Aspects of Male Mating Strategies in the African Elephant (*Loxodonta africana*)

M.Sc. Thesis (Speciale)
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This thesis is dedicated to all the rangers throughout the African continent who, under difficult conditions daily risk, and sometimes loose their life in the interest of conservation.

Preface

This thesis has been handed in to the Department of Zoology, University of Aarhus, Denmark in fulfilment of the requirements to obtain the ”Cand. Scient. Biol.” (M.Sc.). The work has been structured as a report with a general introduction followed by six chapters, two written as manuscripts with short introductions. The final chapter is written as a combined discussion of the results in the previous five chapters.

During my work, numerous people have helped me. Especially, I would like to thank my supervisors Dr. Fritz Vollrath and Dr. Thiemo Krink, University of Aarhus and Dr. Iain Douglas-Hamilton, Save the Elephants (STE) for their support. I am also grateful to David Dabellen and Kantri Lenantampash for their professional assistance and pleasant companionship in the field, and the ever present help from STE field officer Onesmas Kahindi and the STE team in Samburu: “Baringo”, Richard and Benjamin. I am also indebted to STE Scientific advisor Dr. Juliet King and the Nairobi team: Njoki, Peter, Wainaina and Elena for their cheerful way of receiving my cries for help over the VHF radio and arranging for “Airdrops” of essential bits and pieces; One day I will pay you back! The fieldwork could not have been done without the support from the Kenyan Wildlife Service and the Samburu and Isiolo County Council that allowed me to work within the Samburu and Buffalo Springs National Reserve. Especially, I would like to thank all the rangers working in the reserves for the help they have provided. The background monitoring data made available to me by Save the Elephants has largely been collected by George Wittemyer, without his tremendous effort since 1997, nothing would have been known about the Samburu elephant population. Last, but not least, I am grateful to Jeanette Vollmer, Morten Bjerrum, David Mayntz and Lars Back for the critical and constructive comments on earlier drafts of the report.

The project was financially supported by EvAlife through a grant from The Danish Research Council, by Save the Elephants and by a grant from the Elephant Research Trust Fund in Kenya. Furthermore, Indianapolis Zoological Society enabled me to return between December 2000 and May 2001 for additional data collection.

- Or said in the words of the dolphins in “A hitchhikers guide to the Galaxy”(Adams 1986):

“So long and thanks for all the fish”

Aarhus 10th of September 2001

Henrik Barner Rasmussen

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Chapter 1: Introduction

1.1 Research context

In the spring of 1999, the EvAlife research group was established at the University of Aarhus, Denmark. Headed by Dr. Thiemo Krink and Prof. Brian Mayoh (Computer Science, University of Aarhus), the EvAlife project is an interdisciplinary project between biology and computer science using general mechanisms from behavioural and evolutionary ecology as inspiration to novel computing techniques. The primary goal is the creation of models for decision-making and description of self-organisation and robustness in complex systems. These general models will later be used for the development of new techniques in adaptive and distributed computing.

Dr. Iain Douglas-Hamilton and Save the Elephants (STE) have, in collaboration with Kenyan Wildlife Service (KWS) and a number of scientists carefully been monitoring the national elephant population in Kenya. Over the last decade a wide range of field data from radio, and later GPS tracking to population surveys have been collected.

Elephants are long-lived animals with complex social structure and advanced learning abilities. Furthermore, their large size and their ability to carry burdens of advanced equipment like GPS tracking devices, radio transmitters and motion sensors without influencing their behaviour make them ideal for recording large scale movement patterns. This, combined with their relative low population number and few natural enemies (apart from man) make elephants ideal study-organisms when constructing analytical and computer models of behaviour and decision-making.

The first contact between EvAlife and Dr. Iain Douglas-Hamilton was made shortly after the establishment of the EvAlife research group. Since many of the questions concerning elephant behaviour and decision-making were of mutual interest, a long-term collaboration was agreed upon between STE and EvAlife. The joint research program is focusing on combining GPS tracking data with on ground observations of behaviour, forage availability and quality, as well as human land use. The long-term aim is to create behavioristic computer models describing individual and group decisions in relation to foraging and reproduction in the light of competition, risk avoidance and different habitat quality.

During my biology study at University of Aarhus, Denmark, I have developed an interest for behavioural and evolutionary ecology. I have participated as field assistants in a project on mating strategies in male muskoxen (*Ovibos moschatus*) in West Greenland as well carried out smaller projects on the effect of parasites on developmental stability and red coloration in sticklebacks (West Greenland) and on “Behavioural and morphological differentiation among bumblebee *Bombus polaris* workers” (Northeast Greenland)

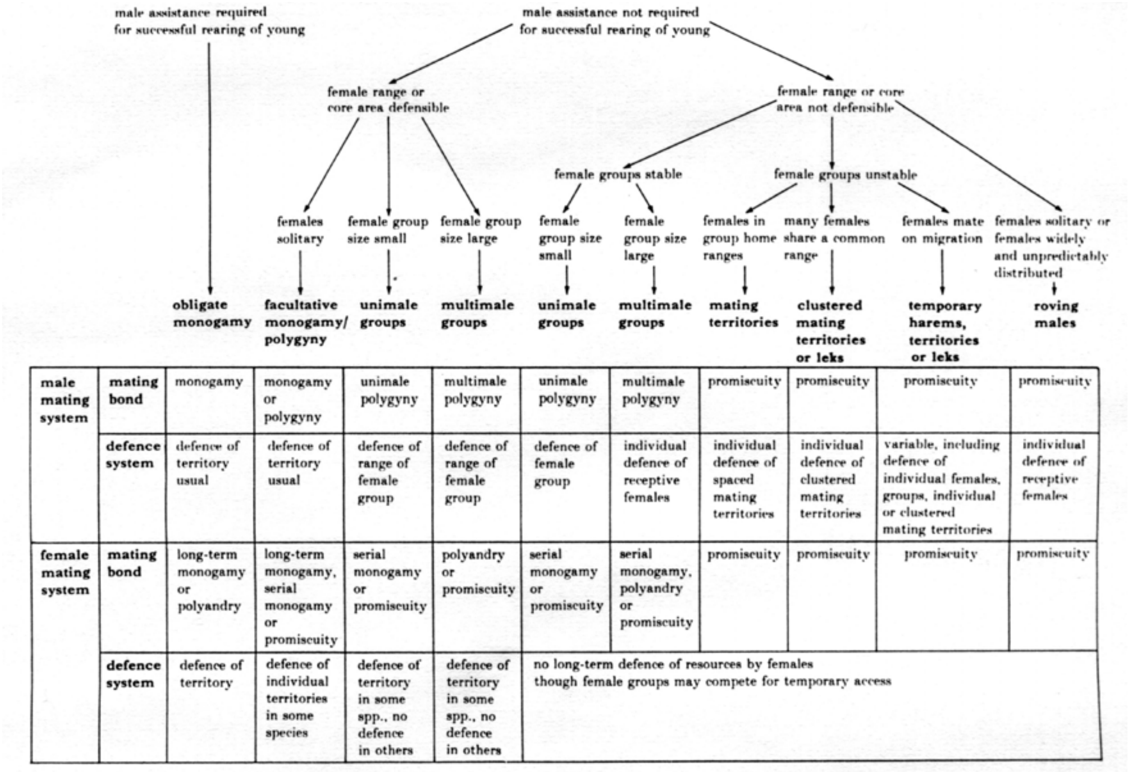
(Rasmussen 1998). Although mainly working with Arctic biology, I have travelled extensively in East and Southern Africa. Therefore, a small hand-written note saying: "Do you want to work with elephants" caught my interest at a time when I was looking for a project for my M.Sc. After talking with my supervisor-to-be Dr. Thiemo Krink, the possibility of doing behavioural work on elephants within the EvAlife framework sounded interesting. Furthermore, since the elephant part of the EvAlife project was still at an early stage, it would provide me with the chance and the challenge of shaping my own project. Soon after joining the EvAlife research group in May 1999, I became interested in the reproductive behaviour and strategies of bull elephants. Since the pioneering work on the description of musth in the African elephant by Joyce Poole in the early and mid Eighties, relative little work had been done in this field. The different tactics and strategies played by bulls of different age and under varying conditions are still poorly understood. Many of the questions related to individual optimisation and strategies fitted into the overall objectives of the EvAlife project and the framework for the scheduled long-term collaboration between EvAlife and Save the Elephants. Therefore, I decided to make my M.Sc. thesis on some of the aspects of male mating strategies in the African elephant, the outcome of which is presented in the following.

1.2 Background

The topic of sexual selection and allocation of reproductive effort was first introduced by Charles Darwin (Darwin 1871). Since the 1960's the theoretical framework and the number of field studies on optimal reproductive strategies under varying ecological and social conditions has undergone a rapid development and some general patterns are now emerging. (E.g. (Trivers 1972; Clutton-Brock and Harvey 1978; Rubenstein 1980; Clutton-Brock 1989)) (Figure 1.2.1). Male reproductive strategies can, largely be explained by the spatial and temporal distribution of females. As stated by Clutton-Brock:

> *"Variation in male mating behaviour is related to the effect of male assistance in rearing young and to the defensibility of females by males. The latter is in turn related to female ranging behaviour and to the size and stability of female groups. Much of the variance [in male reproductive strategies]…can be attributed to differences in these three variables"*(Clutton-Brock 1989).

Understanding the distribution and organisation of females and especially variations within these parameters is thus important in order to understand the reproductive decisions made by males.



		obligate monogamy	facultative monogamy/ polygyny	unimale groups	multimale groups	unimale groups	multimale groups	mating territories	clustered mating territories or leks	temporary harems, territories or leks	roving males
male mating system	**mating bond**	monogamy	monogamy or polygyny	unimale polygyny	multimale polygyny	unimale polygyny	multimale polygyny	promiscuity	promiscuity	promiscuity	promiscuity
	defence system	defence of territory usual	defence of territory usual	defence of range of female group	defence of range of female group	defence of female group	individual defence of receptive females	individual defence of spaced mating territories	individual defence of clustered mating territories	variable, including defence of individual females, groups, individual or clustered mating territories	individual defence of receptive females
female mating system	**mating bond**	long-term monogamy or polyandry	long-term monogamy, serial monogamy or promiscuity	serial monogamy or promiscuity	polyandry or promiscuity	serial monogamy or promiscuity	serial monogamy, polyandry or promiscuity	promiscuity	promiscuity	promiscuity	promiscuity
	defence system	defence of territory	defence of individual territories in some species	defence of territory in some spp., no defence in others	defence of territory in some spp., no defence in others	no long-term defence of resources by females though female groups may compete for temporary access					

Figure 1.2.1 Examples of predicted mating systems depending on female distribution and organisation. From (Clutton-Brock 1989)

Furthermore, mating systems are now seen as the outcome of individual strategies rather than a species-specific characteristic (Clutton-Brock and Harvey 1978). Consequently, variation can be expected both between populations as a result of varying social or ecological parameters or between individuals within populations resulting from variation in individual capabilities (Rubenstein 1980).

Since the various observed mating systems are highly diverse and associated with a wide range of mate guarding, territorial defence and mate bonding, a general review of the topic is outside the scope of this work. In the following sections, a more specific review of the literature on elephant social organisation and reproductive behaviour will be made and linked to theoretical and empirical work done on related mating systems in other mammals.

1.3 Social organisation and reproductive behaviour in the African elephant:

Females:

Female African elephants associate in family units consisting of on average 2-4 related breeding females and their immature offspring, but occasionally do contain up to nine adult females (Douglas-Hamilton 1972; Laws, Parker et al. 1975). The family unit is headed by the matriarch - often the oldest female and the individual members spend most of their time in close association with the unit (Douglas-Hamilton 1972). Individual family units occur either alone or in congregations of up to 5-10 family units containing several hundred individuals. The average group size is often season dependent, with the largest congregations occurring during the rainy seasons (Moss and Poole 1983; Poole and Moss 1989). Specific family units often associate regularly with groups of 1-3 other families. This higher-level association termed kinship groups (Douglas-Hamilton 1972) or bond groups (Moss and Poole 1983) is believed to be groups of related families, possibly formed by splitting of larger family units.

The home range of individual females (family units) as well as the overall density varies greatly throughout the African continent, depending on the type of habitat. Reports of home ranges, using minimum convex polygons (MCP), range from 150 km^2 in the Zambezi Valley (Dunham 1986) up to 6000 km^2 in Namibia (Lindeque and Lindeque 1991) and northern Kenya (Thouless 1996), with the largest home ranges occurring in arid or semi-arid regions. Caution on the use of MCP for calculating home ranges should be taken, since resent results show that this technique grossly overestimate the actual range with up to a factor 7 (Douglas-Hamilton and Krink in prep.). However, MCP ranges do give a relative measure for comparison. In semi arid regions, forage resources are often unevenly distributed and geographically variable between years due to variable rainfall patterns. This, in combination with the large home ranges, result in a wide and to some degree unpredictable distribution of females. The concept of territoriality among elephants has been widely discussed. Groups of family units do tend to stay within certain, very large, “Clan Areas” (Moss and Poole 1983) but defence of well-defined territories by specific groups of females is not present (Poole and Moss 1989).

Females reach sexual maturity around 10-12 years of age (Perry 1953; Laws 1969). The female oestrus cycle is not fully understood, but a 12-week cycle between oestrus events are believed to be the norm, if the female does not conceive. (Wasser, Papageorge et al. 1996; Fiess, Heistermann et al. 1999) The period of behavioural oestrus is short, lasting not more than 3-6 days with the receptive period possibly shorter (Moss and Poole 1983). The gestation period is approximately 21.5 month and is followed by a period of post-partum (lactational) an-oestrus (Laws, Parker et al. 1975; Barnes 1982). The mean inter-calving interval varies between different populations but is on average around 4-5 years. (Range 3- 9 years) (Laws, Parker et al. 1975; Poole 1987). The seasonal pattern of conception and birth varies between populations but seems to be closely linked to the local rainfall patterns. (Laws, Parker et al. 1975; Hall-Martin 1987; Poole and Moss 1989). In areas with no distinct rainy season little variation in monthly conceptions are seen, whereas the vast majority of conceptions occur in or just following the rain in areas with seasonal rainfall (Figure 1.2.2). However, in most populations oestrus females can occur year round (Poole and Moss 1989).

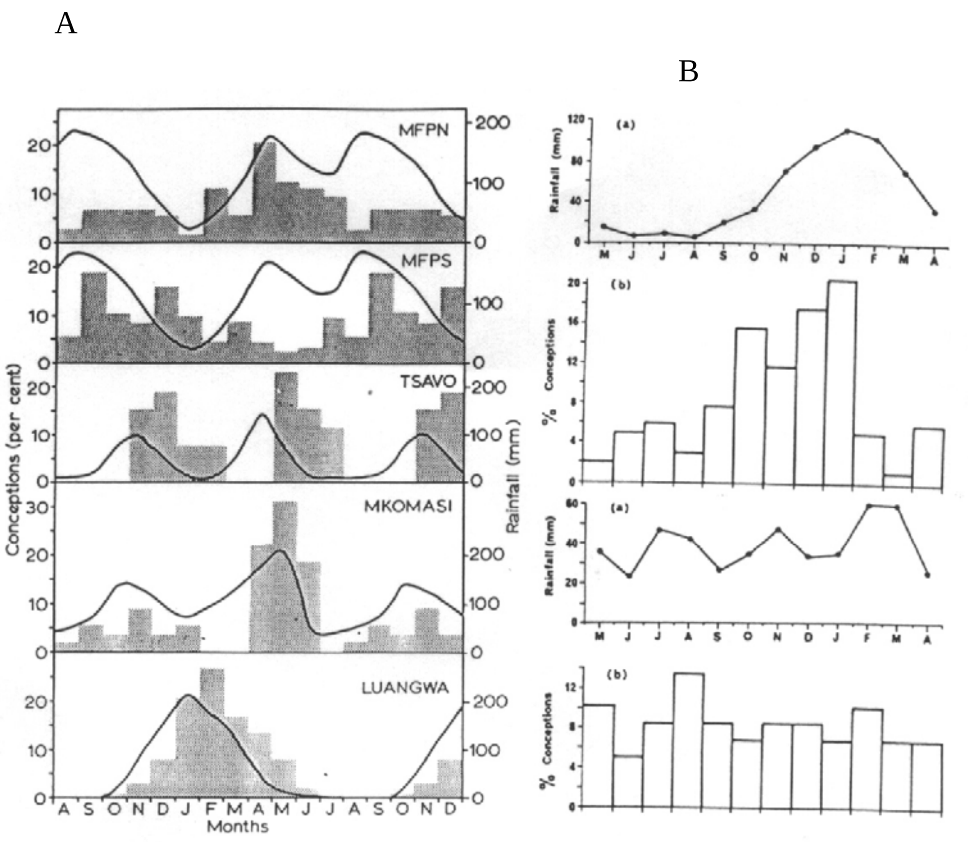


Figure 1.3.1 Conceptions and mean monthly rainfall in A: Murchinson Falls North and South, Tsavo, Mkomasi and Luangwa National Park (Laws, Parker et al. 1975) and B: Kruger (upper graphs) and Addo National Park (lower graphs), South Africa (Hall-Martin 1987).

With an inter calving interval of approximately four years, on average only 25% of the females come in oestrus per year. This, in combination with the absence of a distinct breeding season, results in a highly skewed operational sex ratio in male favour. thus in summary, some of the important aspects of female social organisation and ecology in the African elephant, expected to influence male reproductive strategies are:

1) Non-territorial females with large and non-defensible female home ranges.
2) Small very stable female groups.
3) No well defined breeding season, receptive females occurring throughout the year, with the majority occurring during and after the rainy season(s).
4) Large seasonal congregations of females, coinciding with the peak time for receptive females.
5) Long inter calving intervals, resulting in a skewed operational sex ratio in male favour.
6) No paternal care.

Males:

Bulls leave their natal family after puberty, around the age of 14-17 years (Laws, Parker et al. 1975). At this age, they are the size of, or slightly bigger than the adult females. Post mature growth continue throughout most of the their life, with fully grown bulls around the age of 40-45 years reaching almost twice the size of the females. (Laws 1966; Hanks 1972; Laws, Parker et al. 1975). Comparable degrees of sexual dimorphism and to some degree post mature growth are seen in males among other mammals such as Elephant seals *Mirounga angustirostris* (Le Boeuf 1974), Eastern grey kangaroos *Macropus giganteus* (Jarman and Southwell 1986) and Polar bears, *Thalarctos maritimus* (Ramsay and Sterling 1986) and are usually associated with strong size dependent male competition for mates (Whitehead 1994). A positive correlation between size (and thus age) and reproductive success and dominance rank has also been found in male African elephants (Poole 1987; Poole 1989) and according to Poole, bulls in Amboseli National Park, Kenya are not believed to have any reproductive success before the age of 30-35 years (Poole 1994).

During their adult life, bulls alternates between periods of sexual activity and inactivity. The periods of sexual activity among individual bulls are synchronised between years but not in synchrony at population level, with sexual active bulls occurring year round. (Moss and Poole 1983; Poole 1987). This is probably due to receptive females occurring throughout the year in most populations. Furthermore, it indicates that the sexually active periods are limited, probably due to energetic constrains, since individual bulls do not remain sexually active throughout the year.

The association and interaction with other bulls or females depend on the sexual state of the individual bull. When sexually inactive, the bulls often stay within “Bull areas” either alone or in association with other bulls (Moss and Poole 1983; Poole 1994). Within these bull or “Bachelor” groups, the interactions are relaxed and amicable. The associations within bull groups are loose with groups breaking up and individual bulls coming and leaving. However, some reports indicate that certain individual bulls tend to associate more frequent than others do. (Moss and Poole 1983). At present, it is not known whether these individuals are related or which other forces are determining bull-bull associations. When sexually active, the bulls starts searching for oestrus females and are associating more frequently with family units. Associations with other bulls are mainly limited to encounters when associating with females and interactions between bulls become more aggressive.

Due to the large and somehow unpredictable female home ranges, male elephants are unable to defend territories containing the home range of one or more females. In such systems, males often either attach themselves to a particular group of females, defending that group against competing males (herd bull) or adopt a roving strategy searching for oestrus females. Examples of herd or harem holding males can be seen in red deer (Clutton-Brock, Guiness et al. 1982), whereas male Polar bears (Ramsay and Sterling 1986) and Eastern grey kangaroos (Jarman and Southwell 1986) has been found to rove between groups.

Previously, it was believed, that sexually active bulls mainly associated with specific family units and could be viewed as herd bulls guarding a group of females. (Rushby 1965; Sikes 1971; Poche 1974). Now, this view has been abandoned (Douglas-Hamilton 1972; Croze 1974; Laws, Parker et al. 1975; Poole and Moss 1981) and it is generally believed, that bulls can be viewed mostly as rovers. However, the majority of studies on elephants have been performed within national reserves usually associated with high densities of elephants. Here, the distance between female groups are low and a roving strategy is thus more likely to occur. At low densities of females, Barnes (Barnes 1982) showed that guarding a group of females could theoretically be a better strategy than roving. A pure rover or “stayer” strategy may not be the only option. In a model for optimal mating strategies in non-territorial ungulates, Forchhammer (Forchhammer and Boomsma 1998) showed that the degree of roving, i.e. the mean staying time within a group of females depends on several factors:

> *An increase in female group density, operational sex ratio and age specific fighting success of males are predicted to reduce the average exploitation time of female groups, leading to roving of males… In contrast, an increase in female rejection rate of males and in the time spent by males on non-mating activities…are predicted to increase the average exploitation time of female groups and favour staying behaviour of males…Consequently, the model predicts that younger males will tend to be stayers whereas middle-aged and older males are predicted to be rovers.* (Forchhammer and Boomsma 1998)

The model was tested on muskoxen, *Ovibos moschatus* in West Greenland, and the correlations were all in the predicted direction with bulls staying longer time within female groups outside the peak oestrus season, and younger bulls spending longer time within female groups than older bulls. (Forchhammer and Boomsma 1998)

Changes in reproductive strategy depending on age and rank are also evident in elephants. In Asian elephants, a special state in sexual active bulls, known as musth has been known for the last 2000 years. (Eisenberg, McKay et al. 1971). Musth was earlier not believed to occur in African elephants, (Perry 1953; Sikes 1971) but is now generally accepted also to occur here (Poole and Moss 1981; Hall-Martin 1987). Musth is associated with conspicuous signals such as continuos dribbling of urine and excretion from the temporal glands. Musth bulls experience an increase in dominance rank during musth and females have been shown to prefer mating with bulls in musth (Moss and Poole 1983; Poole 1987). During musth, the bulls have elevated concentrations of testosterone, (Hall-Martin 1984; Poole, Kasman et al. 1984; Rasmussen, Hall-Martin et al. 1996) show an increased level of aggression and are more likely to escalate antagonistic interactions with competing bulls. (Poole and Moss 1981; Poole 1987; Poole 1989). Fights mainly occur between bulls in musth and often result in serious injuries or even death (Hall-Martin 1987; Poole 1989). Therefore, the elevated level of aggression and increased probability of fighting seen among musth bulls is probably associated with a cost in terms of reduced future reproductive success. Thus, musth can be viewed as a competitive reproductive strategy compared to the more non-competitive strategy displayed by sexually active, but non-musth bulls. The signals associated with this strategy are probably serving a dual function, both as a signal to other males of competitive intent and as a signal to the females of high rank and dominance.

Hall-Martin suggested that musth is an alternative mating strategy displayed by younger 25-35 year old bulls (Hall-Martin 1987). However, Poole showed that the occurrence and duration of musth periods are positively correlated with age and are most often seen among high-ranking bulls. Furthermore, she showed that older bulls (35 + years) normally spend most of their sexual active period in musth and focus their reproductive effort during and immediately after the rainy season, when the majority of the females come into oestrus, whereas the younger, medium ranking bulls normally come into musth in less attractive periods of the year and for shorter periods. (Poole and Moss 1981; Poole 1987; Poole 1989). That musth is a strategy displayed by older high-ranking bulls seems most plausible. In a system with a large size-dependent male competition for mates, a competitive breeding strategy is not expected to be favoured before late in life. (Whitehead 1994)

The temporal distribution of musth observed in Amboseli, with the oldest bulls coming in musth at the time of year with most oestrus females and younger bulls focusing on less attractive periods is probably due to older (Larger) bulls forcing younger bulls out of musth during attractive periods. Several reports indicate that smaller musth bulls ceased to signal musth shortly after encountering a larger musth bull (Poole 1989). This suggests that musth may be an honest male-male patrolled signal of rank and fighting ability. However, younger musth bulls were often able to dominate much larger non-musth bulls indicating that relative fighting ability could not alone explain the occurrence of musth (Poole 1987; Poole 1989). Instead, Poole (Poole 1989) suggested that musth depends on the time specific value placed on winning by the individual bull. If so, the value of a resource, either an individual receptive female or a general area should vary between individual bulls, depending on their sexual state or physiology. In situations where smaller (musth) bulls dominate larger (non-musth) bulls, the variation in the resource value between individual bulls should then outweigh the difference in relative fighting ability. This could be possible. If an individual has made an initial investment into reproduction, (for example an investment in increased search or a physiological cost of being in musth) this individual will place a higher value on a given resource compared to an individual that has invested less. This situation would be comparable to the asymmetry between a holder of a territory and an intruder (Parker 1978).

Bulls significantly reduce the time spend feeding during periods of musth compared to when sexually inactive. Furthermore, bulls have been reported to loose condition during periods of musth (Poole 1989). Musth bulls have also been reported to travel far away from their normal non-musth range (Hall-Martin 1987; Douglas-Hamilton 1998). This, combined with the female preference for musth bulls and the fact that the majority of guarding of oestrus females is done by musth bulls, has lead to the general belief that sexual active non-musth bulls have little reproductive success and allocate few resources to reproductive behaviour. Furthermore, it has been suggested that they do not engage in far ranging searches for oestrus females (Hall-Martin 1987). However, the study by Poole compared the behaviour of older bulls between periods of musth and sexually inactive non-musth. A comparison between sexually inactive and sexually active non-musth was not carried out. Furthermore, preliminary genetic results from Addo National Park, South Africa, suggest that a large proportion of the calves were not fathered by the dominant bull, indicating that subordinate bulls do obtain a significant reproductive success (Whitehouse 2001). The lack of behavioural data on sexually active non-musth bulls makes it impossible to know if the large allocation of time and energy to reproduction seen in musth bulls, are associated with the state of musth or with being sexually active in general. Furthermore, since Poole’s work in Amboseli is the only thorough study of musth bulls, it is not known whether the results are generally applicable or are associated with a specific set of conditions. Amboseli National Park is somewhat special, with very high densities of elephants, one main oestrus peak season during the year and a larger number of older males compared to most other present day populations in Africa.

In general, it is not well understood how the individual bulls trade off the investments in current and future reproduction nor how they maximise their current reproductive success by distributing themselves temporally and spatially, in an environment of constantly changing resource value (density of receptive females) and competition. Furthermore, it is not known under which set of conditions it pays to engage in a competitive (musth) or non-competitive (non-musth) strategy and if differences in the optimal level of resource investment exist between the two strategies. If musth is associated with a basic energetic cost or an increased probability of sustaining injuries, a threshold level in the density of oestrus females may exist, where below a competitive musth strategy does not pay off. Additionally we must ask how decisions made by competitors are influencing the optimal behaviour of the individual bull (and vice versa).

1.4 Research objectives

The objectives of the work described in this report, were to investigate how sexually active bull elephants distribute themselves, depending on age and the local set of conditions such as number of oestrus females and number and relative rank of competitors. Furthermore, I wanted to investigate how the choice between a competitive (musth) versus a non-competitive (non-musth) reproductive strategy is influenced by bull age, competition and the density of oestrus females and to compare the level of investments in reproduction between musth and sexually active non-musth bulls. The following questions were addressed during the thesis work:

1) How does bull elephants distribute themselves in time and space in relation to age, distribution of receptive females and competing bulls?
2) Must a certain set of conditions be present before a bull engages in a musth strategy and, if so, is that depend on the age of the bull?
3) Do sexually active musth and non-musth bulls differ in the amount of time and energy allocated to sexual activity?
4) How do bulls change their daily movement patterns when they become sexually active and are there differences in the daily movement patterns between sexually active non-musth and musth bulls?

The general goal was to investigate some of the effects of varying local and individual conditions on the reproductive strategies of males elephants. At intra- and inter-population levels, a wide range of strategies have been observed. The late recognition of the occurrence of musth in African elephants could be because this strategy only occurs under certain sets of conditions not present in all populations and that the strategy for this reason was not easily recognised as a pattern. Alternatively, the complexity seen on the level of populations may be better understood by a “bottom up” approach looking at the factors influencing the individual from it’s immediate surroundings and by introducing space as a factor (Bascompte and Sole' 1995). In other fields of research, a better understanding have been obtained by this approach with the complexity of the system emerging from the interaction of locally much simpler rules for decisions (see for example (Krink and Vollrath 1998) on spider web-building behaviour).

