nine were confirmed to be caused by humans though only two deaths were clearly the result of poaching for ivory (these carcasses were found with bullet holes and their tusks had been removed). Distinguishing between poaching and human-elephant conflict as the cause of death in the remaining carcasses was not possible, as individuals with human inflicted wounds (spear and bullet holes) were found with tusks in the carcass or observed with injuries prior to their death. Over half (n = 5) of confirmed human related deaths were individuals from the oldest age class. However, only 37.9% (n = 36) of carcasses were located, the majority of which were calves. Elephants with spear and bullet wounds have been observed in the study area numerous times, including individuals within family units that had recently lost individuals. Such wounds suggest that some

individuals recorded as “missing” were likely dead as a result of conflict with people. Furthermore, poaching events occurred outside the protected reserves during the study period. Although these individuals could not be identified, it is likely some of these carcasses were those of individuals recorded “missing presumed dead” from the study population, making the number of illegally killed individuals greater than reported here.

Due to the importance of tourist traffic, the wildlife authorities offer a high level of surveillance and the elephants are currently well protected within the study site. Elsewhere in the Samburu/Laikipia MIKE Site there is less patrolling. With births exceeding deaths we conclude that in our central study area there was little impact of ivory poaching on the population from 1998 to 2003. This contrasts with the heavy mortality reported during the 1970s in the Samburu area caused by ivory poaching (Ottichilo *et al.*, 1987). Although our study area is only a segment of the whole, the monitoring of known individuals provides a sensitive early warning system that would detect any serious increase in poaching. Current recording of carcasses within the entire MIKE site by the Kenya Wildlife Service and analysis of the causes of death will give a broader picture of mortality trends throughout the ecosystem and set a base line for measuring poaching impact in the future.

Age Class	Males	Females	Unknown	Total Deaths	Total Individuals	Annual Mortality
0-5	20	11	11	42	336	2.1%
6-15	4	5	0	9	198	0.8%
16-30	11	7	0	18	133	2.3%
Over 30	10	16	0	26	126	3.4%

Table 1: Deaths presented by age class from 1998-2003 and the average annual mortality per age class

Cause of Death	Total	Sub-Adult	Adult ♂	Adult ♀
Carcass Not Found	59	30	10	19
Disease	12	6	4	2
Predation (Lion)	10	10	0	0
Human	9	1	6	2
Injury/Drowning	3	2	1	0
Unknown	2	2	0	0

Table 2: Causes of Mortality (disease was not tested for but prescribed to carcasses symptomatically)

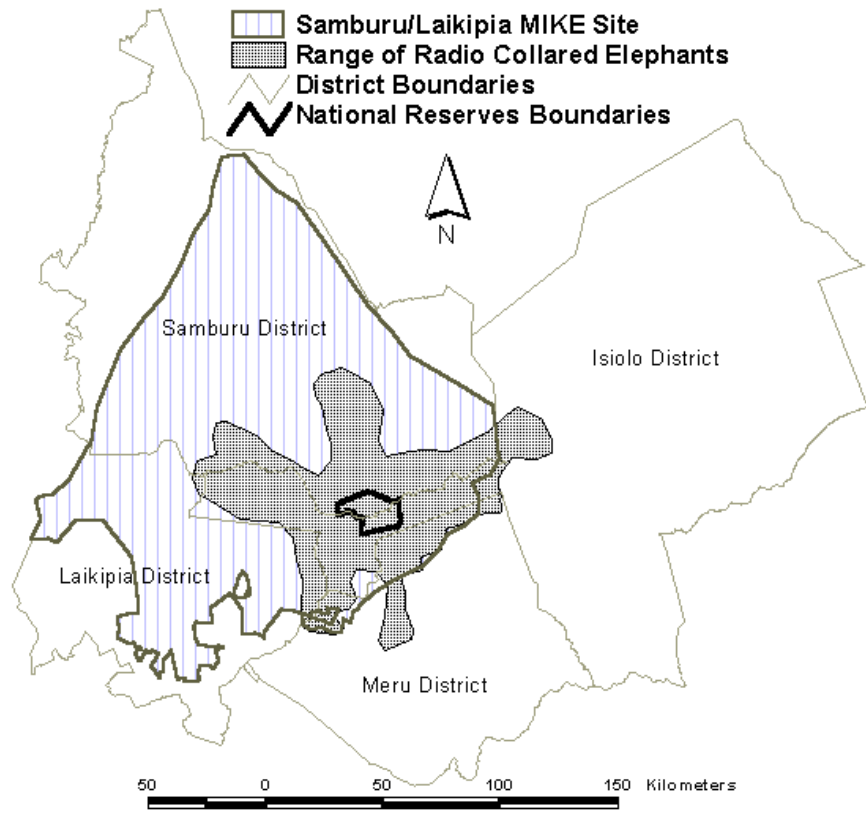


Figure 1: The range of 14 radio tracked reserve elephants, District boundaries, and National Reserve boundaries in relation to the Samburu/Laikipia MIKE site.

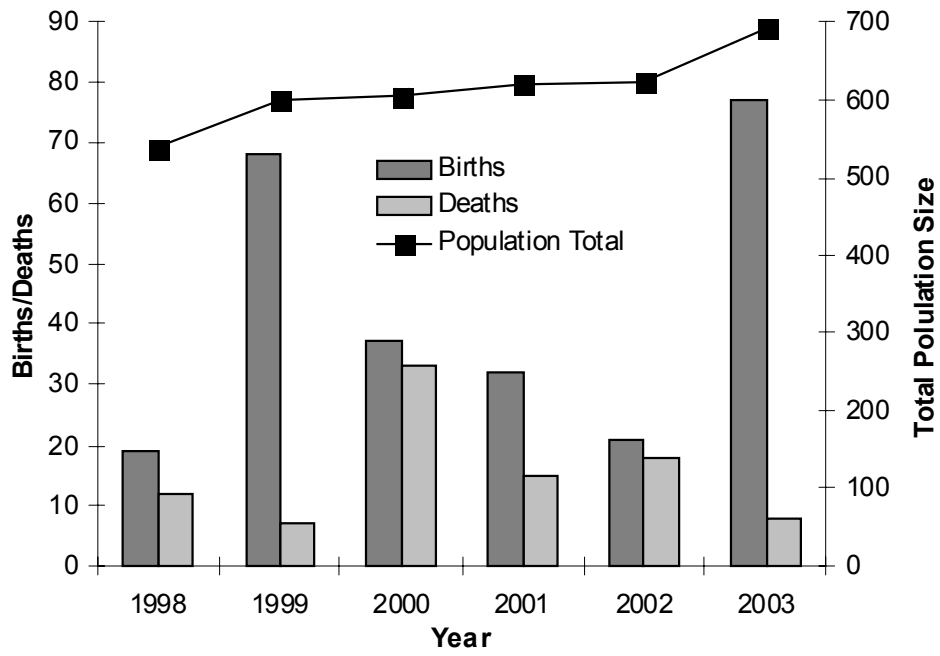


Figure 2: Annual population total, births, and mortalities.

Chapter Four

The influence of variability in primary productivity on female elephant reproductive strategies

G. Wittemyer, H. B. Rasmussen, I. Douglas-Hamilton

Introduction

The impact of the temporal distribution of resources on population dynamics has been the focus of increasing research prompted by the availability of long time-series studies (Saether, 1997). Resource availability affects the ability of mothers to allocate resources to offspring, thereby influencing recruitment, a parameter to which population dynamics in ungulate populations are highly sensitive (Gaillard et al., 2000). The ability to time reproductive activity to coincide with periods of increased resource availability can help to cover the energy costs of reproduction and, thus, can impact lifetime reproductive success (Kennish, 1997; Pianka, 1976). As such, it is not surprising that for many species the phenology of reproduction is closely related to temporal variation in food availability (Drent & Daan, 1980; Kennish, 1997; Langvatn et al., 2004; Rubenstein & Wikelski, 2003; Sinclair et al., 2000).

The reproductive strategy and resulting phenology employed by a species is impacted by both life history constraints and ecological influences (Clutton-Brock & Coulson, 2002). In northern temperate regions, parturition in most ungulates occurs predictably during the period of highest primary productivity in the spring, which relates to the constraints of a short growing season in the strongly seasonal environments of this region (Stearns, 1992). In contrast, parturition phenology in tropical and subtropical regions is not predictable across all species and the influence of life history constraints appears to impact reproductive strategies to a greater extent than in other latitudes (Sinclair et al., 2000). Savanna elephants (*Loxodonta africana*) exhibit life history traits characteristic of large ungulates in that they are strongly iteroparous, have low fecundity and high adult survivorship, generally produce only one offspring

per reproductive bout, and have long generation times. As compared to ungulates, however, elephants exhibit distinct life history traits that impact their ability to respond to ecological variability or other factors influencing population demographic fluctuations. Each reproductive bout in an elephant includes the longest gestation period experienced by a terrestrial mammal (approximately 656 days), extended parental care of young in which weaning typically occurs after 2-5 years, and overlapping, dependent offspring necessitating extensive, long term energy investment in offspring. These life history constraints, in combination with the stochastic ecological variability in primary productivity characteristic of savanna ecosystems, necessitate a distinctive reproductive strategy to overcome the costs of reproduction.

Reproductive phenology may be shaped by resource needs and ecological conditions during parturition, conception, or a combination of both. Many studies of the factors influencing reproductive activity are focused on parturition events, probably in relation to the importance of offspring survivorship to ungulate population dynamics (Gaillard et al., 2000) and the high cost of lactation (Oftedal, 1984). Additionally, conception in many mammals (e.g. large ungulates) is hidden, making research on the factors influencing conception more difficult to study. In order to understand the proximate cues for reproductive phenology, however, the factors influencing the timing or rate of conceptions (in which the concerns for the mother's vitality are paramount (Hogg et al., 1992)) should be distinguished from those influencing parturition (in which the survivorship of offspring is paramount (Gaillard et al., 2000)). Research on the timing of conception and parturition events can offer insight into the interaction between life history constraints and factors influencing fitness as well as further

understanding of the processes causing fluctuations in population dynamics. Here we investigate the relationship between temporal variability in primary productivity at different periods in the elephant reproductive cycle, distinguishing the influence of ecological variation on the timing of conception versus the timing of parturition.

The parturition rates of African elephants, the largest terrestrial mammal, have been shown to vary widely across years in multiple populations, resulting in cyclic recruitment of different age classes (Douglas-Hamilton, 1972; Laws et al., 1975; Moss, 2001). Synchronicity in reproductive parameters, necessary for the emergence of cyclic demographic fluctuations in a population, has been related to variability in food availability, population density, and predation pressure in other organisms (Gaillard et al., 2000; CluttonBrock et al., 1997). The mechanisms influencing elephant population fluctuations, however, remain poorly understood despite investigation of these pertinent factors on elephant demography (Laws et al., 1975). Here we demonstrate that factors influencing both parturition and conception in elephants are essential to understand the emergence of such demographic fluctuations. In this paper, we compare the time-specific reproductive rates, recorded over a seven year period from an individually identified, wild elephant population in northern Kenya, with remotely sensed NDVI (Normalized Differential Vegetation Index), a direct measure of spatially explicit vegetative productivity (Goward & Prince, 1995). Through our assessment of reproductive responses to variations in primary productivity, we are able to evaluate the reproductive phenology of this generalist herbivore in both the pre and postnatal phases of reproduction. This information is important for the management of wild populations and captive breeding programs.

Material and Methods

Data Sets

The reproductive activities of the individually identified members (following established methodology (Moss, 1996)) of the elephant population inhabiting the semi-arid Samburu National Reserve in northern Kenya have been monitored intensively since 1997 (Wittemyer, 2001; Wittemyer et al., 2005). Between November 1997 and August 2004, 265 births were recorded from the 172 most frequently observed and hence best known breeding females (i.e. seen within the study area at least 9 months of each year). Almost all births are believed to have been recorded during this period, as few of the studied females' inter-calf intervals exceeded the 4.5 year average recorded in the closely studied Amboseli elephant population (Moss, 2001). Conception dates of females that died while pregnant were not recorded but unlikely to bias results as mortality rates were low during the study period (Wittemyer et al., 2005). Using the aging techniques established with known aged elephants (Moss, 1996), the birth date of calves less than one month old can be estimated accurately to within one week, providing detailed longitudinal data on the timing of reproductive events. The estimated ages at the first sighting of calves used in this study averaged 12 ± 15 days (S.D.), with 253 of the 265 calves (95%) being observed less than one month after the estimated parturition date. In order to approximate the date of conception for the known parturition events, we subtracted the average gestation period of 656 days (approximately 22 months) from the estimated date of birth (Moss, 1983).

Because analysis of conceptions in this study may be biased by not accounting for the effect of prenatal mortality on observed parturition events, an analysis of a smaller data set of observed estrus events was conducted. Estrus activity was defined by the observations of mate guarding/mating by males and distinct estrus behavior by females (Moss, 1983). Fewer estrus events were observed than the number of births, however, probably in relation to the relatively short duration (4 – 6 days) of behavioral estrus (Moss, 1983). Thus our record of estrus events is incomplete. We compared known estrus events occurring during a 4-year period in the study (November 1997 and November 2001) with estimated conception dates to assess the robustness of relying on parturition data for the calculation of conception probabilities. A total of 31 behavioral estrus events were observed. Two (6.5%), however, were definitively mistakes by the male elephant in that the bull was attempting to mate with a female during mid pregnancy when the female could not have ovulated. Thus, our analysis is conducted on the 29 potentially true conception events.

In many tropical and sub tropical areas, rainfall has generally been used as an indirect measure of the seasonal changes in green biomass (Sinclair et al., 2000; Georgiadis et al., 2003). Studies of savanna ecosystems have also found that seasonal flushes in grasses, occurring concurrently with seasonal rains, contain the highest concentrations of proteins and therefore may be of great significance for savanna inhabitants (Sinclair, 1977). Variability in factors such as rainfall pattern, soil type, and the degree of habitat degradation in an area, however, can have significant effects on the response of vegetation to rain (du Plessis, 2001). NDVI (Normalized Differential Vegetation Index), available from the NOAA AVHRR (Advanced Very High

Resolution Radiometer) and SPOT (Satellite Probatoire d'Observation de la Terre) programs, is a remote sensing index value calculated as the ratio between red and near infrared reflection. It is highly correlated with green biomass (Goward & Prince, 1995). Thus, NDVI acts as a direct assessment of the spatial and temporal variability in vegetation growth (Rasmussen, 1998; Diallo et al., 1991).

To measure time-specific vegetation productivity, we used 10-day composite NDVI values recorded by the NOAA-AVHRR (1995 - 2001) and SPOT (1998 - 2004) systems. NDVI values from these two systems were calibrated and combined using a 2-year overlap in order to cover the study period (Fig. 1). We calculated mean NDVI values for each 10-day period for a 1,158 km² region covering the population's core area, defined by the 95% kernel isopleth (Worton, 1989) calculated using hourly G.P.S. data collected from 12 breeding females tracked for 10-14 months between 2001 and 2003. Vegetation productivity is most accurately estimated by NDVI when values are averaged over a generalized large area (du Plessis, 1999). We found both maximum and minimum NDVI values in the core area were closely correlated with average values per 10 day period, demonstrating that average values were representative of variability in productivity across the core area. Each wet/dry cycle was defined as starting with an increase in the mean NDVI values greater than or equal to 2 standard deviations above the dry season baseline (i.e. the mode of the distribution of composite NDVI values during the study period) and lasting until the next increase of two standard deviations (i.e. encompassing contiguous wet and dry seasons).

Analysis

Studies of reproductive phenology focus on the ecological variability occurring within a year (e.g. Sinclair et al. 2000). Because our study system receives two distinct periods of rainfall per year, in April and November, we focus on the relationship between variability in primary productivity and reproduction both within a seasonal cycle (2 per year) and between cycles across the seven-year study (13 cycles). Specifically, our study investigates between-season reproductive activity (“if to breed”) and within-season reproductive phenology (“when to breed”).

Because of elephants’ long gestation period, each individual is not able to respond reproductively to each pulse in primary productivity. Rather, the number of non-pregnant, breeding (of reproductive age) females varies across cycles in relation to the number of females impregnated. In addition, seasons vary markedly in the duration and degree of primary productivity (Fig. 1). This between-season variability is likely to influence reproductive activity (“if to breed”). We investigated the relationship between between-season variation in vegetative productivity and the proportion of females conceiving. A strong correlation between these two variables indicates that the initiation of a reproductive bout is influenced by differences in between-season ecological conditions and, as such, would synchronize reproduction in a population. In contrast, a weak correlation indicates the initiation of an elephant’s 3-5 year reproductive bout is unaffected by stochastic variation in primary productivity, resulting in little variability in seasonal reproductive rates. In order to investigate the affect of such between-season variability on elephant reproductive phenology, we used a multiple regression analysis to compare the proportion of non-pregnant, breeding-aged females conceiving per season with two indices of primary productivity between-season variability—the cycle

specific maximum NDVI value and duration of elevated NDVI values above the dry season baseline. Non-pregnant periods for females were defined as starting at the onset of the cycle following parturition. The proportion of females conceiving during each cycle was normalized by arcsine transformation before analysis (Zar, 1999).

Conception and parturition events are linked by a fixed gestation period making it difficult to assess which of the two events are governing within-season reproductive phenology (“when to breed”). To determine whether conception or parturition were linked to time-specific primary productivity within each season, we analyzed the relationship between the timing of both reproductive events and within-season variation in the onset of increased primary productivity associated with the start of the seasonal rains. If females conceive at a fixed interval after the actual seasonal start, regardless of variation between seasons, the timing of conception events appear to be a response to season-specific conditions. Such a scenario indicates greater importance of available resources during early pregnancy, where conception occurs after a fixed period of increased resource availability. In contrast, a delay in the occurrence of conceptions in early-starting as compared to late-starting seasons is indicative that within-season reproductive phenology occurs around a static calendar date. This scenario suggests within-season reproductive timing is driven by parturition events, such that parturition occurs during the average period of increased primary productivity as a result of the adjusted timing of conception. Furthermore, the strength of the relationship between parturition phenology and primary productivity would be demonstrated if reproductive timing results in parturition events occurring concurrently with the average onsets of a

wet season such that reproductive energy expenditure is closely correlated with the increased quality of available food resources.

To investigate which of these scenarios occurs in our study population, we analyzed the median season-specific timing of reproductive events (the median number of days between actual season start and conception dates) and compared this with relative seasonal start. Some seasons had too few conceptions to estimate accurately the timing of conceptions. Thus, we limited this analysis to seasons containing 10 or more events. The variability in timing was not normally distributed across all cycles, so nonparametric analysis was conducted to determine if the timing of conceptions varied significantly across seasons. All other data were normally distributed, enabling the employment of parametric techniques. Statistical tests were conducted using S-PLUS 6.0©.

Results

Comparisons of estimated conception dates and start date of the wet/dry cycle demonstrated that conception events do not coincide with the cycle onset. Instead, conceptions tended to occur much later than the onset with the median delay of conception after the cycle onset being 76 days (inter-quartile range: 52–98 days; Fig. 2). The median number of days after the seasonal NDVI peak (maximum wet/dry cycle NDVI value) that conceptions occurred was 38 (IQR range: 15–63 days) with 86% percent of all conceptions occurring after the peak in vegetation productivity, when NDVI values were declining.

In contrast, parturition coincided with the start of the wet cycle, occurring a median of 4 days before the cycle onset (inter-quartile range: -27–27 days; Fig. 2). The dates of conception events were compared to the specific cycle onset dates during the study period to assess the influence of the variability in cycle-specific timing on reproductive activity. The difference between conception dates and the actual date of cycle onset (1st increase in NDVI values) per season varied significantly across seasons (Kruskal-Wallis test: $\chi^2 = 34.126$, $df = 7$, $P < 0.001$). The differences between the start date and median conception date for each cycle were negatively correlated to that cycle's relative start date ($R^2 = 0.658$, $y = -0.7166x + 72.55$, $P = 0.008$; Fig. 3), indicating females conceive later in early starting cycles and earlier in late starting cycles. Parturition dates were also negatively correlated with relative cycle start dates ($R^2 = 0.778$, $y = -1.1547x - 2.2117$, $P = 0.002$).

The effects of the two wet/dry cycle quality indicators, duration of increased NDVI values and maximum NDVI value, on conception probabilities were investigated in a multiple regression model. The duration of increased NDVI did not add significant information to the model ($t = 1.31$, $P = 0.219$; model results: $F = 31.438$, $R^2 = 0.863$, $P < 0.001$) and was therefore removed. A simple regression model with maximum NDVI explained a significant proportion of the variability in conception probabilities ($R^2 = 0.839$, $y = 1.7547x - 0.5298$, $P < 0.001$). Conception rates ranged from 0.0% in one of the poorest cycles to 58.7% during the wet/dry cycle with the greatest maximum NDVI value (Fig. 4). No relation was observed between parturition rates and cycle specific maximum NDVI values ($R^2 = 0.0004$, $y = 0.0289x + 0.1784$, $P = 0.948$). Of the

combined births recorded over the 7-year study comprising 13 wet/dry cycles, over 55 % were conceived during the four best cycles and less than 15% in the six poorest.

This correlation between the proportion of successful pregnancies and vegetation productivity could be the result of high rates of prenatal mortality during poor cycles or condition dependent estrus. To distinguish between these possibilities, we assessed the proportion of estrus events that resulted in births from observations of behavioral estrus events (Moss, 1983) during the first four years (eight cycles) of the study. Estrus events were not correlated with the number of available females ($R^2 = 0.120$, $y = 0.023x + 1.696$, $P = 0.317$). Observed estrus events were correlated with the number of conceptions carried to term ($R^2 = 0.674$, $y = 0.133x + 0.752$, $P = 0.0067$) and positively but not significantly correlated with maximum wet/dry cycle NDVI values ($R^2 = 0.355$, $y = 10.978x - 2.0639$, $P = 0.090$). Of the 29 observed estrus events, six (20.7%) did not result in calf birth 21-22 months later. Of these, four females gave birth approximately 16 weeks later than the estimated birth date from the observed mate-guarding event corresponding to a delay of one ovarian cycle (Hodges, 1998). It appears these females failed to conceive during the mate-guarding event, experienced their full ovarian cycle, and subsequently ovulated and conceived. In 3 of the 4 cases, this missed estrus event and subsequent conception occurred within the same wet/dry cycle (thus not affecting the results in our analysis). In the last two cases, females gave birth more than four years after the observed mate-guarding event (corresponding to the duration of two full pregnancies). This indicates that either the calf was carried to term but lost before it was observed or the estrus observation was erroneous (see Methods).