The aims of the long-term plan is among others, the creation of individual based models on reproductive decisions of bulls, including optimal search patterns depending on female distributions. However, the main goal of this project was not to create these models but to obtain the first preliminary background information on some of the key factors expected to influence the system and to use these as an inspiration for the creation of the first generation models.

When working with reproductive strategies, an obvious important factor is the actual payoff obtained in terms of sired offspring resulting from the various strategies. This is relatively easy to obtain when working with females, but notoriously difficult when working with males. Various factors like number of matings or monopolised females have been used in different studies (see for example (Clutton-Brock, Guiness et al. 1982)). However, the value of a mating, depend on when it is achieved relative to the time of female ovulation and on factors like sperm competition (Cockburn 1991). Furthermore, the guarding of a receptive female or a group of females during a breeding season does not necessarily imply siring all of the offspring, since “satellite” or “sneaky” males may obtain some (often unknown) success. One of the few useful techniques is paternity analysis of the resulting offspring using DNA microsatellites (Bloudin, Parsons et al. 1996). The use of DNA analysis was beyond the scope of the current project and results would in any case not have been available yet due to the almost two year gestation period. However, future plans do involve paternity analysis of the calves and results will be viewed in the light of results from the present study, hereby obtaining a measure of the success of the different strategies.

Apart from these four main scientific questions, the following conservation and management related questions relevant for the local elephant population were addressed.

1) Which areas are of importance to the local population of elephants
2) Do the elephants use special travel corridors between highly utilised areas
3) In which areas could a future conflict between elephants and human development arise.

These questions belong to some of the key objectives of Save the Elephants research project in Samburu, especially Dr. Iain Douglas-Hamilton’s GPS tracking program. The results obtained during this study partly rely on data from that program and should not be viewed in isolation, but as an integrated part of Save the Elephants ongoing work in the area.

Information on large distance movements of individuals will help elucidate some of the underlying mechanisms governing these movements. The study elephant population is not, and cannot be confined to the protected areas (unless drastic and undesirable measures like fencing and culling/translocation programs are carried out). Therefore, an understanding of these movements, like corridors used for travelling, areas used for foraging at specific times of the year and response to human activities and settlements are vital for the creation and implementation of effective management plans. In addition, a better understanding of male mating strategies is important for conservation issues. Size and fighting ability are known to play a key role in the reproductive success of males. Bull elephants may therefore be more willing to enter into good foraging habitats but high-risk areas, i.e. human settlements with crops, in order to maximise energy intake, whereas females may prefer safer, but less attractive, forage habitats i.e. protected areas. Furthermore, bull elephants are known to travel over large distances and to shift between different areas depending on sexual state. Therefore an understanding of the parameters governing male mating strategies and decision making in relation to reproduction is important for our ability to understand the underlying mechanisms behind male movements. This may furthermore enable us to predict possible changes in mating strategies and hence movements as a result of changes in parameters like male age structure and female densities. These changes could occur as a result of poaching, if another surge in the demand of ivory occurs.

1.5 Hypothesis

Bulls are expected to become sexually active at the time and in the area where they are able to maximise the number of sired offspring. Therefore, the number of sexually active bulls is expected to peak during the peak oestrus seasons in the area where the bulls will expect the highest number of receptive females to be present. The place and time with maximum number of oestrus females will not necessarily be the optimal for the individual bull. Factors such as number and rank of competitors are expected to influence the probability of a given bull gaining access to the available females. The oldest and largest bulls are expected to become sexually active at the time and in the area with most oestrus females, since they, due to their high rank and fighting ability, will be able to suppress younger, lower ranking individuals. Medium and low ranking bulls are expected to distribute themselves depending on a combination of rank among sexually active bulls and density of oestrus females. If the cost of sexual activity is constant between seasons, this would be expected to result in a constant ratio between number of oestrus females and number of sexually active bulls in a given age group.

In order for a bull to engage in a competitive reproductive strategy (musth) instead of a non-competitive strategy (Sexually active non-musth) the increased payoff from signalling musth, must be larger than the cost involved. Receptive females have been shown to prefer mating with bulls in musth. This female preference will increase the reproductive success of musth bulls. Furthermore, the increased relative rank of musth bulls results in musth bulls having primary access to receptive females, hereby increasing the probability of siring the offspring. It has been suggested, that the increased levels of androgens associated with musth as well as some of the signals are energetically costly. If bulls pay an energetic price for musth, being in musth will reduce the number of days a bull can be sexually active. Furthermore, the competitive reproductive strategy of musth is expected to increase the likelihood of escalated antagonistic interactions with competitors, and is likely to result in physical injuries for the contesting individuals. Therefore, engaging in a musth reproductive strategy will negatively influence the expected future reproductive success of a bull. The reproductive payoff in terms of sired offspring depends on the density of receptive females, whereas the physiological cost of musth and possibly the likelihood of injuries during fights with competitors are expected to be unrelated to the density of receptive females. Therefore, one would expect a threshold to exist in the density of receptive females below which the cost involved in a musth strategy outweighs the increased payoff.

Poole suggested that smaller musth males might dominate larger males when the value placed on winning outweighs the difference in fighting ability. However, instead of a varying value placed on winning it could be due to a varying cost paid in fighting. The cost related to physical injuries is paid in terms of a reduction in the residual reproductive value (RRV). RRV is a function of mortality and age specific reproductive success. Since reproductive success increases with age, and the mortality is approximately constant (Laws, Parker et al. 1975; Poole 1989) older bulls probably have a higher RRV than younger bulls. As an example of the relation between age, survival, reproductive success and residual reproductive value (RRV) the theoretical values have been calculated using equation 1.5.1 and the below mentioned parameter estimates. The estimate of age dependent reproductive success is based on data of matings obtained by bulls in different age groups from Amboseli (Poole 1989) giving the following relation between age and reproductive success Rep Succ. = $age^2 *$ 0,0014-age*0,0232. The results can be seen in figure 1.5.1. The parameter estimates tries to mimic an elephant population. However, the results are purely theoretical and ONLY presented to show the initial increase of RRV with age

$$RRV_{agex} = \sum_{i=x+1}^{i=50} RS_i * (0.95^{i-x}) \qquad \text{Equation 1.5.1}$$

Stable population

Number of calves per year = 40

Annual mortality = 5 %

Age at maturity (Bulls) = 15 years

RS_X = Age dependent reproductive success at age X

Maximum age = 50

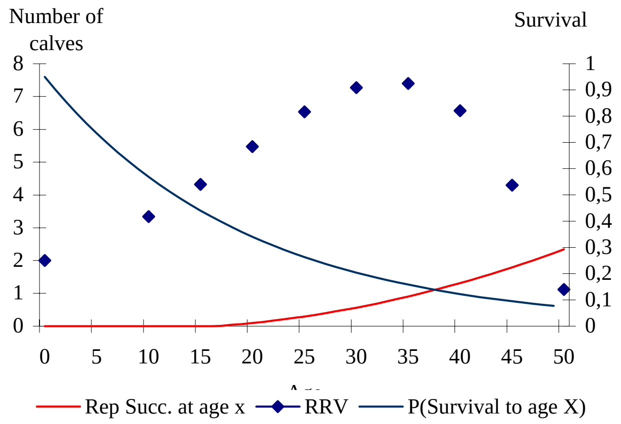


Figure 1.5.1

If the RRV varies and increases (to a certain point) with age, a threshold in the density of receptive females where below a musth strategy does not pay will be age dependent, with older bulls having a higher threshold than younger bulls. The density of females varies between areas and the number of oestrus females changes with season and between years. If the threshold for the differently aged bulls lies within the resulting variation in the density of receptive females, one would expect a temporal and spatial distribution of musth between different aged bulls, depending on the density of receptive females, with older bulls avoiding low-density areas. Furthermore, if the highest ranking bull who is willing to engage in musth is able to suppress musth in lower ranking individuals, the number of musth bulls in areas with densities above the lowest lying threshold will be constant, with the age and rank of the musth bulls increasing with increasing density of oestrus females.

If periods of sexual activity is under energetic constraints, the bulls are expected daily to allocate the amount of time and resources and engage in the search type, that maximises the number of oestrus females encountered per unit resource. It is not clear whether high-ranking competitive bulls should invest differently than non-competitive bulls. It will depend on several factors such as i) the relation between investment and number of receptive females encountered ii) if basic costs are attached to the state of musth iii) the probability of other bulls with a given rank being present and probably also female distribution and group size. However, the optimal amount of time allocated from foraging to searching is expected mainly to depend on female distribution rather than rank and strategy. Therefore, sexually active musth and non-musth bulls are expected to behave similarly in terms of time/resource allocation.

1.6 Material and methods

The study was carried out in and around Samburu and Buffalo Springs National Reserves, Kenya (Fig 1.6.1), in close collaboration with Save the Elephants’ ongoing monitoring and GPS tracking program in the area. George Wittemyer established the monitoring program in 1997, based on the technique developed by Dr. Iain Douglas-Hamilton (Douglas-Hamilton 1972) for identification and recognition of individual elephants. The program collects baseline data on the occurrence and associations of elephants within the study area, as well as recordings of demographic data on reproduction and mortality. Data from the monitoring program, collected mainly by George Wittemyer and Onesmas Kahindi has kindly been made available to me by Save the Elephants and has been used in addition to similar data collected by me.

1.6.1 Study area

Covering some 15.000 km^2 the Laikipia/Samburu area consists of two main regions; the cool dry high altitude area to the southwest, consisting mainly of privately owned farmland, and to the north, the hot and dry low-lying rangeland with isolated mountain forests. (Thouless 1996). The northern low-lying part consists of a matrix of protected national reserves, semi-protected wildlife conservancies and unprotected open areas. The areas outside the national reserves are inhabited by a number of different tribes, mainly Samburu, Borana, Turcana and Somalis. Outside the few towns, the people live in traditional small pastoral communities, mainly depending on grassing cattle and other livestock.

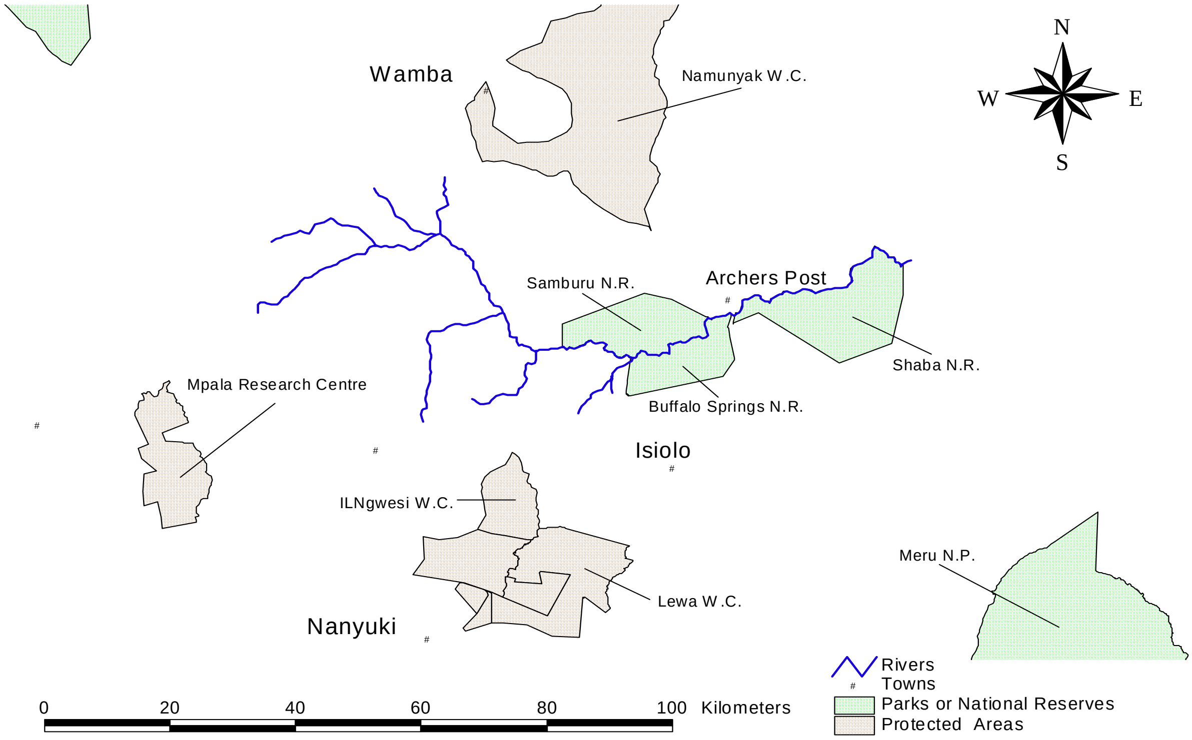


Figure 1.6.1 Study area and surroundings. The greater study area stretches along the Ewaso Ngiro River, from Shaba N.R in the east to app. 30 km west of Samburu N.R, with the core being Samburu and Buffalo Springs N.R (National Reserve = N.R; National Park = N.P; Wildlife Conservancy = W.C).

The study area is situated in the low-lying rangeland along the Ewaso Ngiro River, the only semi-permanent river in the area, just north of the equator on longitude 37º East. The core of the study area lies in and around Samburu and Buffalo Springs National Reserves (560 km^2 combined). The area consists of large, relatively flat regions, with isolated hills and small mountain ranges. The rainfall and plant growth is highly seasonal. The rainfall is highly variable between years but average around 200 mm per annum. The majority of the rain is falling during the two rainy seasons between March/May and November/December. The vegetation mainly consists of low, medium dense, bush-land with the 0-500 m strip on either side of the river dominated by a riverine vegetation of tall Acacia trees (mainly *Acacia eleator* and *Acacia tortillis*) and Doum Palms (*Hyphaene dichotoma*).

1.6.2 The elephant population

The greater Laikipia-Samburu elephant population is estimated to number around 3,000 individuals (Thouless 1993), making it the largest population existing primarily outside protected areas in Kenya. This continuous population has been suggested sub-divided into several overlapping sub populations, with home ranges ranging from 100 to 5500 km^2 (Thouless 1996). Aerial counts and radio collaring indicates that approximately half of this population primarily use the low-lying rangeland and isolated mountain forest areas to the north.

The monitoring program, carried out by Save the Elephants (SERP) has since 1997, observed and identified 910 individual elephants, consisting of 216 breeding females, 536 calves and 157 adult males. This indicates, that a large proportion of the northern Laikipia/Samburu population utilises this area along the Ewaso Ngiro River. However, only half is observed on a regular basis and all spend significant time outside the national reserves. The last two years, few unknown adult females have been seen and identified and the number of new bulls is levelling off with the majority of new bulls being between 15 and 25 years old. This indicates, that the vast majority of the elephants utilising this area along the Ewaso Ngiro River has been recorded. In general, the elephants are believed to range over larger areas and occur at lower densities than in Amboseli National Park. Furthermore, the population contains fewer older males. In figure 1.5.2, the age distribution among the 397 males (Calves, Sub-adults and adults) is shown.

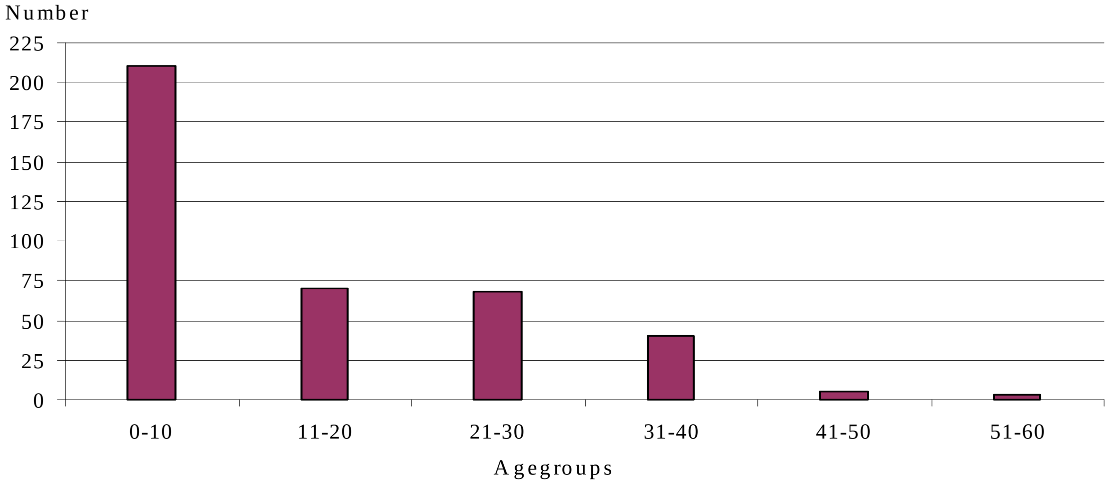


Figure 1.6.2 Age distribution among the 240 male calves and 157 adult bulls in the study population (N= 397)

A constant natural adult mortality of 3-5 percent per year and a maximum longevity of app. 60 years have been reported from other populations (Laws, Parker et al. 1975) On the basis of that, males between 10 and 20 years and again above 40 seems to be under represented in the study population. Probably the “missing” younger males are partly due to some individuals still not being identified, whereas very few (if any) unknown older bulls are expected still to occur in the study population. This combined with the slight female biased adult sex ratio of 1:1,37 may be a remnant effect of the ivory poaching in the mid eighties, mainly affecting the larger bulls (for a thorough description of the study population see (Wittemyer 2001)).

The estimation of bull age has been done by combining height (when available), facial appearance, tusk circumference (Visual) and general body shape. This method is not precise but normally accurate within +/- 3 years up to the age of 35 years (Moss 1996).

1.6.3 Background data collection

Background data on occurrence, associations and sexual state of individual elephants were collected between October 1999 and June 2000 and again between December 2000 and April 2001. A total of more than 3000 observations, consisting of elephant ID, time, position, activity and associating adult individuals were made in addition to comparable data collected by SERP. When newborn calves were observed, the date of birth was estimated using a combination of physical appearance of the calve and last observation of the mother without calf. Bulls were categorised into three sexual states, sexually inactive (IA), sexually active non-musth (SA) and musth. The following definitions were used:

- Sexual inactive: Alone or associating with other bulls and not showing signs of urine dribbling, swollen temporals or temporal gland secretion.
- Sexual active non-musth: Associating with females, did or did not test females and did or did not have slight swollen temporals and weak temporal gland secretion.
- Musth: Regardless of associations was dribbling urine at any rate in combination with swollen temporal glands and temporal gland secretion.

Between 20 and 25 days a month was spend in the field with field days spent on background data collection being equally distributed within the two national reserves.

1.6.4 Focal observations

Focal observations on bulls (estimated to range between 25 to 45 years) were carried out between 21st of January and 4th of July 2000. The focal bulls were categorised into the same three sexual states (sexual inactive, sexual active non-musth and musth) using the same criteria as above, except for sexual active non-musth bulls. In this group, urine dribbling was not allowed to having been present 10 days before or after the time of observation. This was done to avoid including musth bulls that for shorter periods seized urine dribbling. On observation days, a bull was located and followed for 4-8 hours, depending on when it was located. During focal observations ‘on the minute’ observations on activity was done every 15 min. as well as the place of the focal individual in the group. Furthermore, all adult individuals associating with the focal individual was noted as well as any changes, like herd shifts or individuals joining or leaving the focal individual during the focal period. The 15-min interval between observations was chosen after a number of trial observation periods. Ideally, detailed 1 min. observations would have been preferable giving accurate measures of the amount of time spend on the different activities. However, the analysis of frequent observations are sensitive to data gabs and the vegetation made it impossible to have continues visual contact with the focal individual without coming so close that the behaviour was influenced by the presence of the observer.

1.6.5 GPS Collars

Since 1998, Dr. Iain Douglas-Hamilton has carried out a radio and GPS tracking program in the Samburu/Laikipia area. In order to link the large-scale movements previously observed in individuals tracked by that program to associations and sexual states, collars from that program were allocated to track bull.

Four bulls around 30 years old were immobilised and collared during January 2000, using GPS collars from Lotek ltd. Canada (For collar details, see (Douglas-Hamilton 1998)). Two of the bulls were re-collared in January 2001 after the original collar had ceased to function. The collars were set to record positions every hour, hereby obtaining detailed information on daily distance travelled and general ranging patterns. Data was downloaded from a plane or car via a remote radio link approximately once every month. The GPS collared bulls were attempted located every 10-14 days within the study period. When located, either spot observation of associations with other individuals as well as the degree of TGS and urine dribbling was noted, or a period of focal observation was carried out. After the 4th of July 2000, the collared bulls were located at a more infrequent rate, due to reduced field personnel. If a collared bull associated with females on consecutive observations, not separated by more than 14 days it was regarded as sexual active within that period. If it was observed alone or associating with other males on consecutive observations, it was regarded as sexually inactive. Within sexual active periods, bulls were occasionally observed alone. These single observations were disregarded and the whole period assigned as sexual active. Despite the radio beacon in the collars, all bulls “disappeared” for periods of time. If no observations had been obtained for more than three weeks, the sexual state of the bull was regarded as unknown for that period.

1.7 Research plan and thesis outline

In order to meet objective 1 and 2 (section 1.4), background information on the spatial distribution of females as well as the temporal distribution of oestrus had to be obtained. In chapter two, a new way of estimating spatial densities of elephants is investigated. Apart from being used in this study, the method can be generally applied within certain semi-arid regions as an alternative method of estimating elephant densities.

In chapter three the frequency and number of new born calves observed within the study population between 1998 and 2000 is used to create a model for estimating the monthly number of females coming in oestrus, depending on the seasonal rainfall. This model is combined with the results on the spatial distribution of elephants from chapter two in order to obtain the distribution and density of receptive females in both time and space.

The results from chapter two and three form the background for chapter four, where the questions relating to objective one and two is discussed in the light of results on the occurrence and association of bulls in the various sexual states and ages. (methods described in section 1.6). In chapter five the questions in objective three and four is addressed using a combination of focal observations of known bull elephants during different sexual states as well as data from GPS collared bulls obtained from the collaboration with Dr. Iain Douglas-Hamilton’s on-going tracking program.

The conservation related questions are discussed in chapter 6 using the result from all previous chapters, but mainly relying on data from the GPS collars and result from chapter two. In chapter 7 a combined discussion of the results presented in chapter two-six is made together with an outline of implications and future research plans.

Chapter 2: Spatial distribution of elephants

2.1 Introduction

In order to investigate the effects of different densities of receptive females on the bull behaviour and distribution, it was important to obtain information on the spatial distribution of elephants within the study area.

Traditionally three methods have been used to estimate the total number of elephants namely 1) Total or census aerial counts (Ottichilo, Kufwafwa et al. 1987) 2) On-ground counts of droppings (Barnes 1993; Barnes 2001) or 3) Continuously covering an area on-ground with recording of individual known elephants. The first two methods were unavailable for this project. Counts of droppings are time consuming if large areas are to be covered and are unreliable unless time specific decomposition and defecation rates are known (Jachmann 1984). Total aerial counts would have been possible but were too expensive if large areas were to be covered. The last method was already in use in the study area as a part of ‘Save the elephants’ Samburu Elephant Research Project (SERP) and data could be combined with additional data collected in connection to this project.

Only the area within Samburu and Buffalo Springs National Reserves is covered by SERP in this way. Since the area within the reserves is only (500 km^2) compared to the 5000-km2 home ranges of the elephants in the area (Thouless 1996), only changes within this area would be available using traditional methods. A potential alternative method for estimating large-scale spatial densities was therefore tested when the semi-permanent Ewaso Ngiro River dried out and the elephants started digging wells for water in the river sand. If the number of wells and/or the droppings left in the riverbed would be highly correlated with the number of elephants in the area, a spatial estimate of a much larger area could be obtained by counting those wells and droppings. Although this would reflect total elephant density and not female density a rough estimate of areas with low, medium and high female density could be made from the known sex ratio and group composition. In the following manuscript, the method used for the estimation of elephants densities along the Ewaso Ngiro River is presented. This method will be used in chapter three to obtain the spatio/temporal distribution of oestrus females.

2.2 Estimating elephant densities from wells and droppings in dried out riverbeds

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Abstract

In this paper, we present a new way of estimating relative numbers and densities of elephants, and possibly absolute numbers of elephants by counting elephant wells and dung boli within dry seasonal flooding rivers. A combination of aerial and on-ground counts of elephant wells and dung boli in the Ewaso Ngiro River were related to elephant densities, estimated from an on-going monitoring program of individually identified elephants in Samburu and Buffalo Spring National Reserves, Kenya.

Both the total number of elephant observations and the number of different individuals correlated highly with both densities of wells and dung boli when a spatial scale of 4-km river-sections was used. This indicates that both counts can be used for estimating densities at such spatial level. This study show that ground counts of wells or dung boli and aerial counts of elephant wells, along seasonal flowing rivers, can be used as a quick and reliable method for estimating elephant densities. The method is sensitive to differences in the time when different parts of the river dry out and will be unreliable in areas with secondary water sources. High-density areas turned out to be difficult to count from the air due to the high number of wells. The method could possibly be further developed to estimate the absolute number of elephants if an estimate of the number of wells and dung boli made per elephant per day in the river could be obtained. A shortening of the 7-week delay between the river dry out and the count used in this study is recommended, due to an error induced by a level of well reuse and the difficulties in counting high densities from the air

Introduction:

Getting reliable information on the number and density of elephants in often remote and inaccessible regions is important for both conservation, wildlife management and as a background for scientific questions. A number of different methods are available ranging from aerial surveys to dung counts. Estimating the total number of elephants from counts of droppings is both time consuming and has been shown to be difficult due to differences in defecation rates between seasons and changing rates of decomposition due to factors like rainfall and insect activity (Jachmann 1984). Total or census aerial counts have been used successfully, but are carried out infrequently due to the high costs involved in covering large areas by plane.

Many elephant populations throughout the African continent are found in semi arid regions where available water sources are limited for prolonged periods of the year. When the seasonal flowing rivers dry out after the rainy season, elephants are often forced to dig for water in the riverbed if no other sources of water are available in the area. Often, they are confined to areas along the rivers due to water constrains (Viljoen P. J. 1989).

When a river ceases to flow it leaves a clean transect through an area with no droppings or wells. With time, the number of wells in the river increases as will the number of droppings left during the period used for drinking. If the number of droppings and wells in the river are correlated to the number of elephants, a count of wells and droppings can be used as a method to estimate elephant numbers and densities along rivers.

The advantage, compared to census counts over large areas in traditional dung count, is that a smaller area, the river, has to be counted. The period where the dung and the wells have been produced is known and no significant decomposition of the dung has taken place if the count is done less than 2-3 month after the river has seized to flow (Jachmann 1984). The count could possibly be carried out from the air, covering large areas in short time with less flight time compared to direct aerial counts of individuals.

Certain assumptions have to be met for the method to be reliable. 1) No other water sources apart from the river must be available in the area. 2) If the number of droppings is used for the estimate, all elephants must on average spend the same fixed amount of time drinking and not spend a significant time in the river when not drinking. 3) If the number of wells is used, these must to a large extent be used only once.

Information on water availability in the area must be accessible to fulfil assumption 1. Elephants do not spend time in the river sand unless drinking or mud-bathing and normally spend between 30-45 min digging and drinking (Pers obs.). Elephants do sometimes reuse wells. However, a level of well reuse per unit time can be incorporated in a correlation between the number of wells and elephant density/ number. If well reuse is a function of density of wells already present in the river, minimising the time from the river dry out until the count is done will reduce the level of well reuse.

Since the number of wells and dung boli will be a measure of “elephant days” spend in the area around a part of the river it cannot differentiate between x elephants in one day and one elephant in x days. Therefore, the area covered must be large enough to ensure that the majority of elephant movements occur within the sampling area. Minimising the period between the river dry out and the count will reduce the distance individual elephants have moved and therefore reduce the number of elephants leaving or entering the sampling area.

In order to test the validity of this method the counts of wells and dung must be related to a known number of elephants present in specific areas. Such a chance occurred when the semi permanent Ewaso Ngiro River ceased to flow on the 19th of January 2000. This river runs through the core study area of the Samburu Elephant Research Project (SERP) where detailed knowledge about the occurrence of individual known elephants is being collected continuously.

A combined aerial and ground count was carried out to answer whether relative and or absolute number and density of elephants can be estimated by counting droppings or wells in dry riverbeds and if this type of count can be carried out from the air.

Material and methods:

Study area and population

The study area is situated just north of the equator on longitude 37º, in and around Samburu and Buffalo Springs National Reserves, Kenya. The area consists of low-lying semi-arid rangeland along the Ewaso Ngiro River, a semi-permanent river in the area. The river is the only available water source during the dry season apart from two small springs and a tributary that elephants rarely use for drinking, in the southeastern part of the Buffalo Spring National Reserve. The total elephant population within the greater Laikipia/Samburu area has been estimated to around 3000 individuals (Thouless 1996). Of those, app. 900 are using the area in and around the national reserves and have been identified individually by Samburu Elephant Research Program (SERP), a basic monitoring program carried out by “Save the Elephants” in Samburu and Buffalo Springs National Reserves.