Discussion

Our study of the reproductive phenology of a wild elephant population indicates conception rates are influenced by between-season variability in primary productivity while parturition is coordinated to coincide with expected within-season variability in primary productivity. The majority of conceptions carried to term occurred during cycles with increased NDVI values and happen approximately one month after the maximum level of vegetation productivity was reached in the ecosystem. This delay of conceptions until after the period of peak vegetation productivity indicates that elephants consume the majority of high quality resources associated with the seasonal rains prior to becoming reproductively active, potentially enabling the assessment of the relative value of that season prior to investing in a reproductive bout. The proportion of non-pregnant females conceiving and later giving birth varied greatly between wet/dry cycles and was strongly correlated with cycle specific vegetation productivity (Fig. 4), with the cycle maximum NDVI value explaining over 83 % of the variation in conception probabilities. The proportion of females giving birth, however, was not correlated with the cycle-specific vegetation productivity at the time of birth, as expected in an organism unable to predict future conditions at the time of conception or adjust to conditions at the time of parturition. Thus our study indicates initiation of an elephant's 3-5 year reproductive bout is gauged by ecological conditions at the season of conception. Elephants appear to accumulate resource stores prior to ovulation and conception and may forgo expending energy in reproduction when ecological conditions are poor. This response suggests the existence of condition dependent estrus and a physiological threshold below which reproductive activity ceases. Such traits are

characteristic of a capital breeding reproductive strategy, in which a species stores resources prior to initiating a reproductive bout (Madsen & Shine, 1999).

In order to ensure the relationship between conception rates and vegetation productivity was not caused by prenatal mortality, we analyzed a smaller data set of observed estrus events. If prenatal mortality was the factor causing this observed correlation, the mean number of estrus/mate-guarding events is expected to be equal across wet/dry cycles regardless of conditions or at least correlated with the number of non-pregnant breeding females; that is, proportional to the number of available females rather than ecological conditions. Observed estrus, however, was not correlated with the number of non-pregnant females but significantly correlated with the number of conceptions carried to term, indicating prenatal mortality in response to poor vegetation productivity is an unlikely explanation for the observed correlation with seasonal specific quality. Evidence for prenatal mortality linked to low vegetation productivity was also not found, indicating that the majority of conceptions are carried to term. The most likely cause of error in our analysis, at a maximum of 7% in our sample of estrus events, appears to be calves that die after birth but before we observe them. Thus, we conclude that conception rates were strongly related to ecological quality with few to no conception events occurring during wet/dry cycles with low vegetation productivity.

Contrary to conceptions, which are correlated with inter-cycle variation, parturition is strongly shaped by within-cycle variability. The differences between conception dates and the corresponding cycle onset dates varied significantly between seasons, indicating the temporal cue for elephant estrus is not simply the onset of wet seasons. The differences between the dates of specific cycle onsets and the

corresponding mean conception dates were negatively correlated with the relative onset of that cycle (Fig. 3), indicating elephants time conception around fixed calendar dates (during either the April or November rains). Thus, conception is delayed in relation to the cycle onset during seasons with earlier starts causing the resulting dates of parturition to coincide with the average initial increase in vegetation productivity in the ecosystem. The differences between the dates of specific cycle onsets and the corresponding mean parturition dates were also significantly negatively correlated indicating parturition is timed around calendar dates such that elephants give birth after the cycle onset in early starting seasons and prior to the cycle onset in late starting seasons. These results indicate gestation periods in elephants cannot be altered in response to ecological conditions, rather conception dates are adjusted such that the average birth date over the study period occurred during the average cycle onset date. The reproductive energy costs of post-partum investment (lactation) occur in coordination with the onset of future expected high quality ecological conditions, allowing ingestion of resources during lactation to cover the costs of the postnatal reproductive stage. Relying on ingested resources to cover reproductive energy costs is characteristic of an income reproductive energy allocation strategy (Stearns, 1992; Jönsson, 1997).

The mechanism by which elephants time these events is not clear since specific seasonal onset is not the cue. It seems reasonable to assume they use a general environmental stimulus such as photoperiod or temperature to time reproduction. However, photoperiod does not seem likely because reproductive activity occurs twice a year in relation to the two wet seasons, which are separated by approximately 6 months.

Furthermore, the study area is situated half of a degree north of the equator such that day length varies by less than 30 minutes across the year. Temperature, also, does not appear to be the cue as most conceptions occur during the January “hot” season or during the June “cold” season, though temperatures also do not fluctuate substantially across the year.

Elephants, having long gestation periods and high levels of postpartum offspring investment, face an ecological conundrum regarding how to budget resources for reproduction when living in unpredictable environments. Elephant calves are generally not fully weaned until the birth of their sibling, meaning females are lactating at the time of conception and, at times, successive suckling calves may overlap. This constraint of overlapping dependent calves is potentially the major factor shaping the reproductive phenology of elephants. As is common in north temperate species, elephants coordinate parturition to within-season flushes in primary productivity (Stearns, 1992). The life history constraint of their extended reproductive bout, however, inhibits the ability of elephants to predict resource quality at the time of parturition. In making the best of this limitation, elephants initiate their extended reproductive bout based on the quality of the season at the time of conception. Thus, we suggest elephants maximize their use of experienced ecological conditions at the time of conception and rely on probabilistic resource availability during parturition when resource quality cannot be predetermined, employing distinct reproductive strategies during the different stages of reproduction.

The influence of cycle-specific primary productivity on conception rates has the effect of synchronizing reproduction in a population. During our study, the El Niño-

Southern-Oscillation (ENSO) resulted in a period of unusually high primary productivity in the study ecosystem during 1997 and early 1998 (Fig. 1). This major perturbation in the dry and wet season primary productivity cycle strongly influenced elephant conception rates, acting to synchronize reproduction across the population. Additionally, poor rains and resulting low levels of primary productivity in 2000 resulted in no known conceptions, again affecting the synchronization of population reproductive activity. In contrast to other ungulates in which climatic or density driven mortality of juveniles drives population fluctuations (Gaillard et al., 2000), our study population experienced low mortality rates the duration of our study (Wittemyer et al., 2005). Thus time-specific recruitment in elephants does not necessarily relate to mortality rates. Rather, climatically-elicited synchronization in reproductive rates is the likely cause of fluctuations in population age structure recorded in several other populations (Laws et al., 1975; Douglas-Hamilton, 1972).

The characteristic ecological variability and annual dry periods in savanna ecosystems when energy allocation is most strained may have disposed elephants to a capital breeding strategy, encouraging the development of energy buffers for periods of stress. The size of this species limits the cost of carrying excess energy stores (Jönsson, 1997). However, due to their 22-month gestation period and the variability in ecological quality over a year, energy stores at the time of parturition are likely depleted pushing elephants towards a reliance on income resources during post-parturition lactation. Thus, elephants must rely on both energy stores and available resources to ensure successful offspring recruitment. Energy constraints in other species have also required switching between reproductive energy allocation strategies (Shanbhag, 2003)

or a mixed strategy approach (Lourdais et al., 2002; Lourdais et al., 2003).

Investigation of the reproductive strategies employed by an organism during both the pre and post-natal phases of reproduction can serve to enhance understanding of the constraints impacting a species and can offer insight to the factors influencing population demographic cycles.

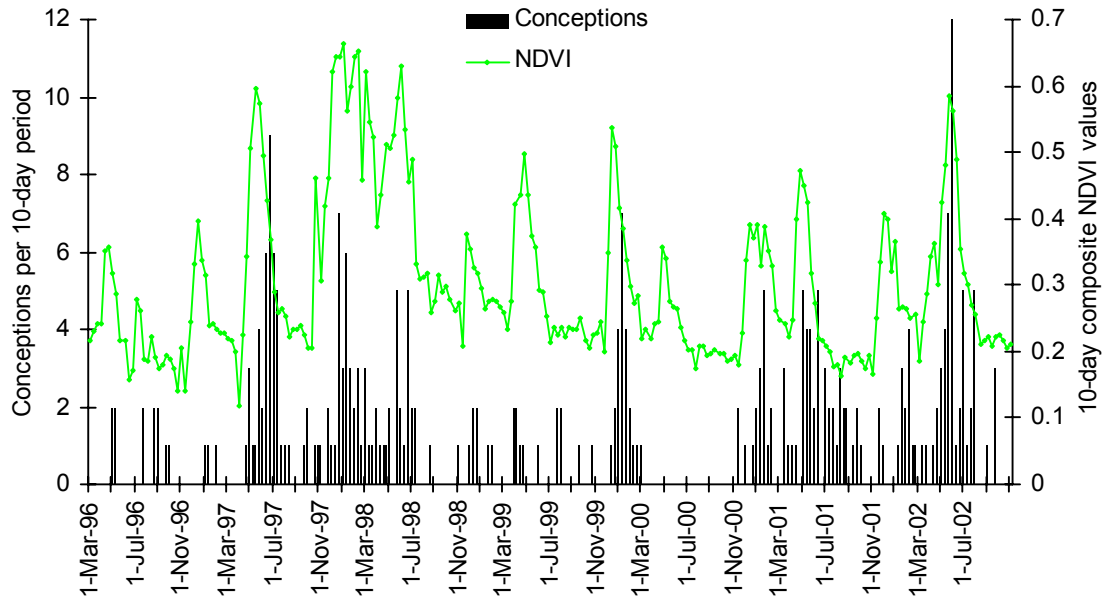


Figure 1. The mean 10-day composite NDVI values (line) for the core study area and total number of conceptions per 10-day interval (bars; calculated by subtracting 656 day gestation period from known time of birth). The high NDVI values and corresponding number of conceptions in 1997-98 resulted in few non-pregnant females available during the following 22-month period. The relatively low NDVI values associated with the April 2000 “drought” occurred concurrently with the only season with 0 conceptions.

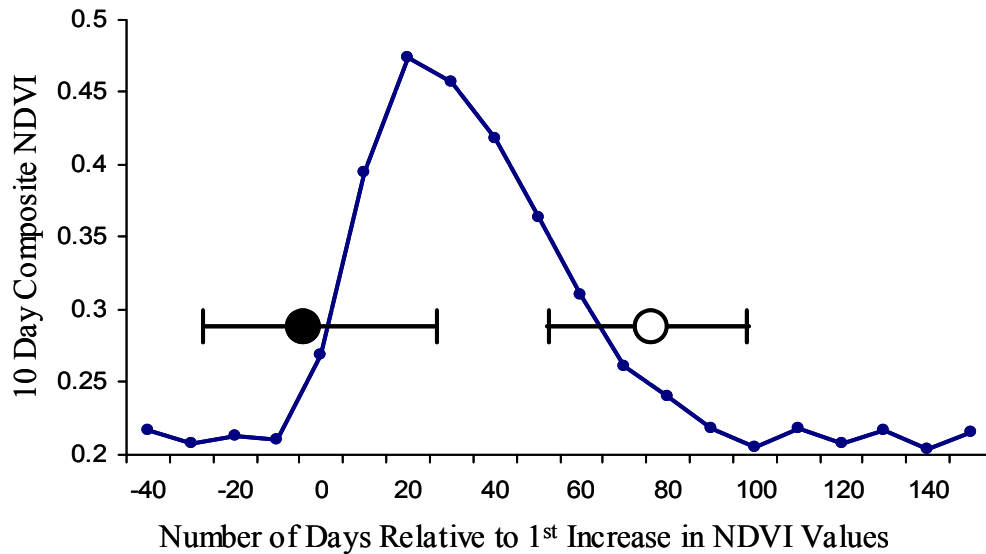


Figure 2. Parturition events (solid circle) coincide with initial increases in NDVI values (employed as a surrogate for resource quality in this study) enabling post-partum costs to be covered by available resources. Conception events (open circle) occurred after periods of increased NDVI values, enabling an individual to gauge and store the best available resources before committing to reproduction. The NDVI values presented characterize the average duration and maximum values of wet season periods during the study. The timing of reproduction in the study population is depicted, where the median date of parturition events (solid circle) occurred 4 days before the initial rise in NDVI values and the median date of conception events (open circle) occurred 76 days after the initial rise in NDVI values; error bars on the circles represent corresponding inter-quartile ranges.

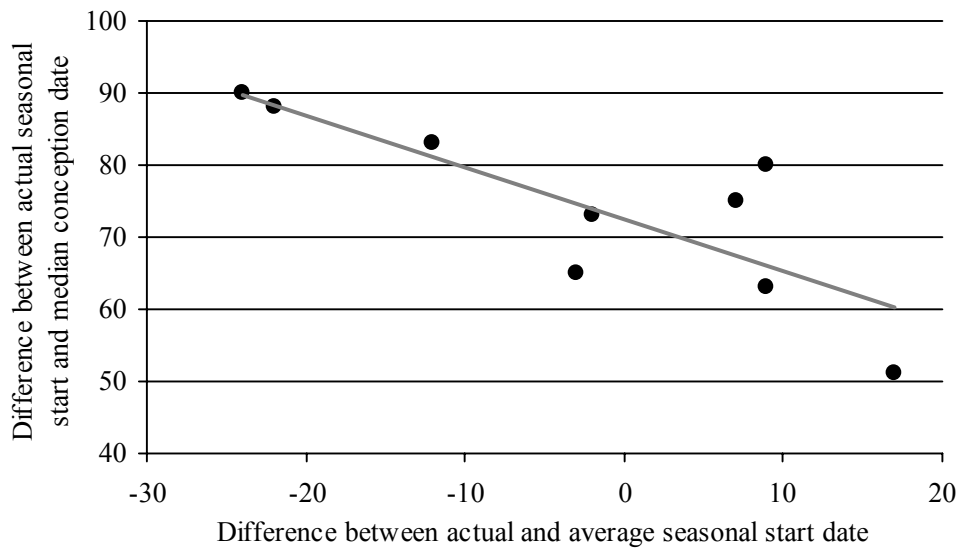


Figure 3. The median delays of conceptions occurring per wet/dry cycle are negatively correlated with the relative start date of that cycle—the difference between the average and actual seasonal start date. In cycles where the initial increase in NDVI values occurred later than average (positive values on the X-axis) the average date of conceptions for that cycle occurs earlier (lower values on the Y-axis). Thus, females are generally conceiving later in early starting seasons and earlier in late starting seasons ensuring births occur around the average date the rains begin. Seasons with less than 10 births were excluded from this analysis (N = 9).

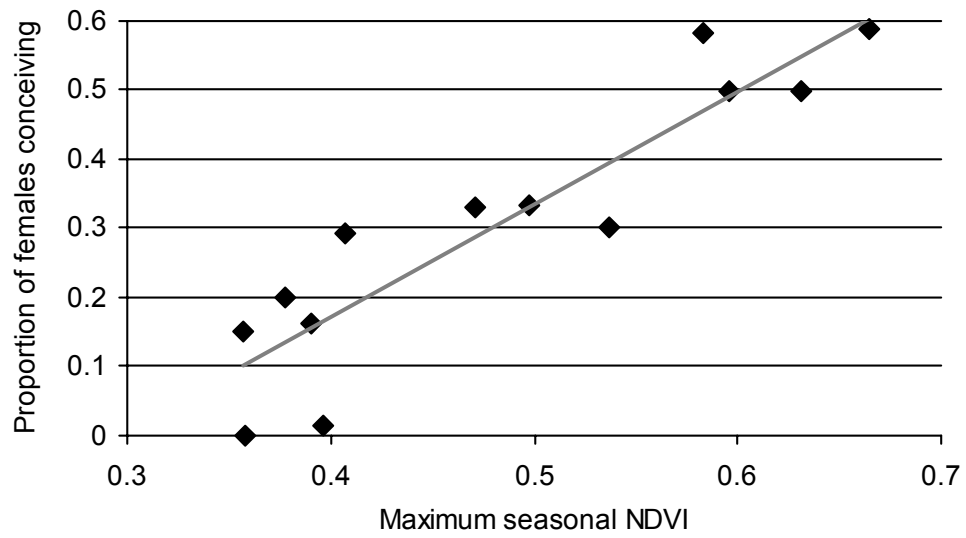


Figure 4. The proportions of non-pregnant females conceiving per cycle were highly correlated with maximum seasonal NDVI values ($R^2 = 0.839$, $y = 1.755x - 0.530$, $P < 0.001$; proportional data is normalized by arcsine transformation in the regression). Few conceptions occur in seasons with low NDVI values, signifying an ecological threshold level below which elephant females cease reproductive activity.

Chapter Five

**The socio-ecology of elephants: Analysis of the processes creating
multi-tiered social structures**

G. Wittemyer, I. Douglas-Hamilton, and W. M. Getz

Introduction

Ecological constraints, by impacting both mating systems and population structure, are formative factors in the evolution of social systems (Emlen & Oring, 1977; Clutton-Brock & Harvey, 1977). In combination with their genetic underpinnings, the type and structure of individual-based interactions relates to the abundance and distribution of food or predation (Alexander, 1974; Wrangham, 1980; van Schaik, 1989; Isbell, 1991). The socio-ecological hypothesis serves as a framework for studies of this particular relationship between ecological factors and social behaviour (Emlen & Oring, 1977; Vehrencamp, 1983; Terborgh & Janson, 1986; Emlen, 1995; Kappeler & van Schaik, 2002).

The ecological factors affecting a species sociality vary across time and space. Ecological and social costs and benefits play a role in determining social unit size in fission-fusion societies (Devore & Washburn, 1963; Kummer, 1968). Fission-fusion societies limit the effect of within unit competition through unit splits during periods of high competition (Dunbar, 1992; Kummer, 1995) and enhance cooperative effects through unit cohesion when the ecological costs of aggregating are low or benefits of sociality arise (Takahata et al., 1994; van Schaik, 1999). Aggregating behaviour is generally thought to be a response to predation pressures (Hamilton, 1971). Widely distributed food resources are believed to promote the evolution of fission-fusion social organizations as a response to fluctuations in the costs of feeding competition (Schaller, 1972; Altmann, 1974; Jarman, 1974). However, individual based studies focusing explicitly on the variability of social unit structure in relation to ecological factors are few. Here we use individual association behaviour to assess the impact of season and

time on social unit composition and cohesion, looking at the influence of ecological factors on the social organization of a free-ranging African elephant population.

In many animals social relations are enigmatic or cryptic and thus difficult to record (Whitehead, 1997). Using Hinde's (1976) framework for the study of social behaviour based on interactions among individuals, recent work has used association indices to assess the social properties of populations (Cairns & Schwager, 1987; Whitehead, 1995). The objectives of studies employing these methods are testing the deviation from randomness of animal associative behaviour and identifying preferred and avoided associates (Myers, 1983; Whitehead & Dufault, 1999; Kerth & König, 1999). Despite the importance and variability of social layering in human societies (Freeman, 1992; Cummins, 2000), little attention has been given to such structuring in animal societies, apart from some work on cetaceans (see Mann et al., 2000). Building on these associative based methods, we used clustering techniques to identify social delineation in elephant society. Our methods empirically substantiate previous inferential descriptions of six hierarchical tiers of organization (Buss, 1963; Laws, 1970; Douglas-Hamilton, 1972; Moss & Poole, 1983): mother-calf units (tier 1), families (tier 2), bond/kinship groups (tier 3), clans (tier 4), subpopulations (tier 5), and populations (tier 6). Identification of the form and function of nested social tiers can serve to further studies of sociality in numerous animal species that have more than one level of social organization, such as prairie dogs (Hoogland, 1995), cetaceans (Mann et al., 2000, Conner, 1992), geese (van der Jeugd et al., 2002), and multiple primate species (Strier, 2000). In this paper, we focus on the relationship between socio-ecological forces and the emergence of a multi-tiered social structure that appears to

conform to the above 6-layer paradigm. Identification of the primary factors influencing the fission-fusion process at each social tier provides insight into the ecology of a species and can enhance studies on the evolution of complex social structures.

Being generalist herbivores with low digestive efficiency, elephants spend 60-80% of each 24-hour day feeding (Owen-Smith, 1988). The patchy distribution of resources in savannah ecosystems, in combination with their heavy feeding requirements, makes elephants susceptible to intra-specific competition. Such competition in other animals limits both social unit size and their proximity to one another (Jarman, 1974; Clutton-Brock & Harvey, 1977). Slight variation in forage quality and quantity may have marked impacts on elephant interactions. In order to explore this, we examine social unit structural variation across the wet and dry seasons over a four-year study period. Further, we look at temporal changes in social structure in order to assess social dynamics occurring due to the longer-term process of population growth. Potential benefits derived from the described social structure are also discussed. Building upon the socio-ecological framework, this study focuses on the factors influencing individual social behaviour and their relation to the fission-fusion social dynamic in a multi-tiered social organization.

Methods

Study Area

Samburu and Buffalo Springs National Reserves are small, protected areas in the greater Samburu/Laikipia ecosystem of northern Kenya. These reserves hold the largest elephant population, numbering approximately 5200 individuals, residing primarily outside protected areas in Kenya (Omondi et al., 2000). As a result of heavy tourist use

of the parks, the elephants using these reserves are habituated to vehicles, enabling easy observation of their behaviour. Between November 1997 and May 1999, all elephants using the two reserves were individually identified and tentatively categorized into two subpopulations, termed resident and non-resident, based upon their degree of reserve use (Wittemyer, 2001). The parks are unconfined and the primary land use in this semi-arid region is livestock grazing in communally owned group ranches that have few or no fences.

The majority of the observations in this study were collected within the boundaries of Samburu and Buffalo Springs National Reserves between June 1998 to August 1999 and May 2000 to December 2002. The total study area lies between the 0.3-0.8° N, 37-38° E. Samburu and Buffalo Springs National Reserves are 320 km², comprising less than 2% of the greater Samburu/Laikipia ecosystem and generally 15-25% of the study elephants' home range (unpublished G.P.S. radio-tracking data). The reserves are centred on the Ewaso Ngiro River, which is the only permanent water source in this semi-arid region and, as such, a focal area for wildlife (for further description of the study area see Wittemyer, 2001).

This region is drought prone and rainfall is sporadic, with the majority of rain falling during the two wet seasons in April and November. Because rainfall is unpredictable, seasons were defined using daily rainfall totals collected on the reserve boundary. Dry seasons were defined as beginning after 30 days of 0 mm rainfall. Wet seasons were defined as beginning after one week with 15 mm or greater rainfall (the approximate amount of precipitation required to get a vegetative response). Single day

showers between two-week periods of 0 mm rainfall were not considered to elicit a seasonal change.

Data collection

For purposes of clarity, we define the following terms used throughout this paper to describe the social context of elephants.

- (1) Aggregation: A collection of elephants in the wild observed at a particular time to be associated with one another (see below for spatially explicit definition of association)
- (2) Cluster: structural unit of a tree constructed using clustering methods (Romesburg, 1984)
- (3) Tier i units: social or supra-social units (assemblages of individuals defined from analysis of clustering results following the methods described below) within a hierarchical organization where tier i units are composed of tier $i-1$ units, $i=2-6$.

Our study focuses on the social behaviour of breeding female elephants, defined as individuals with dependent calves, because the distribution and organization of females is generally thought to relate to the pattern of resources and risks in their environment, whereas males organise themselves around the distribution of receptive females in time and space (Trivers, 1972; Emlen & Oring, 1977). All females over 20 years of age in the study population have at least one dependent calf. Generally, a breeding female is associated with her juvenile offspring 100% of the time, though this bond weakens as juveniles mature (10-13 years) with males dispersing from their mother's social unit after puberty (Douglas-Hamilton, 1972; Moss, 1988). Such tight

bonds result in identical association behaviour between a mother and her calf (tier 1 social units); thus, for purposes of analysis, these mother-calf units were treated as a single entity represented by the mother. Our analysis of social behaviour focused on the “resident” (5th tier) subpopulation comprising 112 breeding females and their calves, representing 382 elephants and 46% of the total (6th tier) population of breeding females identified within the study area (Wittemyer, 2001).

The majority of observations used in this study were collected by observers recording all individuals encountered along one of 4 set routes travelled per day. Routes followed existing roads running the length of the reserves both to the North and South of the Ewaso Ngiro River, where routes 1 and 2 were within 500 meters of either riverbank and routes 3 and 4 were located approximately 5 kilometres from the river on either side. Observations of elephant aggregations during non-transect movements in the study area (opportunistic sampling) were also collected and used in this study. All observations were recorded following the same protocol. Once elephants were spotted, observers approached to within 100 meters or less of the aggregation and recorded the following for each observation: (a) identity of individuals present, (b) accuracy of the observation (recorded in categories: 1) 100% identification of all individuals, 2) identification of all breeding females and males excluding calves, and 3) incomplete identification), (c) location of aggregation (G.P.S.), and (d) the date, time, observer name, and route name. The observer stayed with the aggregation until all individuals were recognized, unless thick vegetation did not allow a complete accounting. The data presented in this study is compiled from 2889 observations of aggregations where the observer was confident of registering all associating breeding females, i.e. observation

accuracy 1 and 2. Each individual's aggregation was recorded only once per day to avoid non-independence of observations. In all instances of multiple observations per day, the first observation was retained to avoid potential observer (preordained) bias regarding the location or social context of individuals. The average number of observations per breeding female was 132 (minimum = 73, maximum = 284).

Elephant aggregations, for calculation of association indices, were defined as individuals estimated to be within a 500 m radius of an observationally estimated aggregation centre (elephants are generally clustered within a small area, thus social aggregations are easily recognized). When aggregations exceeded this 500 m radius definition, we used a modified criteria where an aggregation was defined by being separated from the nearest other aggregation by a distance greater than its diameter. In order to standardize observations between the individuals used in the study, aggregation data were converted into simple association indices between all dyads in the study

population (Ginsberg & Young, 1992): $\frac{X_{AB}}{N - D}$ where X_{AB} is the number of

observations during which A and B are together, N is the total number of observations, and D is the number of observations during which neither A nor B were observed (thus including only observations when A or B were observed). Because association indices are a ratio of the total observations of two individuals together and separate, results are robust against sample size differences between individuals.

Difference from random structure

Previous studies of social structure based on individual association behaviour focused on assessing the differences between observed and random patterns of association (Manly, 1995; Bedjer, et al. 1997; Whitehead, 1997). We applied these

established methods to our elephant association data in order to verify that observed elephant associations deviate from random. SOCPROG 1.2 (Whitehead, 1999) performs this analysis by generating random association data sets by switching 1 (associated) and 0 (not associated) values in rows of recorded association data (Bedjer et al., 1997). These random data sets are constrained such that the number of observations per individual and group sizes per observation match the original data, and are then used for comparison with actual indices of association in order to identify non-random properties of the study system (Bedjar et al., 1997). Additionally, SOCPROG 1.2 offers a method for assessing the change in individual association behaviour over time by estimating the probability two animals will associate at the same level across time lags (Whitehead, 1995). We ran 20,000 routines to assess the robustness of associations over time, as described in Bedjer et al. (1997). In order to evaluate preferences in associations, observation data must be partitioned into sampling periods. A sampling period of 10 days was selected for this analysis, because the primary observer was able to cover all sampling routes at least twice within this period, increasing the likelihood of encountering those elephants present. All possible sample periods were assessed in the analysis of lagged association rates (Whitehead, 1995).

Structuring

Hierarchical social tiers were defined through a two-step analysis employed to identify emergent properties of the association data: 1) A cluster analysis—the simplification of multi-dimensional information into a two-dimensional representation—of the raw data was conducted to objectively represent the structure of the study population (Strauss, 2001). In order to determine the most appropriate

clustering method for our data, we assessed the degree to which cluster results fit the observed data using the cophenetic correlation coefficient (CCC) (Romesburg, 1984). Only clustering results with CCC values >0.8 (the accepted standard—Romesburg, 1984) were used in the second step. 2) For each of the clustering trees we obtained (Figs. 2 and 4), we created a cumulative graph of the number of bifurcations (branches) occurring per 0.05 bifurcation distance (d) increment (the bifurcation distance is the Y-axis of a cluster tree, increasing up the tree as the degree of association between individuals decreases). This cumulative bifurcation graph was then used to identify putative knots, defined as points on the cluster tree where the rate of bifurcations below the knot was significantly different from rates above the knot (see below for further description). Thus, knot values indicate points of structural changes in the cluster method tree and were subsequently defined as social tier delineations.

We created hierarchical trees and cumulative bifurcation graphs for association data on all 112 breeding females in the study subpopulation (Romesburg, 1984; Strauss, 2001) using four different clustering methods: the Unweighted Pair-Group Method (UPGMA), Ward's Weighted (Ward's), Complete Linkage (CLINK), and Single Linkage (SLINK), were compared (Table 1). The Ward's Weighted Clustering Method yielded the highest CCC value (Table 1) and, consequently, Ward's results were used in subsequent analyses to identify social tiers. We assessed the significance of all potential putative knots (points around which the slope of preceding and succeeding points changes) in the cumulative bifurcation graph by comparing the distribution of bifurcations per stepwise increment above versus below the knot values using the Wilcoxon rank-sum test. The Wilcoxon rank-sum Z-statistics of all contiguous,

significant knots were compared and the putative knots that maximized the Wilcoxon rank-sum Z -statistics were used to delineate social tiers (Fig. 1). The bifurcation value associated with the selected knot was then used to define the social units of the defined social tier where individuals bifurcating below the knot value were considered to be part of the same social unit (Fig. 2). In order to assess the integrity of the defined social units, the compositions of social units characterized using each of the four clustering techniques independently were compared (Table 2).

Significant knot values ($p < 0.05$) separate sets of points that can be fitted with lines of different slope above and below the knot. The formation of units above and below the knot thereby occurs at different rates for a given rate of increase in the bifurcation distance variable d . Biologically the knot indicates where the type of affiliation between individuals in merging clusters is changing from that of a tight, high AI value to a looser, lower AI value. Lower AI values are related to longer term fissions of component groups within a cluster or more frequent rates of fission and fusion of these groups. In social systems where individuals associate at random, knots separating clusters into tiers that aggregate at different rates are not expected to be evident (Fig. 3). In our case, the graph is distinctly concave down suggesting the primary social tier (comprised of the greatest number of bifurcations) occurs at a high AI level, followed by more loosely associated upper tiers with fewer bifurcations. Biologically this implies the core social tier is comprised of stable, tightly associated units: potentially coalitions or kinship based groups such as a family. This contrasts with social systems producing concave up graphs where a high density of linkages occur in an upper tier predicated by a few individuals associating in the lower tier level. Biologically this would indicate the

primary social structure is a relatively unstable, looser aggregation of individuals, potentially in the form of a loose herd.

After definition of 2nd tier units, the data were reduced to include only associations among the matriarchs of each 2nd tier unit (see below for definition of matriarch) in order to identify higher order social tiers. The strengths of 2nd tier associations inundate the weaker higher order relationships, thus all relationships below the identified 2nd tier knot value were excluded from this subsequent analysis. Ward's clustering method, subsequently run on the reduced association matrix, was the only method that yielded a CCC value greater than the 0.80 standard (Table 1; Romesburg, 1984). Consequently, it was the only method we used in the analysis of defined social units at levels above the 2nd tier. Further, multiple significant knot values emerged in two of the data partitions (described below) from this analysis (the wet season and 1998-2000 data while the other sets did not contain more than one significant knot— See Results and Discussion). Identification of multiple knots followed the same procedure as the analysis conducted for the 2nd tier with the additional method of repeated comparisons of potential knots in order to maximize the sum of Z-statistics for both knots simultaneously. The two significant knots were used to define two social tiers: 3rd-tier units were defined as the consortium of 2nd tier units whose bifurcation points lay below the 1st knot of the matriarch tree, 4th tier bifurcation points lay between the 1st and 2nd knot, and the subpopulation (potentially the 5th tier social delineation) used in this study lay above the 2nd knot (Fig. 4).

For evaluation of ecological and temporal effects on social structure, matrices of association indices from observations during the wet and dry seasons and temporal

periods 1998-2000 and 2001-2002 were created. The numbers of aggregations recorded for each partition were (seasonally) 1795 during dry periods, 1094 during wet periods, and (temporally) 1404 during 1998-2000, 1485 during 2001-2002. Differences in the number of observations in the dry and wet season relate to differences in the length of each season (dry periods are typically longer) as well as the tendency of elephants to aggregate in fewer, larger groups during the wet season. Analyses of both seasonal and temporal association matrices were conducted using the methods described above. Structures from each partition were compared with results from the total data set in order to ascertain the degree of social stability. Social stability was assessed in two manners: 1) individual stability—defined as the number of individuals assigned to the same units as found with the total data set and 2) unit stability—defined as the number of units with identical compositions to those defined from the total data set, where a unit is unstable even if a single individual changes membership (Table 3). These analyses provide information on the variation in social structuring seen across seasons, or ecologically distinct periods, and time, or periods differentiated through demographic changes. Furthermore, the social networks of individuals (the number of total study animals with which an individual was observed to associate) were compared across seasonal and temporal partitions using paired statistics.

The matriarch of a social unit was defined, on the basis of behavioural observations, as the individual that was dominant to all other unit members (where dominant individuals physically displaced subordinate individuals from resources). Age estimates of matriarchs were conducted using physical features such as shoulder height, body length, and facial features (Moss, 1996). The ages for 16 breeding females have

been assessed through molar evaluation (a method with an approximate error of ± 2 years; Laws, 1966) either after death or during radio collaring operations (Rasmussen et al., *in press*). Differences between our estimates and molar evaluated ages were minor, averaging 2.5 ± 1.5 years, and estimates were generally greater than molar evaluated ages. Known aged individuals were then used for comparison with estimated individuals.

Correlative Coherence Analysis (CoCA)

Previous studies have used the mean and standard deviation of association index values to look at differences in individual associations (Myers, 1983; Gowans et al., 2001). In a population of size n , the average is taken over $\frac{n(n-1)}{2}$ pairwise indices. These indices, however, are partially correlated with each other and thus not independent, particularly in social units of closely associated individuals such as those found in 2nd and 3rd tier units. Correlative coherence analysis (CoCA) (Getz, 2003) accounts for the fact that a group of n individuals only has $n - 1$ degrees of freedom when finding a single value to represent the “average” degree of association among n individuals, and thus not susceptible to potential problems with non-independence. CoCA produces a single number that generalizes the concept of association from two to n individuals and was developed to generalize the concept of the correlation between two sets of measurements to the correlation among $n \geq 2$ sets of measurements (Getz, 2003). Association indices among pairs of individuals, because they range from 0 to 1, are equivalent to nonnegative correlations among these pairs of individuals. The method for computing the CoC value of an n -dimensional associate matrix A is as follows (Getz,

2003): Calculate the n eigenvalues λ_i ($i=1, \dots, n$) of A . The CoC value of A is then the solution r to the equation

$$(1 + (n - 1)r) \ln(1 + (n - 1)r) + (n - 1)(1 - r) \ln(1 - r) = n \ln n + \sum_{i=1}^n \lambda_i \ln\left(\frac{\lambda_i}{n}\right)$$

We note that if all pair-wise associations in a system had the same value, r , then their CoC value would also be r . In this sense, r is an average measure. We also note that CoC and average AI values are similar in populations where all units have reasonably high levels of association or all units are similarly associated. Whenever the matrix A contains many 0s then the CoC value greatly exceeds the average AI value. This is the reason for the striking differences in AI values and CoC values in the 4th tier and population social levels in Table 4. Intuitively the reason for this difference follows from the fact that for the 3-unit system for which $a_{12} = a_{13} = a_{23} = 1/3$ (i.e. all units associate 1/3 of the time with each other) the CoC value = 1/3, while for the system $a_{12} = 1$, $a_{13} = a_{23} = 0$, the CoC value = 0.702. In both cases, the average value for a_{ij} ($i \neq j$) is 1/3, but in the latter case the measure of coherence should be much higher because we have 2 of the 3 units associating with one another all the time. From this example we obtain an intuitive feel for the reason why CoC values are more appropriate to assess group cohesion than average AI values, particularly in populations where the levels of association among units varies greatly between 0 and 1.

Statistics

Statistical analyses and all clustering methods were conducted using the software package S-Plus 6.0. Non-parametric statistical methods were used in this study except for comparison of seasonal social networks. The Wilcoxon paired-sample test

was used for comparisons of the seasonal differences in social units' CoC values and 2 tailed, paired t tests used to compare the distributions of social networks across seasons and temporal periods. Jackknife techniques were used to get estimates of variances for CoC values of non-replicated events (i.e. the wet and dry matrices for the total population and matrices of a social unit before and after its matriarch's death) (Shao et al., 1996). Median and inter-quartile range (IQR) values are presented for data sets compared with non-parametric techniques, and mean and standard error (SE) values are presented for normally distributed data.

Results

Differences from random structure

Using the methodology of Whitehead (1999), we found the association behaviour of the Samburu elephant population differed significantly from random. Observed association indices were significantly lower than random association indices (observed = 0.085, random = 0.093, $p < 0.0004$), indicating elephants maintain preferred associations within 10 day sampling periods constraining the number of dyads associating (Whitehead, 1999, Gowans et al., 2001). Additionally, the standard deviation of observed association indices was significantly greater than that of random (observed = 0.145, random = 0.086, $p > 0.9999$; this high p value for the 2 tailed test specifies a significantly larger observed value than the random value), indicating elephants maintain preferred associations across 10-day sample periods. Lagged association rates are used to assess the duration of associations in a population, where the rate decreases across the period of the study if associations are short lived or remain constant if relationships are stable (Whitehead, 1999). We found lagged association

rates decreased slightly during the first 7-10 day sampling periods and were relatively stable for all lagged durations exceeding 10 days (Whitehead, 1995).

Seasonal and Temporal Data Set Analysis

Compositions of defined 2nd tier social units were stable across the four clustering methods compared. Structurally, 50 units were defined from three of the four methods, with 51 identified from the fourth (Table 2). In comparison to the Ward's methods, which gave the greatest CCC value (Fig. 2; Table 1), only 4 of the 112 individuals were grouped differently in 2nd tier units defined from the combined three other methods. We used a reduced data set composed of only the 50 2nd tier unit matriarchs for identification of higher social levels. Four distinct, hierarchical social tiers emerged from this analysis of interactions among elephants comprising the studied subpopulation; where delineations of breeding females into 2nd tier units, 2nd into 3rd tier units, and 3rd into 4th tier units were defined statistically (Fig. 4; Table 4).

Association data were partitioned by season (wet and dry) and year of study (1998-2000 and 2001-2002), and then analysed independently to allow comparison of results derived from temporal or seasonal effects. The explicit, individual compositions of 2nd tier units, "family units" (Buss, 1961; Laws, 1970; Douglas-Hamilton, 1972), were largely stable across data set partitions. The greatest change occurred in the 2001-2 partition where 6 of 112 individuals changed by splitting off to form new family units (Table 3). Both seasonal partitions demonstrated greater consistency, with 3 (wet) and 2 (dry) individuals changing social units as well as consistent numbers of social units (Table 3).

Our ability to separate 3rd from 4th tier units, defined from relationships among 2nd tier matriarchs, was greatly affected by the seasonal partitioning. The delineation between these two tiers emerged only during the wet season, as neither dry season nor total data sets demonstrated significant knot values (Table 3). Additionally, this delineation was evident only during the earlier stages of the study, in the 1998-2000 data set, though at a cohesively weaker level with $d = 1.3$ (Table 3).

Social units of the 4th tier were the least cohesive with the greatest variability at both the individual and unit level occurring during the dry season, where 10 matriarchs (20%) were grouped in different 4th tier units and only 5 (62.5%) of identified 4th tier units were identical in composition to those from the total data set (Table 4). Additionally, the number of 4th tier units increased by 2 in the dry season in comparison with the wet season, and increased by 1 in the later half of the study as compared to the first half (Table 4). The 1998-2000 temporal data set was relatively stable with only 2 individual changes and 75% of units identical in composition to the total data set, while the 2001-2 data set was less so, with 6 individuals changing social units and 75% of units identical (Table 3).

Comparison of cohesion between social tiers and among data partitions within social tiers were conducted using CoCA, offering a method to quantify the average cohesion of a matrix while taking into account the correlation among matrix elements (Getz, 2003). CoC and average AI values generally depicted the same trends in behaviour (Table 4), though CoC values are greater than the average AI values especially when many dyads' AI values are zero as occurs in the 4th and 5th social tiers (see methods for explanation of this difference). Previous studies have used the average

AI value to compare social cohesion (Myers, 1983; Gowans et al., 2001). As noted in the methods, however, AI values are not statistically independent. Cohesion, as measured by CoCA, decreased from the 2nd to the 5th tier, with the highest levels occurring among core 2nd tier units. Corresponding to the cluster method results, levels of cohesion differed significantly across each tier (Kruskal-Wallis $\chi^2 = 24.627$, $df = 3$, $p < 0.0001$; Table 4).

Across all social tiers, seasonal effects on CoC values were apparent (Table 5). The CoC values of 2nd tier “families” generally increased during the wet season as compared to the dry season, however the difference was not significant ($p = 0.086$). We used wet season definitions of 3rd tier “bond/kinship” units in order to compare unit cohesion, finding significantly greater wet season CoC values than those of the dry season ($p = 0.002$). Significantly greater cohesion was also found in 4th tier “clans” during the wet season than the dry season ($p = 0.0156$). However, 9 out of 50 2nd tier, 4 out of 25 3rd tier and 1 out of 8 4th tier units demonstrated the reverse with greater cohesion during the dry season than the wet. The 5th tier subpopulation showed the same general seasonal affect found in tiers 2-4, with the wet season CoC value exceeding that of the dry season. Like cohesion, social networks increased in size significantly during the wet season when individuals associated with an average of 98 individuals (87.6% of the total study individuals) in contrast to dry season networks averaging 80 individuals (71.0% of the total) (2-tailed, paired t -test, $t = 12.152$, $df = 111$, $p < 0.0001$). However, social networks were not significantly different across temporal periods of the study (2-tailed, paired t -test, $t = 1.285$, $df = 111$, $p = 0.201$).

Demographic changes in the size of a 2nd tier unit through time are likely to influence its stability, and one might expect the sizes of 2nd and potentially 3rd tier units to be distributed around some ecologically and sociologically determined optimal size. Interestingly, we found no evidence for this: the distribution of the number of 2nd tier units comprising the 26 3rd tier units was not different from random, in this case a Poisson distribution of the same mean ($\chi^2=0.19277$, $df=2$, $p>0.900$), while the distribution of individuals (breeding females and their calves) in the 50 2nd tier units did deviate from random, but was bimodal (Fig. 5). We choose to organise these data into the sum of two distributions based on matriarch age (the generation time for elephants is 17.4 years (Moss, 2001) so elephants twice the age of the generation time, 34.8 years, are more likely than not to be grandmothers). Again, the distributions of each category based on matriarch age did not significantly differ from random (35 years and older: mean=9.85, $\chi^2 = 8.363$, $df = 12$, $p > 0.500$; less than 35 years: mean = 5.02, $\chi^2 = 10.142$, $df = 5$, $p > 0.050$) indicating an optimal group size did not exist when accounting for units with different age structure. Matriarchs younger than 35 years, however, lead significantly smaller families than matriarchs 35 years and older (median_{younger}=4, median_{older}=10: Wilcoxon Rank-Sum: $N_{\text{younger}}=23$, $N_{\text{older}}=27$, $Z=4.666$, $p<0.0001$) thus matriarch age does have an effect on the size of social units.

Discussion

Elephants exhibit stable, non-random social behaviour. From cluster analysis of association data, we were able to delineate four hierarchical social tiers from the continuum of social interactions. These four tiers have significantly different degrees of cohesion (Table 4) and responded differently to temporal and seasonal effects.

Individuals generally displayed strong unit fidelity across time and season, but fusions of lower tier units into higher tier units and fissions of higher tier units into lower tier units occurred regularly. Variability in unit composition across data partitions was generally the result of switches by a few individuals across social units (Table 3). Thus, the majority of individuals' social relations and the 4 tier social organization were relatively consistent during the study period.

Previous studies of elephant social structure describe three social tiers, tier 1-3, and three non-social tiers, 4-6 (Douglas-Hamilton, 1972; Moss & Poole, 1983). Our study is the first to quantitatively demonstrate this multi-tiered social structure. Our 2nd tier units correspond with the definition of “family unit” (Buss, 1961; Laws, 1970; Douglas-Hamilton, 1972), which are groups of closely associated breeding females, most probably relatives, and their calves. Our 3rd tier units appear to equate with Douglas-Hamilton's (1972) description of kinship groups, later termed bond groups (Moss & Poole, 1983), comprised on average of 2.5 family units and 28 (range 14-48) individuals in Lake Manyara National Park. Similarly, 3rd tier units were comprised on average of 2.0 2nd tier units and 16 (range 6-40) individuals in our study area. The difference in average size may be related to ecological differences between the two study areas, because Samburu is much drier than Lake Manyara. Previous research described a 4th tier organization, termed “clan”, as a spatial population structure, roughly grouping elephants according to overlap in their dry season home ranges (Douglas-Hamilton, 1972; Moss & Poole, 1983). The emergent 4th tier delineation in our study does not rely on any spatial information and represents a potentially novel tier not previously recognized to be influenced by social fusions of 2nd and 3rd tier units.

Further, the dry season home ranges of all 4th tier units overlap and some units' ranges are not distinguishable spatially, indicating the previous definition of clans (Douglas-Hamilton, 1972, Moss & Poole, 1983) does not apply to the 4th tier units defined in this study.

This study looks at social structure as a function of behavioural association patterns, though it is likely that spatial properties of the study population influence observed social behaviour. Of particular interest is the influence of spatial interactions on the emergence of 4th tier units. Our observations suggest that 4th tier units are a function of social rather than spatial processes, as the data were collected within or near a small (320 km²), unfenced nature reserve. Elephant movements and resulting social interactions, therefore, appear not to be constricted by distance, landscape features, or any geographical barriers. Furthermore, although some spatial structure is associated with the resource-rich river running through our semi-arid study area, we did not identify any riparian structures that would explain the emergence of as many as eight 4th tier units.

Observations of mutualistic interactions (Mann et al., 2000) among 3rd and 4th tier unit members support our assertion that these tiers are social in origin. Radio tracking data of two 3rd tier associates from different 2nd tier units demonstrate coordinated movements over periods greater than a month within and outside the protected study area (unpublished data). Similarly, observational data of 4th tier associates indicates periods of cohesive movement spanning multiple weeks, both within and outside protected areas. Similar cohesive behaviour for shorter periods (7-14 days) has been recorded for the entire 5th tier subpopulation. Coordinated behaviour

such as this has been used to distinguish social from non-social structures in studies of cetaceans (Whitehead, 2003). Further, large aggregations (>100 elephants) are assembled in relation to social tiers, where 4th tier members are usually spatially clustered within the larger aggregation and 3rd and 2nd tier units are spatially nested within their 4th tier units. Observations of alloparental care were common within 2nd and 3rd tier units and occurred infrequently among 4th tier relations. Specifically, lactating females have been observed suckling another 2nd tier associate's calf in four different units and a 3rd tier associate's calf in two different units. Such interactions are rare and were not observed across different 4th tier units. Non-lactating females, however, have been observed to suckle calves within 2nd, 3rd and 4th tier units though such behaviour is generally limited to calves less than 6 months old and is infrequent across higher tiers associates. Although rates of this interaction were not rigorously recorded across the population, the significance of this behaviour has been studied (Lee, 1987). Individuals defending their 2nd and 3rd tier counterparts are also common, and coalitions of 4th tier units in response to dominance interactions with outside elephants were observed infrequently. These observations suggest a social rather than non-social mechanism in the formation and maintenance to the 4 tier social organization.