A total distance of 55 km river was covered with 20 km inside the reserves and 35 km outside.15 km of the river within the reserves, lying adjacently to the springs, were not included in the count. The count of wells and dung boli was carried out between the 7th and 11th of March 2000, 7 weeks after the river ceased flowing.

Elephant number and density

Data on the presence of individually known elephants within the reserves are continuously recorded by SERP using on-ground observations within the borders of the two reserves, noting position, group composition and identity of all elephants encountered. In case of multiple observations of the same individual elephant on the same day, only the first observation is recorded. A minimum of 20 field days is spend per month, hereby recording all elephants spending a significant time within the reserve (Wittemyer, 2001). Only observations from the 7-week period between the river dry-out and the count were used.

The number of different individuals seen during the 7-week period within a given area was used as a measure of number of different elephants in that area. The number of single observations (including multiple observations of the same individual but on different days) was used as a measure of elephant density.

On ground count

The on ground count was carried out by driving in the dry riverbed. Two types of ground-counts were carried out (Fig 1). 1) A total count where all boli and wells occurring in the river was noted 2) A 10-meter wide subsection count where 5 meters to each side of the car was counted. The car was kept between 15 and 20 meters from the northern riverbank in order to avoid a riverside effect on the subsection count. The subsection count was done over the entire 55-km. Only 35-km was covered by the total count because incoming rain threatened to flood the river, forcing to speed up the count. The total count was made to estimate total numbers and densities and the subsection count was made to test if a faster method could be used for estimating relative numbers and densities.

Dung boli and wells were counted in 500-meter sections of the river by driving slowly in the riverbed. The position between each 500-meter section was taken using a GPS

An attempt was made to distinguish between fresh and old wells. However, the time period from a well was made until it was regarded as old could not be well established and the two groups were pooled. Furthermore, we assumed that no wells had disappeared due to age during the seven weeks prior to the count. A single elephant defecation consists of on average of 3-6 boli. Dung was counted as the number of boli and not as number of defecation’s since it was impossible to distinguish individual defections in some areas.

Aerial count

A total count of wells was carried out from the air using a Cessna 185. The flight path was kept app. 50 meters adjacent to the river, giving the observer full view of the river. The counts were noted every 15 sec. corresponding to app. 700 meters of river. The positions separating the counting sections were taken automatically with the flight GPS. A total of 35 km of the river were covered by air, corresponding to the 35-km where both total and subsection counts were carried out (Fig.2).

Analysis

Ground vs. aerial count:

Aerial and on-ground counts of wells were compared from the 35-km of the river where both a total on-ground count and an aerial count were carried out. The positions separating each counting section were not identical between the ground and air count since the flight path had to be kept adjacent to the river in order to have full view. Furthermore, the aerial counting sections had to be specified in time units compared to distance on ground. However, corresponding positions between aerial and on-ground counts, separated by less than 50 m, occurred every 3-4 km. The total counts within these 8 larger sections were added. The aerial and ground counts in these eight sections were compared using linear regression.

Droppings vs. wells and total vs. subsection ground count:

The number of boli and wells within each 500-meter section were compared in the total count and 10-meter subsection count and between the two counts, using linear regression.

Number and density of elephants vs. subsection count:

The total count of wells was not obtained from within the reserves. Therefore, the number and density of elephants were compared with the 10-meter subsection count of wells and dung boli along the 20 km of the river within the reserve boundaries where elephant observations were available. The total number of all elephant observations within a specified area during the 7 weeks from the river dried out until the count was used as a measure of elephant density. The number of different individuals observed during the 7 weeks was used as a measure of number of elephants.

We tried out three different spatial methods of relating the elephant observations to the number of wells and dung boli. This was done in order to find the maximum spatial resolution in which a high correlation between the number of wells or dung boli and the number, and the density of elephants would emerge.

1) The numbers of wells and dung boli were summed up for non-overlapping sections of 2x500 meter. These values were assigned to the GPS position separating the two 500-m sections (centre position). The elephant observations occurring within a 500-meter radius of that centre position were counted and the number of elephants was analysed vs. the number of dung boli and wells using linear regression (Fig 1b).

2) The numbers of wells and dung were summed for non-overlapping sections of 4x500 meters (2 km of river) and related to number of elephant observations between the longitudes of the section borders using linear regression (Fig 1 b). The grouping of observations using longitudes could be justified since this part of the river runs almost straight from west to east making the sections non-overlapping.
3) Same as method 2 except the sections were doubled to 8x500 meters (4 km of river).

All regressions were forced through origin, as zero elephants would be expected to correspond to no wells or dung boli.

Results:

A map of the area indicating the different types of counts carried out is shown in figure 2. Large differences in the number of wells and boli were observed along the 55-km of river both between general areas and between subsequent counting sections (Fig 3). This indicates general differences in elephant densities and specific points used for drinking along the river.

Aerial counts of wells were hard to obtain when densities exceeded app. 150 wells per 500-meter river. This prevented aerial counting of the 20-km of river inside the reserves. It was not possible to count dung boli from the air.

Ground vs. aerial count:

The comparison between the total on-ground count of wells and the aerial count revealed an almost twice as high count from the air (Air count = 1.9621x ground-count, R2 = 0.73) (Fig 4 a). This discrepancy is probably due to an underestimation in the ground count where wells situated far from the car on the 80-100 meter wide river could have been difficult to detect. This underestimation is not expected to have influenced the 10-meter subsection count since the 5 meters on each side of the car were in clear view.

Droppings vs. wells and total vs. subsection ground count:

In the 10-meter subsection count, the number of wells correlated well with the number of dung boli. The best fit was obtained using a polynomial fit (wells=0.043*boli^2 +2.573*boli, R^2 =0.83) Compared to linear fit (wells = 5.8038*boli, R2 = 0.75) Thus, the number of boli increased faster than the number of wells indicating a level of well reuse (Fig.4 b).

In the comparison between the 10-meter subsection count and the total ground count, the number of wells correlated with Total count = 2.4596x 10-meter count + 1.6109, R2 = 0.79. The number of boli correlated with Total count = 2.6412x 10-meter count + 7.5153, R2 = 0.76 (Fig 4 c). The relative low correlation coefficient between the two counts are probably due to the river meandering in the riverbed causing the 10-meter count to miss the highest densities at intervals. Another factor is the general underestimation of the number of wells and dung boli in the total count found in the comparison between the aerial and the total on-ground count.

Number and density of elephants vs. subsection count:

In method 1, the number of dung boli and wells were compared within a 1-km section of the river with elephant observations within a distance of 500-meter from the GPS position separating the two 500 meter sections making up the 1-km section. With this method, only a weak correlation was found explaining between 50 and 65 % of the variance (Fig 5 a). The total number of observations and the number of individual elephants correlated with the number of dung boli. (Total observations = 0.1621 x boli, R^2 = 0.672), (Individuals = 0.107 x boli, R^2 = 0.523) and with wells (Total observations = 1.061 x wells, R^2 = 0.574) (Individuals = 0.7453 x wells, R^2 = 0.593).

In method 2, where larger 2-km sections of the river were used, the correlation between elephant numbers and boli explained more of the variance (Fig 5 b). For boli (Total observations = .2201 x boli, R^2 =0.817), (Individuals = 0.0999 x boli, R^2 = 0.692) and for wells (Total observations = 1.3911 x wells, R^2 = 0.762), (Individuals =0.6505 x wells, R^2 = 0.754) respectively.

In method 3, the 2-km sections used in the second method were doubled to sections of 4-km of river. By increasing the spatial scale to 4-km sections, a much better result was obtained (Fig 5 c). The correlation between number of boli and total observations (Total observations = 0.2269 x boli, R^2 = 0.992) now explained almost all the variance. The ability to explain number of individuals also increased (individuals = 0.1041 x boli, R^2 = 0.880). With this method, we found a clear non-linear relation between the number of wells and both total observations and the number of individuals. A polynomial fit explained almost all the variance. (Total observations = 0.0017 x wells^2 + 0.483 x wells, R^2 = 0.999) (Individuals = 0.0002 x wells^2 + 0.5872 x wells, R^2 = 0.991).

Discussion:

On a daily basis elephants migrate 3-5 km to and from the river covering 8-10 km per day searching for food and water. (Pers obs. and GPS tracking). Therefore, it was not surprising that a low correlation existed between the number of wells, dung, and elephant observations, when a fine-scaled spatial resolution of one and two km river-sections was used. A very high correlation was found at levels of 4-km river-sections between the 10-meter subsection count of wells, dung boli and the number of elephants. This shows that the 10-meter subsection count of wells and dung in the river could explain the density measured as number of elephant observations as well as numbers of different elephants at a spatial scale of 4-km sections. A comparison of the number of wells or dung boli between areas can therefore be used as a measure of the relative numbers and densities of elephants.

A level of well reuse must be the reason for the non-linear relation found in method 3 between the number of wells and both total observations and the number of individuals, as well as between number of boli and wells over the whole distance counted.

The lack of a total count of wells and dung within the area covered by SERP, prevented the calculation of number of wells and dung produced per day per individual in the river to be used for an estimate of absolute numbers and densities. However, the result from the 10-meter subsection count indicates the possibility for using counts of wells or dung boli as a measure of absolute numbers and densities of elephants.

The number of wells and dung boli explained most of the variance in the number of different individuals observed within the 4-km sections of the river. However, several family units left or arrived at the reserve during the 7-week period and many of the elephants utilised more than one of the 4-km sections. This means that the total number of different individuals in the whole area covered would be grossly overestimated if a simple sum of the number of different individuals within each 4-km section were made. Therefore, if the total number of different elephants should be estimated from river counts one must cover a sufficiently large area to ensure that the majority of elephant movements has occurred within the area covered. Furthermore, the total sum of wells and dung boli counted in the whole sampling area must be used for the estimate of total number of individual elephants. The longer the period from the river dry out, until the count is carried out the more the elephants will have moved around. In that respect, a reduction of the 7-week period used in this study is recommendable. Other advantages of a shorter period is a smaller degree of reuse of wells and a general lower number of wells or dung to be counted, making the count easier.

The big advantage of using well counts instead of dung counts is the possibility of aerial counting. By using aerial counting, large areas can be covered in a short period as well as areas inaccessible from the ground. The higher number of wells seen in the aerial compared to the ground count indicates that aerial counts may be more accurate than total ground counts. Any correction for this underestimation should be done with caution since the underestimation will depend on several variable factors such as the river width, the height of the car used and maybe light conditions during the count. Therefore, a total count on rivers wider than 40 meter is recommended, either by two or more teams, each counting a part of the river, or by aerial counting.

Counting areas with a high density of wells turned out to be difficult from the air which also supports a shorter than 7-week period between the drying of the river and the count, especially in areas with high elephant densities.

The present study has shown promising results for using counts of wells and dung boli in dry seasonal flowing rivers for estimating densities and numbers of elephants in semi arid regions. Before the presented method can be used to estimate absolute numbers and densities of elephants, further studies are necessary to establish the number of wells and boli made per elephant per day in a river.

Acknowledgements

We wish to thank Fritz Vollrath for his critical and constructive comments; Save the Elephants provided unpublished data on elephant observations as well as logistical support. We also wish to thank Flemming Sørensen for helping with the on-ground count. Especially, we are grateful to David Daballen and Kantri Lenantampash for their invaluable help and companionship in the field. This work was supported by EvAlife through a grant from the Danish Research Council and by a grant from the Elephant Research Trust Fund, Kenya.

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Figure legends

Figure 1

A) The methods used for the total and 10 meter subsection on-ground count. Number of wells and dung boli were summed in sections of 500-meters and GPS position was taken on the point separating subsequent sections. The total count included all wells and dung boli within the river. The 10-meter subsection count included only wells and dung within 5 meters on either side of the car. The car was kept 15-20 meters from the northern riverbank. B) The different spatial methods used for relating the elephant observations to the count of dung boli and wells in the river. In method 1, the counts of two subsequent 500-meter sections were summed and related to the observations of elephants lying within 500 meters from the GPS position separating the two sections. In method 2, the counts from four subsequent 500-meter sections were summed and related to the elephant observations lying between the first and last longitude of the combined section. In method 3, the number of sections was doubled to eight compared with method 2.

Figure 2

Map of the area indicating the different types of counts carried out in the different regions of the sampling area.

Figure 3

The number of wells and dung boli per 500 meters counted in the 10-meter subsection count on the 55-km of the Ewaso Ngiro River.

Figure 4

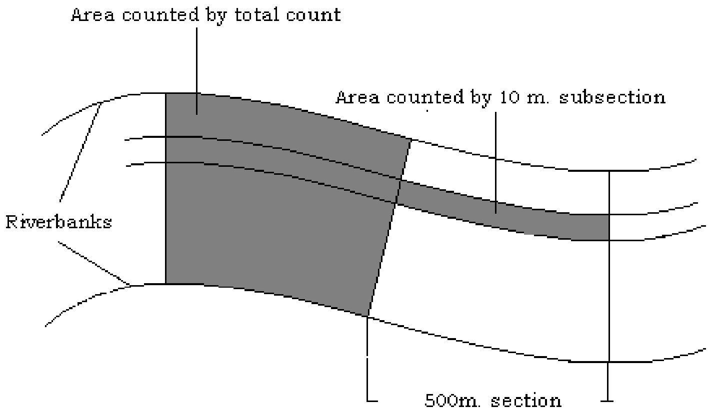
A) The number of wells compared between the total on-ground count and the aerial count. Number of river sections = 8. B) The number of boli versus the number of wells per 500-meter section in the 10-meter subsection ground count. Number of sections = 110. C) The number of wells and dung boli compared between the total ground count and the 10-meter subsection count. Number of sections = 70.

Figure 5

The number of elephant observations and the number of different individuals observed versus the number of wells and dung boli counted in the 10-meter subsection count using method 1 (a, sections N= 20) method 2 (b, sections N=10) and method 3 (c, sections N= 4). Total number of elephant observation N= 1812

Figure 1

A


Area counted by total count
Area counted by 10 m. subsection
Riverbanks
500m. section

B

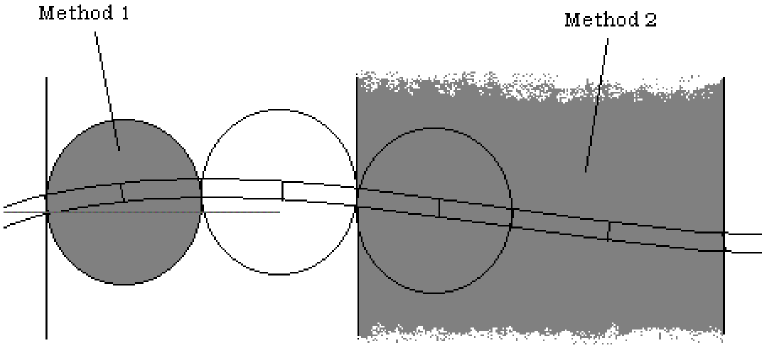

Method 1
Method 2

Figure 2

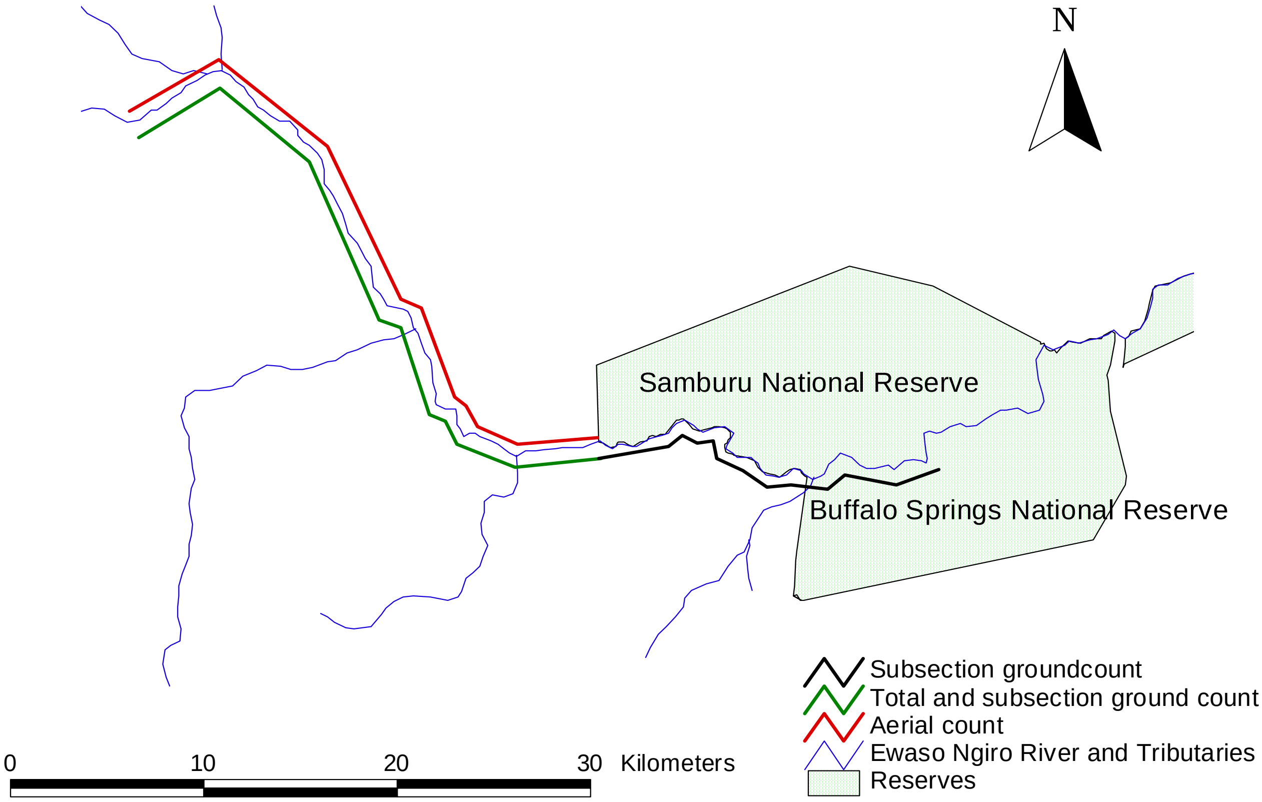

N
Samburu National Reserve
Buffalo Springs National Reserve
Subsection groundcount
Total and subsection ground count
Aerial count
Ewaso Ngiro River and Tributaries
Reserves
0
10
20
30
Kilometers

Figure 3

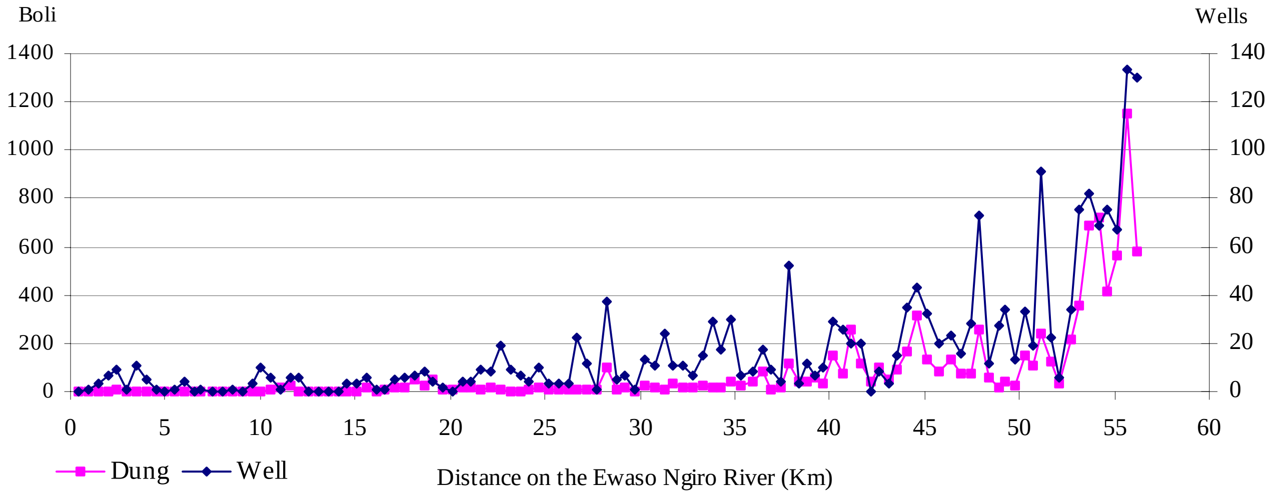
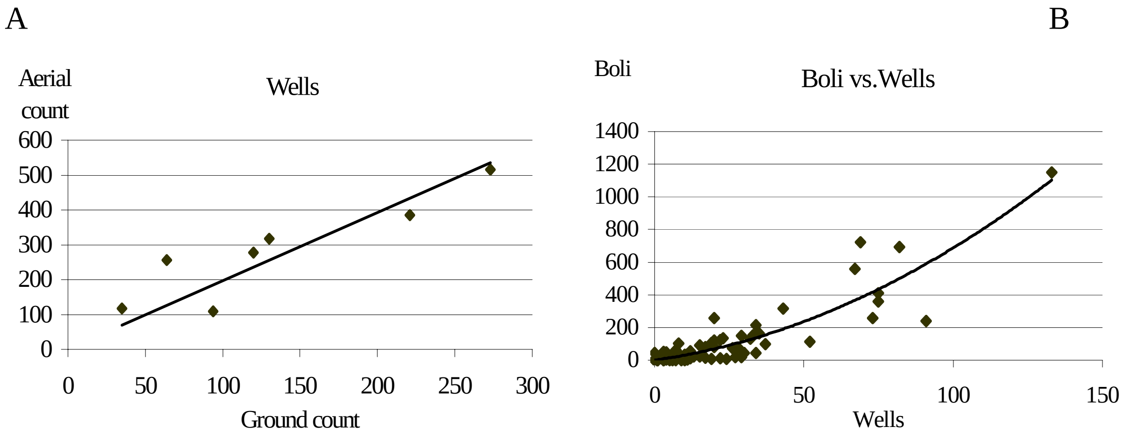
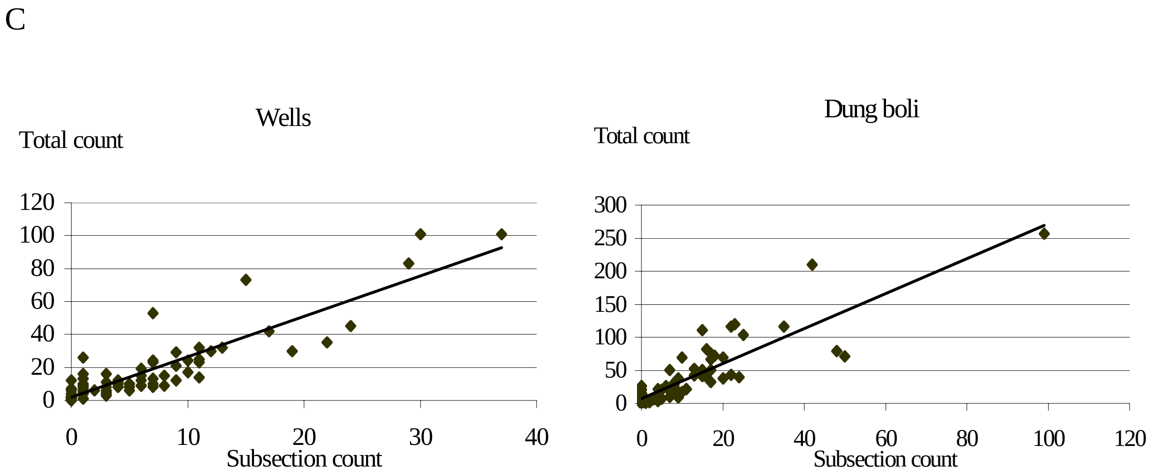

Boli
Wells
1400
1200
1000
800
600
400
200
0
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
45
50
55
60
Dung
Well
Distance on the Ewaso Ngiro River (Km)

Figure 4



Aerial = 1.921 x ground; $R^2 = 0.7313$

Boli = 0.043 x wells^2 + 2.573x wells; $R^2 = 0.825$

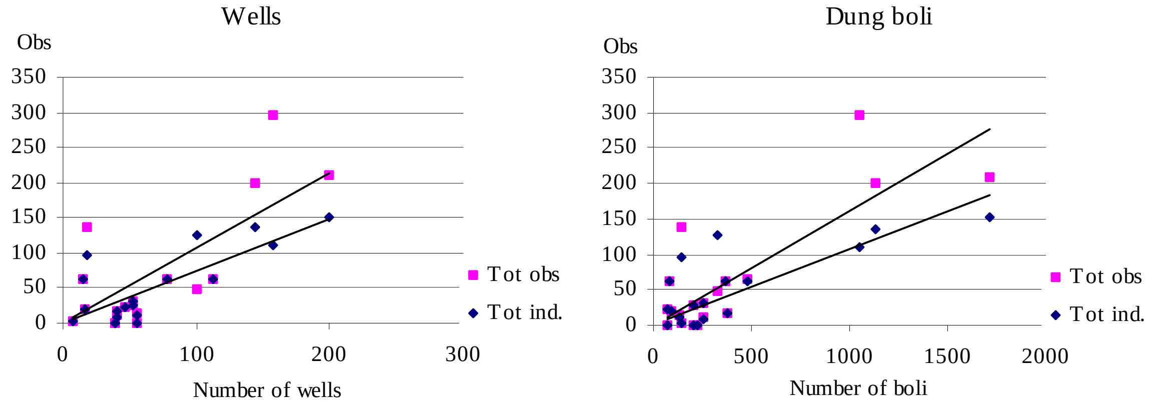


Total =2.4596 x subsection + 1.6109; R^2 =0.788

Total = 2.64 x subsection + 7.515; $R^2 = 0.759$

Figure 5

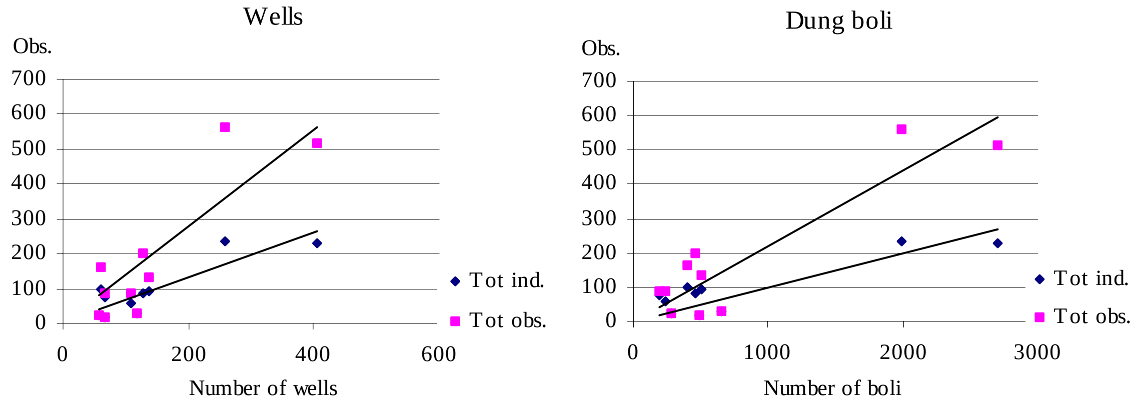
A Method 1



Tot obs = 1.061 x wells; R^2 = 0.574
Tot ind. = 0.7453 x wells; R^2 =0.593

Tot obs = 0.1621 x boli; R^2 = 0.672
Tot ind. = 0.107 x boli; R^2 = 0.523

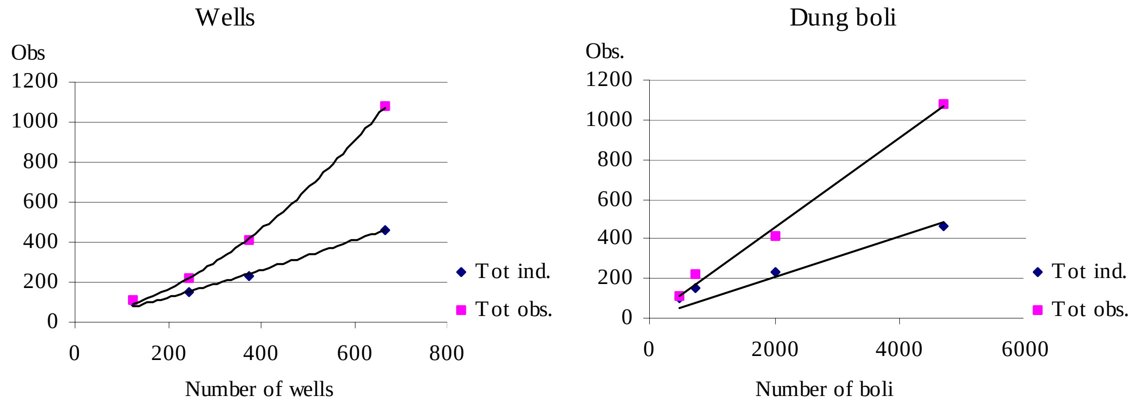
B Method 2



Tot obs = 1.3911 x wells; R^2 = 0.762
Tot ind. = 0.6505 x wells; R^2 =0.754

Tot obs = 0.2201 x boli; R^2 = 0.817
Tot ind. = 0.0999 x boli; R^2 = 0.692

C Method 3



Tot obs = 0.0017 x wells ^{2}; R^2 = 0.999
Tot ind. = 0.0002 x wells^2; R^2 =0.991

Tot obs = 0.2269 x boli; R^2 = 0.992
Tot ind. = 0.1041 x boli; R^2 = 0.880

Chapter 3: Temporal and spatial distribution of oestrus females

3.1 Introduction

In order to estimate the spatio-temporal distribution of oestrus females, the distribution of females must be combined with the frequency of oestrus during the year. The females have a gestation period of 21.5 month and a post-birth refraction period of app. 24 months, resulting in, on average, a quarter of the females coming in oestrus per year. The distribution of oestrus during the year among those females was attempted obtained in two different ways. Namely, by using the number of observed oestrus females among the total number of females observed, and by using the distribution of new born calves during the year and then subtracting the gestation period. The spatial and temporal distribution of oestrus females can then be estimated by the fraction of females expected in oestrus at a given time of the year times the density of females. In the following section, data from the background data collection has been used, combined with demographic data on calve birth as well as data used in chapter 2

3.2 Spatial distribution of females

Normally, densities of elephants are expressed as average number of individuals per km^2, estimated from aerial surveys of large areas. If a fine-scaled estimate of females per km^2 should be obtained, large areas had to be covered intensely in an equal manner. This could not be done due to a combination of time constrains and the inaccessibility of many areas. However, the elephants are dependent on the Ewaso Ngiro River for drinking water during most of the year and are on a daily basis walking perpendicular back and forth between the river and forage areas (Pers. obs. and GPS tracking). In chapter two, it was shown that the activity of elephants drinking in the river reflected the number of elephants occurring in the areas on either side of the river. Therefore, space can be simplified and reduced to a one-dimensional line, namely the river and the density measured as elephants per km river. An estimate of the relative density of elephants (RDE) along the river (Relative number of elephants per X distance river) was obtained using the methods described in chapter two. The correlation between total number of elephant observations and number of boli per 4-km river section (Section 2.2, Method 3, Fig 5c) was used. The RDE was calculated at each 500-m section along the entire distance of the river covered by the on-ground count using equation 3.2.1 and 3.2.2.

$$\text{Density at section X} = D_X = 0.2269 * \sum_{i = \text{Section } x - 4}^{n = \text{Section } x + 4} \text{Boli section}_I \qquad \text{equation 3.2.1}$$

$$\text{RDE at section X} = D_X / \text{Mean } D_{1 \text{ to } 131} \qquad \text{equation 3.2.2}$$

The RDE along the river is shown in fig.3.2.1. An area of high density can be seen between 52 and 58 km corresponding to the central part of the two reserves (See Fig 3.2.2). Medium densities were seen in the remaining part of the reserves (Between 35 and 65 km). Interestingly the medium densities continued to the west almost 20 km outside the protected area.