Seasonal effects on sociality

During the dry season, when resource quality and quantity decreases, ecological constraints increase inter and intra group competition (Jarman, 1974, Altmann, 1974). The socio-ecological framework predicts this increase in competition should shape the social structure of organisms (Wrangham, 1980; Isbell, 1991). Our results indicate that social cohesion of elephant units decreases across all social tiers during the dry season.

However, the effects of the dry season are disproportionate across tiers. 2nd tier units were the most stable across seasonal and temporal partitions (Table 3) and across different clustering methods (Table 2). The number and cohesion of 2nd tier units changed little across season, demonstrating that structural organization at this level was robust against potentially divisive ecological forces.

The effect of season was pronounced on the 3rd and 4th social tiers. In particular, the identification of units in the 3rd social tier was dependent on season and the cohesion of 3rd tier units (defined using the wet season definition) was significantly less during the dry season. This was the only seasonally specific social tier, demonstrating its unique dependence on ecological conditions. The number of units in the 4th tier increased during dry periods and unit cohesion decreased significantly during these periods. This tier, however, was discernable across the seasons and throughout the study. Distinguishing the 3rd from the 4th tier structure in the dry season, when only one higher social tier was observed, was conducted by assessing the similarity in unit numbers and compositions to results from the total data set; results clearly indicated the presence of the 4th tier structure rather than the 3rd tier (Table 3).

Tighter ecological constraints of the dry season thus lead to greater levels of disassociation and splits in higher social units, inhibiting 2nd tier units from coalescing into 3rd tier units for extended periods. As competition increases, individuals tend to spatially separate. Levels of association occur along a continuum and the demarcations between social tiers are affected by interactions across all social levels, thus emergence of one tier can be affected by the state of other tiers. In this case, 3rd tier units with bifurcation distance (d) values slightly less than the 3rd/4th tier knot (those which

bifurcate just below the knot threshold) are marginally more cohesive than 4th tier units with d values slightly greater than the knot. Demarcation of these 3rd tier units is not possible during the dry season because the rate at which individuals bifurcate in 3rd tier units, particularly those close to the 3rd/4th tier threshold, are no longer statistically distinguishable from 4th tier units (Fig. 4). It is likely that 4th tier units are affected by the social attraction among the merged 3rd tier units during the dry season, resulting in the lower knot value of d (Table 3). Such changes affect the stability of 4th tier units; in this case splitting some units identified using the total data set into two dry season 4th tier units. Essentially, during the dry season higher order social units may act as a hybrid between 3rd tier inhibited relationships and typical 4th tier associates.

Temporal effects on sociality

We also found variability in social structure across the study period (Table 3). The 3rd tier social delineation was distinguishable in the 1998-2000 data partition, though it was absent in the later half of the study so comparison between the study periods was not possible. Prior to the start of data collection in June 1998, the “El Niño” climatic event brought excessive rains to the study area. These excessive rains had a major impact on vegetation growth and it is likely 3rd tier units were able to form year round during this period because of the lag effect on vegetation availability acting to supplement typical dry season diminution, thereby limiting intra-unit competition for resources.

Some of the temporal variability observed in social structure may be related to the two-year sample period of temporal partitions. Elephant reproductive intervals are generally between 3.6 and 4.8 years (Moss, 2001; Foley, 2002). The reproductive state

of breeding females and variability in their calves' ages and development are likely to affect social unit stability. Females with calves less than a year old (those with potentially greater nutritional requirements) may be affected by intra-group competition to a greater extent than other breeding females, resulting in temporarily lower cohesion between these females (1st tier units) and their 2nd tier units. Alternatively, such females may exhibit periods of increased levels of association in order to gain anti-predation benefits from their social unit while the calf is of a susceptible age. Predation by lions and humans was a salient cause of mortality in the study population (Wittemyer et al., 2005a). Periodic rainfall events like "El Niño", which led to the greatest observed population increase during the study period, may extenuate the effects of reproductive status on social unit cohesion by synchronizing reproduction across social units and across the whole population. Longer term studies may find greater temporal stability if partitions are for periods matching the population's average inter-birth interval.

Population growth, however, is potentially the major factor affecting temporal variability. The number of units in both the 2nd and 4th tiers increased during the later half of the study, probably in relation to the 3.8% annual growth rate occurring during the study period (Wittemyer et al., 2005a). Structural changes in the numbers of social units as a function of period of study were most obvious among the otherwise stable 2nd tier social units. The 2nd tier average bifurcation distance (average changes in d) was the lowest for the 2001-2 data partition, resulting in six novel 2nd tier units (Table 3). Interestingly, all six of the new units constituted single mothers and their calves that were subordinate to the matriarch of the group from which they split; three had daughters reaching reproductive age or breeding and three were primiparous. Thus, the

effect of unit size on social unit stability appears to be compounded by the age, reproductive state and rank of unit members.

Social unit stability and composition

Although no evidence was found for an optimal group size of 2nd or 3rd tier units, the role and age of the matriarch were found to be salient factors affecting the composition and size of social units (Fig. 5). Potential grandmothers were found to lead larger family units than younger matriarchs. Thus our results suggest that parous daughters remain with their mothers while their own progeny are sexually immature, leading to three-generation families. Because of the stable linear-dominance hierarchies in elephants (apparently a function of both individual size and age; Foley et al., 2001, Moss, 1988), intra-group competition disproportionately affects subordinates and their offspring. As females ranked lower than the matriarch of their social unit become grandmothers, the costs of group philopatry may begin to exceed the benefits derived from remaining with their mothers. Although few females in the study population live to an age where they are likely to be great grandmothers (i.e. around 50 years old given the generation time of 17.4 years (Moss, 2001)), those that live to this age do not lead larger social units (mean size = 8, number of families = 3). Thus, as breeding females become grandmothers, the increased costs of association may cause them to split from their natal social units and form new 2nd tier social units. Familial contacts can still be maintained through 3rd or 4th tier social units while avoiding the costs of high degrees of association.

Previous studies demonstrated a positive correlation between matriarch age and the fitness of social unit members, offering a potential cause for social unit philopatry

(McComb et al., 2001). After the death of its matriarch, we observed a 2nd tier unit fission that resulted in three novel 2nd tier units comprising a 3rd tier unit. Before her death, the social unit's CoC value = 0.749 ± 0.059 (jackknife estimated SE) and after her death the social unit was less cohesive with a CoC value = 0.658 ± 0.055 (jackknife estimated SE). This suggests that 3rd and 4th tiers may well be generated through fissions of 2nd and 3rd tier units respectively, with the components of the fissioning units retaining stronger ties than expected at random. Furthermore, social unit composition appears to affect higher order social interactions. Not all 2nd tier units are members of 3rd tier units during the wet season, particularly larger 2nd tier units. Non-forming 2nd tier units generally have greater numbers of breeding females than those that form 3rd tier units, though this relationship was not significant at the 0.05 level (median_{non-forming}=2.5, median_{forming}=2, Wilcoxon Rank-Sum: $N_{\text{non-forming}}=12$, $N_{\text{forming}}=38$, $Z=1.778$, $p=0.0753$). Our observations suggest that 3rd tier units are most likely to be formed from 2nd tier units that have recently split probably as a function of unit size. Higher tier associations may also be in response to predation pressures. The largest 4th tier unit is composed of 17 2nd tier units (2 to 3 times more than other units), half of which have recently lost an older breeding female or the unit matriarch. This is in contrast to the other 4th tier units, of which only one has lost a high-ranking female to natural causes.

Low ranking primiparous females, experiencing the constraints of calf rearing for the first time, may also split from their natal 2nd tier social unit potentially in relation to the changing social costs and benefits of child rearing. One of the three primiparous females that formed a novel 2nd tier unit in the later half of our study left her natal unit after the death of the matriarch, believed to be her mother, but maintained contact with

original unit members at 3rd tier association levels. Such observations provide anecdotal evidence of the benefits of maternal derived rank and the cost associated with rank alterations for subordinate individuals. Primiparous females were also observed to join non-natal units more frequently than other breeding females, though such visits were usually short lived. Unit switching may serve to enhance the social knowledge of these relatively inexperienced females.

Cohesive and divisive social forces

Inclusive fitness benefits derived from the survival and propagation of kin serve as the general cohesive force in many social organizations (Hamilton, 1964; Vehrencamp, 1983; Emlen, 1995), though other cooperative benefits from group affiliation, such as enhanced success in territorial or resource defence (Schaller, 1972; Harcourt, 1992), may serve as the primary cohesive factor and not be based on kinship. While some species may form multiple tiered social organizations where membership is not stable across years or seasons, elephants are believed to remain in natal units throughout their lives (Moss, 1988). Genetic studies are needed to elucidate the role of kinship in elephant social structure. Previous studies have provided evidence for inclusive fitness benefits derived from elephant sociality, in the form of allomother effects on calf survivorship (Lee, 1987) and fitness benefits relating to matriarch social knowledge (McComb et al., 2001). Our results show 2nd tier units, which are probably the units where inclusive fitness benefits are greatest, are highly stable across time and season. This stability indicates such units are organised below the ecological threshold where variability in the social costs and benefits of units can act to significantly affect

unit formation and cohesion (Fig. 6a), though it is apparent social unit age structure and composition affects where this threshold lies.

Expanding the socio-ecological model to multi-tiered social systems can help to elucidate the factors affecting the emergence of different social delineations. Our observations indicate the social benefits derived from multi-tiered social structure are probably inclusive fitness, resource/territorial defence, and anti-predatory behaviour. Other researchers have suggested clans, probably the equivalent of 4th tier units, form in order to facilitate the exchange of ecological information (Foley, 2002) and to attract mates (Moss & Poole, 1983). Social tiers are influenced by such cohesive and divisive forces, which act throughout the social continuum but may affect relations at each tier to varying degrees (Fig. 6b). With multilevel fission-fusion societies, the nested hierarchy of social tiers can separate into smaller units, down the hierarchy, during times of constraints and increased competition or fuse into larger units, building up the hierarchy, when facilitated by conditions leading to increased cooperative benefits. Social tiers in which the benefits of forming units are only marginally equivalent to the costs of forming those units will be unstable in time and space when variability drives costs to exceed the benefits of the group (Fig. 6c). Degrees of social interactions among members in the study population are affected by ecological and temporal variability, thus delineations (and in some cases emergence of delineations) between social tiers are not fixed but vary over time, both seasonally and with changes in population size. Thus, the net total costs change over time, and depend on the number of social tiers at which a group is interacting (Fig. 6d).

The formation of higher order social delineations has important implications for the evolution of social systems. Though studies of multileveled social structures are few, our study suggests that each tier emerges in response to a different compilation of cost-benefit tradeoffs (Krause & Ruxton, 2002, Whitehead, 2003). Furthermore, time spent in different social delineations and their spatial properties (like distances between 2nd tier units when associating in their 3rd tier units) potentially affect social benefits derived from multiple social tiers. In gelada baboons (*Papio gelada*) inclusive fitness benefits apparently act to maintain families (Hamilton, 1964; Vehrencamp, 1983) but the cohesion of multiple families into a higher social tier may occur in response to predation pressures during periods of increased predation risk (Kummer, 1995). Similarly for elephants, while individuals are essentially always in their 2nd tier units, coalitions of 2nd into 3rd and 3rd into 4th occur less frequently. Individuals maintain the benefits of their 2nd tier units, and may incur the benefits while avoiding the costs of 3rd or 4th tiers by coalescing into the higher order units for limited periods at opportune times. For example, elephants may derive greater social benefits from larger aggregations during the breeding season (coinciding with the wet season) by attracting mates (speculated by Moss & Poole, 1983), which may be the reason individuals coalesce into 3rd tier units more frequently during wet seasons.

Isolating the function of each social tier is difficult in complex animals like elephants. Our study suggests that as 2nd tier units increase in size, social costs are likely to cause fissions that create 3rd tier social units, which can potentially lead to the formation of 4th tier units through the same process. However, 4th tier units were apparent across seasons and temporal periods in contrast to 3rd tier structures, indicating

the dominant forces affecting these two tiers are different. The costs incurred by 4th tier units may be diffused by the lower levels of cohesion in this tier. Alternatively, novel socio-ecological benefits, such as intra-group information exchange hypothesized as the function of clans by Foley (2002), may serve to maintain these units across seasonal periods. It is possible, however, that the 4th tier social structure is an epi-phenomenon, occurring simply as a result of elephants predisposition to socially interact rather than as a function of socially derived benefits. The levels of cohesion, or time spent with 4th tier conspecifics, are relatively low, possibly minimizing the ecological costs of such interactions. Thus 4th tier sociality may have no functional meaning, representing “runaway” sociality comparable in an evolutionary context to Fisherian sexual selection (Fisher, 1930) or superstimulus responses in mate selection (Basolo, 1990). Only with humans is the function of such higher order delineations clear, for example in the context of economic and military alliances (Falger, 1992). Kinship can also dictate the formation of higher social levels in humans, as found in pastoralist communities in East Africa where social tiers are based on patriarchal lineage (Spencer, 1965; Teustch, 1999). Future controlled experiments are needed to directly assess the influence of cohesive and divisive factors on the formation and structure of different social tiers. Identification of the role and relationships of various social levels can serve to elucidate key socio-ecological factors affecting a population and, as such, are salient to conservation efforts and studies of sociality.

Method	Total Breeding Females	Matriarchs of 2 nd Tier Units
UPGMA	0.874	0.529
CLINK	0.890	0.575
SLINK	0.841	0.479
Ward's	0.965	0.820

Table 1: The cophenetic correlation coefficients (CCC) (Romesburg, 1984) of four clustering methods compared for selection of the clustering method which best fits the study association data.

Method	Knot Value	N _A	N _B	Z statistic	p-value	Defined Units
Ward's	0.65	27	13	4.823	<0.0001	50
UPGMA	0.55	29	11	4.867	<0.0001	50
CLINK	0.60	28	12	4.816	<0.0001	50
SLINK	0.50	30	10	4.295	<0.0001	51

Table 2: Results from four cluster methods used to assess the integrity of 2nd tier social unit definitions. Compositions of defined units were robust across clustering methods.

2nd tier Delineation	Knot Value	N_A	N_B	Z statistic	p-value	Defined Units	Individuals Different	Units Identical
Total	0.65	27	13	4.823	<0.0001	50		
Wet	0.6	28	12	4.67	<0.0001	49	3 ^a	45 ^b
Dry	0.75	25	15	4.482	<0.0001	49	2 ^a	48 ^b
1998-2000	0.6	28	12	4.533	<0.0001	49	5 ^a	44 ^b
2001-2002	0.45	31	9	4.586	<0.0001	56	6 ^a	36 ^b
3rd Tier Delineation								
Total	1.1	14	9	1.185	0.2359	-		
Wet	1.05	16	9	2.527	0.0115	25	-	-
Dry	1.15	10	8	1.324	0.1854	-	-	-
1998-2000	1.3	14	14	2.429	0.0151	20	-	-
2001-2002	1.05	14	12	1.582	0.1070	-	-	-
4th Tier Delineation								
Total	1.8	17	14	4.247	<0.0001	8		
Wet	1.85	19	16	3.926	<0.0001	8	0 ^c	8 ^d
Dry	1.65	24	10	4.229	<0.0001	10	10 ^c	5 ^d
1998-2000	2	16	14	2.834	0.0046	8	2 ^c	6 ^d
2001-2002	1.65	18	14	4.062	<0.0001	9	6 ^c	6 ^d

^a out of 112 individuals

^b out of 50 units

^c out of 50 individuals

^d out of 8 units

Table 3: Social unit definitions from subsets of the data (containing association indices calculated during seasonal and temporal periods) were compared with results from analysis of the total data set in order to ascertain the effects of season (ecological variability) and time (population growth) on social structure. Statistical identification of knot values and subsequent unit definitions were conducted by comparing step-wise changes in the number of bifurcations above the knot value (N_A) and below the knot value (N_B) (see methods and Fig. 1).

Delineation	Avg AI	SE	Avg CoC	SE
2nd Tier	0.829	0.017	0.835	0.018
3rd Tier	0.627	0.037	0.706	0.030
4th Tier	0.376	0.058	0.515	0.036
*5th Tier	0.053	0.001	0.281	0.001

Table 4: Comparison of the average association index (AI) value and average social unit Correlative Coherence (CoC) value across social tiers. Average CoC and AI values are similar in tightly associated social tiers, but begin to differ markedly in higher tiers (see Methods for a discussion on the differences between these two measures of association).

Delineation	Wet Median (CoC)	<i>n</i>	IQR	Dry Median (CoC)	<i>n</i>	IQR	Wilcoxon Z (Exact)	<i>p</i> value
2nd Tier	0.875	32	0.780-0.924	0.810	32	0.730-0.882	1.715 (234)	0.086
3rd Tier	0.749	23	0.667-0.824	0.645	23	0.602-0.791		0.002
4th Tier	0.536	8	0.478-0.605	0.511	8	0.462-0.544	(35)	0.016
			Jackknife			Jackknife		
	Wet Mean		SE	Dry Mean		SE		
5th Tier	0.305	1	± 0.0164	0.272	1	± 0.0159		

Table 5: Correlative Coherence (CoC) values for the 2nd-5th social tiers' units were quantified across the wet and dry seasons. The 5th tier CoC values were jackknifed to obtain standard error estimates. The numbers of units compared (*n*) are less than the actual number of units in 2nd and 3rd tiers because comparisons across seasons were not possible in units composed of single breeding females.

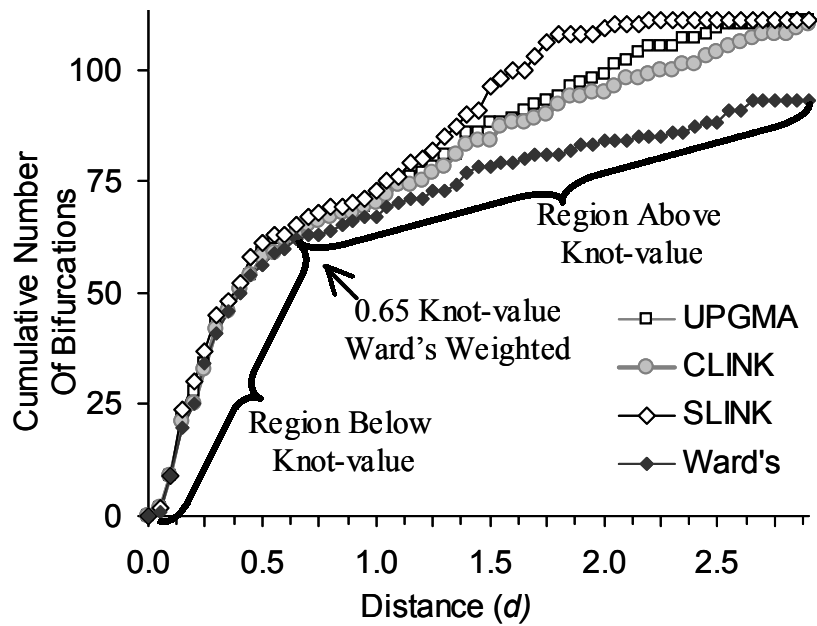


Figure 1. Cumulative numbers of bifurcations across cluster distances (d) for the four different types of cluster analysis listed in Table 1 and 2. Identification of knot values signifying social tier delineations was conducted by maximizing Z -statistics from comparisons of stepwise changes above and below the knot value. The 0.65 (d) knot value for the Ward's Weighted Clustering Method is indicated, as well as the corresponding regions above and below the knot value ($N_A = 27$, $N_B = 13$, $Z = 4.823$, $p < 0.0001$).

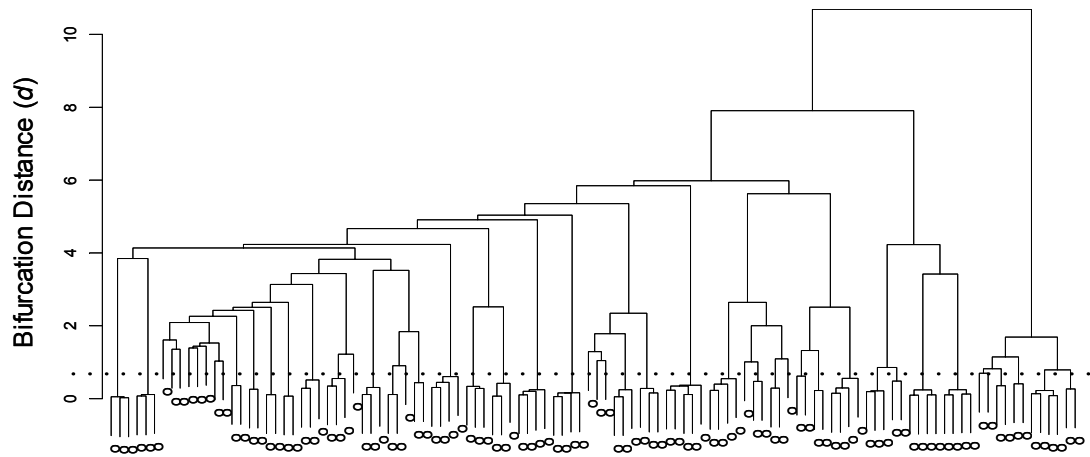


Figure 2. A cluster diagram constructed from the association indices using the Ward's Weighted method identifies putative group relationships among the 112 breeding females used in the study. Each (o) at the base of the tree represents one breeding female. The bifurcation distance (d) is the measure of associative distance between individuals, where $d = 0$ indicates two individuals were observed together 100% of observations (having the same association pattern) and increasing d values represent decreasing degrees of association among individuals. The solid line indicates the $d = 0.65$ cut-off used to delineate 2nd tier social units from higher order social relations (Table 1, Fig. 1). Individuals bifurcating below this line are in the same 2nd tier unit, while those bifurcating above this line are in different 2nd tier units.

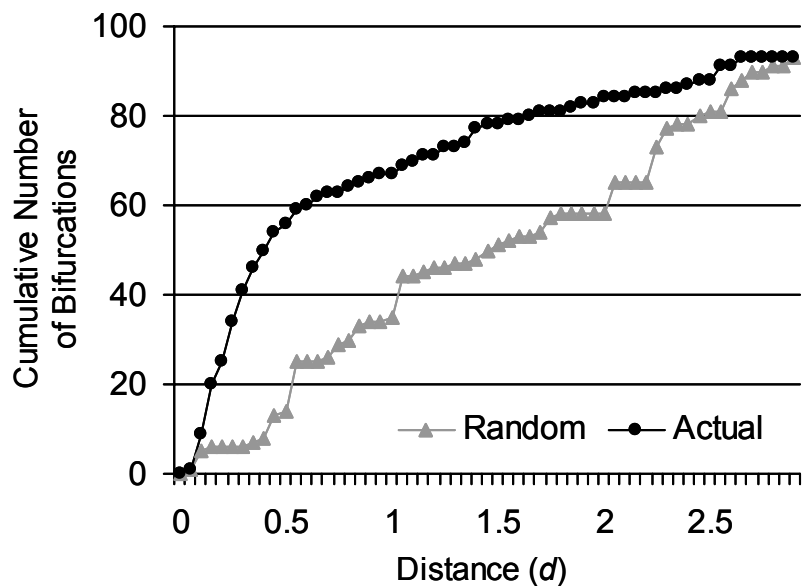


Figure 3. The difference between the cumulative number of bifurcations across cluster distances (d) for actual association data (from the Ward's clustering method) and the data after randomisation. The randomised data set does not have any significant knot values and is relatively linear indicating no social tiers exist. The actual data has a significant knot value ($p < 0.05$) at 0.65 (d) and is concave down indicating the existence of a social tier.

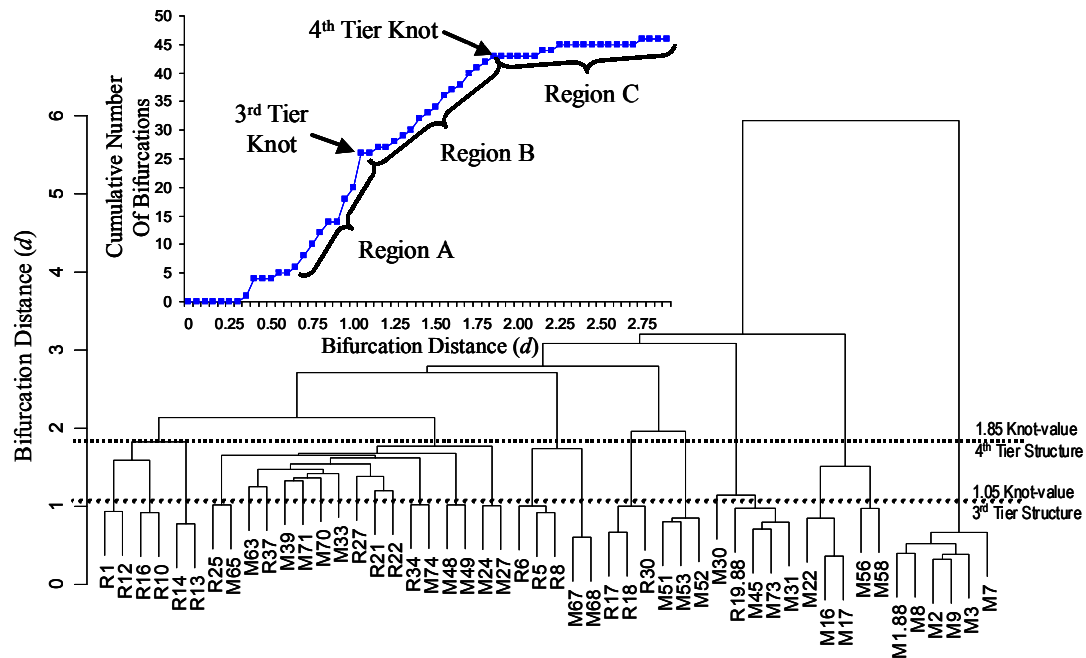


Figure 4. The Ward's cluster diagram and the cumulative bifurcation graph are plotted here for the 50 2nd tier unit matriarchs (listed as letter and number combinations at base of cluster tree: e.g. R1) using wet season data only. The 3rd (Region A, $0.65 < d \leq 1.05$) and 4th (Region B, $1.05 < d \leq 1.85$) social tiers are identified by the slope changes in the cumulative graph of bifurcations (Insert). Region C, $d > 1.85$, is where the 4th tier units aggregate to form the 5th tier subpopulation associated with the study site. Social delineations occur at statistically optimised knot values (see Methods) after all points below $d=0.65$ had been removed (these represented 2nd tier units based on a cluster analysis of all the data). The significances of the knots are: A vs B: $Z = 2.527$, $p = 0.012$; B vs C: $Z = 3.926$, $p < 0.001$. A statistically significant 3rd tier delineation was not distinguishable from the 4th tier delineation in our analysis of dry season data alone ($Z = 1.324$, $p = 0.185$; Table 4).

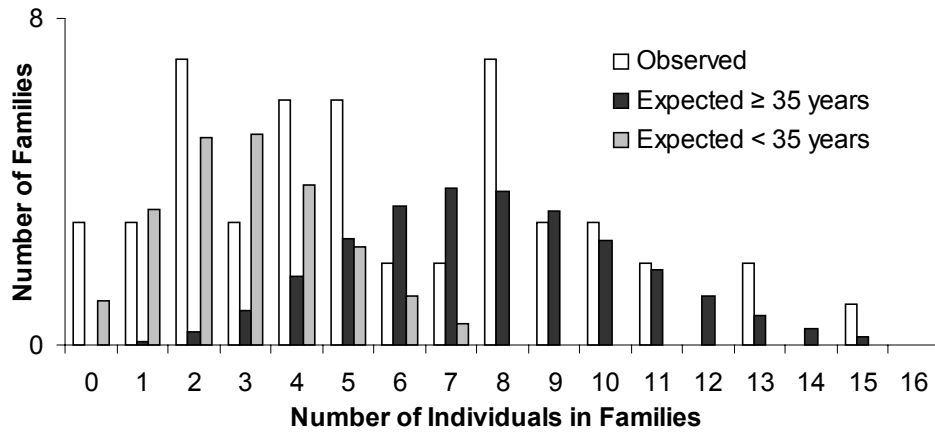


Figure 5. In order to assess if the sizes of social units are distributed around an optimum, we compared observed distributions of unit sizes with Poisson (random) distributions of the same means. The observed distribution of 2nd tier unit sizes (including breeding females and their calves) significantly deviated from the Poisson distribution of the same mean (mean = 7.64, $\chi^2 = 50.870$, $df = 11$, $p < 0.001$), indicating that the sizes of social units are not randomly distributed. Distributions of 2nd tier unit sizes after separation into two classes based on matriarchs' age (< 35 and ≥ 35 years) in relation to elephant generation time (17.4 years), however, did not significantly differ from respective random distributions of the same means (35 years and older: mean=9.85, $\chi^2 = 8.363$, $df = 12$, $p > 0.500$; less than 35 years: mean = 5.02, $\chi^2 = 10.142$, $df = 5$, $p > 0.050$) indicating that an optimal group size did not exist for either category of social unit.

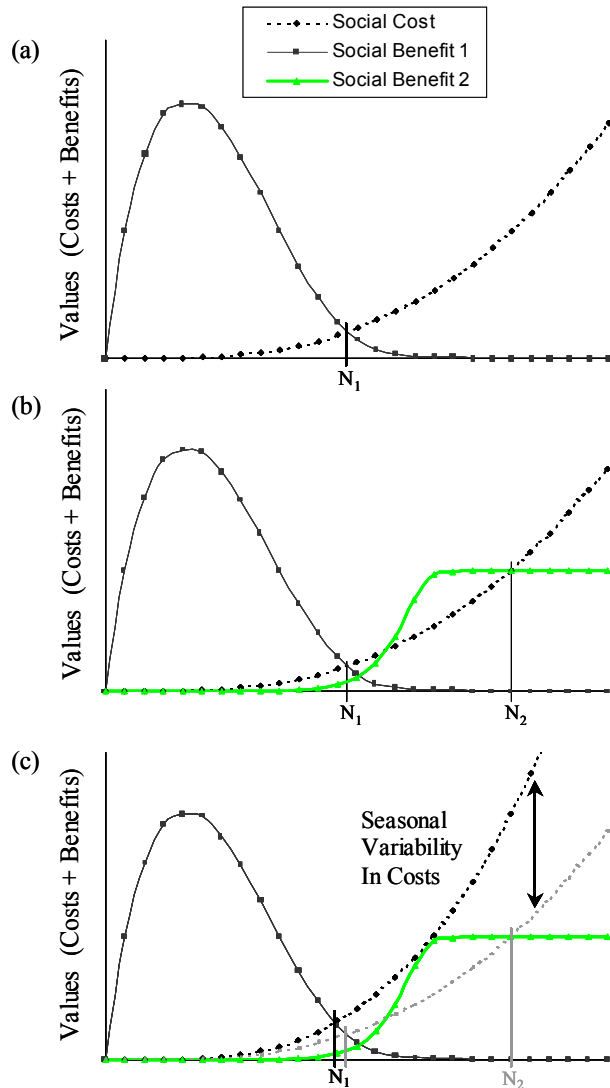


Figure 6. A conceptual framework is presented on the effects of the interactions among social and ecological costs and benefits on the emergence of a multi-tiered social organization. Social benefit 1 (e.g. inclusive fitness benefits) decrease as group size increases, while a social cost (e.g. feeding competition) increase with group size (a). The point at which these forces intersect dictates the threshold (maximum not optimal) size of the social group (N_1), above which costs exceed the benefits of grouping. Certain cohesive or divisive forces may only be salient at specific group sizes as with social benefit 2 (e.g. territorial defence for large groups), such that combined costs and benefits result in multiple threshold group sizes (b). Additionally, social costs and benefits will vary across time and group context affecting these threshold group sizes. In this example, costs exceed the benefits of the second order threshold group size during certain seasonal periods, impeding formation of the higher order social group during high cost periods (as seen with 3rd tier aggregations in elephants) (c). When the net total value of these forces act across the social continuum, multiple social tiers may emerge in relation to a hierarchy of cost/benefit comparisons in which social benefit 1 out ranks social benefit 2 (d).

Chapter Six

A Likely Ranking Interpolation for Resolving Optimal Dominance Orders in Systems with Unknown Relationships

G. Wittemyer and W. M. Getz

Introduction

Dominance relationships are an important construct of social interactions, used to explain behavioural and fitness related differences among individuals (Krebs & Davies, 1987). Dominance structure is also a key factor influencing the spatial properties of animal populations, such as home range size, movement, and resource access. Thus the quantification of dominance interactions is an important aspect of behavioural ecology and the development of quantitative methods to resolve dominance relations has been the focus of numerous studies (as reviewed in de Vries, 1998).

Standard methods for deriving the dominance hierarchy in a system of interacting individuals rely on the scoring of pair-wise competitive interactions (Boyd & Silk, 1983; Martin & Bateson, 1993). The results of these interactions, wins or losses, are arranged in a dyadic interaction matrix where the ij^{th} element represents the observed dominance relationship of i to j (Fig. 1 A). In a discrete formulation, this element is a 1-0 win-loss metric or, in a continuous formulation, it may take on any value between 0 and 1 and represent the probability of dominance (number of wins/number of total contests per pair). Conventions for resolving dominance ordering from dyadic interaction matrices can be broadly grouped into two categories (Albers & de Vries, 2001; Gammell et al., 2003): *optimisation methods* that reorganize the dominance matrix to minimize or maximize a matrix metric to derive the ordinal rankings of individuals (Crow, 1990; de Vries, 1998; Boyd & Silk, 1983) and *strength methods* that derive a cardinal rank measure for an individual's overall position in the hierarchy (Cluttonbrock et al., 1979; David, 1987). However, none of these rank

methods appear to be generally accepted (de Vries & Appleby, 2000; Langbein & Puppe, 2004).

Optimisation methods generally resolve the rank order of individuals by minimizing the number of circular dominance interactions (i.e. interactions of the form A dominates B who dominates C who dominates A). Strength methods, such as David's Score (David, 1987) and Clutton-Brock et al.'s index (Cluttonbrock et al., 1979), use the difference between the sum of wins and the sum of losses as a measure of an individual's strength to produce a dominance hierarchy. Strength methods, unlike optimisation methods, provide a quantitative numerical dominance value that offers insight into the differences in relative dominance strengths of individuals, but may offer sub-optimal ordinal rankings in the presence of circular interactions. Such dominance values can be employed in parametric analyses of differences between individuals; in contrast, optimisation methods result in ordinal ranks requiring non-parametric methods of analysis.

Both methods are challenged by sparse data that does not contain information on the relationships among all dyads. Here we present a *likely ranking interpolation* approach to address the sparse data problem. Our technique incorporates the advantages of both the optimisation and strength methods thereby simultaneously yielding the optimal ordinal rank and the cardinal strengths of individuals in the hierarchy. It provides insights beyond those offered by either method alone and is a more powerful method for ranking individuals when data is sparse.

Description of Method

Our method entails a five step process to resolve the nearest linear rank order from a set of dyadic interaction data. The first two steps find the optimal rank ordering of known dyads through implementation of an optimisation routine following de Vries I&SI method (de Vries, 1998). The third step applies a likely-rank interpolation to estimate unknown relationships. The fourth step employs a dominance strength metric to resolve the relative ranks of unknown dyads. The fifth step solves a minimum matrix metric to arrive at the unique, near linear rank ordering of individuals.

Resolving the Hamiltonian rank order

In systems with full knowledge and perfectly linear dominance relationships, the optimal rank order, termed the *Hamiltonian rank order*, occurs when all individuals are ranked higher than individuals they dominate. Assuming the dominance matrix elements are composed of dominance probabilities or 1-0 metrics, the optimal rank order can be derived by minimizing the sum of the matrix elements to the left of the matrix diagonal or maximizing the sum of the matrix elements to the right of the matrix diagonal.

Formally, let a_{ij} denote the degree (or probability) to which individual i dominates individual j . Since $a_{ij} + a_{ji} = 1$, it follows that

$$a_{ji} = 1 - a_{ij}, \quad i, j = 1, \dots, n, \quad (1)$$

where n is the number of individuals in the system. Define the upper and lower triangular sums of the dyadic interaction matrix A of elements a_{ij} respectively as

$$H = \sum_{i=1}^n \sum_{j=i+1}^n a_{ij} \quad \text{and} \quad I = \sum_{i=2}^n \sum_{j=1}^{i-1} a_{ij}. \quad (2)$$

From relationship (1), this implies

$$H = \frac{n(n-1)}{2} - I. \quad (3)$$

The Hamiltonian rank order occurs when H is a maximum or equivalently I is a minimum. Under conditions of perfect knowledge and linearity (i.e. all relationships are known and dominant individuals always defeat their subordinates), $I = 0$ and the rank order solved using a strength method will be the same as the Hamiltonian rank order obtained using an optimisation method. When conditions of perfect linearity and knowledge are not met the results of these two classes of methods diverge.

The presence of circular polyads (e.g. A dominates B, which dominates C, which dominates A) in the data result in a number of inconsistencies I in the rank order (given by equation 2). In de Vries (1998) method, a flipping algorithm is implemented that switches the relative positions of individuals in the rank order (Johnson et al., 1982; Roberts, 1990) in a direction that ultimately leads to the local minimum for I (equation 2; Fig. 1 A). We adopt this algorithm in **Step 1** of our method.

Once this minimum is obtained, de Vries (1998) method further restricts solutions to the rank order through the minimization of the sum of differences in the ranks of all inconsistency dyads. Specifically if the i - j dyad is inconsistent then $a_{ij} = 1$ (or > 0.5 in the case of probabilistic element values) even though $i > j$. Define

$$\Psi_{ij} = \begin{cases} i - j & \text{whenever } a_{ij} = 1 \\ 0 & \text{otherwise} \end{cases} \quad \text{when } i > j. \quad (4)$$

de Vries's approach is to minimize the total strength of the inconsistencies

$$SI = \sum_{i>j}^n \Psi_{ij} \quad (5)$$

in a procedure that he refers to as the I&SI method (Fig. 1 A). Thus, **Step 2** of our method finds the ordering that minimizes SI . de Vries (1998) compared the I&SI method with a variety of published ranking methods, demonstrating the I&SI method offered the most robust dominance ordering in a near linear system.

Initial ordering of individuals

The I&SI approach finds a local minimum. To ensure a good solution, the procedure is repeated for multiple, different initial orderings of individuals organized according to the following two-step procedure: (a) individuals are first ordered by their win-loss ratio, where pairs with equal ratios are ordered by numbers of wins; (b) a permutation technique is implemented that randomly switches individuals a random number of times from the initial ordering to prove a spectrum of initial conditions are searched. The rank order for each starting position is then solved by inserting dominant individuals above their subordinates. If the total change in the number of inconsistencies (equation 2) followed by the total rank sum different of these inconsistencies (equation 5) increases as a result of the row insertion, the insertion is reversed. Finally, the Hamiltonian rank order is regarded as having converged to an acceptable solution when the value of I followed by the value of SI remains unchanged after repeated permutation runs. Generally, 100 runs is regarded to be sufficient for locating the minimum of both the I and SI metrics (de Vries, 1998). We stress, however, that minimizing I and SI does not in general produce a unique rank order when the data are incomplete (unknown dyadic relationships exist).

Resolving unknown relationships

For many organisms, agonistic interactions may be rare, subtle, cryptic, or occur predominantly through modalities other than physical pair-wise interactions (e.g. scent marking). As a result, dominance relationships among all pairs of individuals may not be known (Fig. 1 B). As an effect of sampling, the number of unknown relationships tends to increase with the number of individuals included in the study. This problem is often encountered in uncontrolled field studies where dyads cannot be forced to compete (e.g. Gende & Quinn, 2004). In many studies, ascertaining the general position of individuals with few observed interactions is essential for the realization of a dominance hierarchy.

Treatment of unknown relationships has been handled in different manners; some methods assign the unknown dyad the equivalent value for a tie (e.g. 0.5 if the dominance is scaled between 0 and 1; Appleby, 1983) and others ignore the relationship between such dyads in their overall ranking system (de Vries, 1998). In strength-based methods both elements of unknown dyads may be assigned zero (Cluttonbrock et al., 1979; David, 1987). Assessing dominance relationships across groups of individuals with large proportions of unknown relationships, however, is difficult using either optimisation or strength methods.

Here we present a linear interpolation technique to quantify a likely dominance relationship between unknown dyads. After execution of de Vries's I&SI approach, if interaction values a_{ij} are not known for dyad i - j , (where i and j are the rankings after Step 2) we use 2nd and higher order relationships of the individuals in the unknown dyad to derive the probable relationship between the individuals. This approach is

similar to the rank based scaling of dominance indices (Bradley & Terry, 1952) and maximum likelihood estimates (Crow, 1990). In **Step 3** of our method, unknown elements are assigned interpolated values

$$\hat{a}_{ij} = 0.5 - (i - j) / 2n \quad (7)$$

where it is clear that $\hat{a}_{ij} + \hat{a}_{ji} = 1$ (note the use of the caret to denote that this is an interpolated element of the matrix A rather than a value obtained from data). Our interpolation is based on the assumption that the greater the separation in ranks between two individuals with an unknown relationship the more likely the higher-ranking individual is to dominate the lower ranking individual, with values ranging from almost one if i is the top individual and j is the bottom individual to almost zero for the reverse situation. After using equation 7 to fill in all the missing values (unknown relationships) in the interaction matrix A , Step 4 of our method is to calculate each individual's relative dominance strength as described next (Fig. 1 C).

Calculating dominance strengths

Strength methods are used to obtain a unique rank order for the individuals in a hierarchical system, modulo those individuals that have identical interaction histories. This uniqueness is an attractive feature for biologists studying the relationship between dominance and other biological measures in a population. In **Step 4**, we apply a strength method to our most current version of A (which in Steps 1-3 has been minimized with respect to inconsistencies and out filled using the interpolating equation 7). In this step all known dominant-subordinate dyads and the optimised rank order of circular polyads are conserved; conditions not met when using strength metrics alone (Fig. 1 D).

In contrast to other strength methods, which explicitly incorporate a contestant's second order relations in the algorithm (e.g. the strengths of each individual defeated by the contestant), second order relations are implicitly incorporated in our algorithm through the interpolation procedure (Step 3). As a result, the dominance strength of both possible rank orders for the unknown dyad (when B is above C and when C is above B or $i = j - 1$ and when $i = j + 1$) must be assessed prior to assigning relative ranks. This entails recalculating the likely rank metric for each unknown element after switching the position of the dyad members. The individual with the greatest dominance strength when in the higher rank position is designated as the actual dominant individual. Specifically, our dominance strength metric δ_i for individual i is generated as follows. Define $a'_{ij} = a_{ij}$ or $a'_{ij} = \hat{a}_{ij}$ depending on whether the element is respectively calculated from data or interpolated using equation 7. Further define “above” (a) and “below” (b) the matrix diagonal, and row (ρ) and column (κ) sums (Fig. 2 A):

$$\rho_i^a = \sum_{j=i+1}^n a'_{ij}, \rho_i^b = \sum_{j=1}^{i-1} a'_{ij}, \kappa_i^a = \sum_{j=1}^{i-1} a'_{ji}, \kappa_i^b = \sum_{j=i+1}^n a'_{ji} \quad (8)$$

$$\delta = \delta^a + \delta^b, \text{ where } \delta^a = \rho_i^b - \kappa_i^a \text{ and } \delta^b = \rho_i^a - \kappa_i^b \quad (9)$$

Note that δ linearly scales between $n - 1$ and $1 - n$, thereby representing the full spectrum of possible defeats and wins; δ can be easily scaled between 0 and 1 by $\frac{n + \delta}{2n}$.

This step in our method allows tied ranks to be incorporated into an individual's dominance strength (de Vries, 1995). Further, in circumstances where likelihood assessment of dominance ranks results in equal ranking, our method assigns tied rank values (0.5 in the case of a 0 to 1 rank system) to the unknown dyad's elements.

The application of this metric may be problematic in circumstances where the number of unknown interactions is skewed across individuals. In such cases, an individual's strength will be artificially boosted when relationships with higher ranked individuals are unknown, resulting from the high proportion of likely ranking metrics in its row score (sum of wins) instead of potential 0 values. Correspondingly, an individual with a larger number of interactions with higher ranks will have 0 scores in its win row and thus have a lower strength score. Such scaling issues are particularly salient when the data has a relatively high proportions of unknown relationships or where the social organization of the study organism results in naturally skewed interaction matrices, e.g. in species which tend to interact only with close or lower ranking individuals. Under such conditions, implementation of our method using δ may not offer an acceptable solution to the relative rankings of unknown dyads. Rather, an individual's rank strength may be better quantified by δ^b (i.e. its interactions with only those it has defeated) or by δ^a (i.e. its interaction with only those to whom it has lost) (equations 9; Fig. 2B). Since this half-matrix approach only includes "wins" or "losses" but not both, circular interaction components are excluded from dominance strength calculations. Thus the approach may not be appropriate in circumstances when circular relationships are evident.

Minimizing the sum of elements below the matrix diagonal

The resolution of the relative ranks of unknown dyads in Step 4 offers a unique rank order to the initial sequence of individuals derived from Steps 1 and 2. As the number of unknown dyads increase, however, the possibility of multiple, equal solutions to steps 1 and 2 increases. To resolve the "best" rank order for the systems

interaction matrix, step 5 of our method solves the minimum sum of the matrix elements below the matrix diagonal (equation 2). Thus the preferred, unique rank order in a system with unknown relationships is one containing the minimum number of inconsistencies (Step 1), the minimum strength of those inconsistencies (Step 2), all unknown relationships ordered according to their dominance strength values (Step 3 and 4), and finally the minimum sum of elements below the matrix diagonal (Step 5).