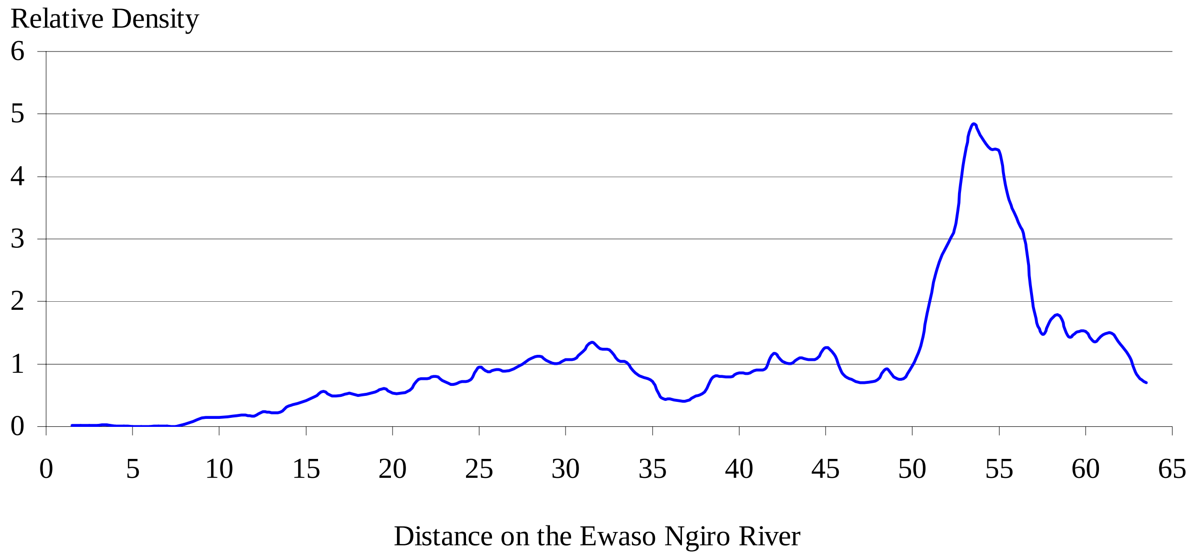


Figure 3.2.1 Relative density of elephants along the Ewaso Ngiro River obtained from counts of Dung boli within the dry riverbed, March 2000. The distance between 35 and 65 km occur within the Samburu and Buffalo Springs National Reserves.

In order to obtain an estimate of the absolute number of individual females along the river the RDE shown in fig 3.2.1 must be corrected for any spatial changes in sex ratio and be linked to a known number of females. An overall sex ratio of 1.4 females to 1 male exists among the adult individuals presently identified in the study population (SERP unpubl.data). In order to investigate if any spatial differences in sex ratios existed, the study area was subdivided into 10 smaller areas (Fig. 3.2.2), and the 3875 single observations on bulls and adult females obtained from the baseline data collection during the study period were assigned to the area where they occurred. In fig. 3.2.3, the area-specific sex ratio is shown. A small town, Archers Post, is situated along the river in area eight and the north-going highway to Ethiopia (A2) runs through it (still just a dirt track). Therefore, few elephants utilises this area and too few observations were available to estimate the sex ratio.

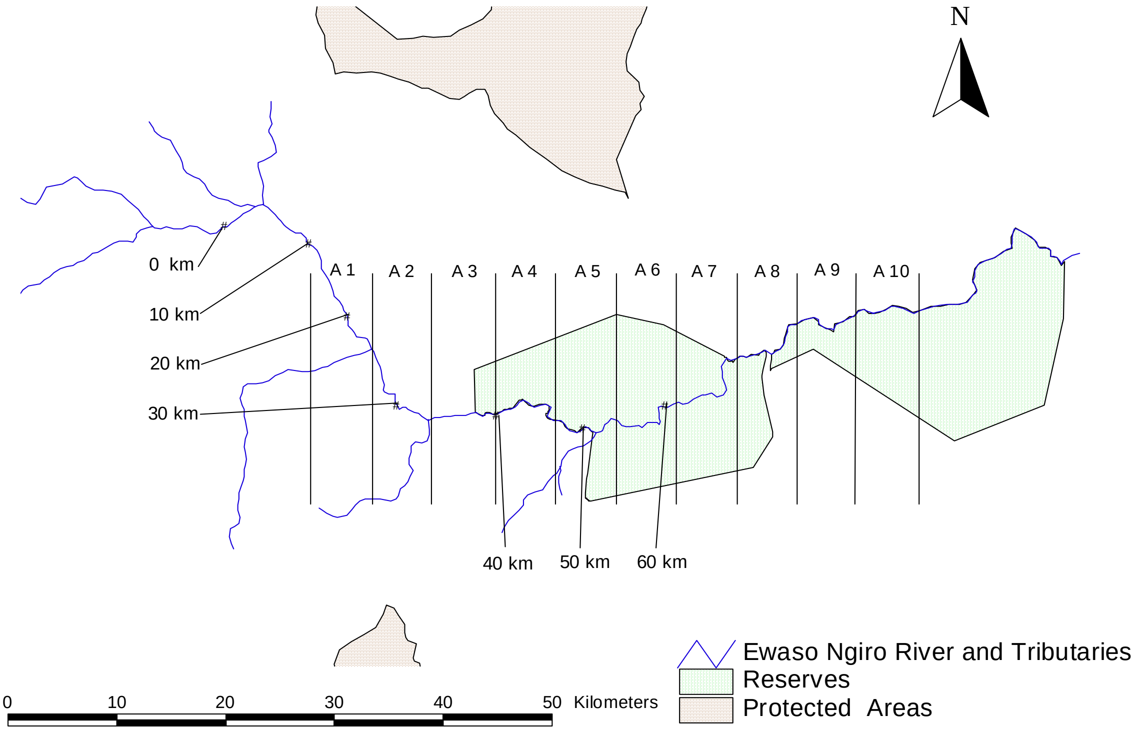


Figure 3.2.2. Areas used for area specific sex ratio and indication of distances on the river used during the river count of boli and wells (A1-A10 = area 1 – area 10)

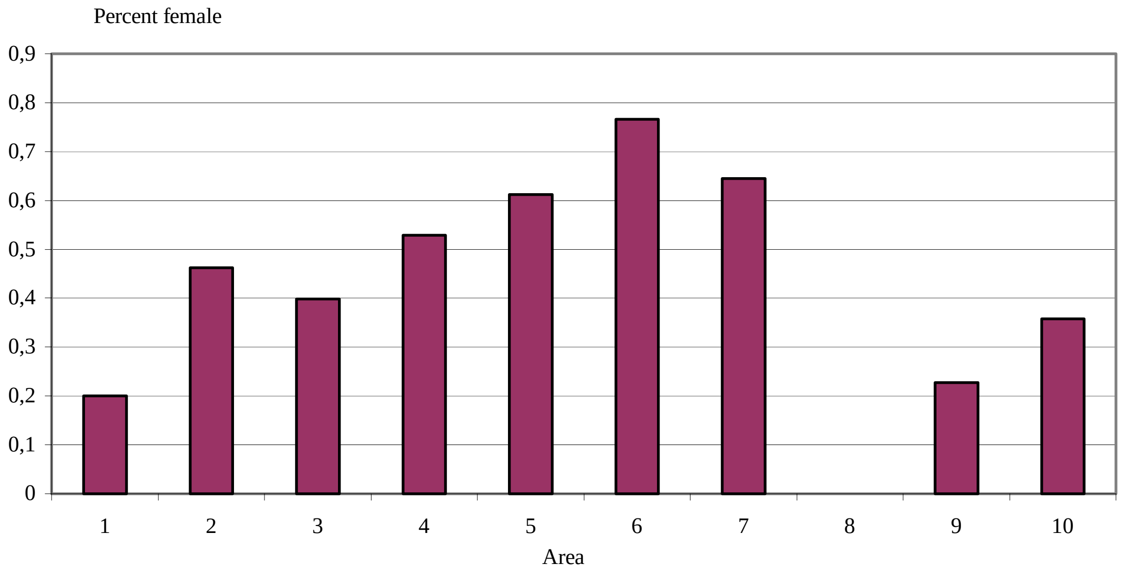


Figure 3.2.3 Percent females of total observations of adult individuals along 10 sections of the Ewaso Ngiro River. (Total N= 3875, 1=15; 2=67; 3=264; 4=346; 5=1130; 6=1728; 7=236; 9=22; 10=67).

In the core area of the reserves, a sex ratio of 3:1 in female favour was observed. Moving further to the west and east a higher percentage of males were observed, reaching a level of 1:4 in bull favour in the area 10-20 km west of Samburu N.R and in Shaba N. R.. Area 9 and 10 situated in Shaba National Reserve were covered at a lower intensity by the baseline data collection and not covered by the river count due to water in the river, Therefore, these areas are not included in the following part. Due to the large differences in sex ratio seen between the different areas, the RDE must be corrected in order to reflect the relative density of females (RDF). The RDE values along the river were therefore multiplied by the sex ratio of the area where they occurred. The RDF values are shown as the red graph in Fig. 3.2.4

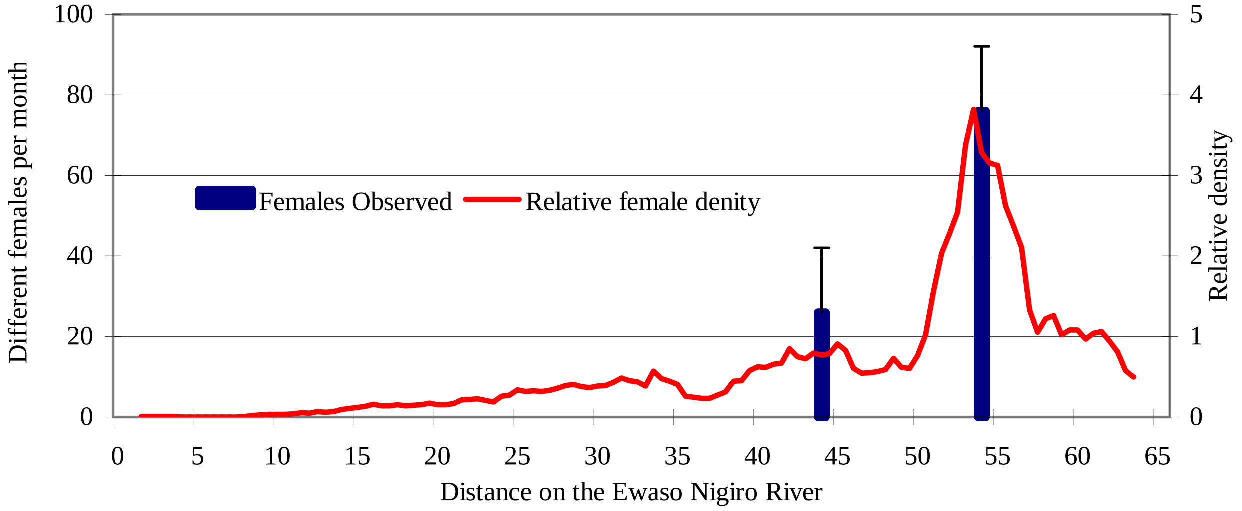


Figure 3.2.4 Relative density of females along the Ewaso Ngiro River and average number of different individual females observed in section 38 to 48 km and 48 to 58 km.

If differences along the river in the number of observed individual females corresponded to the differences in RDF, the RDF could be translated into density of different females (DDF). The area between 38 and 58 km occurred within the two national reserves and had sections of both medium and high RDF. From November 1999 until May 2000 and again from December 2000 until March 2001, continuous baseline recordings of individual females were taken within this area, making it possible to relate the measure on RDF to DDF per month. The average number of different females observed per month in the medium density area between 38 and 48 km and the high-density area between 48 and 58 km is shown in fig 3.2.4 on top of the RDF value. The difference in RDF and DDF between the two areas is almost the same, making it possible to translate the relative density of females into DDF per month. The river count underlying the estimation of RDF was only obtained at one point in time, namely in March 2000. However, if the number of different females per month is relatively stable, the DDF along the river could be extrapolated in time to cover the whole study period. The number of different females seen per month within the reserve is shown in Fig 3.2.5. The number of observations of different breeding females per month is relatively stable. This low variation indicates a more or less constant number throughout the period from November 1999 until March 2001 and allow for the use of the spatial distribution of DDF as an estimate of the general distribution of DDF during the study period.

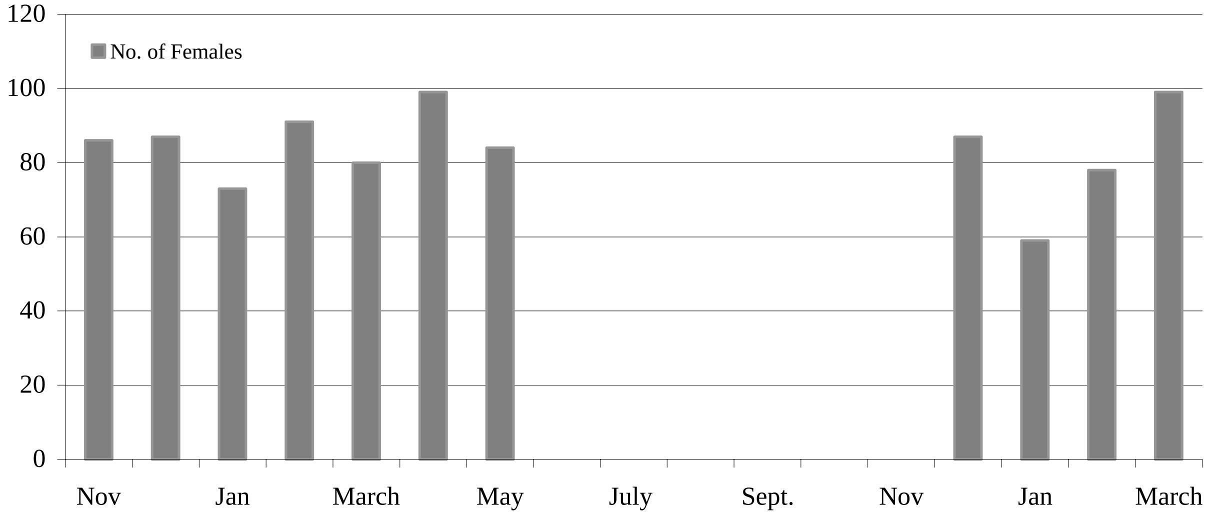


Figure 3.2.5. Total number of different breeding females observed per month within the reserves between November 1999 and March 2001, No observations between June and November 2000.

3.3 Temporal distribution of oestrus females

Female elephants show signs of oestrus for only a short period of 4 – 6 days (Moss and Poole 1983). This short duration of an oestrus event compared with the frequency of observations on specific females, results in only a small fraction of the actual oestrus events being detected. During the fieldwork, only 16 oestrus females were observed. Therefore, the observations of oestrus females can only be used as an indication of possible peaks in number of oestrus females. An estimation of the actual frequency of oestrus events during the year must be done using other methods.

Accurate estimates of calf age (+/- 1 week) can be done until 1 month after birth (Moss 1996). Between 1998 and 2000, 111 of the 153 calves born in the study population (72%) have been observed less than one month after birth (using last observation of female without calf in combination with physical appearance of calf). Assuming the time of year and number of observed new born calves are representative for the remaining number of birth occurring in the population during that year, the number of new born calves can be used to obtain the frequency of oestrus events during the year. The number of oestrus events will be higher than the number of calves born, since some females do not conceive and others miscarry. However, as long as the oestrus to calf ratio does not change greatly with season, the number of calves will reflect the number of oestrus events. Due to the gestation period, a minimum delay of 22-24 month exist before information on oestrus events at a specific time can be obtained. Two methods were tried in order to extrapolate the data on frequency of oestrus between 1996 and 1998 up to the time of the study.

In the first method, the average frequency of oestrus during the year was combined with the number of females expected to come into oestrus.

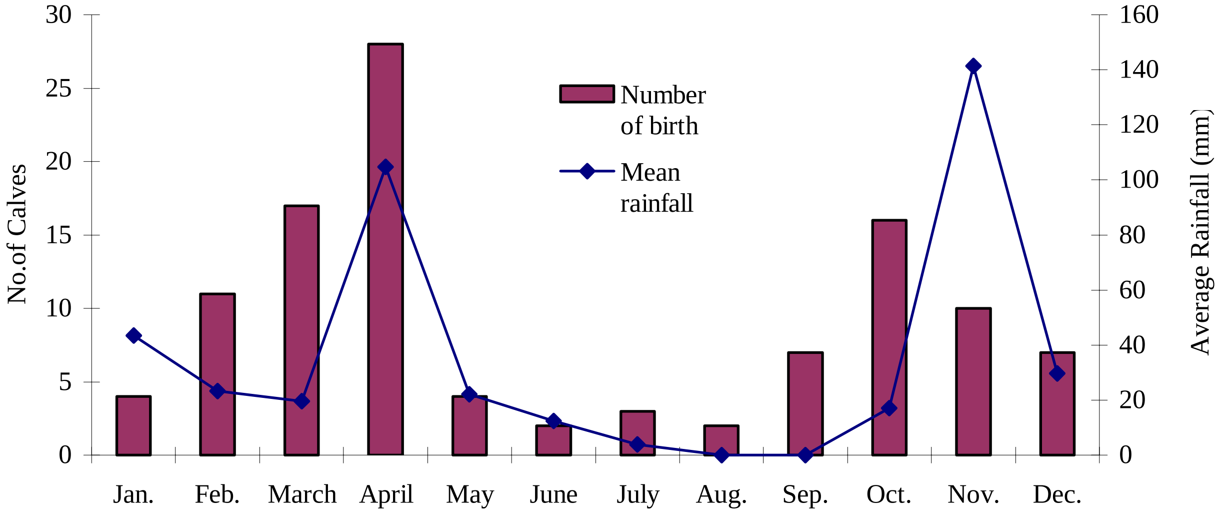


Figure 3.3.1 Average monthly rainfall between 1996 and 1999 measured at Archers Post together with total number of new born calves per month between 1997 and 2000, only calves observed less than a month after birth included (Calves N=111).

The total number of newborn calves per month born between 1998 and 2000, as well as average rainfall for the last 4 years (measured at Archers Post) is shown in fig.3.3.1. A clear correlation between calf birth and rainfall exists, with the majority of calves being born during the two rainy seasons. This relation of calf birth and rainfall is in accordance with findings in other elephant populations (Laws, Parker et al. 1975; Hall-Martin 1987). By subtracting the average gestation period of 21.5 month from the distribution of newborn calves seen in fig. 3.3.1 the distribution of oestrus events during the year has been obtained (Fig. 3.3.2). Two peaks of female oestrus events are apparent. The first peak is from December to January, and the second from May to July, with very low frequencies of oestrus females in the remaining part of the year.

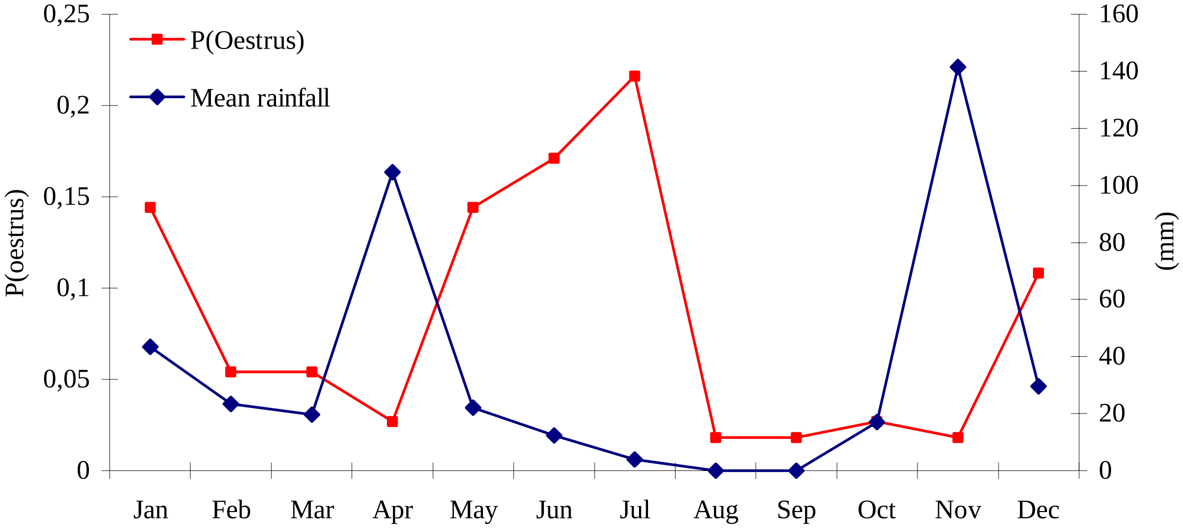


Figure 3.3.2 Average monthly rainfall between 1996 and 1999 measured at Archers Post together with monthly fraction of all oestrus females obtained by subtracting the 21.5 month gestation period from all calves observed less than one month after birth, between 1998 and 2000 (N=111).

In order to get the distribution of the actual number of oestrus females during the year, the frequency seen in fig 3.3.2 must be corrected for the expected number of oestrus females during the year. The number of calves born per year fluctuates significantly between years, (Fig. 3.3.3) indicating that the number of oestrus events must be fluctuating between the years. Normally, females come into oestrus when their youngest calf is between 1,5 to 2,5 years old. Therefore, the number of females in the population with youngest calf within that interval is a better estimate of number of oestrus events within that year than using the simple average of 25% of the females per year.

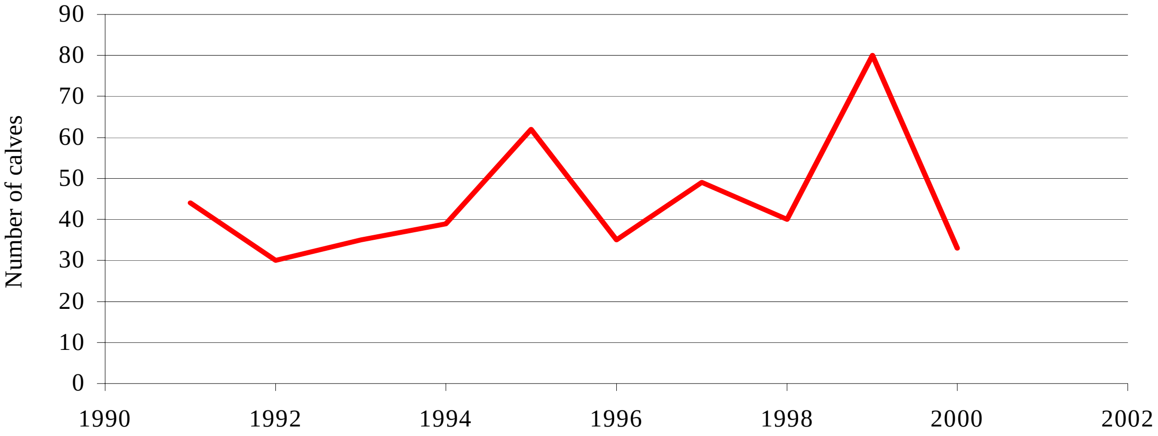


Figure 3.3.3 Total number of calves born per year, N= 412.

At the end of 1999, 42 out of the 216 known breeding females had calves between 1,5 and 2,5 years giving a 20 % probability that any individual female would come into oestrus between mid 1999 to mid 2000. A year later, at the end of 2000, that number changed to 65 females giving a 30 % probability of any female coming into oestrus between mid 2000 and mid 2001. By combining the expected probability of oestrus from figure 3.3.2 with the expected number of females coming into oestrus during the whole year, the expected number of oestrus females per month can be calculated as $P(\text{Oestrus})_{\text{monthX,yearY}} * \#\ \text{oestrus females}_{\text{year y}}$. In figure 3.3.4, the estimated number of oestrus females per month between August 1999 and July 2001 is shown together with the number of observed oestrus females. The number of observed oestrus females is much lower than the expected since not all females are seen every month. However, the timing of the peak in oestrus events correspond between observed and expected, except a complete lack of any observed oestrus females during the expected May-July peak in 2000. It seems unlikely that a large number of females come into oestrus without any being observed. The lack of observed oestrus females during May-July is probably due to the almost complete failure of the April 2000 rainy season (See next section). The strong relation between the average rainfall and the number of calves born (Fig 3.3.1) indicates that females for some reason time their oestrus in response to the rain. The failure of the April 2000 rain is likely to have caused fewer females than expected to come into oestrus. Therefore, the average distribution of oestrus events can probably not be used to predict the number of females coming into oestrus during a specific season.

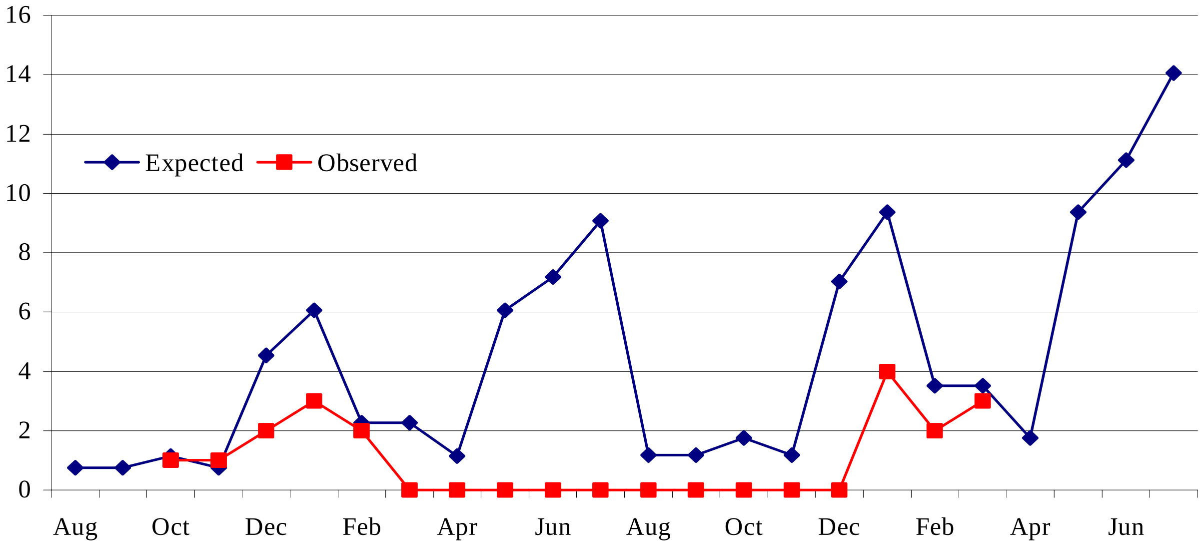


Figure 3.3.4 Estimated and observed number of oestrus females between August 1999 and March/July 2001. Estimated numbers obtained by combining fraction of all oestrus females expected to come into oestrus per month and estimated number of oestrus females per year ($N_{est.}$= 107; $N_{obs.}$= 16).

In the second method, the relation between the amount of rainfall and number of oestrus females were investigated. The gestation period of 21.5 month was subtracted from the date of estimated birth of the 111 calves observed less than one month after birth. The number of oestrus events obtained in this way was adjusted according to equation 3.3.1 with the total number of calves known to be born during that year, in order to reflect the total number of oestrus events.

$$T_{XY} = C_{XY} * (O_Y / C_Y) \qquad \text{equation 3.3.1}$$

T_{XY} = Estimated total number of oestrus females in month X year Y.

C_{XY} = Number of oestrus females in month X year Y, estimated from observed new born calves.

O_Y = Total number of oestrus females in year Y, estimated from all calves born 2 years later.

C_Y = Total number of oestrus females in year Y, estimated from observed new born calves.

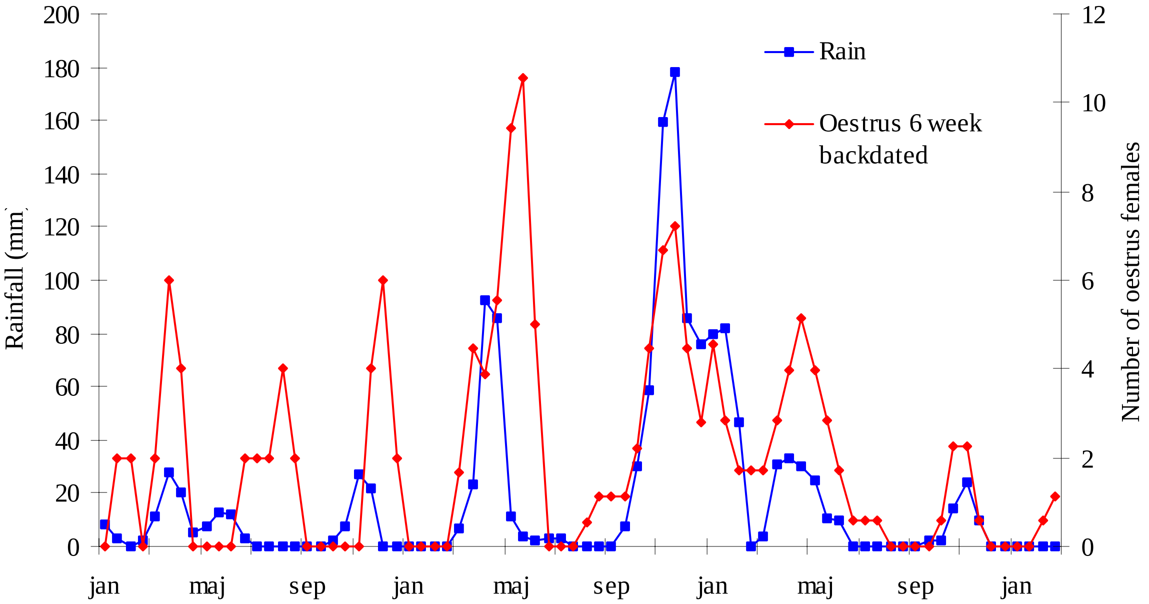


Figure 3.3.6 Monthly rainfall (2 week overlapping average) together with monthly number of oestrus females (2 week overlapping average). Oestrus females estimated from newborn calves and corrected for total number of calves born per year. The number of oestrus females has been back dated 6 weeks in order to overlap with the rainy season.

In figure 3.3.6 the 2-week overlapping monthly average of rainfall and estimated oestrus events (T_{XY}), are shown for the period between January 1996 and January 1999. The number of oestrus females has been backdated 6 weeks (i.e. June oestrus are shown under April) in order to overlap with the rainy season they are resulting from. The monthly rainfall and the number of oestrus females are weakly correlated (Oestrus = 0.037 * Rain +2.73; R^2 = 0.294). The low amount of variance explained is probably due to the slight change in response time between rain and oestrus. This slight shift in response time can be overcome by looking at the total amount of rain received during each of the six rainy seasons and compare that with the total number of oestrus females coming 5-7 weeks later (table 3.3.1). In fig. 3.3.7 a+b oestrus females vs. rainfall is shown. The number of oestrus females per season was found to be a linear function of the reciprocal amount of rain (oestrus = -1920.5* rainfall $^{-1}$ + 44.13; R^2= 96.12). The large correlation coefficient indicates that the seasonal amount of rainfall is a good indicator of the number of females coming in oestrus after the rain.

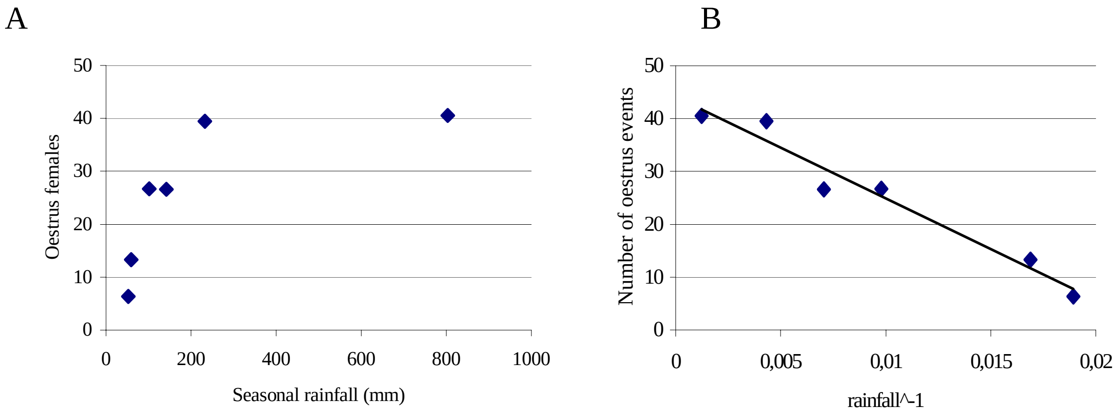


Figure 3.3.7 A: Number of oestrus females vs. seasonal rainfall N=6 B: The total number of oestrus females per season vs. reciprocal amount of total rainfall (Seasons N=6) (Oestrus females = -1920.5 * Seasonal rainfall $^{-1}$ 44,14; R^2 = 0.9612).

The non-linear correlation indicates that the effect of additional rain decreases with increased amount of rain. This would be expected, since the females probably respond to the vegetation resulting from the rain and as the soil becomes more satiated with water the effect of additional water on vegetation growth is reduced. The intercept is around 44 females (corresponding to the number of females coming in oestrus during a season with unlimited rainfall). This number corresponds roughly to 25 % of the breeding females, the average number of females expected in oestrus per year. This indicates, that if optimal conditions exist during a season, all potential available females will come into oestrus. Furthermore, no females are expected in oestrus during seasons with less than 40 mm of rain. ($0 = -1920*Rain^{-1} + 44 \Rightarrow Rain = 43mm$). The correlation does not take into account the varying number of females capable of coming into oestrus (Females with new born calves or females already pregnant cannot come into oestrus). After the heavy rain in 1997-1998, caused by El Ñino weather phenomenon, some females came into oestrus (and later gave birth) not more than 6-12 month after their latest calf was born. Therefore, the number of available females was calculated as the number of females at a given season having calves between 0.5 and 2.5 years old. In Fig 3.3.7, the fraction of available females coming in oestrus in each season is related to the reciprocal rainfall (Fraction Oestrus =-21.39 *rainfall $^{-1}$ + 0,4812; R^2 = 0.9925).

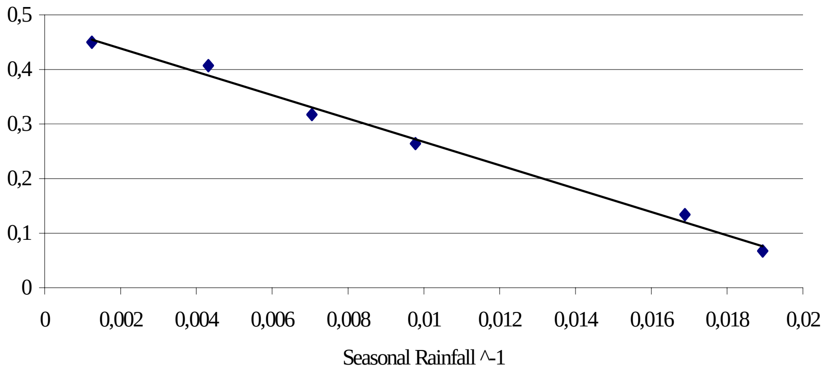


Figure 3.3.8 Fraction of females with calves between 0.5 and 2.5 years coming in oestrus vs. seasonal rainfall^{-1} (Fraction Oestrus =-21.39 *rainfall $^{-1}$ + 0,4812; R^2 = 0.9925)

Using the fraction of available females rather than total oestrus females make intuitively sense and the higher correlation coefficient indicates that this method is more accurate. For an overview of the data used, see table 3.3.1.

Rainy season	Oestrus season	Rainfall (mm)	Number of oestrus from known birth	Total number of calves born 2 years later	Est. number of oestrus from calve birth	Available females	Est. number of oestrus females from rainfall
April 96	June 96	102.2	6	40	26.7	101	
November 96	January 97	59.2	3		13.3	99	
April 97	June 97	231.9	37	80	39.5	97	
November 97	January 98	803	38		40.5	90	
April 98	June 98	141.8	21	33	26.7	84	
November 98	January 99	52.8	5		6.3	93	
April 99	June 99	101	N.A.	N.A.	N.A.	89	24
November 99	January 00	154.2	N.A.		N.A.	105	36
April 00	June 00	63,3	N.A.	N.A.	N.A.	120	17
November 00	January 01	81,1	N.A.		N.A.	120	26
April 01	June 01	121,7	N.A.	N.A.	N.A.	113	35

Table 3.3.1 Data on rainfall and observed and predicted number of oestrus females between 1996 and 2001

Using the correlation between seasonal rainfall and fraction of oestrus, a seasonal specific estimate of the number of oestrus females between August 1999 and July 2001 can be made. A rainy season was defined as a period with rain events not separated by more than 30 days. The number of oestrus females resulting from that season was estimated according to equation 3.3.2 obtained from the correlation found in Fig 3.3.8

$$\text{No. of oestrus females season} =((-21.39/ \sum \text{rain within season}) + 0.4812)* \text{Available females} \qquad \text{Equation 3.3.2}$$

The total number of oestrus females in a season is in some way distributed over the period following the rain. In figure 3.3.6, the distribution of oestrus females somehow resembles the distribution of the rainfall. Therefore, a method to distribute the estimated number of oestrus females based on the distribution of the rainfall was attempted. The distribution was made in the following way: The rainy season was divided into k, non-overlapping 15 day periods (either 1^{st}-15^{th} or 16^{th} to 31^{st}) With the first period being the last 15-day period without rain and the last period being the first 15-day period without rain. The number of oestrus events resulting from each period was then calculated according to equation 3.3.3

$$\text{No. of oestrus in period i+6 weeks} = \frac{\sum \text{Rain in period i}}{\sum \text{Rain in season}} * \text{Number of oestrus in season} \qquad \text{Equation 3.3.3}$$

The number of oestrus events per calendar month was then calculated using equation 3.3.4. For a graphic illustration, see fig 3.3.8.

$$\text{Oestrus}_x = \text{Oestrus in month}_x = \sum \text{oestrus in the two periods in month}_x \qquad \text{Equation 3.3.4}$$

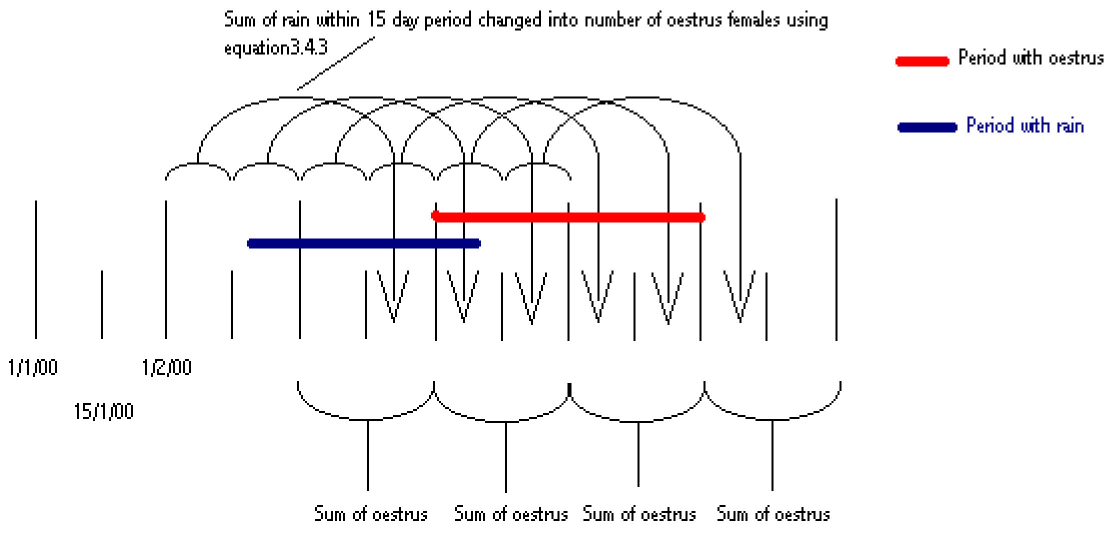


Figure 3.3.8 Method for obtaining the distribution of oestrus females within each season.

The actual distribution of oestrus females between 1996 and 1998, obtained from known calve birth as well as the distribution calculated using equation 3.3.3 and 3.3.4 can be seen in figure 3.3.9. Apart from the first season, the predicted distribution follows the actual distribution relative closely. Therefore, this method was used to the distribute the estimated number of oestrus events between August 1999 and July 2001 (figure 3.3.10)

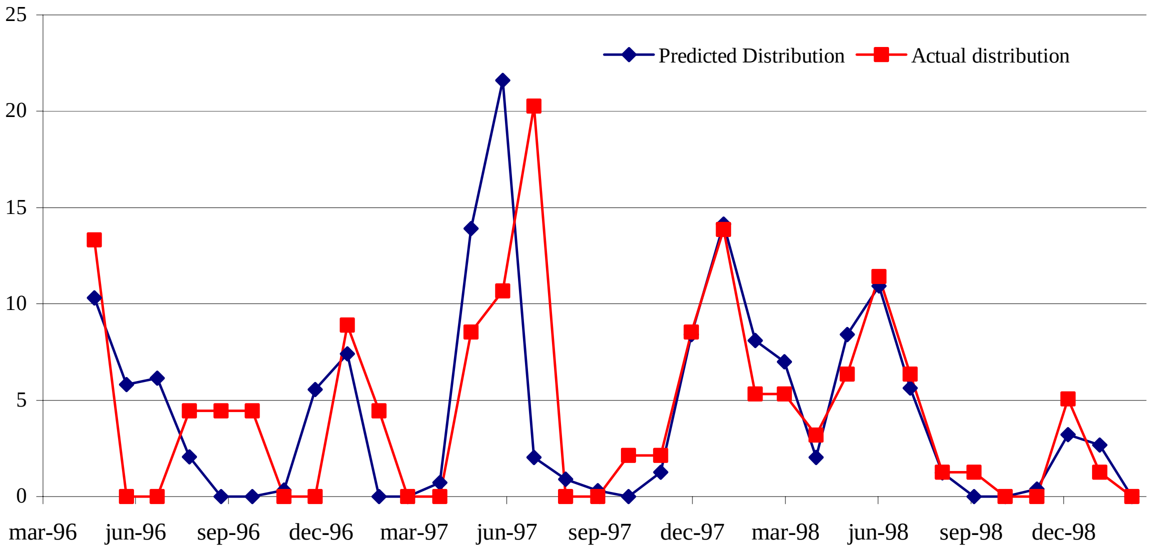


Figure 2.4.9 Actual and predicted distribution of oestrus females using equation 2.4.3 and 2.4.4.

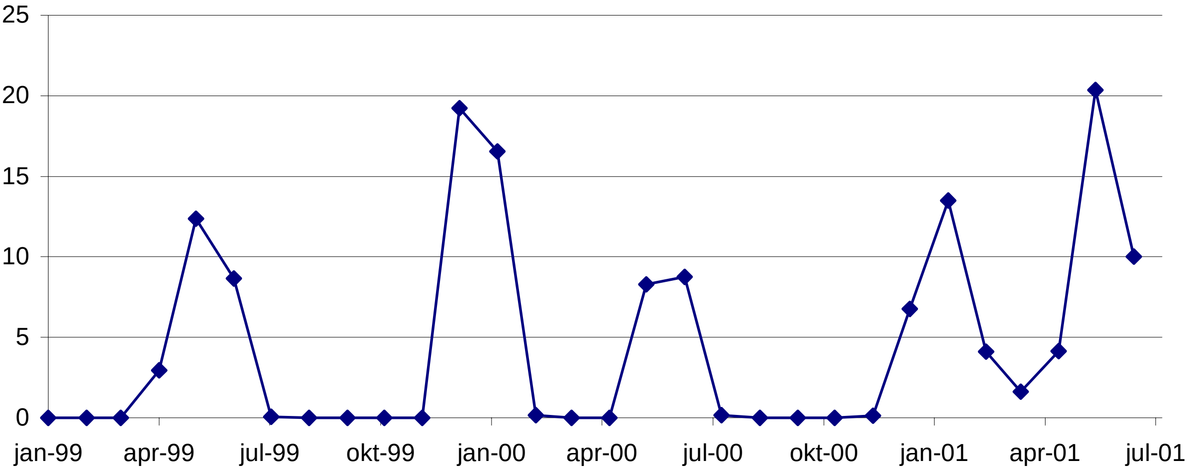


Figure 3.3.10 Estimated number of oestrus females per month between January 1999 and July 2001, using equation 3.3.3 and 3.3.4.

3.4 Spatial and temporal distribution of oestrus females

The predicted number of oestrus females per month found in section 3.3 can now be combined with the spatial distribution of females found in section 3.2, hereby obtaining the spatio-temporal density of oestrus females during the study period. The number of females occurring at river section i in month x and expected in oestrus during month x (Oestrus $_{(xi)}$) was calculated using equation 3.4.1, hereby obtaining an estimate of the number of oestrus females occurring at given section of the river during a given month.

$$\text{Oestrus}_{(xi)} = (\text{Oestrus}_{x} / c)^{*}\ \text{DDF}_{i} \qquad \text{Equation 3.4.1}$$

c = Number of breeding females in the population, currently 216

In fig. 3.4.1, the resulting spatio-temporal density of oestrus females between August 1999 and July 2001 along the 65-km section of the Ewaso Ngiro River, constituting the study area is shown.

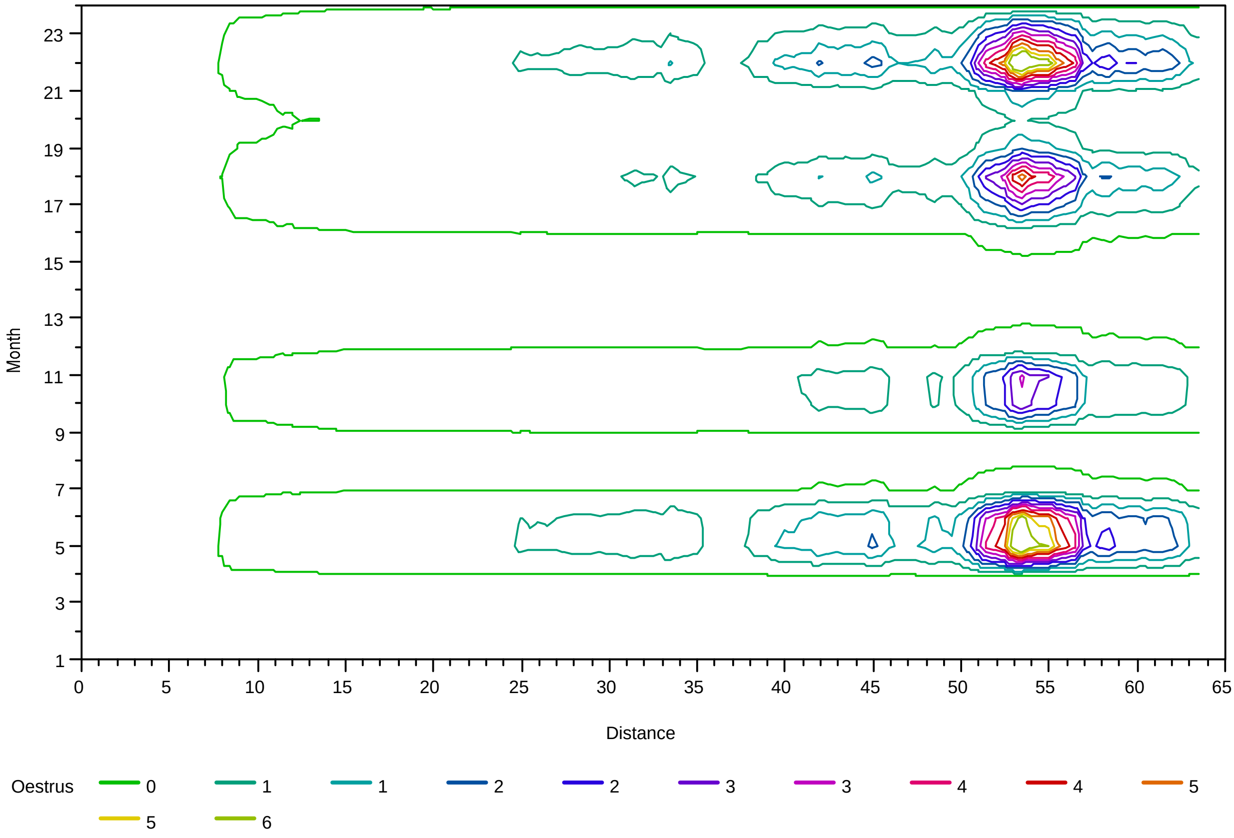


Figure 3.4.1. The spatial and temporal density of oestrus females along the Ewaso Ngiro River between August 1999 and July 2001

3.5 Discussion

Large differences were found in the spatial density of females within the study area. The core of the two reserves had very high densities compared to the areas outside the two reserves. The preference for the reserve could be due to risk avoidance. Even though illegal hunting is at a low, occasionally poaching and harassment do occur outside the reserves. It could also be caused by differences in forage quality. The areas outside the reserves have large amounts of cattle and over grassing and soil erosion are evident in most areas.

Large seasonal variations in the frequency of oestrus were also found with both the timing and total number of oestrus females depending on the seasonal amount of rainfall. This seasonal timing with peak numbers of oestrus females occurring shortly after the rain has been seen in other populations and can have several explanations. If an energetic cost is associated with coming into oestrus, females may need a period of ample forage in order to obtain a good body condition before oestrus. If oestrus is not in itself costly, females may not want to start a long and costly gestation period unless in prime condition. Thirdly, the rain could be a signal used by the females to time the birth to coincide with an expected period of good forage 22 month later hereby securing high energy intake during the first period of lactation.

By combining the spatial density of females with an estimate of the number and distribution of oestrus events, a spatio-temporal distribution of oestrus females could be obtained (Fig. 3.4.1). This distribution must be viewed as crude approximation. It is based on the extrapolation of a spatial distribution into time as well as a calculation of probability of oestrus depending on rainfall and the number of available females. Certain underlying assumptions must also be kept in mind. The number of oestrus females was calculated as a given fraction of the females occurring in a given area. If oestrus females tend to aggregate or associate, for example to constitute a larger target for the bulls, the distribution of oestrus females will not be similar to the distribution of all females. However, the very large differences seen between areas, both in time and space are unlikely to be an artefact. The large differences in the distribution of oestrus females are expected to influence the reproductive decisions among the bulls, since different areas have highly variable resource value in terms of receptive females.

Chapter 4: Temporal and spatial distribution of sexual activity in bulls

4.1 Introduction

Bulls must choose at which time and in what place to become sexually active. Furthermore, sexually active bulls can choose between a competitive musth strategy, or a non-competitive, non-musth strategy. Three main factors are expected to influence these decisions, namely: 1) the rank and condition of the individual bull, 2) the distribution of oestrus females and 3) the distribution and relative rank of competing bulls. The ranking order is not necessarily fixed over time, but may change depending on the sexual state of the individual bull, or the type of dispute. Furthermore, the overall ranking may not be linear (A<B<C does not necessarily imply A<C). The relative rank between two bulls can, in a given situation often be observed from disputes over some resource (a muddying place, the shade of a tree, forage, or proximity to a receptive female). However, since individuals place different values on different resources at different times, the retreating part in a dyadic interaction is not always the same, especially if the ranking distance between the interacting individuals is small. During the study period the outcome of all interactions between bulls were noted. Since the total number of possible bull pairs in a population with 150 bulls are more than 11.000 relatively few were ever observed together. Furthermore, since several interactions have to be recorded before the actual ranking can be established this could only be done for a small number of bulls. However, the individual rank is highly dependent on size and thus age (Poole 1989). Therefore, the estimated age was used to categorise the bulls into 4 age/rank groups namely: age group 1 (15-25 years); age group 2 (25-30 years); age group 3 (30-35 years) and age group 4 (35+ years).

For most of the bulls, too few observations were available to assign individual periods of sexual activity or inactivity. Therefore, if a bull was observed in association with females it was regarded as sexually active and if it was alone or with other bulls it was regarded as inactive. Bulls do occasionally associate with females during periods of sexual inactivity and do spend some of the time alone when sexually active. However, these “wrong” classifications are expected to be few, compared to the overall association pattern and are likely to cancel out. The distribution of sexual activity between age groups in time and space as well as individual patterns of sexually active periods was obtained from the background data collection carried out in this study, as well as comparable data collected by Save the Elephants baseline monitoring program. The distribution of bulls was compared to the temporal and spatial distribution of oestrus females estimated in chapter two and three. As an example of a spatial distribution of individual bulls, depending on rank and density of oestrus females, data on the ranging during January and February 2000 of one un-collared bull (in musth) and the four collared bulls (sexually active non-musth) is presented in section 4.4.

4.2 Age dependent distribution of sexual activity and musth

4.2.1 Frequency of sexual active non-musth and musth in time

Some of the bulls are seen very infrequently. Therefore, the individual patterns of sexual cycles in the four age groups are based on the individuals with the most complete longitudinal data sets. Since only incomplete records are available for many of the bulls, some of the bulls presently not having been observed in musth are expected to have regular periods of musth. This is especially true for the two oldest age groups. The prevalence of the different sexual states over time in the four age groups as well as examples on individual sexual cycles can be seen in figure 4.2.1 A-D.

The youngest bulls in age group 1 associates with females throughout the year with no clear focus on the peak oestrus seasons. Furthermore, individuals show no clear cyclic pattern of sexual activity. Since 1997, three of the 91 bulls in this age group have been observed in musth. However, musth events lasted only for brief periods between 1-3 days. To date, the youngest bull observed showing signs of musth is Edison (BNN1082), estimated to be around 20 years old. Older bulls were not present on any of the occasions where age group 1 bulls were observed in musth.

In age group 2 (25-30 years), the bulls show signs of cyclic sexual behaviour. The majority of the bulls have their sexual active period during the peak oestrus seasons. Three of the 17 bulls in this group have been observed in musth. The periods of musth, lasting up to one month are mainly occurring at the beginning or termination of the peak oestrus seasons.