Assumptions

Few assumptions are required to implement the I&SI method (de Vries, 1998) and, hence, our method which uses the I&SI for the initial sorting procedure. The primary assumption of our method is that the study system is a near linear dominance hierarchy, but we recommend this assumption be tested statistically, where possible, following established conventions (e.g. de Vries, 1995). Such tests become computationally difficult in systems including large numbers of individuals with multiple unknown relationships. Thus for large, sparse data sets, we suggest the following alternative tests of the near-linearity assumption. Either (1) statistically test linearity following established methods on a reduced dataset comprised of the most frequently observed individuals and assume near-linearity scales up to the full data set, or (2) assess the plausibility of linearity based on previous studies or anecdotal information. In social systems where linear hierarchies cannot be assumed, our method is not appropriate and different techniques such as controlled experiments are needed to assess the context specific relationship of dominance outcomes between individuals (e.g. territoriality and dominance in resident versus non-resident birds).

Some optimisation methods avoid the assumption of independence in dominance encounters, a condition not often met in animal systems (Kramer &

Schmidhammer, 1992), by making the observational unit of analysis the dyad and assigning the rounded 1 or 0 value to dyad members with variable numbers of wins and losses. Unfortunately, this procedure may under-represent the available dominance information if numerous interactions with variable results have been observed. Probability values for the elements a_{ij} may be preferred over simplified 1-0 values in studies that employ strength metrics in parametric analyses, as the results of strength metrics are more accurate when using probabilities. The illustrative example presented here (Fig. 1) follows the more statistically robust technique of using 1-0 interactions, but our technique allows versatility in this assumption of independence in the observational unit. The employment of probabilities instead of rounded values is simply implemented by assigning dominance to the i th individual in the flipping algorithm of steps 1 and 2 whenever $a_{ij} > a_{ji}$.

Analysis of simulated data

In order to test the accuracy of our method, we created two complete dominance matrices containing 20 individuals where the first had a completely linear dominance hierarchy and the second contained a non-linear dominance hierarchy with 5% probability of circular polyads imposed across all dyads (Fig. 1 A is the non-linear matrix). The most likely rank order was found for the complete matrices by minimizing the number of inconsistencies (I) and sum of inconsistencies (SI). We then randomly removed 20%, 40%, 60% and 80% of elements from both the linear and non-linear dominance matrix (Fig. 1 B shows 60% removal of elements in the non-linear matrix). Our dominance rank algorithm was run on each of the resulting matrices containing unknown dyads. This process was conducted 10 times on each category of matrix, e.g.

60% removal of the non-linear matrix, in order to get an estimate of the accuracy of the algorithm's performance with the different data regimes. The relative difference in position between the known rank and the solved rank for each individual in each dominance matrix category was calculated ($n = 200$ per category), from which the average and variance of differences was determined.

Not surprisingly, our technique ranked individuals from linear matrices significantly better across all categories of data removal than individuals from non-linear matrices (Table 1). Generally, the algorithm performed well on both linear and non-linear data sets when at least 60% of dyads were known, with the average difference in ranks being less than 1 and the maximum difference in rank found being 6 among the permuted 40% removed non-linear matrices (Table 1). The accuracy of rankings in matrices with 60% and 80% removal of data decreased markedly. However, the average (\pm SE) difference between the solved rank and known rank was still only 3.03 ± 0.18 positions for the non-linear case with 80% missing data, and no constraints on the minimum number of interactions per individual (Table 1). Such resolution is potentially suitable for categorizing individuals in course rank-order groups like high, medium, and low ranking. However, the maximum and 75th quartile differences in an individual's ranking, respectively equal to 13 and 4 positions, demonstrate that large errors may arise when data is sparse (Table 1).

This lowered performance in the sparser data sets is due in part to the increased number of individuals for which no or little dyad interaction data is available. In reality, individuals with no known relationships should be excluded from analyses. By implementing a simple constraint whereby each individual in the matrix is required to

have a minimum of 3 known relationships (the maximum possible in a 20x20 matrix where 80% of dyads are unknown), the performance of our method improves (Table 1). Particularly relevant to studies containing few known relationships is our result that the maximum difference in rank order declined by around a quarter when a minimum constraint of three dyads per individual was implemented for the data set containing 5% circular relationships. The bottom line appears to be that for a group of 20 individuals greater than half the dyads need to be measured to know that the maximum placement error in a truly linear system is not more than 3.

We also explored the impact of the number of individuals in the system by running our method on a linear system comprising 50 individuals with 40% and 60% removal of data. Interestingly, the ranking performance in the larger data matrices (40% removed averaging 0.52 ± 0.047 and 60% removed averaging 1.28 ± 0.088) was similar to that of the smaller matrices, indicating error rates do not increase in direct proportion to the number of individuals in a system. The maximum displacement in rank also remained similar to the results found for the smaller matrix (*viz.* 4 on the 40% and 8 on the 60% removed in contrast to 3 and 7 in the 20 individual system). These results suggest that for sparse data sets, useful levels of resolution are going to be obtained, even for large systems.

Discussion

Our likely dominance ranking method combines the strengths of two existing and complementary approaches to ranking hierarchies of individuals. First, our method uses an optimisation paradigm to solve the nearest Hamiltonian rank order, followed by employment of a strength paradigm to ensure the final order is a unique solution. The

primary advantage of our method is its ability to resolve and incorporate unknown relationships in the total ranking of individuals in a dominance matrix. By employing a likely rank interpolation, our method can be used to determine rank orders in datasets containing fewer known dominance relationships than previous methods. Furthermore, our method does not weaken or undermine the results of known interactions. Rather it uses the information from multiple orders of separation to arrive at the likely rank relationship between individuals in unknown dyads. An additional advantage to our technique is the versatility of data types that can be used to resolve the rank order: the observational unit can be designated at the categorical 1-0 (win-lose) dyad level or the graded value arising from scoring multiple interactions of the same pair.

Of particular relevance to many studies of dominance is the calculation of continuous dominance strength metrics. The benefits of such a metric include resolving the rank order among closely ranked individuals, identifying dyads with truly tied ranks, and providing a continuous variable with which to compare behavioural correlates. Employing the strength metric in our method in parametric analyses, as is often desired in behavioural studies, may be difficult because circular polyads can result in a non-linear relation between a strength-based order and the order derived using an optimisation method (Fig. 1 D). Such differences may highlight relationships or areas in the dominance matrix of interest in the study system. Additionally, the relative strengths of linearly ranked portions of the interaction matrix can be used in parametric comparisons. The incorporation of our strength metric, the sum of elements in an individuals row (wins) minus the sum of elements in an individuals column (losses), to solve unresolved components of the rank order consistent with the I&SI result (de

Vries, 1998) offers a novel combination of the two conventions of ranking techniques that improves on either technique's independent results.

In order to test the accuracy of our method, we created two complete interaction matrices, one linear and one non-linear, with known rank orders. We then randomly removed data from elements in the matrices and subsequently ran our algorithm on the altered matrices. We compared the solved rank order with the known rank order, providing a quantified assessment of algorithm performance (Table 1). The algorithm provided useful information on relative ranks even when large proportions of the matrix elements were empty. We found that relatively simple rules, such as setting limits to the number of unknown dyads per individual, can greatly increase the accuracy of rank orders, particularly as the size of the system increases. Furthermore, our results indicated that our approach could be effectively used as an aid in determining key unknown dyads whose relationship when known will disproportionately improve the solved rank order. Thus, in addition to solving the best rank order, our method may be usefully employed to explore the structure of behavioural data and improve data collection regimes.

(A)

	A	B	C	D	E	F	G	H	I	J	K	L	N	M	O	P	Q	R	S	T
A	*	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
B	0	*	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
C	0	0	*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
D	0	0	0	*	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
E	0	0	0	0	*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
F	0	0	0	0	0	*	1	1	1	1	1	1	1	1	0	1	1	1	1	1
G	0	■	0	0	0	0	*	1	1	1	1	1	1	1	1	1	1	1	1	1
H	0	0	0	0	0	0	0	*	1	1	1	1	1	1	1	1	1	1	1	1
I	0	0	0	0	0	0	0	0	*	1	1	1	1	0	1	1	1	1	1	1
J	0	0	0	0	0	0	0	0	0	*	1	1	1	1	0	1	1	1	1	1
K	0	0	0	■	0	0	0	0	0	0	*	1	1	0	1	1	1	1	1	1
L	■	0	0	0	0	0	0	0	0	0	0	*	1	1	1	1	1	1	1	1
N	0	0	0	0	0	0	0	0	0	0	0	0	*	1	1	1	1	1	1	1
M	0	0	0	0	0	0	0	0	■	0	■	0	0	*	1	1	1	1	1	1
O	0	0	0	0	0	■	0	0	0	■	0	0	0	0	*	1	1	1	1	1
P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	1	1	0	1
Q	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	1	1	1
R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	1	1
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	■	0	0	*	1
T	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*

(B)

	A	B	C	D	E	F	G	H	I	J	K	L	N	M	O	P	Q	R	S	T
A	*	1				1	1						1					1		1
B	0	*		1		0	1							1						
C			*	1		1	1		1		1	1					1	1	1	
D				*			1		1			1		1		1	1		1	
E		0	0		*			1								1				
F		0				*		1	1		1	1		0	1		1			
G		1	0	0			*		1			1	1	1					1	
H		0		0				*	1	1	1	1		1				1	1	
I		0				0			*	1		1		1				1		
J			0	0		0	0	0	0	*	1		1					1		
K				■				0	0	0	*	1		0	1					1
L		■	0			0	0	0	0	0	*	1	1	1			1		1	1
N		0	0	0		0	0	0	0	0	0	*		1			1		1	1
M		0				0		■		■	1	0		*		1		1		1
O				0		1	0	0	0	■	0	0	0		*		1		1	
P					0	0								0		*		1	0	1
Q			0	0								0		0			*	1		
R		0			0		0	0	0			0	0	0	0		0	0	*	1
S			0	0			0	0				0		0	1				*	
T		0									0	0	0	0	0		0	0		*

(C)

	C	D	A	G	B	E	H	F	I	J	K	L	M	N	O	S	P	Q	R	T
C	*	0.52	0.55	1	0.6	1	1	0.67	0.69	1	0.74	1	0.79	1	0.83	1	0.88	1	1	0.95
D	0.48	*	0.52	1	0.57	0.6	0.62	0.64	0.67	1	0.71	0.74	0.76	1	1	1	0.86	1	0.9	0.93
A	0.45	0.48	*	0.52	1	0.57	1	1	0.64	0.67	0.69	0.71	0.74	1	0.79	0.81	0.83	0.86	1	1
G	0	0	0.48	*	1	0.55	0.57	0.6	0.62	1	0.67	0.69	1	1	1	1	0.81	0.83	0.86	0.88
B	0.4	0.43	0	0	*	1	0.55	0.57	1	0.62	0.64	0.67	1	0.71	0.74	0.76	0.79	0.81	0.83	0.86
E	0	0.4	0.43	0.45	0	*	1	0.55	0.57	0.6	0.62	0.64	0.67	0.69	0.71	0.74	1	0.79	0.81	0.83
H	0	0.38	0	0.43	0.45	0	*	0.52	0.55	1	1	1	0.64	1	1	1	0.74	0.76	1	0.81
F	0.33	0.36	0	0.4	0.43	0.45	0.48	*	1	1	0.57	1	0.62	1	0	0.69	1	0.74	1	0.79
I	0.31	0.33	0.36	0.38	0	0.43	0.45	0	*	1	0.55	1	0.6	0.62	1	0.67	0.69	0.71	1	0.76
J	0	0	0.33	0	0.38	0.4	0	0	0	*	1	0.55	0.57	1	0.62	0.64	0.67	0.69	1	0.74
K	0.26	0.29	0.31	0.33	0.36	0.38	0	0.43	0.45	0	*	1	0	0.57	1	0.62	0.64	0.67	0.69	1
L	0	0.26	0.29	0.31	0.33	0.36	0	0	0	0.45	0	*	1	1	1	1	0.62	1	0.67	1
M	0.21	0.24	0.26	0	0	0.33	0.36	0.38	0.4	0.43	1	0	*	0.52	0.55	0.57	1	0.62	1	1
N	0	0	0	0	0.29	0.31	0	0	0.38	0	0.43	0	0.48	*	1	0.55	0.57	0.6	1	1
O	0.17	0	0.21	0	0.26	0.29	0	1	0	0.38	0	0	0.45	0	*	1	0.55	1	0.6	0.62
S	0	0	0.19	0	0.24	0.26	0	0.31	0.33	0.36	0.38	0	0.43	0.45	0	*	1	0.55	0.57	0.6
P	0.12	0.14	0.17	0.19	0.21	0	0.26	0	0.31	0.33	0.36	0.38	0	0.43	0.45	0	*	0.52	1	1
Q	0	0	0.14	0.17	0.19	0.21	0.24	0.26	0.29	0.31	0.33	0	0.38	0.4	0	0.45	0.48	*	1	0.55
R	0	0.1	0	0.14	0.17	0.19	0	0	0	0.31	0.33	0	0	0.4	0.43	0	0	*	1	0.55
T	0.05	0.07	0	0.12	0.14	0.17	0.19	0.21	0.24	0.26	0	0	0	0	0.38	0.4	0	0.45	0	*

Figure 1. (A) A sample interaction matrix with a 5% chance of circularity randomly imposed upon each dyad. Wins by an individual are denoted by a 1 in the individual's row and correspondingly a 0 in the individual's column. Initially this 20x20 matrix had 9 inconsistencies (I) with the sum of inconsistencies (SI) equalling 47, but the relative ranks of individuals N and M were switched resulting in $I = 8$ and $SI = 48$. (B) Unknown relationships are depicted as empty elements in an interaction matrix. In order to test our method, 60% of elements from the complete matrix were randomly removed and the results of our analysis compared with the known rank order (note the four inconsistencies that were randomly eliminated in the data set). (C) The unknown elements in the matrix are filled in using a likely-ranking interpolation (equation 7). The best rank order has been solved for the sparse data set by minimizing the values of I and SI (equations 2 and 5), yielding $I = 2$ and $SI = 9$ for this example, then resolving the relative ranks of unknown dyads using a strength metric (equation 9), and finally minimizing the sum of elements below the matrix diagonal. Note the changes in the position of individuals B + G and P + S as a result of resolving their inconsistencies in the previous matrix. (D) The optimised individual rank orders and their strengths calculated from matrix 1 C, as described in the text. Note that the individual strength metrics are not completely monotonic. This is a consequence of initially deferring to the I&SI minimization procedure as producing the best ordering. For example, the strength of individual F is greater than that of individual H but H is ranked higher as a result of the minimizing the sum of inconsistencies between F + O.

(A)

	A	B	C	D	E
A	*	1	1	0.75	0.83
B	0	*	0.58	1	1
C	0	0.42	*	1	0.67
D	0.25	0	0	*	1
E	0.17	0	0.33	0	*

(B)

	A	B	C	D	E
A	*	1	1	0.75	0.83
B	0	*	0.58	1	1
C	0	0.42	*	1	0.67
D	0.25	0	0	*	1
E	0.17	0	0.33	0	*

Figure 2. (A) Our dominance strength metric δ_i subtracts the sum of i -th row elements (wins) from the sum of i -th column elements (losses) for individual i . The dominance strength for individual B = 1.16 and C = 0.18. (B) The half-matrix metric may be used when the biology of a study organism affects the distribution of interactions, where an individual is prone to interact more frequently with individuals above or below their rank order. The dominance strength calculated from interactions below the individual in the rank order for individual B = 2.16 and C = 1.34.

Linear	Average difference	SE	Maximum difference	75th percentile
20%	0.28	0.034	2	1
40%	0.55	0.046	3	1
60% no min. ¹	1.19	0.082	8	2
60% min. 3 ²	1.16	0.085	7	2
80% no min. ¹	2.28	0.142	9	3
80% min. 3 ²	2.10	0.139	8	3
5% Circularity				
20%	0.42	0.056	5	1
40%	0.89	0.084	6	1
60% no min. ¹	1.74	0.123	12	2
60% min. 3 ²	1.47	0.112	9	2
80% no min. ¹	3.03	0.183	13	4
80% min. 3 ²	2.61	0.150	10	4

¹ No constraint was implemented on the minimum number of interactions per individual

² The minimum number of interactions per individual was constrained to 3

Table 1: Accuracy of method on simulated data

Chapter Seven

Seasonal movement, spatial segregation and social dominance in the African elephant

G. Wittemyer, W. M. Getz, I. Douglas-Hamilton

Introduction

Intra-specific competition for access to limited resources is hypothesized to be one of the most salient selective forces acting on individuals (Alexander, 1974). Such competitive interactions are broadly categorized into two classes: interference/contest competition, where individuals actively block other individuals from accessing resources, and scramble/exploitative competition, in which every individual attempts to consume available resources before their conspecifics. The type and degree to which either competitive regime occurs in an organism is thought to be a function of both its diet selectivity and the spatial distribution of resources in its environment (Isbell, 1991; van Schaik, 1989; Wrangham, 1980). Research on this topic has related the effects of different competitive regimes to social organization, mating systems, and spatial structuring of a population (Emlen & Oring, 1977; Clutton-Brock & Harvey, 1977; Isbell & Young, 2002; Sterck et al., 1997).

An important impact of the type and function of competitive interactions is the likelihood and strength of dominance hierarchy formation both within and between groups (Isbell, 1991; van Schaik, 1989; Wrangham, 1980). Established dominance hierarchies can benefit individuals by minimizing potentially costly contest interactions, facilitating resource monopolization by higher ranked individuals without constant reaffirmation of rank relationships (Clutton-Brock, 1982; Krebs & Davies, 1987). The socio-ecological framework predicts such dominance regimes are prevalent in species experiencing interference competition, in relation to reliance on monopolizable resources, but weak and poorly defined in those competing through scramble interactions occurring where resources are widely distributed (Sterck et al., 1997).

According to this framework, dominance hierarchy formation can be a function of within group interference competition, between group interference competition, or interference competition both within and between groups, but is not predicted to occur in species competing primarily through scramble competition (van Schaik, 1989; Isbell, 1991). Large herbivores are generally thought to exhibit scramble competition in response to the widely distributed, low quality herbivory comprising their diets (Clutton-Brock et al., 1987). Linear dominance hierarchies, however, are common to females of many large ruminants. The factors influencing the formation of such hierarchies in species predominantly experiencing scramble competition offers an interesting deviation from the predictions of the socio-ecological framework (see review by Sterck et al., 1997). The co-occurrence of these traits is not well understood and offers an important area for the study of the impact of resource distribution on social behavior. In this paper we explore the application and shortcomings of the socio-ecological framework to understanding the factors influencing dominance hierarchy formation in the African elephant (*Loxodonta africana*), a species predominantly experiencing scramble competition.

Elephants are characterized as generalist herbivores in that they feed on a wide diversity of plant types including regularly switching from grass to browse (Cerling et al., in review), and they demonstrate low levels of selectivity in their diet (Owen-Smith, 1988; Laws, 1970). Elephants do not have fixed territories, though competition over spatially explicit resources, such as water holes, does occur (pers. obs.). Despite these ecologically related characteristics of a scramble competitor, elephant social behavior demonstrates characteristics of a despotic society in that females are bonded

(Wrangham, 1980) and dominance relationships are well defined within familial groups (Archie et al., in press). Agonistic interactions among elephants are generally pairwise conflicts, like most ungulates (Clutton-Brock, 1982). However, elephants also develop long term group alliances, similar to those found in many primates (Janson, 2000), among which between group competition also occurs. The impact of between group dominance hierarchies on the organization of elephants spatially and socially has not been studied, although it is likely the formation of such a hierarchy is important to alleviating the potential high costs associated with contest interactions in this largest terrestrial mammal (Buss, 1990). Such characteristics make elephant sociality an interesting system in which to explore the relationship between scramble competition, dominance hierarchy formation, and resource availability.

In this paper, we investigate the relationship between spatial use and dominance rank between elephant social groups to understand the social factors that influence spatial organization in a wild elephant population. We first characterize dominance relations within the study population by analyzing observations of agonistic interactions among individuals and familial groups from a free-ranging African elephant population. Because the spatial behavior of familial members is the same, we focus our analysis on between group variations. We use the defined dominance order to assess the explanatory power of rank to observed differences in spatial use and movements. Specifically, we test the following predictions using continuously recorded G.P.S. radio tracking data: (1) high ranking groups move less than low ranking groups, (2) high ranking groups use smaller areas (home ranges) than low ranking groups, (3) high ranking groups access areas in close proximity to permanent water (an important limited

resource in the study area) to a greater extent than low ranking groups, and (4) high ranking groups spend a greater proportion of time within protected areas than low ranking groups. Finally, we explore the relationship between changing resource distribution and the manifestation of rank specific behaviors by testing the four predictions during both the dry season, when resources are limited and potentially monopolizable, and the wet season, when resources are ubiquitous and less monopolizable. If dominance hierarchies in elephants are a function of competition for resources, we expect to see strong differences in behavior between seasons.

This study offers novel insight into the application of the socio-ecological hypothesis to social structures shaped by scramble competition by assessing the degree to which social hierarchy impacts spatial organization during periods of increased competition. Furthermore, by characterizing the social properties influencing spatial population structure in elephants, the results from this work offer information important to the conservation and management of wild elephant populations. With range constriction leading to increased confinement in spatially limited protected areas, information on spatial use is particularly important to elephant conservation and the future management of this species.

Methods

Study of the relations between rank and spatial use were conducted on the elephants inhabiting the Samburu and Buffalo Springs National Reserves in northern Kenya. This semi-arid region is dominated by acacia-comiphora savanna and scrub bush and the reserves are focused on the major permanent water source in the region, the Ewaso N'giro River (Barkham & Rainy, 1976). Rainfall averages approximately

350 mm per year and occurs during biannual rainy seasons generally taking place in April and November. For a more detailed description of the ecology of the study area see Wittemyer (2001).

The elephants using these reserves are largely habituated to the presence of vehicles, enabling easy observation of behavior. These elephants are individually identified following well established methodology (Moss, 1996) and have been closely monitored since 1997 (Wittemyer, 2001). Over 900 elephants have been observed within the reserves over the course of the eight year monitoring project. The level of reserve use across a year, however, varies between individuals and was used to delineate two subpopulations among the reserve users (Wittemyer, 2001). Individuals entering the reserves during all four seasons, two wet and two dry, within a year were designated resident while those that used the reserve seasonally or rarely were termed sporadic. Further structuring of the population occurs along social delineations, defined using individually based association data (Wittemyer et al., 2005b).

Communal areas managed by multiple pastoralist tribes surround the national reserves. As a result, the reserves are not fenced and the study population of elephants is free ranging. The parks have been found to comprise less than 10% of the area used by the study population (Wittemyer et al., 2005a), and are part of a complex spatial arrangement of patches connected by corridors in the ecosystem (Douglas-Hamilton et al., 2005). Elephants move in and out of the reserve continually and no elephants stay within the park year round (pers. obs.). Thus, the spatial behavior reported here is assumed to be relatively natural since neither fences nor other hard boundaries impact

the spatial use of the study elephants. This combination of factors makes Samburu an excellent population for the study of the population spatial properties of elephants.