Bulls between 30-35 years (Age group 3) have clear sexual cycles and almost all bulls have their sexual active periods during the peak oestrus seasons. To date, of the 29 bulls, 13 have been seen in musth. The musth period typically lasts between one and two months, with extensive periods spent in sexually active non-musth. The individual sexual cycles are, however widely different between bulls in this group. Some have two cycles of sexual activity per year without coming into musth, some with musth periods in both, others come into musth in one of the sexually active periods but not in the other and again some only have one sexually active period either with or without musth.

In the last age group of bulls above 35 years, few were observed in sexually active non-musth. Of the 19 known individuals, 15 have been observed in musth. Bulls in this age group almost exclusively come into musth in or around the time of expected peak numbers of oestrus females. Musth periods typically last between 2 and 3 months. In this group, the individual sexual cycle also vary. Some bulls have two musth periods a year, others one longer.

Age group 1 (15-25 years)

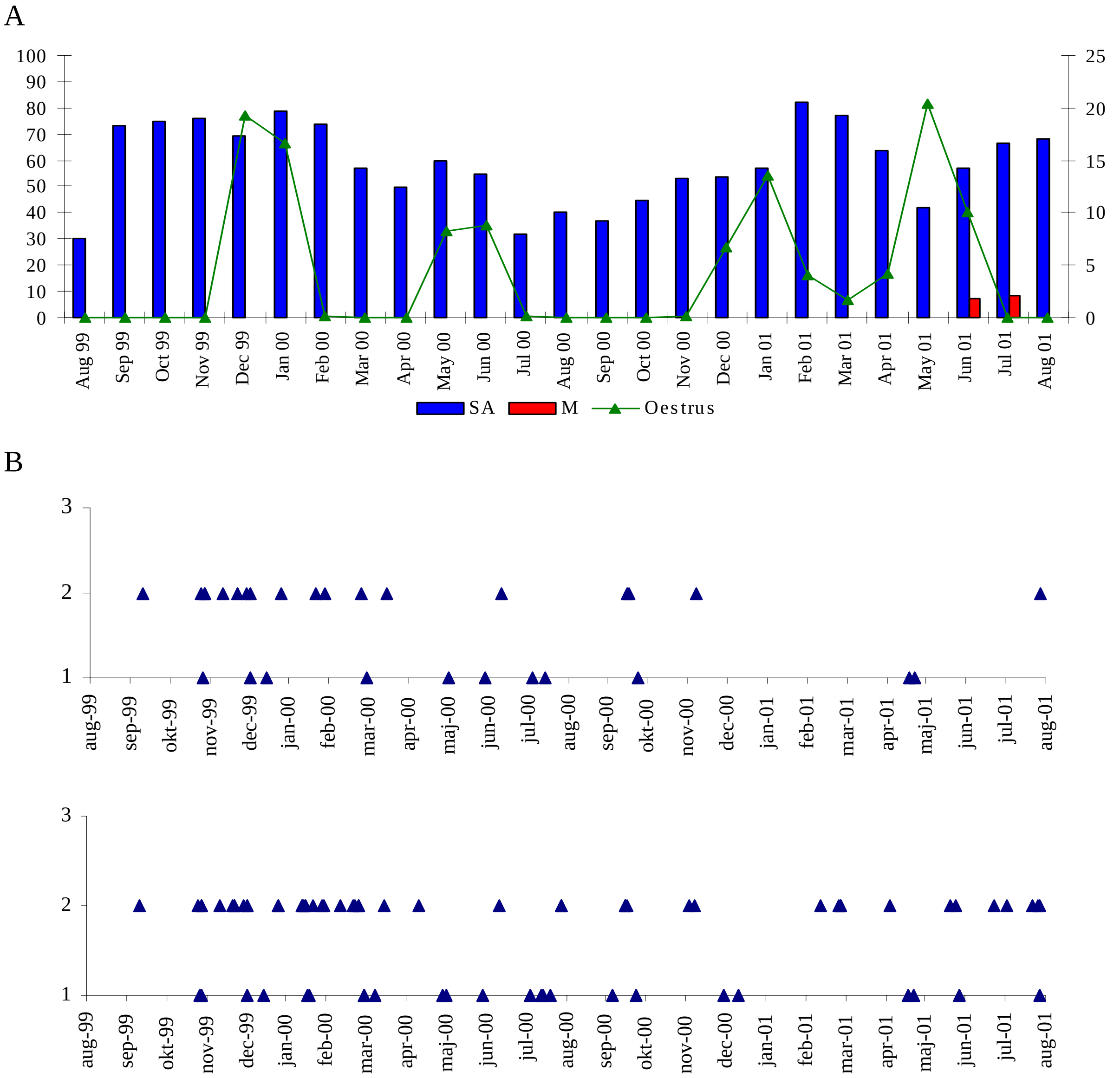
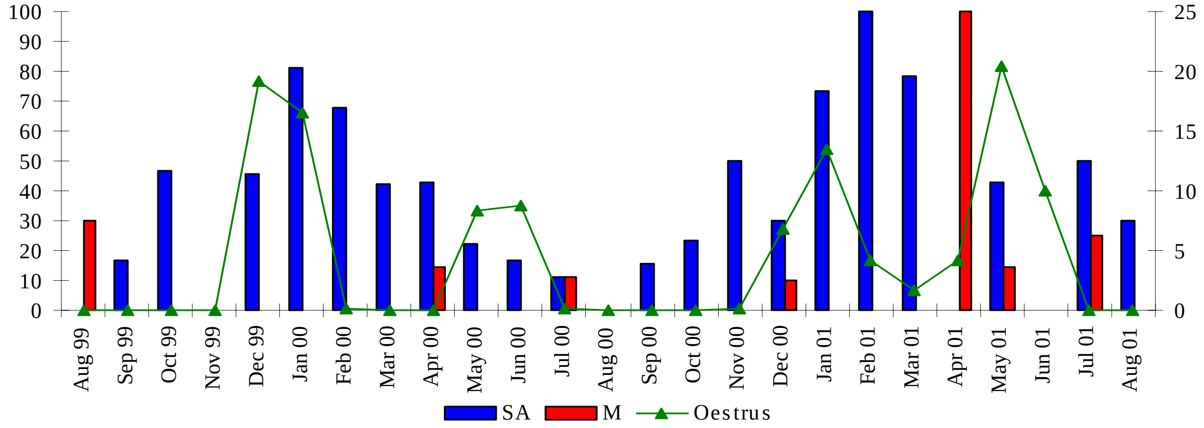


Figure 4.2.1 A: A) Percent observations of bulls associating with females or in musth in age group 1 between August 1999 and August 2001 and estimated number of oestrus females. (Number of observation N= 683, Month with less than five observations omitted) B) Examples of individual bull associations in two bulls (BNN1066-Arthur and BNN1082-Edison), 1= Alone or with other bulls, 2= With females, 3= In musth

Age group 2 (25-30 years)

A



B

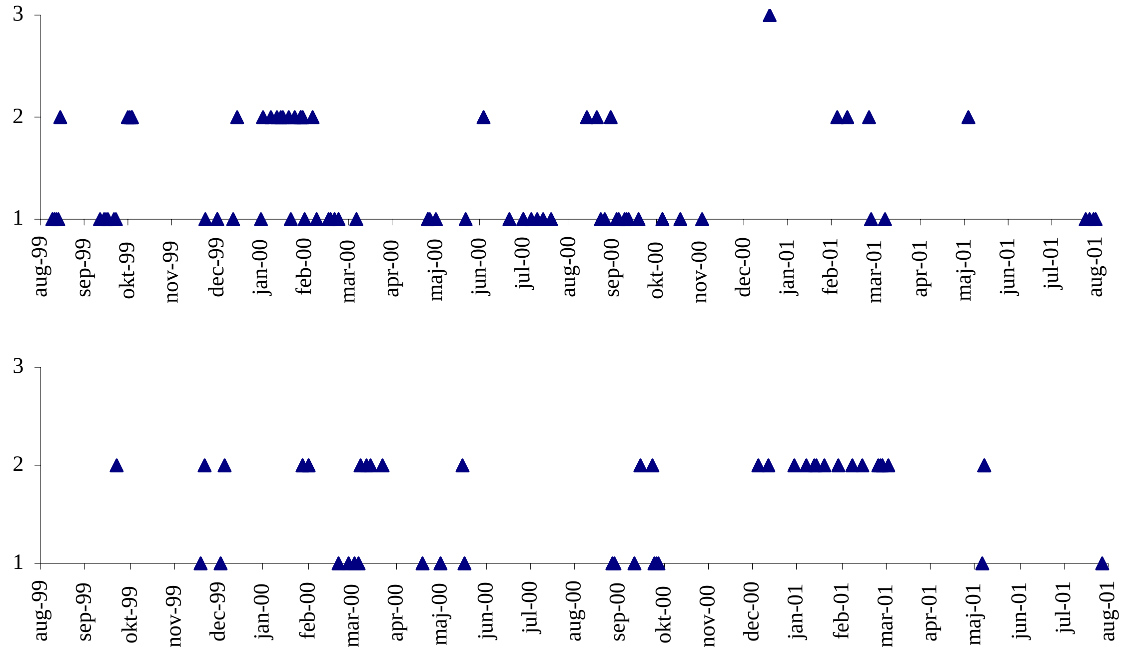


Figure 4.2.1 B: A) Percent observations of bulls associating with females or in musth in age groups A2 between August 1999 and August 2001 and estimated number of oestrus females. (Number of observation N= 274 Month with less than five observations omitted) B) Examples of individual bull associations in two bulls (BNN1040-Yearger and BNN1039-Ansel), 1= Alone or with other bulls, 2= With females, 3= In musth

Age group 3 (30-35 years)

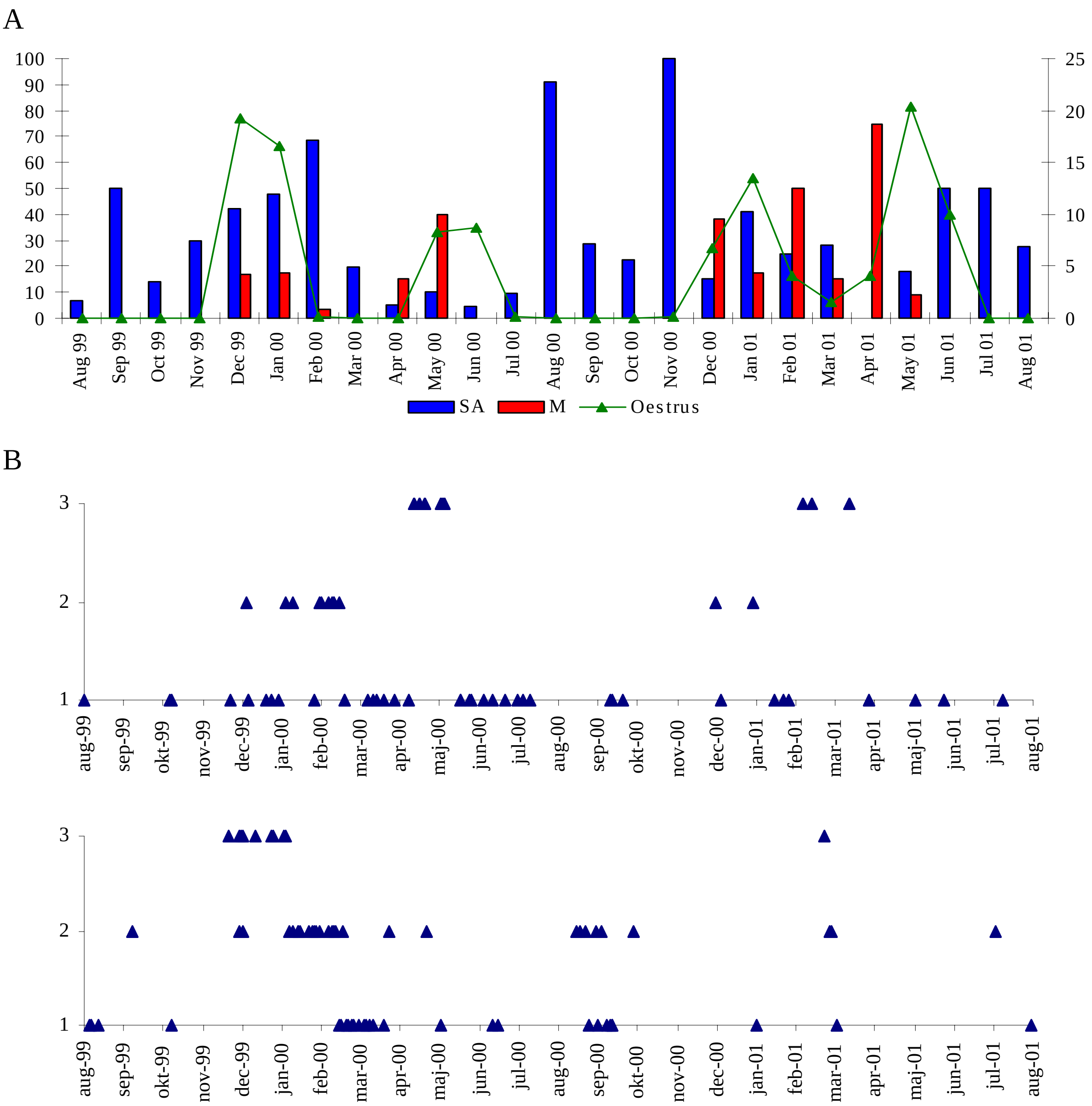


Figure 4.2.1 C: A) Percent observations of bulls associating with females or in musth in age groups A3 between August 1999 and August 2001 and estimated number of oestrus females. (Number of observation N= 472 Month with less than five observations omitted) B) Examples of individual bull associations in two bulls (BNN1019-Lpaus and BNN1027-Esidai), 1= Alone or with other bulls, 2= With females, 3= In musth

Age group 4 (35 + years)

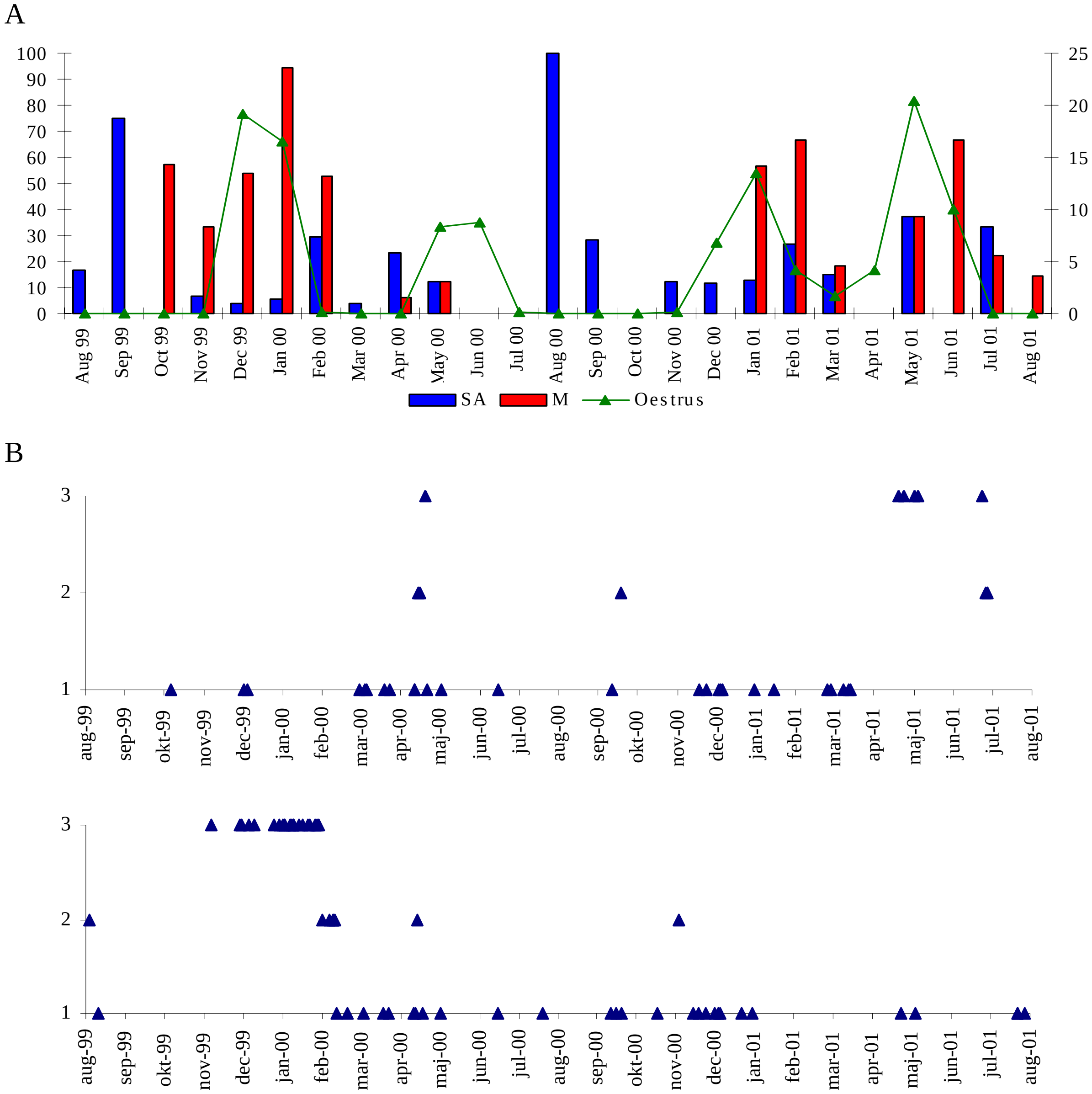


Figure 4.2.1 D A) Percent observations of bulls associating with females or in musth in age groups A 4 between August 1999 and August 2001 and estimated number of oestrus females. (Number of observation N= 315 Month with less than five observations omitted) B) Examples of individual bull associations in two bulls (BNN1001-Mungu and BNN1011-Mandela), 1= Alone or with other bulls, 2= With females, 3= In musth

4.2.2.Number of musth bulls in time

The number of different musth bulls in each age group per month is shown in figure 4.2.2.1 In general, the total number of musth bulls follows the estimated total number of oestrus females. However, the age of the bulls in musth vary depending on the number of oestrus females. During the April-June season 2000 where few females were expected in oestrus due to the poor rainfall, only two different age group 4 bulls were observed in musth. One of the bulls was only observed once (BNN1022-Thesiger) the other (BNN1001-Mungu) was only in musth for one week before returning to foraging. Mungu has during 1998, 99 and 2001 had musth periods lasting 2-3 months during the same time of year. This suggests that the conditions during the April-June 2000 season were unsuitable for musth to occur in older bulls. However, several younger, age group 3 bulls were in musth during the same season, with one (BNN1019-Lpaus) spending more than one month in musth. Conditions were more favourable during the following two seasons, with oestrus females expected to occur throughout the period between December 2000 and June 2001. However, during the period with few oestrus females between the two main seasons, no age group 4 bulls were observed in musth.

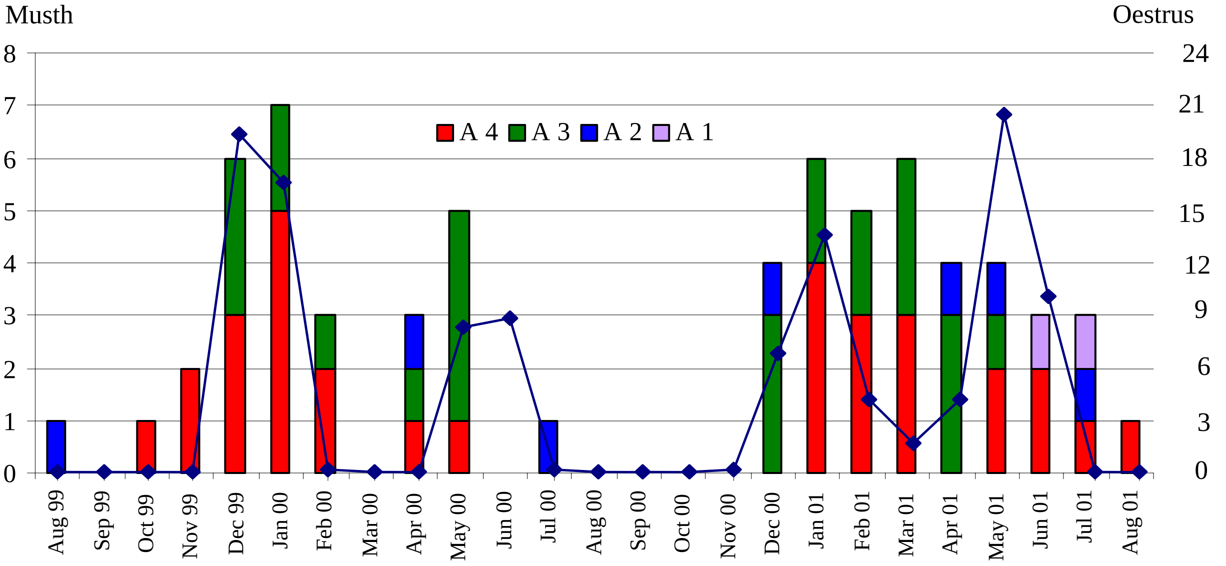


Figure 4.2.2.1 Number of different musth bulls observed per month in the four age groups between August 1999 and Aug 2001. (A1=15-25y; A2=25-30y; A3=30-35y; A4=35+y). Number of different bulls=29

4.3 Spatio-temporal distribution of bulls

In order to see if the occurrence of musth and sexually active non-musth could be linked more directly to the space/time specific density of oestrus females, the observations on bulls were overlaid on the spatio-temporal distribution of oestrus females obtained in Chapter 3. Only the area between distance 30 to 64 km (from the count of wells) was included, since areas outside were covered by the background data collection at a more infrequent rate. Furthermore, the relative density of bulls in time/space regions of different oestrus densities was calculated. This was done by calculating the number of bull observations within a time/space region lying within a given oestrus density interval (intervals between 0; 0-0.5; 0.5-1; 1-2; 2-3; 3-4; 4<) divided by the total number of observations and by the size of the region (see equation 4.3.1). The relative density (dividing by total number of observations of bulls in each sexual state) was only used in order for an easier comparison between the sexual states and age groups due to varying number of total observations.

Eq. 4.3.1

$$\text{Relative density of bulls}_{\text{state x y}} \text{ in interval i} = \frac{\sum \text{obs}_{\text{state xy}} \text{ in T/S density interval i } / \sum \text{obs}_{\text{state xy}}}{\text{\# of S/T areas within interval i}}$$

T/S area= Time/ Space area, a 500m*1 month area where the oestrus density was calculated (total number of T/S areas = 68 (34 km) * 24 (24 month) =1632)

i = Oestrus density interval. Values of i = (0);(0-0.5);(0.5-1);(1-2); (2-3); (3-4) (4<)

State xy = Sexual state of bull, either IA,SA or Musth in age group y

The correlation between the relative density of bulls in the different intervals and oestrus densities will reflect whether bulls in a particular state avoids areas with oestrus females (negative), are indifferent (constant) or attracted (positive). If positive, a linear correlation would indicate a fixed bull/female ratio, whereas a non-linear increasing relation would indicate an over-dispersal of bulls towards areas of high female density. Any positive correlation can either be due to an attraction of bulls to oestrus females or an attraction to some common resource. A comparison of the shape of the relation between the three sexual states would indicate if the response differs between them. In figure 4.3.1 A-D the distribution of inactive, sexually active non-musth and musth bulls in the four age groups are shown together with the predicted density of oestrus females as well as the correlation between the relative density of bulls and density of oestrus females.

The density of both inactive and active non-musth bulls in age group one is positive correlated with the density of oestrus females indicating that the young bulls tends to aggregate around females regardless of sexual state, whereas inactive bulls in age group 2-4 are only slightly positive affected by the density of oestrus females. In the older age groups, a positive, increasing non-linear correlation exists between the relative density of sexually active musth and non-musth bulls and density of oestrus females except active non-musth bulls in age group four. Generally, few of these bulls were active without being in musth and did not seem to be strongly affected by oestrus densities.

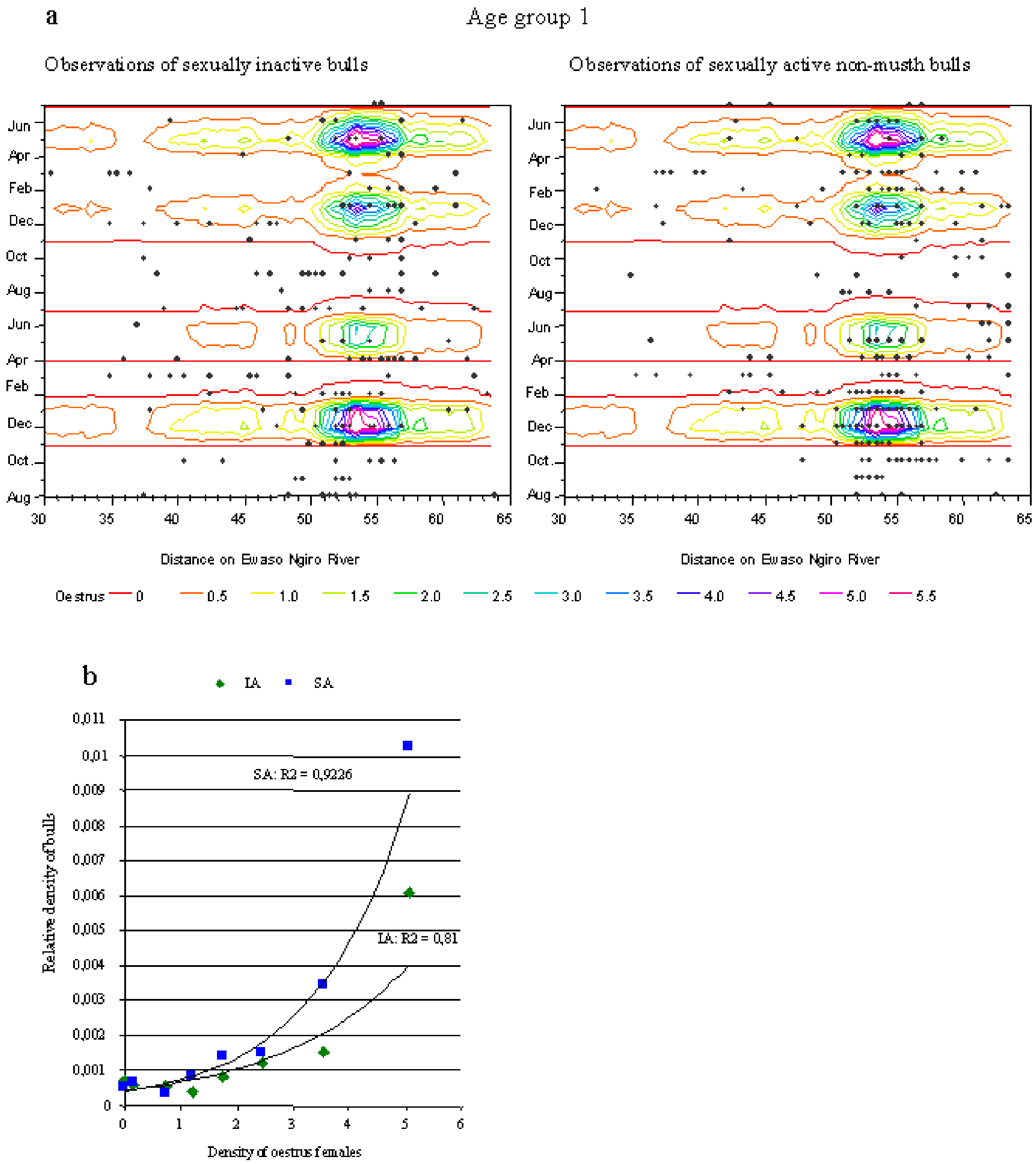


Figure 4.3.1 A: a) Spacio/temporal distribution of observations on sexually inactive and active non-musth bulls in age group one and density of oestrus females, shown as isoclines b)Relative density of bull observations as a function of oestrus density. (number of observations = 604)