Dominance Analysis

Studies of agonistic interactions in elephants have shown agonistic interaction rates between individuals in the same family group, where individuals spend over 80% of their time in close association, are low (Lee, 1987; Archie et al., in press). A recent study calculated rates of such interactions at an average \pm SE of 0.14 ± 0.02 interactions per hour in mother-calf pairs and 0.05 ± 0.01 per hour in non-first order relationships (Archie et al., in press). In relation to the hierarchical fission-fusion social organization of elephants, contacts between individuals from different social groups occur at significantly lower rates than within social groups (Wittemyer et al., 2005b). Thus, rates of non-familial agonistic interactions are rare, resulting in unknown relationships for many non-familial pairs of individuals. Here we present an analysis of interaction data collected between July 2001 and December 2003 within the study area using *ad-libitum* sampling (Altmann, 1974), where the initiator and recipient of agonistic interactions were recorded opportunistically. As a result of our sampling method, interactions cannot be related on a temporal scale so rates of agonistic interactions were not calculated. Rather, the observations were used to formulate the most likely rank order among the study elephants using methods developed to address the problem of unknown relationships (Wittemyer & Getz, in review).

Types of agonistic interactions observed included chases, pokes, pushes as well as displacements. Displacements occurred when the initiator moved directly toward the recipient leading to the recipient moving away from the initiator. The role of each

individual during such interactions was clear because individual defined as the loser of the interaction would usually move away while looking at the winner over its shoulder. Observations where the rank relationships were not obvious, such as occasionally occurred when two individuals faced off and both moved off in opposite directions, were noted but not included in this analysis. Thus, we used only overt interactions to characterize dominance interactions in our study population.

In this analysis, we focus on agonistic interactions among mature females in different social units in an attempt to understand dominance relationships across social units. The number of agonistic interactions observed among members of family groups was much greater than between individuals across different groups, thus we exclude observations of interactions within family units in this quantitative description of the dataset. During the study period, we observed 419 agonistic interactions across family groups involving 124 different individuals. Each individual interacted with an average \pm SE of 3.8 ± 0.42 individuals outside her family unit and was observed in an average of 5.7 ± 0.53 agonistic interactions.

As a result of the low numbers of agonistic interaction observations among individuals in different families in the study population, the relationship in many dyads was unknown. Thus, we employ a likeliness-based approach to solve the relative ranks of unknown pairs and derive the best dominance rank ordering of the study individuals (Wittemyer & Getz, in review). This method minimizes the number and strength of inconsistent dominance relationship (de Vries, 1998); that is, interactions where a lower ranking individuals dominates a higher ranking individual. Minimization of inconsistencies is achieved by switching the relative positions of individuals in the

dominance rank until the sum of values below the matrix diagonal are minimized. The robustness of results using this technique have been demonstrated to relate to the proportion of relationships known in the dominance matrix (Wittemyer & Getz, in review). We created two interaction matrices for the study population containing different sub-samples of individuals in the study population that were most frequently observed in agonistic interactions (either as a winner or loser). For pairs with ambiguous dominance relations, where A sometimes beat B and vice versa, we assigned a dominance probability of 0.5 for both individuals, and for pairs where the winner or loser were consistent across observations 1 or 0 was assigned as the dominance probability. The first matrix contained our best dataset of 20 family unit matriarchs in which 37% of dyads were known (Fig. 1). The second matrix was composed of 73 females that were observed interacting with at least two females outside their family group, resulting in 13% known dyads (not shown). We then compared the resolved ranks of each focal individual across the different matrices to ensure the robustness of our rank assignments. Because of the relative sparseness of our interaction data, we categorized the assigned ranks into 3 broad categories (Table 1).

Radio Tracking Data Collection

To assess the degree to which rank relations affect spatial use, we analyzed data collected from G.P.S. collars fitted on 7 different individuals representing distinct families (as defined by Wittemyer 2005b) in the Samburu elephant population. The rank of the matriarch of each family was defined using the methods described above and used for rank based inter-group comparisons, since the matriarch directs family movement and spatial use (Moss, 1988). The ranks of these families were not known at

the time of collaring. The collared families differed in respect to their rank status within the population (Table 1), but were of similar sizes (range 9-13 individuals) and all lead by mature matriarchs estimated to be over the age of 35 years (Wittemyer et al., 2005b). Age estimates were conducted following methodology outlined in (Rasmussen et al., in press). These elephants were radio collared by a Kenya Wildlife Service (KWS) veterinarian following the protocol established by KWS. The data used in this study are part of an ecosystem wide assessment of elephant ranging behavior being conducted on the Samburu/Laikipia elephant population by Save the Elephants under the auspices of KWS. Secondary breeding females in most of the social groups were fitted with radio collars rather than the matriarch, in order to avoid unnecessary stress on families and older aged individuals. We assumed that the range and movement patterns of all individuals in a group are essentially the same because the individuals comprising these quantitatively defined groups have been shown to spend between 85-100% of their time together (Wittemyer et al., 2005b).

Dry season data analyzed in this study were collected from the 7 focal individuals between July 10 and October 1, 2001, consisting of 84 days. We initiated our analysis on July 10th because all 7 focal individuals had been collared for at least 24 hours by this date and rainfall had not occurred in the study area for over 30 days (a definition previously used to define dry seasons). We ended our analysis on October 2 because the first rain of the “November” 2001 wet season occurred on this date. Thus our dry season study period incorporated movement and spatial information carried out by the study elephants during a period without rainfall in the study area and, as a result,

localized rainfall was not a potential factor impacting the recorded movements and spatial use.

Wet season data analyzed in this study were collected between November 1, 2001 and January 2, 2002, consisting of 62 days. This period was defined using NDVI (Normalized Differential Vegetation Index) data: an increase in the mean NDVI values greater than or equal to 2 standard deviations above the baseline for the whole year (the mode of the distribution of NDVI values) marked the onset of the wet season, and a decrease in NDVI values below this demarcation defined the cessation of the wet season. Thus our wet season study period incorporated movement and spatial information carried out by the study elephants during the seasonal period of increased primary productivity as measured by NDVI (Goward & Prince, 1995).

During the dry season, G.P.S. radio collars were programmed to record the positions of the collared individual on an hourly basis. Failure to obtain fixes occurred infrequently in each of the collars during the three month dry season study with a median of 11 (range 4-56) failures during the 2016 hour period. Collar performance and the resulting data set were not as good during the wet season period of the study. Two of the seven collars were programmed to record G.P.S. data at 3-hour intervals during this period. One collar failed on December 15, 2001 spanning the last 17 days (415 hours) of the 1488 hour wet season period and another collar failed for an eight day (196 hour) period between December 12th and 19th 2001, after which it operated normally. The remaining three collars performed well with failures ranging from 5-16 hours. Although this data set had more failures than that collected over the dry season, positions were recorded for at least 45 days during the wet season for all individuals and

we could not find any evidence of bias in the collected data. Analyses of these wet season data were collated on a 3-hour basis in order to ensure similar samples sizes among the seven individuals during this period.

Analysis of G.P.S. data obtained from the radio collars was conducted in ArcView 3.2© and ArcGIS 9.0© (Environmental Systems Research Institute), using the Animal Movement extension (Hooge & Eichenlaub, 1997). Hourly distances moved were calculated for each individual for all possible hours where successful fixes were taken, and 2-hour distances moved were calculated where fix failures occurred and used in calculation of daily movement distances (covering a 24 hour period). However, 2-hour movement data were excluded from analyses of hourly movement behavior. Likewise, in our analysis of wet season data 6-hour distances were calculated when fix failures disrupted 3-hour distance calculations and used to estimate daily movement distances (covering 24 hour periods).

Two types of home range estimation techniques were used to analyze the data, minimum convex polygons and fixed kernel estimates (Worton, 1995). Home range analysis was conducted in ArcView 3.2© (ESRI). Minimum convex polygon home ranges and kernel home ranges were calculated using the Animal Movement Extension (Hooge & Eichenlaub, 1997). The fixed kernel method was used to create density isopleths. Although the Kernel Least Squares Cross-Validation (LCSV) technique is preferred (Seaman et al., 1998), the amount of data collected for each individual made such estimation unwieldy. Therefore, the smoothing parameter used for all individuals on a 1 meter grid was $h = 1000$. Both 50% and 95% density isopleths were calculated.

The spatial analyst extension of ArcView 3.2© (ESRI) was then used to calculate the areas of different isopleths.

Analysis of the location of fixes in relation to protected status of areas and proximity to permanent water was conducted in ArcGIS 9.0© (ESRI). The proportions of fixes located within 1 kilometer, between 1 and 2.5 kilometers, 2.5 and 5 kilometers, and greater than 5 kilometers from permanent water were calculated using the assign attribute function to buffer shape files created for these distances from permanent water. Land use in the study region varies in protective status from national reserves to community or private conservancies, to unprotected communal areas. To determine how differently ranked individuals used space in relation to these different protective designations, the proportion of fixes occurring within each land use type were also calculated using the assign attribute feature in ArcGIS 9.0© (ESRI). This data was used to compare time specific use of the reserves during the dry season.

Hard boundaries do not exist in the study region, making explicit study area definitions difficult. To test for spatial selectivity, we defined the study area as the MCP range of the combined data from the seven tracked elephants during the dry season. The proportion of the MCP area occupied by different habitat criteria was then compared to the amount of time spent in each habitat. Wet season data was analyzed for preferences only within the dry season defined study area as individuals used disparate ranges during this period making definition of a wet season study area for comparative purposes problematic. Habitat selection in relation to proximity to permanent water (4 classes described above) and protected status (2 classes protected and not protected) was conducted using the Neu Method (Neu et al., 1974; Alldredge &

Ratti, 1992). χ^2 Goodness of Fit statistics were Bonferroni corrected to account for multiple comparisons. Selectivity was assessed for each individual elephant as well as across the pooled data of the 7 tracked individuals. Comparisons between the wet and dry season were conducted. The assumption of independence of data points for habitat selectivity analysis was not met. Due to the high resolution of the data set, however, our analysis is conducted on a close approximation of real time spatial use over the study period and the results are thought to be robust despite this violation of the assumption of independence.

Statistical Analysis

We analyzed movement and spatial use data during the wet season using data collated at 3-hour intervals across all individuals, because two of the seven collars were at this resolution. Where the resolution of the data was finer, we sub-sampled the data so that the G.P.S. fixes matched those of the 3-hour interval collars, collected at 0:00, 3:00, ..., 21:00. Analysis of movement and spatial use within the dry season was conducted using data collected at hourly intervals. For comparisons between dry and wet season data, however, dry season data were sub-sampled at 3-hour intervals. Analyses of movement data were conducted using non-parametric techniques as both hourly and daily data sets were not normally distributed across all individuals. Pairwise comparisons were conducted using Wilcoxon rank sum tests; comparisons of hourly and 3 hourly distances moved were conducted across all pairs within both seasons, thus 21 tests were conducted within each season between the 7 individuals. Significance of p -values was assessed after Bonferroni correction for multiple comparisons of the alpha level (Zar, 1999). Comparisons of more than two individuals were conducted using

Kruskal-Wallis tests. The correlation between social rank and movement and spatial use was conducted with Spearman rank correlations. All comparisons to rank were conducted on ordinal groupings where the rank of each of the seven individuals was categorized as 1 (high), 2 (mid-high), or 3 (mid-low) in order to ensure the robustness of the rank relationships (Wittemyer & Getz, in review). Data within categories was not pooled but analyzed as independent samples. M54, M5, and R28 were grouped together as the highest-ranking individuals since they were dominant in all of their recorded interactions. M31 and R22 were categorized as mid-high ranking because they were grouped together in both analyses of dominance data sets. Finally, M46 and R37 were grouped as mid-low ranking individuals as they also were also consistently grouped together and below M31 and R22 in both analyses of dominance relationships. All statistical analyses were conducted in JMP 4.04 Student Version (SAS Institute ©1989-2001).

Results

Between Group Dominance Relationships

Although data was sparse in relation to the low frequency of dominance interactions between individuals, our results indicate that between family group dominance hierarchy was nearly linear. In the dominance matrix consisting of 20 individuals in which 37% of relationships were known, only 2 circular relationships were found (Fig. 1). In the sparser data set consisting of 73 individuals with 11% of dyads known, only 4 of 290 known relationships were circular. Results from both data sets were closely correlated (Table 1). Because of high numbers of unknown pairs

causing lower resolving power (Wittemyer & Getz, in review), these results were used to categorize the radio-tracked individuals into 3 dominance categories of high, mid high, and mid low.

Differentiation in Movements

Individuals within the study population demonstrated diverse spatial use and movement behavior during the long dry season of 2001 (Fig. 2). Hourly distances moved differed significantly across individuals (Kruskal-Wallis rank sums: $\chi^2 = 519.39$, $df = 6$, $p < 0.0001$), as did the daily distances moved (Kruskal-Wallis rank sums: $\chi^2 = 287.24$, $df = 6$, $p < 0.0001$). We related these differences in movement to the social rank category of the study individuals. Both hourly movement (Spearman's $\rho = 0.808$, $p = 0.028$) and daily movement (Spearman's $\rho = 0.794$, $p = 0.033$) were significantly correlated with rank (Table 2). Combined, the three highest-ranking individuals averaged 251 meters/hour and 5.93 kilometers/day, approaching half the average distances moved by the four lower ranking individuals, which averaged 456 m/hour and 10.78 km/day. Total distances moved during the dry season, calculated by summing all consecutive G.P.S. fixes regardless of interval, were also significantly correlated with rank (Spearman's $\rho = 0.869$, $p = 0.011$).

Results from analyses of correlations between rank category and movement during the wet season differed from those found during the dry season (Table 2). Hourly distances traveled differed significantly across individuals (Kruskal-Wallis rank sums: $\chi^2 = 80.93$, $df = 6$, $p < 0.0001$), as did the daily distances moved (Kruskal-Wallis rank sums: $\chi^2 = 60.22$, $df = 6$, $p < 0.0001$), though the degree of differentiation across individuals was weaker than during the dry season. Furthermore, rank was not a

significant predictor of 3-hour, daily or total movement during the wet season (Table 2). General differences in seasonal movements were apparent as 6 of the 7 tracked individuals moved significantly greater distances per 3-hour period and per day during the wet season than the dry season (Table 4 and 5). Only one individual from the lowest rank category, R37, did not demonstrate significantly greater movements in the wet season.

Pair-wise comparisons of differences in hourly (dry season) and 3-hourly (wet season) movements between all pairs of individuals were conducted (Table 3). Alpha levels were Bonferroni corrected because of overlapping multiple comparisons, resulting in significance being assigned to p -values < 0.0028 . During the dry season, 15 of 21 pairs demonstrated significant differences in movements. Members of the highest-ranking group were found to have similar movement behavior, where 2 of 3 comparisons between the three dominants were not significantly different. Similarity also existed among lower ranking individuals where 3 of the 4 individuals did not demonstrate significant differences. The fourth, however, moved significantly less than each of the other three and was found to move distances more similar to one of the dominant individuals than any of the lower ranking ones. Pair-wise comparisons during the wet season showed a different pattern, where the relationship between rank status and movement was not obvious. During this period only 7 of the 21 comparisons were significantly different, where 6 of the significantly different comparisons were the result of the movements of one dominant individual who moved less than all other elephants (Table 3).

Differentiation in Spatial Use

Home range sizes of elephants varied across groups and were related to differences in rank category as well (Table 2 and 6). Analysis of dry season data found MCP ranges were significantly correlated with rank (Spearman's $\rho = 0.775$, $p = 0.044$), where lower ranked individuals tended to have larger ranges (Table 6). Similarly, the sizes of the 95% kernel density isopleth were positively though not significantly correlated to rank (Spearman's $\rho = 0.699$, $p = 0.080$). The sizes of the 50% kernel density isopleth, used to define an individual's core range, were not significantly correlated with rank (Spearman's $\rho = -0.227$, $p = 0.625$). The location of the 50% density kernel, however, was related to rank, where higher ranking individuals had a greater proportion of their "core" range located within protected areas than lower ranking individuals during the dry season (Spearman's $\rho = -0.784$, $p = 0.037$). In relation to this result, the proportion of fixes occurring within protected areas was significantly correlated to rank (Spearman's $\rho = -0.850$, $p = 0.015$). The inverse was also true, where lower ranking individuals showed a greater propensity towards using regions outside protected areas (Spearman's $\rho = 0.850$, $p = 0.015$). Interestingly, we found that lower ranking individuals significantly decreased their use of the national reserve as the dry season progressed ($R^2 = 0.460$, p value = 0.015), while the use of high ranking individuals did not change significantly ($R^2 = 0.113$, p value = 0.285; Fig. 3). Weekly proportions of time spent in the national reserves was calculated for each individual and normalized by arcsine transformation for this analysis.

Although all individuals spent a greater proportion of time outside protected areas during the wet season (Fig. 4 and Table 7), neither time in or out of protected

areas nor MCP or kernel home range size were significantly correlated with rank (Table 2). Interestingly, the proportion of “core” range located in the national reserves was still correlated with rank (Table 2). Further, the proportion of time spent in proximity to permanent water at the 1 km, 2.5 km, and 5 km distances were all significantly correlated with rank. Although proximity to water was correlated with rank, decreasing proportions of fixes occurred in proximity to permanent water during the wet season for all individuals (Fig. 5 and Table 7).

The study elephants demonstrated significant preference for areas within 1 kilometer and avoidance of areas greater than 1 kilometer from permanent water during the dry season (Table 7). Area selection in relation to permanent water differed substantially in the wet season, where only selection for areas between 1 and 2.5 kilometers from permanent water was significant. Across both seasons, elephants demonstrated strong selection for areas within protected areas and avoidance of areas outside protected areas (Table 7). The strength of this selection, however, decreased during the wet season. Analysis of individual habitat preferences during the dry season demonstrated preference for areas within 1 kilometer of permanent water and significant avoidance of area greater than 5 kilometers from water was found in each of the seven elephants (Table 8). Differentiation of area use during the dry season was not found to be strongly correlated with rank except at the 5 km resolution (Table 2). Interestingly, while all elephants, except for one dominant, used areas between 1 and 2.5 kilometers at expected levels during the dry season, dominant individuals showed significant avoidance of areas between 2.5 and 5 kilometers while lower ranking individuals did not. One lower ranking individual proved to be the exception to this

rank related differentiation by avoiding all areas over 1 kilometer from permanent water, though she was the only individual which demonstrated significant avoidance of protected areas (Table 9). Only the lowest two ranking individuals did not demonstrate significant selection for protected areas and avoidance of unprotected areas during the dry season (Table 9).

Discussion

Seasonal variation in rank related behavior

Strict territory exclusion, indicative of contest competition and monopolizable resources, was not observed in the study elephant population. In periods with limited resources, however, competition between elephants appears to result in the partitioning of preferred habitats (Fig. 2). Observations of agonistic interactions between families, recorded in the national reserves, predominantly occurred during the dry season in relation to point samples of resources, including water, fruiting trees, or recently felled trees. Additionally, lower ranking individuals moved significantly greater distances, had larger home ranges, tended to use areas outside protected areas and further from permanent water to a greater degree than high-ranking individuals during the dry season (Fig. 4 and 5). Our results indicate that the costs of being lower ranking in an area occupied by a dominant become acute as resource quality declines or becomes more clumped and defendable. Thus, we found evidence for spatial segregation and differentiation in movement behavior among the studied elephants in relation to rank during the dry season, behavior consistent with predictions of the socio-ecological

framework for despotic systems but not normally associated with a social structure shaped by scramble competition.

Our results from the wet season indicate factors causing resource partitioning and differential spatial use did not occur during the wet season. Seasons were defined using time-specific NDVI data and, thus, is the period in the study area with increased primary productivity (Goward & Prince, 1995). We found no significant correlation between rank and movement and little correlation between spatial use and rank during the wet season (Table 2). Interestingly, correlations between rank and water proximity were significant across all distances during the wet season even though the total time spent near water decreased for all individuals (Fig.5). Although dominant individuals had a greater proportion of their core range, as defined using the 50% isopleth of the kernel home range estimate, within the national reserves in both seasons, these core ranges were much less contiguous during the wet than the dry season, changing from a single contiguous core region during the dry season to multiple (ranging from 5-7) widely dispersed core patches for each of the dominant families in the wet season. Our results indicate spatial partitioning in the study area does not occur during the wet season when resources are generally of higher quality and less clumped spatially. Thus, wet season behavior was consistent with prediction from the socio-ecological framework for species experiencing scramble competition.

Complexity in the relationship between scramble competition and dominance relations appears to result when fluctuating ecological factors influence both the type of competitive interactions and the strength of dominance related differences. As density of conspecifics increase or resources decline, intra-specific competition influences

access to limited resources. Thus, resource configuration in highly seasonal environments may lead to changes in the competitive landscape across seasons. Interestingly, cursory analysis of movement and spatial use of two of the dominant groups during a successive dry season, during which NDVI dry season values were higher than those recorded during the 2001 dry season, found increased distances moved and range sizes as compared to those presented here. Data, however, was not available for the other individuals studied here, thus thorough analyses could not be conducted. This may indicate that rank derived advantages only occur during infrequent periods of high competition, as occurs during extended periods of below average rainfall, but are not apparent as resources increase.

Impacts of rank related differentiation

The differentiation in hourly and daily movement is expected to reflect differentiation in energy expenditure by high and lower ranking elephants. Movement by elephants at very slow speeds and at speeds greater than 1 m/sec are energetically expensive for elephants (Langman et al., 1995). Hourly G.P.S. data can be used to define periods exceeding energy efficient movement speeds. Not surprisingly, costly high-speed movements exceeding the 1 m/sec threshold were rare across all individuals. Interestingly, the top hourly speeds reached by elephants exceeded this threshold most frequently in lower ranking individuals, with R37 exceeding this speed in 9 different hours during the dry season. Although we are not able to assess the degree to which access to resources of different quality differs in relation to rank, it is possible that dominants, moving less frequently and spending greater periods in protected areas, may encounter a cost in resource quality in relation to reduced search area and time.

However, preferred habitat characteristics of all elephants, demonstrated in analyses of pooled data (Table 3), were most frequently used by dominants. Distinguishing the variation in resource quality access across individuals of different rank and relating caloric intake to energy expenditure, however, is beyond the scope of this study.

The motivation for spatial preferences by the study elephants for protected areas is of importance to the management of this species. The national reserves are a focal area for elephant use in the study region and thus subject to high elephant density (Wittemyer, 2001; Douglas-Hamilton et al., 2005), but the habitat type within the reserves does not appear to vary substantially from that outside these reserves. As such, intra-specific competition for resources is expected to be higher within the reserves. Dominant individuals, however, were found to avoid non-protected areas during the dry season when competition for resources was greatest, relying almost exclusively on the reserves during this period. This spatial preference may be the result of inter-specific competition between elephants and human lead livestock herds occurring outside the protected areas in community owned areas. In support of this hypothesis, analysis of diurnal water use within and outside the reserves shows differences in behavior. Elephants tend to spend a greater proportion of the hotter, daylight hours within 100 meters to permanent water when in the reserves ($n = 1128$ hours during the day vs $n = 482$ at night) as compared with use outside the protected areas ($n = 794$ hours during the day vs $n = 675$ at night). Livestock is often on the river during the mid day outside the protected areas but confined to corrals during the night as a predator protection precaution. Thus, diurnal access to the river for elephants may be limited to a greater extent outside the protected areas.

Application of results to socio-ecological theory

Spatial behavior is thought to directly relate to the type and strength of different competitive regimes (Isbell, 1991). Within group scramble competition is predicted to impact daily travel distances in relation to group size where larger groups will move greater distances in relation to increased resource requirements. Between group scramble competition is hypothesized to impact the range size of groups where larger groups will have larger ranges in order to fulfill resource requirements (Isbell, 1991). In our study we focused analysis on movements and spatial behavior of a scramble competitor across groups of different rank, where rank and group size were not correlated across the seven focal groups (Spearman's $\rho = -0.3922$, p -value = 0.3841). Our results demonstrate differentiation in spatial behavior in relation to rank during the dry season is similar to that hypothesized to be related to social group size in other scramble competitor social systems. Specifically we found that ranges were generally larger for subordinates despite the fact that portions of subordinates' ranges overlapped with the majority of the range of dominants. Additionally, subordinates tended to move more than dominant groups. In elephants, high-ranking groups do not appear to be impacted by resource competition to the same degree as their lower ranking conspecifics, enabling dominants to move less and use smaller areas during periods of constrained resources.

In relation to the formation of linear dominance hierarchies within and between groups, elephants can be characterized as despotic rather than egalitarian. The lack of strict territoriality during periods of constrained resource availability, however, indicates that these animals are relatively tolerant of lower ranking conspecifics despite

the fact that segregation of spatial use across differently ranked individuals was found. It seems unlikely displacement of subordinates by dominants (low tolerance) can explain such behavioral differentiation since the areas being used are large and levels of agonistic interactions are low. Rather, it appears subordinates may avoid areas used by dominants as resources become increasingly constrained (Fig. 3), potentially to avoid contests over generally low quality resources.

Well defined dominance hierarchies have been found in numerous large herbivores in which intra-specific interactions are typically characterized as scramble competition, including cape buffalo (Prins, 1989), caribou (Barrette & Vandal, 1986), prong horns (Dennehy, 2001) and red deer (Appleby, 1980). Although much research has been conducted on factors, such as predation, influencing group formation in societies experiencing scramble competition for resources (Jarman, 1974), little research is conducted on the factors impacting the formation of dominance hierarchies in such societies. As we found with elephants, rank derived benefits in these species are typically related to resource access by dominants over subordinates. Monopolization of resources in relation to rank in scramble competitive systems, however, is often ephemeral or not overt. For instance, the propensity of socially dominant pronghorn antelope to access higher quality portions of widely distributed resources than subordinates was detected through analysis of nutrient content in dung (Dennehy, 2001) but not found during focal observations of behavior (Byers, 1997). Similarly, spatial segregation among elephants was not found in the form of territoriality typical to contest competitive systems. Rather, segregation was found in the form of differentiation in habitat use only during periods of increased competition.

Our results offer a potential extension to the socio-ecological hypothesis to systems in which scramble competition dominates. In such systems, dominance hierarchy formation is probably indicative of resource competition during temporal periods of increased competition or in relation to ephemeral key resources. Limited contest competition occurring during highly constrained periods may drive the formation of social hierarchies and rank related behavioral or fitness differentiation. The identification of the salient factors influencing social hierarchy formation can offer important insight into the constraints impacting a population or species.

NK		M52	M2	M33	R27	R17	M8	M3	M24	M31	R10	R22	S30	R37	M45	M63	M65	R1	M73	R25	M30	
1	M52	*				1			1		1	1	1	1	1			1		1		
2	M2		*	0.5			1	1		1		1	1		1				1			
3	M33		0.5	*				1		1		1			1					1	1	1
4	R27				*	1						1			1			1	1		1	
5	R17	0			0	*			1	1					1			1				
6	M8		0				*	0.5		1						1						1
7	M3		0	0			0.5	*						1								
8	M24	0				0			*	1		1		0	1							
9	M31		0	0		0	0		0	*	1	1			1					1		1
10	R10	0								0	*		1					1		1		
11	R22	0	0	0	0				0	0		*	0.5	1	1		1		1	1		
12	S30	0	0								0	0.5	*			1					1	
13	R37	0			0			0	1			0		*	1	0		1				
14	M45	0	0	0		0			0	0		0		0	*	1			1			1
15	M63						0						0	1	0	*		1		1	1	1
16	M65				0							0					*				1	1
17	R1	0			0	0					0			0	0			*				1
18	M73		0							0		0			0					*		
19	R25	0		0	0						0	0	0			0	0				*	
20	M30			0			0			0					0	0	0	0				*

Figure 1. Dominance matrix of 20 matriarchs in which 37% of relationships between dyads are known. Identification letter-number combinations in bold type are the matriarchs of the seven family groups radio tracked in this study.

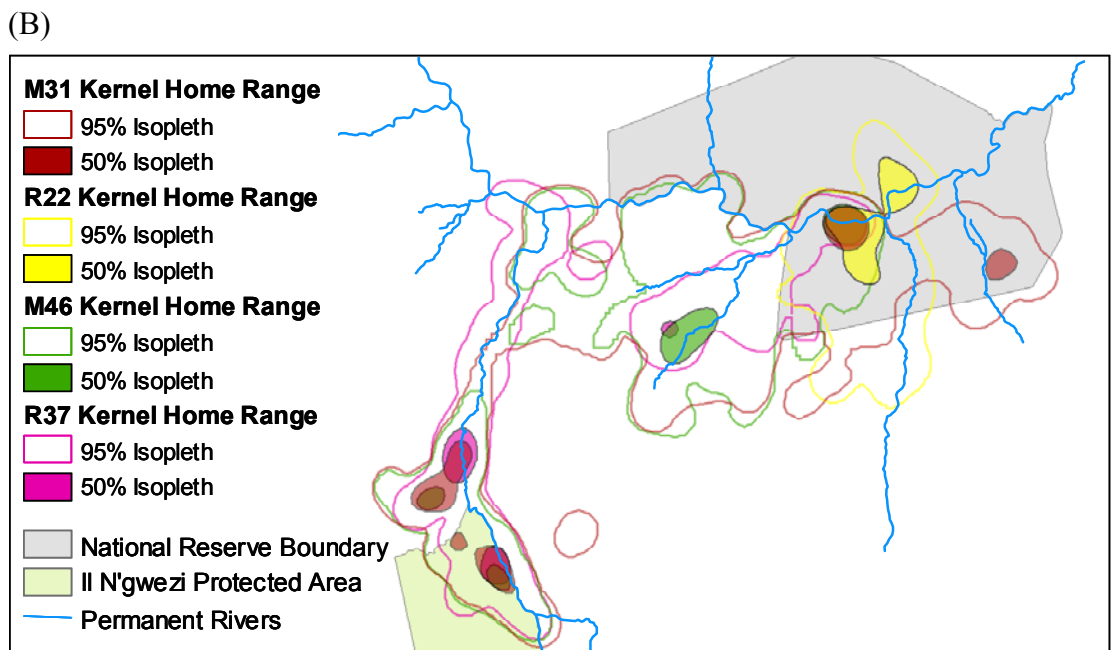
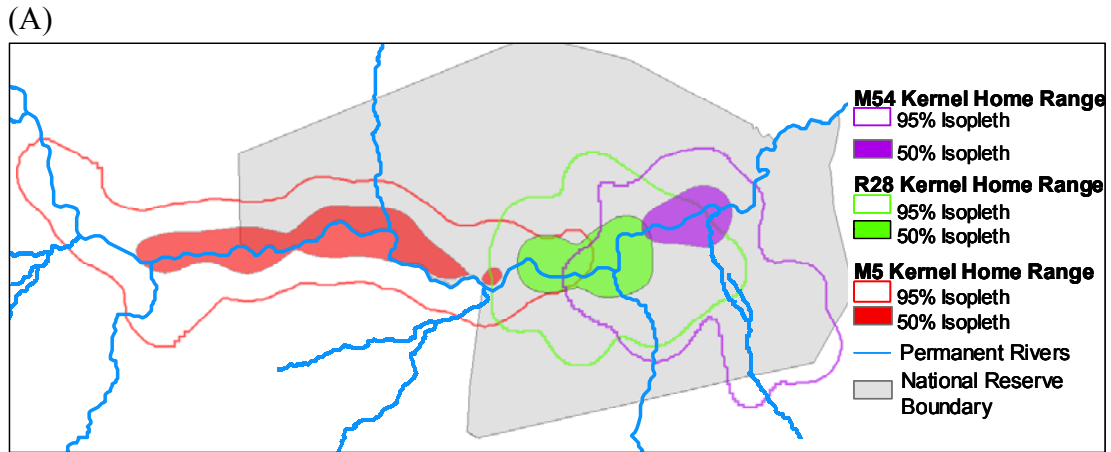


Figure 2. Kernel home range for the three dominant individuals (A) and four lower ranking individuals (B) during the dry season. All individuals with the exception of R37 have part of their core range within the boundaries of Samburu and Buffalo Springs National Reserves. The ranges of the three dominant individuals are cohesive and focused on the main river in the study area while ranges of the lower ranking individuals are more dispersed and focused at various points within and outside the protected reserves.

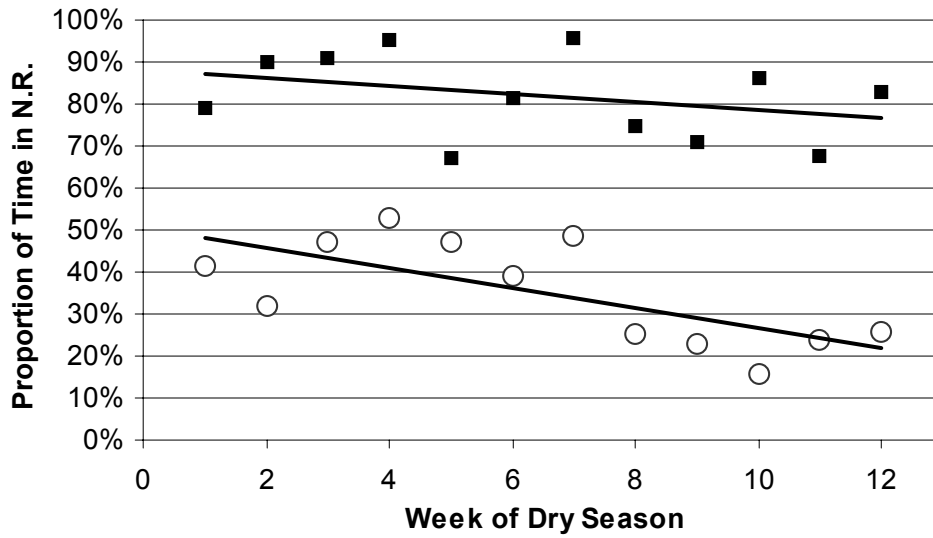


Figure 3. Use of protected areas by lower ranking individuals (open circles) decreased significantly as the dry season progressed (Arcsin normalized: $R^2 = 0.460$, p value = 0.015, $y = -0.025x + 0.525$), while use by dominant individuals (black squares) did not change significantly over the 12 week dry season (Arcsin normalized: $R^2 = 0.113$, p value = 0.285, $y = -0.018x + 1.099$).

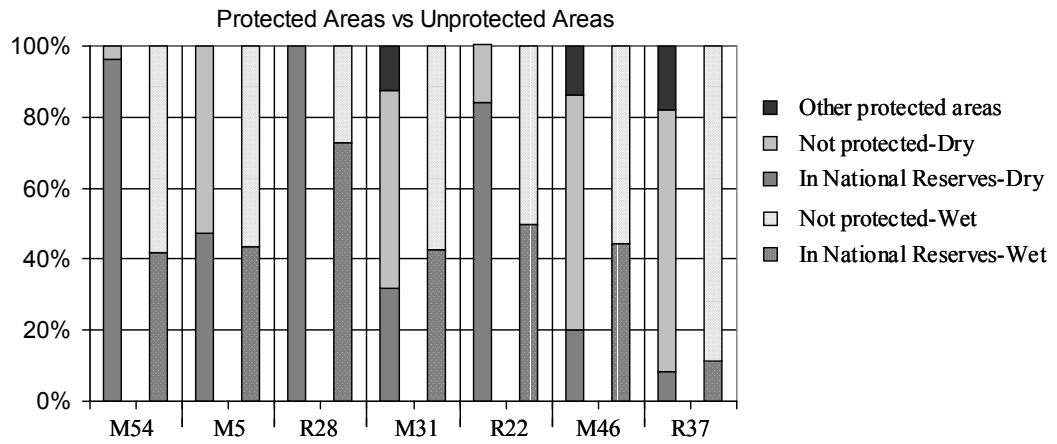


Figure 4. Proportion of time spent within and outside protected areas in both the dry and wet season.

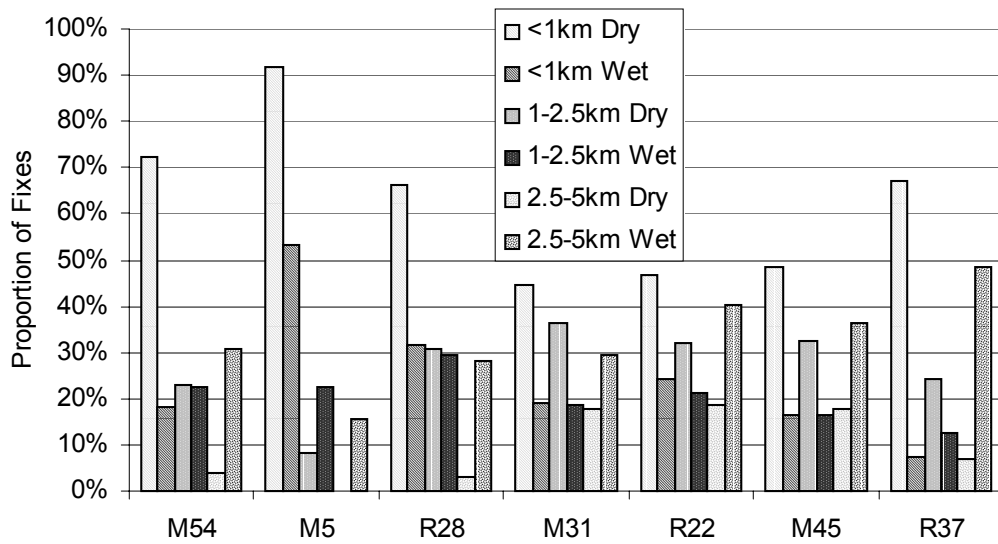


Figure 5. The proportion of time spent by the seven tracked individuals within 1 km, between 1 and 2.5 km, and between 2.5 and 5 km of permanent water sources during both the wet (black and white bars) and dry season (gray and white bars) in the study area.

ID Number	Relative Rank	20 40% known	73 25% known
M54	Top	1	1
M5	Top	2	3
R28	Top	4	2
M31	Mid	9	12
R22	Mid	11	16
M45	MidLow	14	29
R37	MidLow	13	28

Table 1: The rank of focal individuals was assessed from two dominance matrices with varying degrees of information. The first matrix contained 20 matriarchs and 37% of pair-wise relationships known (labeled n=20, 37% known). The second matrix contained 73 individuals and 13% of pair-wise relationships known (labeled n=73, 13% known). Results from analyses of both matrices were analogous.

Season		3 Hour Dist	Daily Dist	Total Dist	Time in N.R.	Time in Unprotected
DRY¹	Spearman's ρ	0.808	0.794	0.869	-0.85	0.85
	<i>P</i> value	0.028	0.033	0.011	0.015	0.015
WET²	Spearman's ρ	0.302	0.378	-0.264	-0.246	0.246
	<i>P</i> value	0.51	0.403	0.668	0.595	0.595

Season		MCP HR	K95 HR	K50 HR	K50 in N.R.	1km Water	2.5km Water	5km Water
DRY¹	Spearman's ρ	0.775	0.699	-0.227	-0.784	-0.472	-0.718	-0.76
	<i>P</i> value	0.041	0.08	0.625	0.037	0.284	0.069	0.047
WET²	Spearman's ρ	0.265	0.113	0.302	-0.775	-0.756	-0.85	-0.699
	<i>P</i> value	0.566	0.809	0.51	0.041	0.049	0.015	0.08

1 Dry season G.P.S. data were analyzed at an hourly interval

2 Wet season G.P.S. data were analyzed at a 3 hourly interval in relation to data collected for 2 of the seven elephants (See Methods)

Table 2: Spearman rank correlations comparing individual rank with various measurements of movement and spatial use behavior. Correlations significant at the $\alpha < 0.05$ are highlighted.

	M54	M5	R28	M31	R22	M45	R37
M54	*	12.025	2.176	171.69	7.119	100.13	114.72
M5	37.064	*	4.282	276.77	36.357	180.53	192.19
R28	0.051	31.322	*	207.99	17.255	128.53	145.06
M31	2.947	61.18	3.722	*	99.674	7.239	1.985
R22	1.718	55.534	2.578	0.139	*	49.941	63.988
M45	0.253	41.509	0.635	1.424	0.628	*	1.413
R37	2.267	21.078	1.19	10.395	8.606	3.907	*

Dry Season

Wet Season

Table 3: Pairwise comparison of hourly movements in the dry season (above the matrix diagonal) and wet season (below the matrix diagonal). Wilcoxon rank sum test χ^2 are presented for each pair. After Bonferroni correction for 21 multiple comparisons, significant χ^2 statistics highlighted in gray.

ID Number	Dry Median (Inter-Quartile Range)	Dry Max 3Hourly	Wet Median (Inter-Quartile Range)	Wet Max 3Hourly	Wilcoxon Z (p)
M54	0.47 (0.22-0.97)	5.39	1.01 (0.47-2.09)	10.19	11.00 (<0.0001)
M5	0.40 (0.18-0.71)	4.95	0.64 (0.33-1.29)	8.98	8.37 (<0.0001)
R28	0.50 (0.24-0.90)	3.45	1.05 (0.46-1.91)	7.61	10.35 (<0.0001)
M31	0.92 (0.39-1.84)	8.36	1.19 (0.53-2.31)	10.84	3.82 (0.0001)
R22	0.58 (0.25-1.28)	7.17	1.20 (0.47-2.22)	10.21	9.54 (<0.0001)
M46	0.81 (0.34-1.71)	9.11	1.07 (0.46-2.18)	10.92	3.97 (<0.0001)
R37	0.81 (0.32-2.06)	12.10	0.98 (0.38-1.93)	9.20	1.06 (0.2886)

Table 4: 3 Hourly Movement Distances between the Wet and Dry Season

ID Number	Dry Median (Inter-Quartile Range)	Dry Max Daily	Wet Median (Inter-Quartile Range)	Wet Max Daily	Wilcoxon Z (p)
M54	5.46 (4.21-6.66)	11.23	11.22 (7.79-15.95)	33.26	7.85 (<0.0001)
M5	3.79 (3.12-5.16)	15.31	6.53 (5.12-8.14)	29.26	6.70 (<0.0001)
R28	5.31 (4.61-6.00)	9.05	10.01 (8.05-11.73)	23.47	8.25 (<0.0001)
M31	9.92 (8.01-11.91)	22.16	12.15 (10.31-15.06)	28.83	3.42 (0.0006)
R22	6.99 (5.30-8.41)	17.99	11.70 (9.18-15.59)	25.37	7.49 (<0.0001)
M46	9.40 (7.55-11.99)	19.94	11.87 (9.23-14.61)	24.37	3.13 (0.0017)
R37	9.31 (7.19-13.71)	38.75	9.95 (7.79-13.54)	29.50	0.72 (0.4712)

Table 5: Daily Movement Distances between the Wet and Dry Season

ID Number	MCP km ²	95% Kernel km ²	50% Kernel km ²	Number of Core Areas	Core Areas in SNR km ²
M54	112.7	82.77	8.23	1	8.23
M5	207	114.87	25.68	1	11.31
R28	68.25	72.07	15.94	1	15.94
M31	585.3	372.23	21.54	4	8.28
R22	123	109.94	17.24	2	17.24
M45	443	261	15.61	4	5.07
R37	910.5	117.8	9.31	3	0

Table 6: Home Range Size and Core Areas (defined using 50% Kernel home ranges) during the dry season

Area	Proportion Study Area	Dry Fix Obs	Dry Fix Exp	χ^2	Wet Fix Obs	Wet Fix Exp	χ^2
< 1km ¹	26.22%	8705	3660	869.221	733	689	0.346
1-2.5 km ¹	30.30%	3738	4229	7.138	594	797	6.439
2.5-5 km ¹	29.95%	1347	4180	240.065	936	787	3.508
> 5 km ¹	13.53%	169	1889	195.761	366	356	0.037
Protected ²	21.36%	8774	2982	2812.933	1054	562	107.946
Unprotected ²	78.64%	5185	10977	764.081	1575	2067	29.322

1 Bonferroni corrected for 8 comparisons

2 Bonferroni corrected for 4 comparisons

Table 7: Proportion of time spent in proximity to permanent water and within and outside protected areas during both the wet and dry season. χ^2 statistics are Bonferroni corrected for multiple corrections

	<1 km			1-2.5 km			2.5-5 km			>5 km		
	Obs	Exp	χ^2	Obs	Exp	χ^2	Obs	Exp	χ^2	Obs	Exp	χ^2
M54	1449	527	57.6	459	609	1.32	75	602	16.48	27	272	7.881
M5	1797	514	114.4	163	594	11.16	0	587	20.96	0	265	9.473
R28	1328	527	43.58	616	608	0.003	63	601	17.21	1	272	9.633
M31	902	528	9.492	730	610	0.849	353	603	3.691	27	272	7.891
R22	934	526	11.33	646	607	0.087	373	600	3.077	52	271	6.332
M45	971	524	13.63	648	605	0.107	350	598	3.682	29	270	7.696
R37	1324	515	45.29	476	596	0.859	133	589	12.6	33	266	7.291

Table 8: Selection for areas in relation to the nearest permanent water source was tested across individuals during the dry season. χ^2 statistics, Bonferroni corrected for 28 multiple comparisons, with post correction $\alpha < 0.01$ are written in bold. All individuals demonstrated strong preference for areas within 1 km of permanent water and avoidance of areas over 5 kilometers from water. The three dominant individuals demonstrated significant avoidance of areas between 2.5 and 5 kilometers from water, while lower-ranking individuals did not with the exception of R37. Most individuals used areas between 1 and 2.5 kilometers near expected levels.

Elephant	Within Obs	Within Exp	ChiSq	Outside Obs	Outside Exp	ChiSq
M54	1939	429	379.171	77	1581	102.172
M5	984	419	54.531	1032	1541	12.022
R28	2016	429	419.480	0	1579	112.792
M31	638	430	7.207	1120	1582	9.646
R22	1691	428	265.937	325	1577	70.980
M45	400	427	0.120	1319	1571	2.892
R37	168	420	10.796	1441	1546	0.510

Table 9: Selection for areas in relation to protected status was tested across individuals during the dry season. χ^2 statistics, Bonferroni corrected for 14 multiple comparisons, with post correction $\alpha < 0.01$ are written in bold.

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