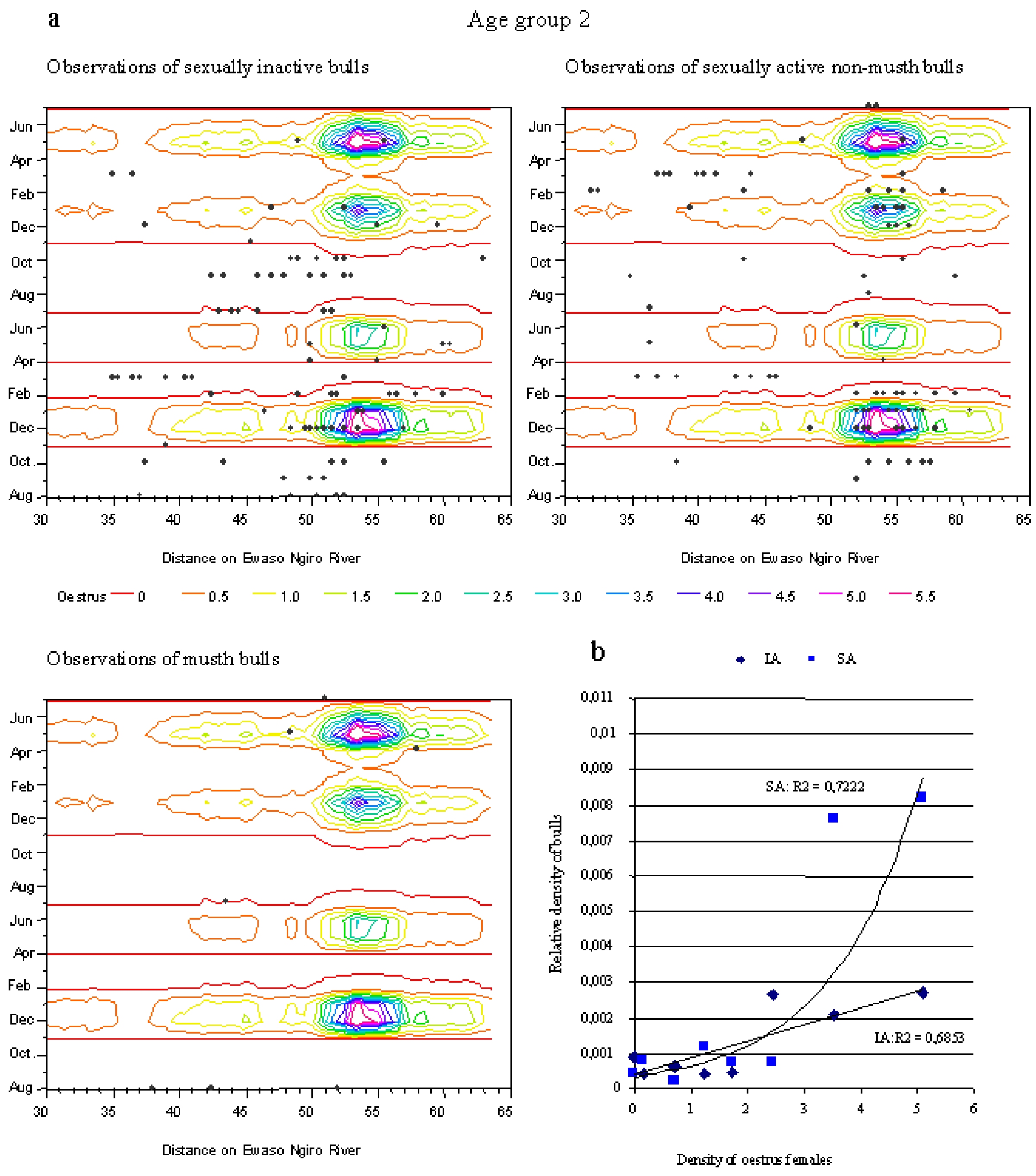
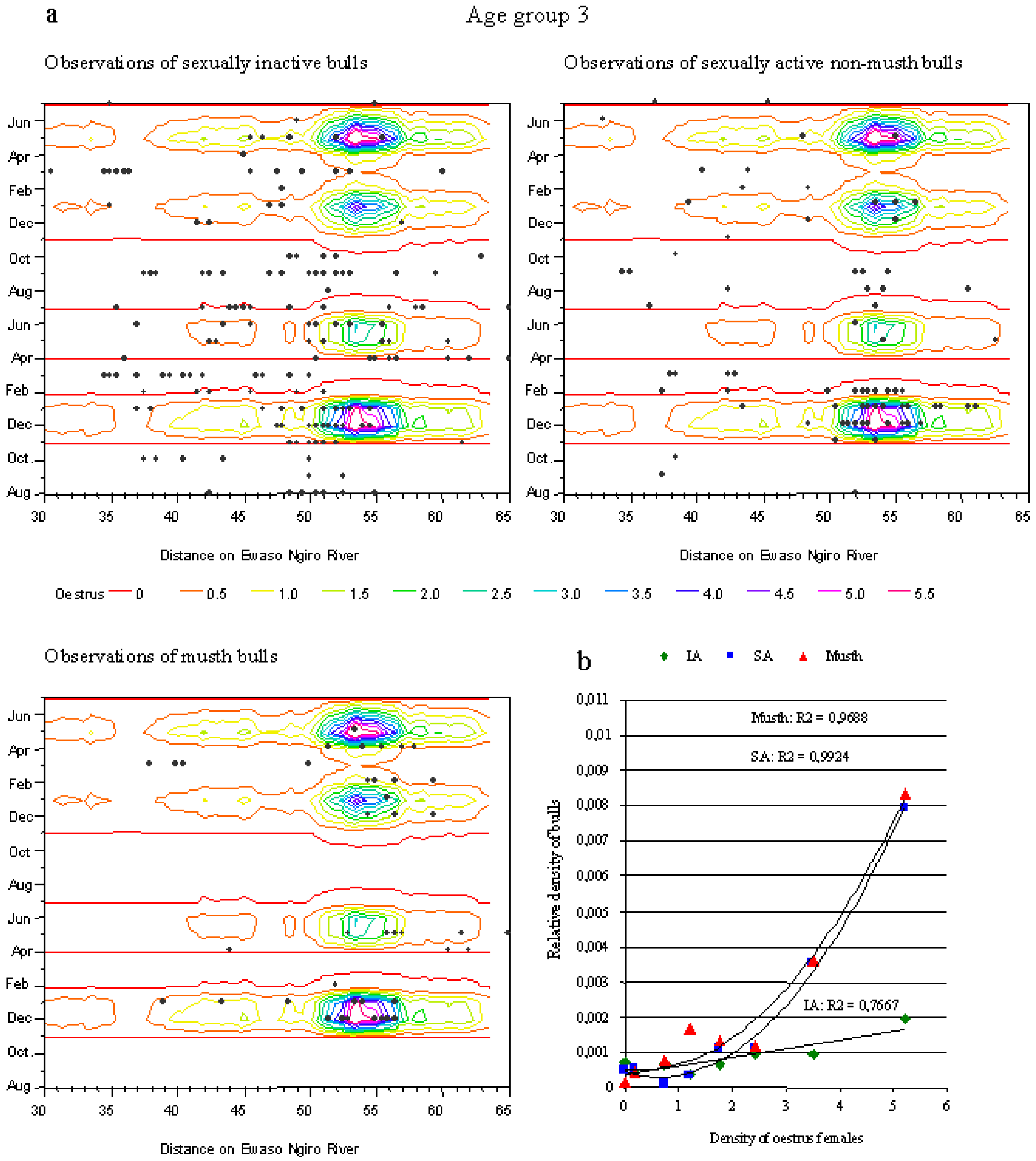


Figure 4.3.1 B: a) Spacio/temporal distribution of observations on sexually inactive, active non-musth and musth bulls in age group two and density of oestrus females, shown as isoclines b)Relative density of bull observations as a function of oestrus density. (number of observations = 235)



a

Age group 3

Observations of sexually inactive bulls

Observations of sexually active non-musth bulls

Observations of musth bulls

b

Figure 4.3.1 C: a) Spacio/temporal distribution of observations on sexually inactive, active non-musth and musth bulls in age group three and density of oestrus females, shown as isoclines b)Relative density of bull observations as a function of oestrus density. (number of observations = 408)

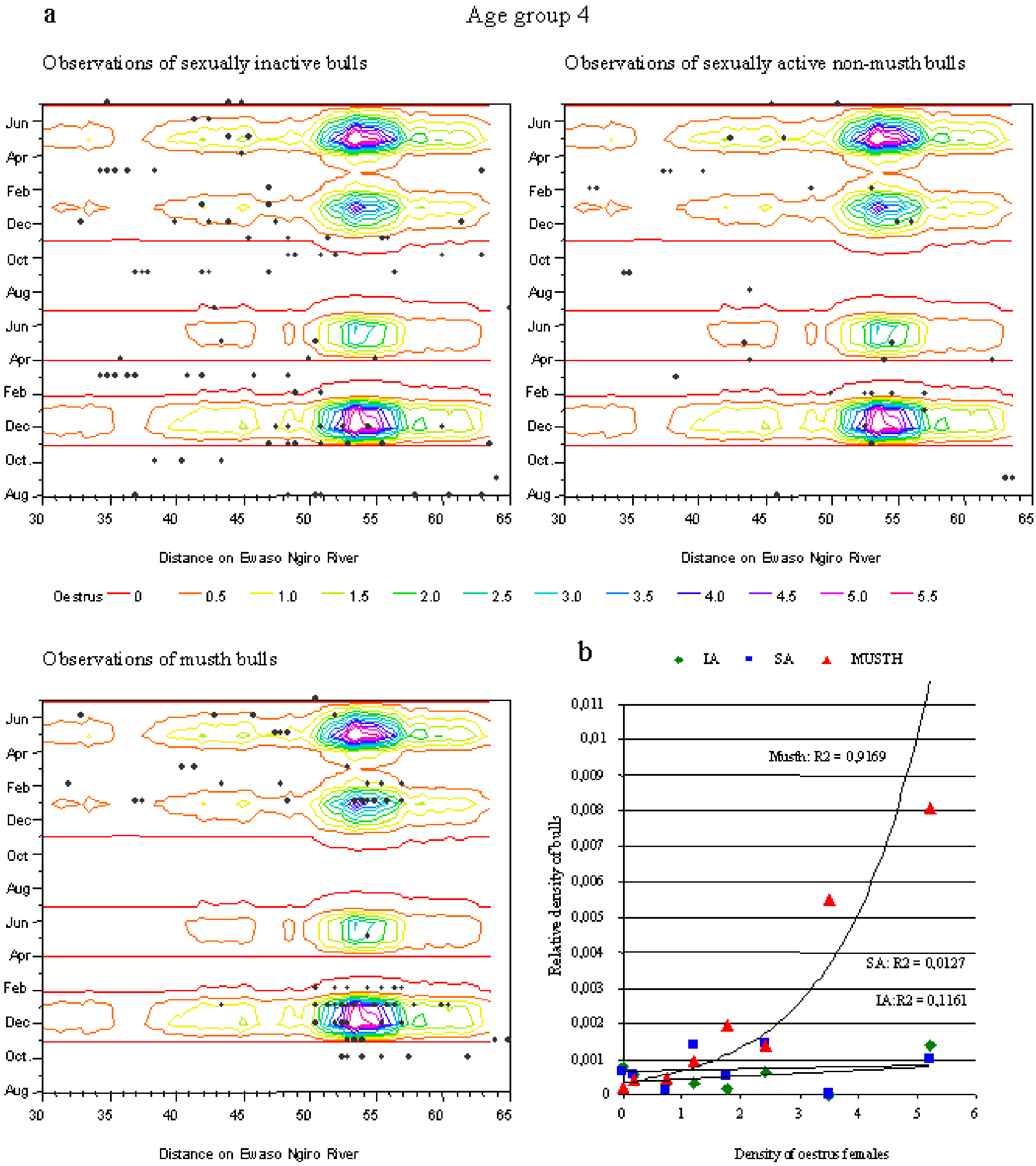


Figure 4.3.1 D: a) Spacio/temporal distribution of observations on sexually inactive, active non-musth and musth bulls in age group four and density of oestrus females, shown as isoclines b) Relative density of bull observations as a function of oestrus density. (number of observations = 260)

4.4 Distribution of individual bulls

The spacing of individual sexually active bulls depending on rank and area quality requires detailed knowledge of the rank and ranging of all active bulls within a given area and period as well as area quality in terms of oestrus female density. This combined information is difficult to obtain, unless all bulls are collared with radio or GPS collars. During the period from mid January to end February 2000, five bulls above 25 years were seen sexually active within the study area. Of these five bulls, four were GPS collared and the fifth was seen on a regular basis (every 2-3 days). Unfortunately, one collar was giving a high rate of fix failures but recorded a minimum of one position per day. All five bulls were well known individuals and their ranking well established. Furthermore, the period coincided with the count of wells and dung in the Ewaso Ngiro River (Chapter 2) hereby giving an accurate estimate of the spatial density of females.

In figure 4.4.1, the minimum convex polygon ranges are shown for the five bulls. The highest-ranking bull BNN1011 (Mandela est. 35 years, un-collared) was in musth but only ranging over a short 10 km section of the river corresponding to the area with the highest female density. Since he was not collared, he could have been outside this area. He was however seen minimum every second or third day, making it unlikely for him to have ventured far away from the area he was observed in. Secondly, if he had spend a significant time in another area he would most likely have been observed in that area. None of the lower ranking bulls was in musth. The second and third ranking bulls BNN1026 (Winston, est. 31 years) and BNN1027 (Esidai, est. 33 years) are very closely ranked. Esidai is slightly older and bigger, however he backed away from Winston on two occasions and was estimated to be the lowest ranking of the two during that particular period. Winston moved over a much larger 40-km long section of the river to the west of the area used by Mandela. This area was less favourable with medium to low densities of females. Thus, Winston was second in rank at the time but first in rank in the area in which he was ranging. Esidai completely overlapped with Mandela, but covered a slightly larger section of the river. He was thus third in rank at the time but second in rank in the area with the highest densities of females. The fourth ranking bull BNN1019 (Lpaus, est. 31 years) was overlapping with Mandela and Esidai but stayed mainly 5-10 km south of the river in some of the areas utilised by the females for foraging. The last, fifth ranking bull BNN1039 (Ansel, est 25 years) overlapped with most of the other ranges, but mainly had a range similar to Winston. After the end of February, the four bulls became sexually inactive and subsequently shifted range. They were now all overlapping and often seen in the same bull herd just west of the reserve.

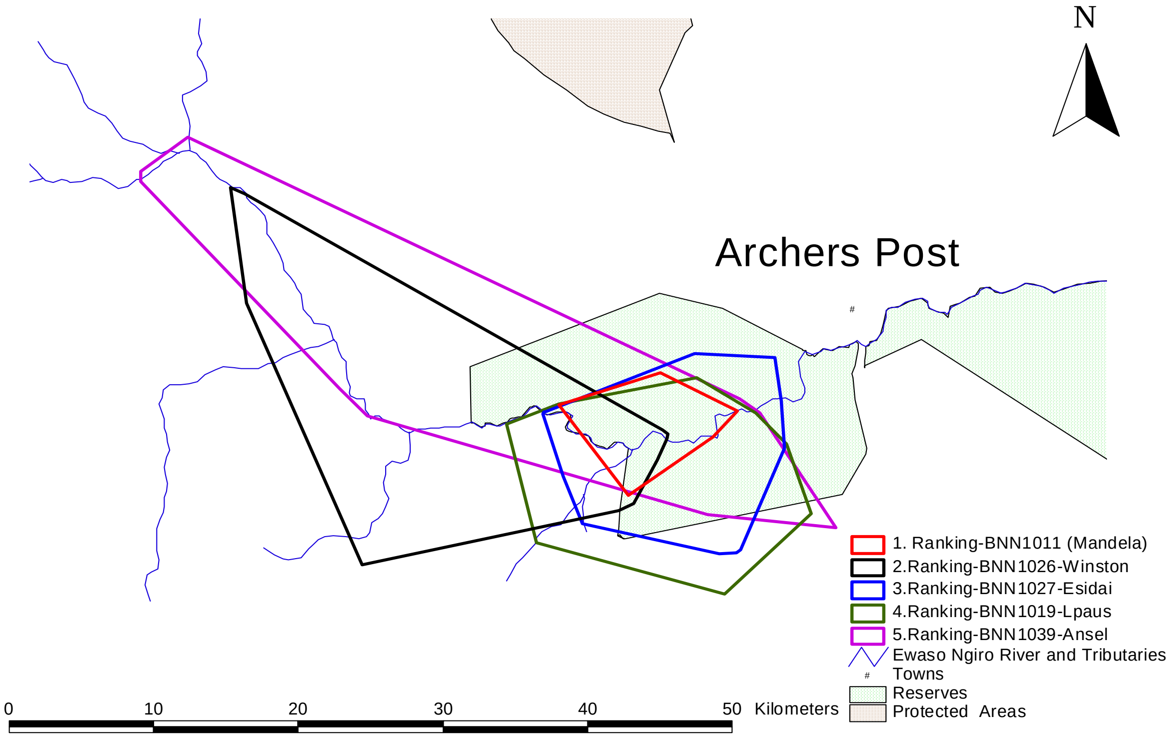


Figure 4.4.1 Minimum convex polygon ranges of the five highest ranking bulls within the study area between mid January and end February 2000. Highest-ranking bull, BNN1011-Mandela in musth, rest sexually active non-musth. (BNN1011 based on 21 observations not separated by more than 3 days, BNN1026, BNN1027 and BNN1039 based on 1 hour recordings, BNN1019 based on minimum one recording per day)

4.5 Discussion

The bulls start having distinct periods of sexual activity and inactivity around the age of 25. The first sporadic musth events occur around the same time. However, no bulls were observed in prolonged periods of musth before around the age of 30. This is comparable to observations from the Amboseli National Park.

The almost complete lack of older age group four musth bulls during the April- June season 2000 and again during April 2001 (Fig.4.2.1) indicates that these bulls tend not to come into musth during periods with low to medium numbers of oestrus females. This can have three explanations: 1) The oldest bulls spend all their available resources during periods with high numbers of oestrus females and are therefore not capable of being in musth longer. 2) The resources are better invested at another time (following seasons) or, 3) The resource value, in terms of receptive females is too low to pay for a competitive musth strategy. The first seems unlikely. The older bulls expected in musth during April-June 2000 had not been in musth immediately prior to that period and most likely had the necessary resources available. Furthermore, one bull, Mungu seemed to have the intention of coming into musth but dropped out of musth again after only one week. Again, between the December-February and May-June season 2001, a period occurred with no age group four bulls in musth. Several large bulls, that had not been in musth for over a year were in the general area, and the bulls dropping out of musth in March did not appear to be in particular bad condition, making it likely that they could have continued for another month. This indicates that the older age group 4 bulls did not come in musth due to extrinsic rather than intrinsic reasons. During the same periods of time, younger age group two and three bulls were observed in musth indicating that the resource value was adequate for them to engage in a competitive strategy. Whether the older bulls refrained from musth due to better payoff from invested resources at a later stage or the level of receptive females were to low to pay for a musth strategy in general, cannot easily be separated. However, both hypothesis points towards a threshold value in the density of receptive females needed before a competitive musth strategy is profitable. Since younger bulls did come into musth, this threshold may be age dependent.

When looking at the response of the bulls to the time/space specific resource value, a general over-dispersal of sexual active musth and non-musth bulls was seen towards areas with high densities of oestrus females (section 4.3). This is unlikely to be caused by a response to a common resource since the inactive bulls responded much less than sexually active bulls (except age group one). The comparable responds of active and inactive bulls in age group one is in accordance with the general lack of distinct sexual periods described in section 4.1 and is probably caused by these young bulls generally staying within female areas.

Sexually active age group four bulls did not seem to respond to areas of high oestrus densities. However, few bulls in this age group were observed in this state and some of the bulls identified as being in sexual active non-musth are most likely bulls having short (1-2 week) periods of pre- and post-musth, coinciding with the beginning and end of the oestrus seasons.

An increase exist in the bull/oestrus ratio towards areas of high oestrus densities, this is seen among all musth bulls and among sexually active non-musth bulls in age group two and three. This is contrary to what would be expected under an ideal free stability of the bulls with a fixed bull/female ratio, but in accordance with the existence of a threshold in female density mentioned above. However, a similar degree of over dispersal was seen both among sexual active musth and non-musth bulls and between age groups indicating that it is not affected by age or state.

The example on spatial distribution of individual bulls in section 4.4 is somewhat descriptive. Furthermore, the difference in payoff between being first, second or third ranking bull in an area is unknown. However, it never-the-less shows one incident where the bulls seems to position themselves at an optimal place depending on a combination of both area specific resource value and own rank.

The larger bulls seem to postpone their reproductive investment if the resource value is below a certain threshold. This, combined with the example of the spatial distribution of sexually active bulls (musth and non-musth) depending on both area specific resource value and number and rank of competitors (section 4.4) suggest, that the individual bulls are capable of tuning their reproductive strategies according to the local set of conditions. This tuning includes both position in space, level of investment (musth/non-musth) and the trade off between current and future reproduction. This capability of responding to local sets of conditions could also explain the highly variable patterns of sexual cycles and musth, especially observed among age group three bulls.

Chapter 5: Male investment in reproductive activities

5.1 Introduction

In order to answer the questions in the introduction, relating to objective three and four regarding the level of investment between sexually active non-musth and musth bulls, the amount of investment in reproduction had to be measured. Measuring the allocation of resources to reproduction is difficult. First, it can be measured in terms of different units such as energy or time allocation. If energy is chosen, one must first know the metabolic requirements linked to different activities and then measure the increase or decrease of time spend on the various activities. Furthermore, the total amount of energy allocated is a combination of the energy spent, and the amount of energy not acquired due to reduced time spend foraging. The amount of energy not acquired depends on seasonal energy content in ”would be” forage and on which area the individual would have chosen to forage in, if not sexually active. In short, getting a realistic estimate of energy allocation is not possible. Instead, the amount of time spend on different activities can be used as an approximation. Certain limits to that approach exits, since equal time spend on different activities cannot be directly compared. However, for a comparison between different sexual states or ages one can measure the amount of time spent on the different main activities such as foraging, walking, resting, standing etc. and hereby obtain an estimate of the relative focus on foraging versus non-foraging activities.

Focal observations were carried out in order to compare the level of time allocation to different activities between inactive, sexually active non-musth and musth bulls. Furthermore, in order to compare the mate-searching strategies, the number of females encountered, the number of herd shifts and the amount of time spent in association with females were noted. In addition, four GPS collars from Save the Elephants’ tracking program were allocated to the tracking of bulls in order to obtain detailed information on changes in the daily and seasonal movements depending on the sexual state. In the following manuscript, the results on the focal observations and GPS collars are presented.

5.2 Reproductive investments by male African elephants *Loxodonta africana* (Blumenback)

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Abstract

The phenomenon of musth, occurring in sexual active male African elephants *Loxodonta africana* is associated with large investments in reproduction in terms of reduced feeding and far ranging searches for receptive females. In order to investigate if sexual active non-musth bulls (SA) have comparable levels of investments and ranging behaviour to musth bulls, focal observations of daily activity patterns were carried out on 23 bulls and combined with detailed recordings of daily movements of 3 of the bulls, using GPS radio collars. No differences were found between SA and musth bulls in the numbers of females encountered per hour or the number of shifts between female herds. Furthermore, SA bulls significantly reduced the time spend feeding compared to inactive bulls but less than musth bulls. No GPS collared bulls came into musth, although all collared bulls experienced periods of both sexual activity and inactivity. During sexually active non-musth periods, the bulls on average doubled the daily travelling distance and shifted range compared to inactive periods. Although sexually active non-musth bulls did not reduce feeding as much as musth bulls, the change in activity and ranging patterns as well as the large increase in daily travelling distance is comparable to the changes normally associated with musth. The results presented in this paper suggest that the behavioural changes regarding search intensity and time allocation to reproduction described in musth bulls may be generally associated with sexual active periods. In light of these results, musth should exclusively be viewed as a competitive strategy, signalling dominance and willingness to fight for the position as highest-ranking male but not as a mating strategy deviating in the way of searching for receptive females.

Introduction:

Male African elephants (*Loxodonta africana,* Blumenback) become sexually mature at the age of approximately 14 years (Poole 1987). When reaching the age of 20-25 years the bulls starts alternating between periods of sexual activity and inactivity (Poole, Kasman et al. 1984). In sexually inactive periods, the bulls mainly engage in feeding and are either associating with other bulls, or alone (Moss and Poole 1983; Poole 1994). When becoming sexually active, the bulls start associating with females and testing females for oestrus (Moss and Poole 1983). During sexually active periods, bulls may or may not enter into a state known as musth (Poole and Moss 1981; Poole 1987). Musth is characterised by an increased level of aggression and continuous dribbling of urine in combination with streaming from the temporal glands. Furthermore, musth bulls walk with a distinct “musth walk” and often have a strong odour (Poole 1987; Poole 1989). These physical and behavioural characteristics are conspicuous and make it easy to recognise bulls in musth. Musth is associated with an increase in dominance rank (Poole 1987; Poole 1989) and has been likened to the rutting behaviour of ungulates (Eisenberg, McKay et al. 1971). The occurrence and duration of musth is positively correlated with age, with the average age of first musth being 29 years in Amboseli National Park, Kenya (Poole 1987). During periods of musth, the bulls spend significantly less time on foraging and resting and more time on walking than when not in musth (Poole 1987; Poole 1989). Musth bulls are also known to shift range compared to the range when not in musth (Moss and Poole 1983; Hall-Martin 1987; Douglas-Hamilton 1998). Musth bulls are more successful in guarding and mating oestrus females and are believed to have a higher reproductive success than sexual active non-musth bulls (SA bulls) (Hall-Martin 1987; Poole 1987; Poole 1989).

No visible physical differences exist between sexually inactive and sexually active non-musth bulls. Recording of bull associations and behaviour is necessary in order to identify periods of sexual activity. The amount of resources allocated to reproduction by sexually active non-musth bulls are not well documented. Since musth behaviour was identified in the African elephant (Poole and Moss 1981) most studies on male reproductive behaviour have been dealing with musth bulls and often, sexual inactive and sexual active non-musth bulls have not been clearly differentiated or sexual activity has been equalled to musth (Poole 1989).

Receptive females occur year around in most populations, although peak numbers of receptive females occur in and immediately following the rainy seasons (Laws, Parker et al. 1975; Hall-Martin 1987). Since SA bulls do not stay sexually active year around, but have prolonged periods of inactivity this can be viewed as indirect evidence for an energetic constrain on the duration of sexual active non-musth period. Barnes described a reduction of feeding and increased walking among sexual active bulls that did not appear to be in musth, in

Ruaha National Park Tanzania (Barnes 1982), which also indicate some level of investment among SA bulls.

During sexually inactive periods, bulls are expected to maximise the intake of surplus energy. This extra energy can either 1.) Be used on present reproductive effort during sexually active periods or 2.) Be allocated to growth (Investment in future reproduction). Since individual bulls are expected to maximise the sum of current and expected future reproduction and the investment of resources in any of the two is complementary, the pay-off from current investments is expected to outweigh (or equal) the reduction in future reproduction. Apart from a reduction in the amount of energy available for growth, a reduction in future reproduction can also be caused by increased mortality/injuries if risks are associated with reproduction.

The high level of aggression and increased likelihood of engaging in physical fights seen in musth bulls (Hall-Martin 1987; Poole 1989) indicates that musth can be viewed as a competitive strategy compared to sexually active non-musth. Therefore, the cost in terms of increased mortality due to fights, are most likely only paid by musth bulls. In a system with post mature growth and large size-dependent competition for mates, a competitive strategy is not expected to pay before late in life (Whitehead 1994) Younger bulls are also rarely seen engaging in the competitive musth strategy, hereby avoiding to pay the costs associated with fighting.

Although SA bulls probably obtain a generally lower reproductive success than musth bulls, due to their lower rank and non-competitive strategy, this does not necessarily imply that they should invest less or search differently for receptive females than musth bulls. Any difference in the optimal daily allocation of resources to reproduction between the two sexual states will depend on the shape of the relation between resource allocation and reproductive success, the trade off between current and future reproduction, and if any basic energetic cost is associated with musth.

In this paper, we compare the amount of time allocated to different activities as well as the daily travelling distance and number of females encountered, between inactive, sexual active non-musth and musth bulls in order to compare search strategy and intensity between the two sexual states.

Material and methods

Study area and population:

The study area is situated just north of the equator on longitude 37º, in and around Samburu and Buffalo Springs National Reserves, Kenya. The area consists of low-lying semi-arid rangeland along the Ewaso Ngiro River, the only permanent water source in the area.

Within the study area, ‘Save the Elephants’ has since 1997 carried out a monitoring program based on identification of individual elephants (Wittemyer 2001). At present, approximately 900 elephants consisting of 156 adult males and 216 breeding females have been seen and identified. The study population is part of the larger free ranging population in the Laikipia/Samburu area estimated to number around 3000 individual (Thouless 1996). Few unknown elephants (mainly younger bulls) have been recorded within the study area the last two years, and all adult individuals occurring regularly within the study area are believed to be known.

Focal observations

Focal observations on bulls were carried out in the study period between 21st of January and 4th of July 2000. The age of the bulls was estimated to range between 25 to 45 years using a combination of height, facial shape, and general appearance (Moss 1996). The bulls were categorised into three sexual states, Sexually inactive (IA), Sexual active non-musth (SA) and Musth. A bull was regarded as sexual inactive when alone or associating with other bulls and not showing signs of urine dribbling (UD) or temporal gland secretion (TGS). When a bull was associating with females during the focal observation period without having a combination of UD and TGS and without UD having been present 10 days before or after the time of observation, it was regarded as sexual active non-musth. A bull was regarded as in musth, when it regardless of associations was dribbling urine at any rate in combination with swollen temporal glands and TGS.

On observation days, a bull was located and followed for 4-8 hours depending on when it was located. During focal observations ‘on the minute’ observations on activity was done every 15 min. as well as the place of the focal individual in the group. On the hour positions were taken using a handheld GPS. Furthermore, all adult individuals associating with the focal individual were noted, as well as any changes like herd shifts or individuals joining the focal individual were recorded.

GPS Radio-collars

Four bulls around 30 years of age were immobilised and collared during January 2000 using GPS collars from Lotek ltd. Canada (For collar details see (Douglas-Hamilton 1998)). Two of the bulls were re-collared in January 2001 after the original collar had ceased to function. The collars were set to record positions every hour, hereby obtaining detailed information on daily distance travelled and general ranging patterns. Data was downloaded from a plane or car via a remote radio link approximately every month.

The GPS collared bulls were attempted located every 10-14 days within the study period. When located, either spot observation of associations with other individuals as well as the degree of TGS and urine dribbling was noted, or a period of focal observation was carried out.

After July 4, 2000, the collared bulls were located at a more infrequent rate due to reduced field personnel. If a collared bull associated with females on consecutive observations, not separated by more than 14 days it was regarded as sexual active within that period. If it was observed alone or associating with other males on consecutive observations, it was regarded as sexually inactive. Within sexual active periods, bulls were occasionally observed alone. These single observations were disregarded and the whole period assigned as sexual active. Despite the radio beacon in the collars, all bulls “disappeared” for periods of time. If no observations had been obtained for more than three weeks the sexual state of the bull was regarded as unknown, for that period.

Results

Daily activity patterns:

During the study period a total of 380 hours of focal observations were made on 23 different bulls distributed as 180 hours on 18 IA bulls, 100 hours on 10 musth bulls and 100 hours on 7 SA bulls. The allocation of time to the four main activities, Standing, Walking, Resting and Foraging were highly dependent on the time of day (Figure 1) but the general pattern of the daily activities did not change between the sexual states. A significant overall effect of sexual state existed on time spent walking (ANOVA, DF = 2, P = 0.0028), standing (ANOVA, DF = 2, P= 0.0099) and foraging (ANOVA, DF = 2, P= 0.023) (significant at 0.05 after sequential Bonferroni adjustment) but not on resting (ANOVA, DF = 2, P= 0.94). When comparing each state, SA bulls spend significantly less time foraging and more time standing compared to sexually inactive bulls (Table 1) but more time foraging than musth bulls (Table 1). Thus, SA bulls were intermediate between musth and inactive bulls (Fig 2).

Herd shifts and females encountered

The frequency of herd shifts was calculated as the number of times a bull left or joined a group of females divided by the observation period. The frequency of herd shifts was not significantly different between SA and musth bulls, with SA bulls and musth bulls leaving or joining a group of females at a rate of 0.33 and 0.37 shifts per hour respectively (t test: DF= 24; t=0.444; P>0.661).

The female encounter rate was calculated as the total number of different breeding females observed less than 200 meters from the focal bull during an observation period divided by the observation period. The number of different females encountered per hour was not significantly different with SA bulls and musth bulls encountering on average 2.27 and 1.65 females per hour (t-test: DF=24; t = - 1.273; P>0.215). However, SA bulls spent more time in association with females (69.5%) than musth bulls (46.4%) (t-test: DF= 24; t= - 2.241 P<0.035).

Observation periods, where the focal bull followed or guarded an oestrus female was excluded from the analysis of both herd shifts; female encounter rate and time spent in association with females. This was done, since bulls are expected to cease searching for other receptive females during the period they follow one.

GPS collars

The accuracy of the collar GPS was measured by leaving one of the collars on a fixed spot for one week. The accuracy was comparable to most handheld GPS units with all the 164 test positions lying within 170 meters of the mean position and 62 percent being between 0 - 50 meters and 32 percent between 50 – 100 meters. The GPS collars fitted on three of the four bulls operated to satisfaction with a mean percentage of fix failures being 8,0 %, 5.7% and 2.2% respectively. The majority of the fix failures coincided with the resting periods where the elephants are typically standing under a large tree or lying down. The collar on the last bull was giving 75 % fix failures the first eight weeks. Thereafter the collar flipped around leaving the GPS units pointing inwards giving almost 100 percent fix failures. In the following, data from that bull has been excluded.

Of the 24966 positions recorded after the collars were put on the elephants, 8 was deleted due to their un-likelihood of being situated between 10 and 7000 km away from the previous and following recording. The recording of positions every hour made detection of “bad fixes” lying at an unlikely distance and direction from the previous and following recording relatively easy and very few un-deleted positions are expected to be more than 200 meters from the actual position.

Sexual state and daily travelling distance

Unfortunately, the only collared bull (BNN1019) seen in musth had the failing GPS collar. One other bull, BNN1027, has previously been seen in musth. All collared bulls had both sexually active and inactive periods. The sexually active periods mainly coincided with periods expected to have peak numbers of oestrus females, during or just following the rainy seasons. The daily distance travelled was calculated as the 24-hour sum of the distance between hourly positions. In figure 3, the daily travelling distance is shown for the three bulls as well as the sexual state when known. During the periods where the sexual state were known, all bulls covered significantly longer distances per day when sexually active compared to when they where inactive (ANOVA: DF=1;F=304,8; P<0.0001) (figure 4).

Ranging patterns

The ranges were compared between the sexual states in the three collared bulls using the period between January and June 2000, where the most detailed information on associations were available. In figure 5, the ranges during periods of sexual activity and inactivity are shown for the three bulls. All three bulls spent their inactive periods in a relative small area along the Ewaso Ngiro River, just west of Samburu National Reserve. During sexually active non-musth periods, they both increased and shifted their range toward south, east and north. BNN1026, Winston was not observed during the period between April and June. However, the data retrieved from the collar showed that he had spend most of the time in an area far to the west, during the same time he covered long distances per day. During his sexually active period in January 2001, he returned to the same area and was continuously observed together with females without being in musth. The following month, when sexually inactive, he returned to the same bull-area as 8 month earlier. This suggests, that he may have been sexually active during the period in April and May 2000.

Discussion

In general, the sexually active non-musth bulls were younger (est. range 25-35 years) than musth bulls (est. range 30 - 45 years) with the youngest bulls exclusively being seen in sexual active non-musth and the oldest bulls almost exclusively in musth. This is in accordance with the observations made by Poole (Poole and Moss 1981; Poole 1987; Poole 1989). Musth and sexually non-musth can thus be viewed, as alternative mating strategies, displayed by different aged bulls, where bulls do not engage in a competitive strategy before late in life.

The allocation of time to foraging, walking and resting among sexually inactive bulls and the reduction in foraging and increased walking among musth bulls observed in this study is comparable to the levels reported from Amboseli National Reserve. (Poole 1989) The reduction in foraging and increase in walking seen among sexually active non-musth bulls were intermediate compared to musth and inactive bulls. However, a possible confounding effect of age may be present. The continued post-mature growth in elephants, probably resulting from a strong size dependent male-male competition is levelling off around 30-35 years and place a higher energetic demand on younger bulls. Consequently, older bulls may be capable of reducing their daily energy intake more than younger bulls. Therefore, the higher reduction in foraging among musth bulls could partly be an effect of age and not musth. With the current data set, it was not possible to separate the effect of age and musth.

The 20 % reduction in foraging by SA bulls combined with the large increase in daily travelling distance seen among the collared bulls indicates a significant investment into reproduction. Furthermore, the comparable level of herd shifts and number of females encountered between SA and musth bulls, as well as the general shift in range, previously reported in musth bulls, indicates a somewhat similar search strategy between the two sexual states. This indicates, that the main difference in the mating strategy between younger non-competitive and older competitive bulls is limited to the cost the individuals are willing to pay to obtain the position as highest-ranking male, whereas the allocation of resources to searching and search tactics are comparable. This level of investment seems unlikely unless some reproductive success is obtained by these bulls

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Figure legends

Figure 1:
Allocation of time to the four main activities, Walking, Resting Standing and Foraging during the day between Sexually inactive (IA), Sexually active non-musth (SA) and musth bulls (Observation hours: IA, N=180; SA N=100; Musth N= 100).

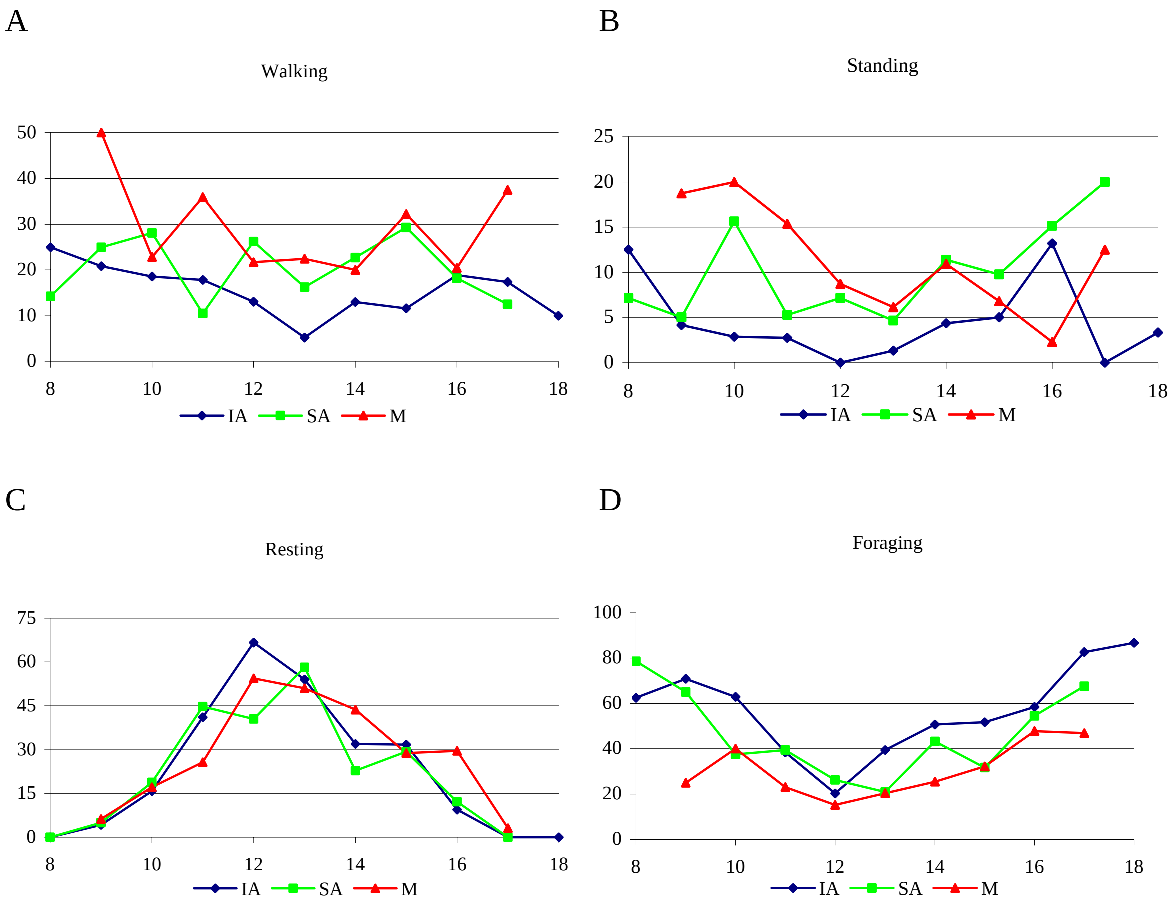
Figure 2:
Total daily allocation of time to the four main activities, Walking, Standing Resting and Foraging between Sexually inactive (IA), Sexually active non-musth (SA) and musth bulls, Columns not sharing a letter significantly different

Figure 3:
Daily travelling distance for the three GPS collared bulls. Red line at the base corresponds to sexual active periods and green lines to sexual inactive periods. The data gabs in Winston and Ansel corresponds to the period between collar failure and replacement.

Figure 4:
Average daily travelling distance during periods of sexual activity and inactivity for the tree collared bulls.

Figure 5:
Ranges of the three collared bulls during their active and inactive periods between January and June 2000.

Figure 1


A
Walking
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20
10
0
8
10
12
14
16
18
IA
SA
M
B
Standing
25
20
15
10
5
0
8
10
12
14
16
18
IA
SA
M
C
Resting
75
60
45
30
15
0
8
10
12
14
16
18
IA
SA
M
D
Foraging
100
80
60
40
20
0
8
10
12
14
16
18
IA
SA
M

Figure 2

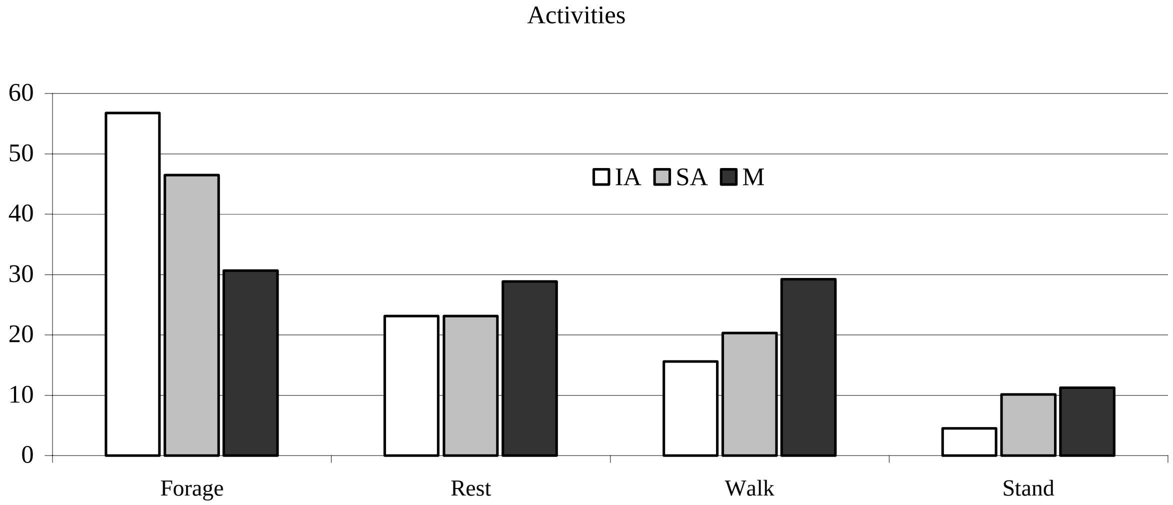


Table 1		Paired t-test
Foraging	Df.	Prob.
IA vs. SA	9	0.021
IA vs. Musth	9	0.0007
SA vs. Musth	8	0.025
Walking		
IA vs. SA	9	0.203
IA vs. Musth	9	0.0016
SA vs. Musth	8	0.0967
Standing		
IA vs. SA	9	0.0337
IA vs. Musth	9	0.0287
SA vs. Musth	8	0.769
Resting		
IA vs. SA	9	0.57
IA vs. Musth	9	0.52
SA vs. Musth	8	0.38

Figure 3

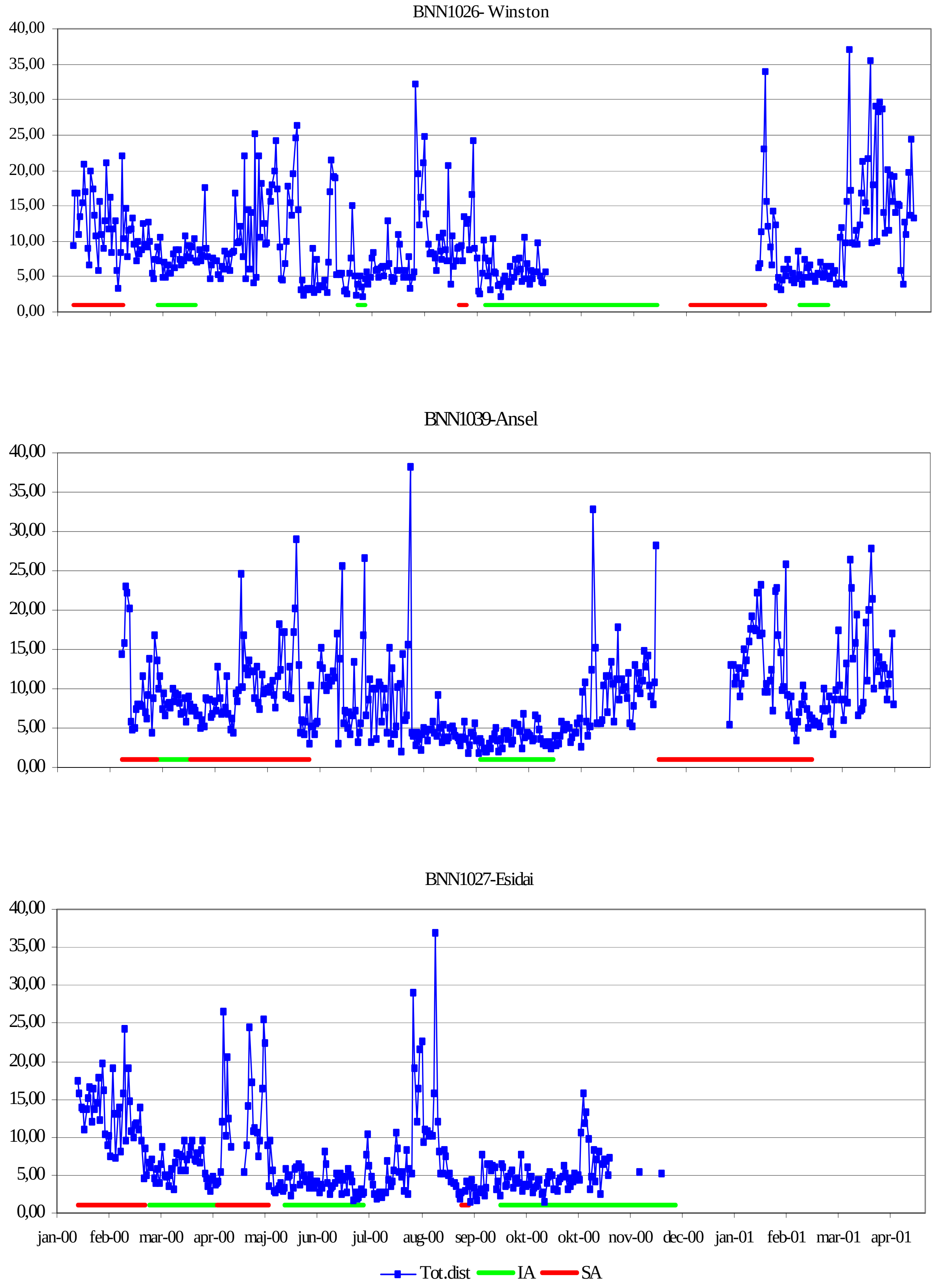

BNN1026- Winston
40,00
35,00
30,00
25,00
20,00
15,00
10,00
5,00
0,00
BNN1039-Ansel
BNN1027-Esidai
jan-00
feb-00
mar-00
apr-00
maj-00
jun-00
jul-00
aug-00
sep-00
okt-00
okt-00
nov-00
dec-00
jan-01
feb-01
mar-01
apr-01
Tot.dist
IA
SA

Figure 4

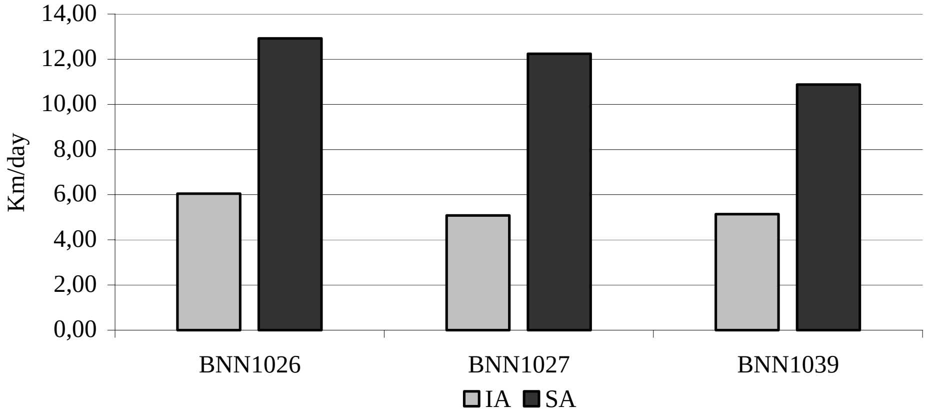

14,00
12,00
10,00
8,00
6,00
4,00
2,00
0,00
Km/day
BNN1026
BNN1027
BNN1039
IA
SA

Figure 5 A

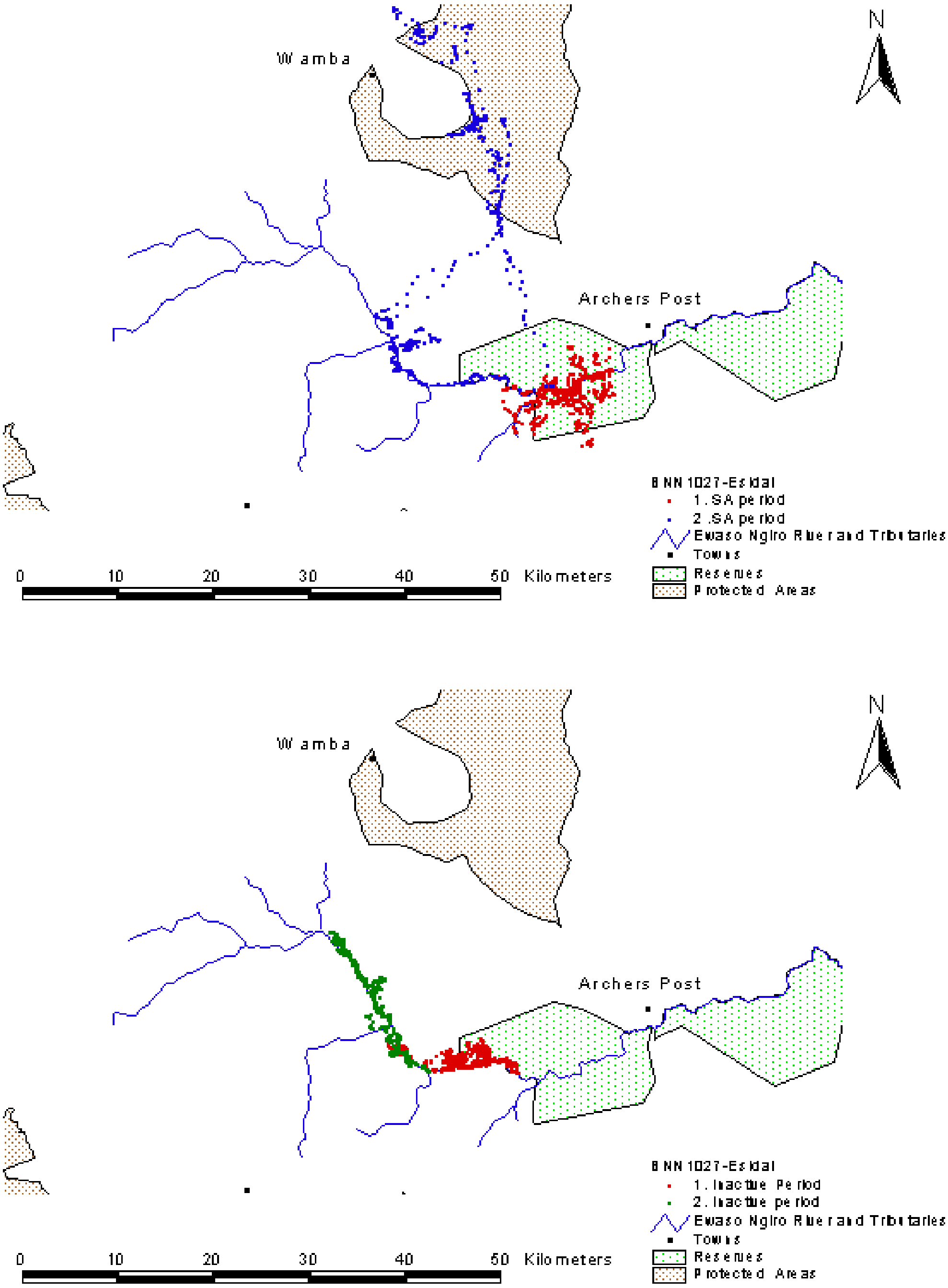

Wamba
N
Archers Post
BNN 1027-Esidai
1. SA period
2. SA period
Ewaso Ngiro River and Tributaries
Towns
Reserves
Protected Areas
0
10
20
30
40
50
Kilometers
Wamba
N
Archers Post
BNN 1027-Esidai
1. Inactive Period
2. Inactive period
Ewaso Ngiro River and Tributaries
Towns
Reserves
Protected Areas
0
10
20
30
40
50
Kilometers

Figure 5 B

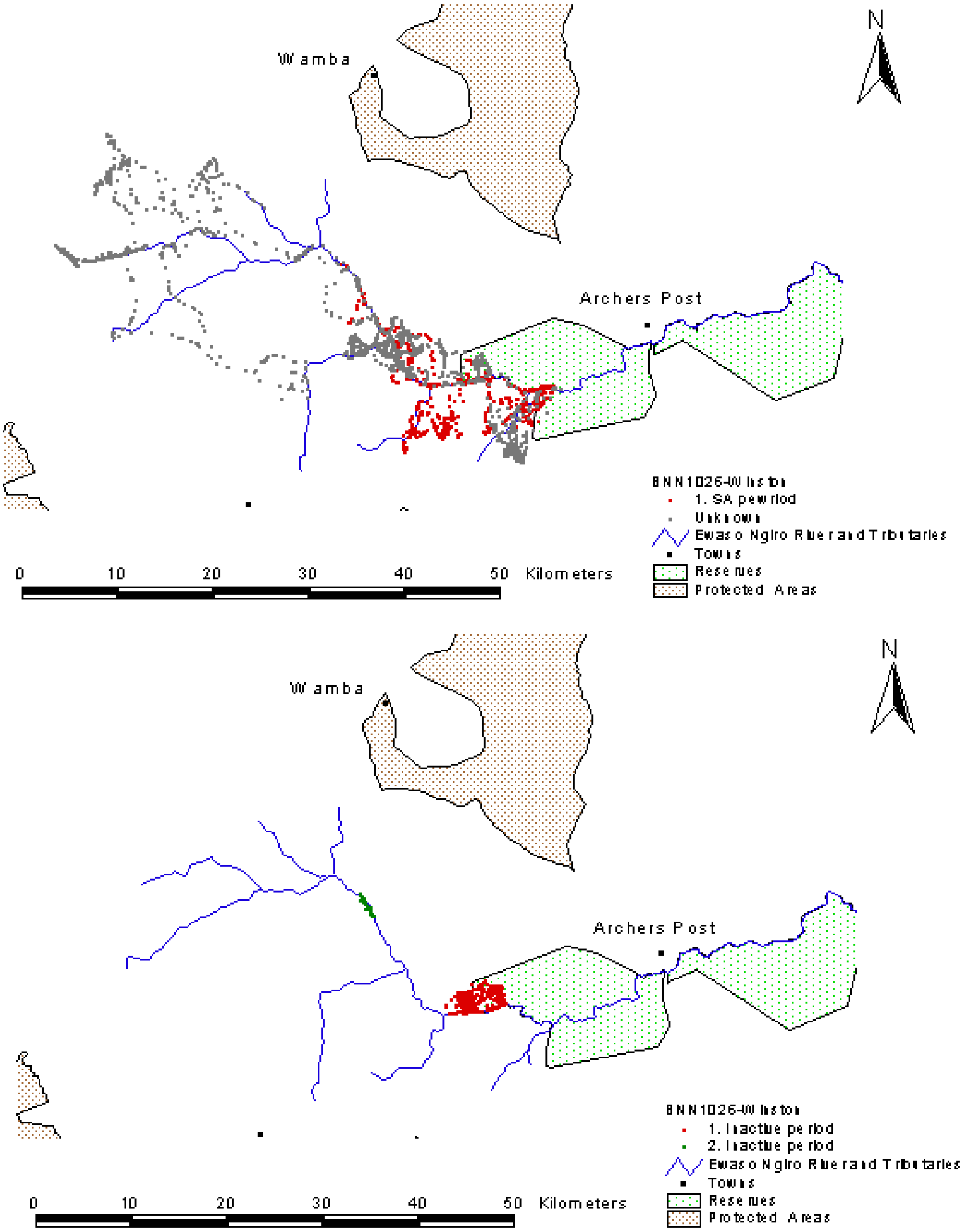
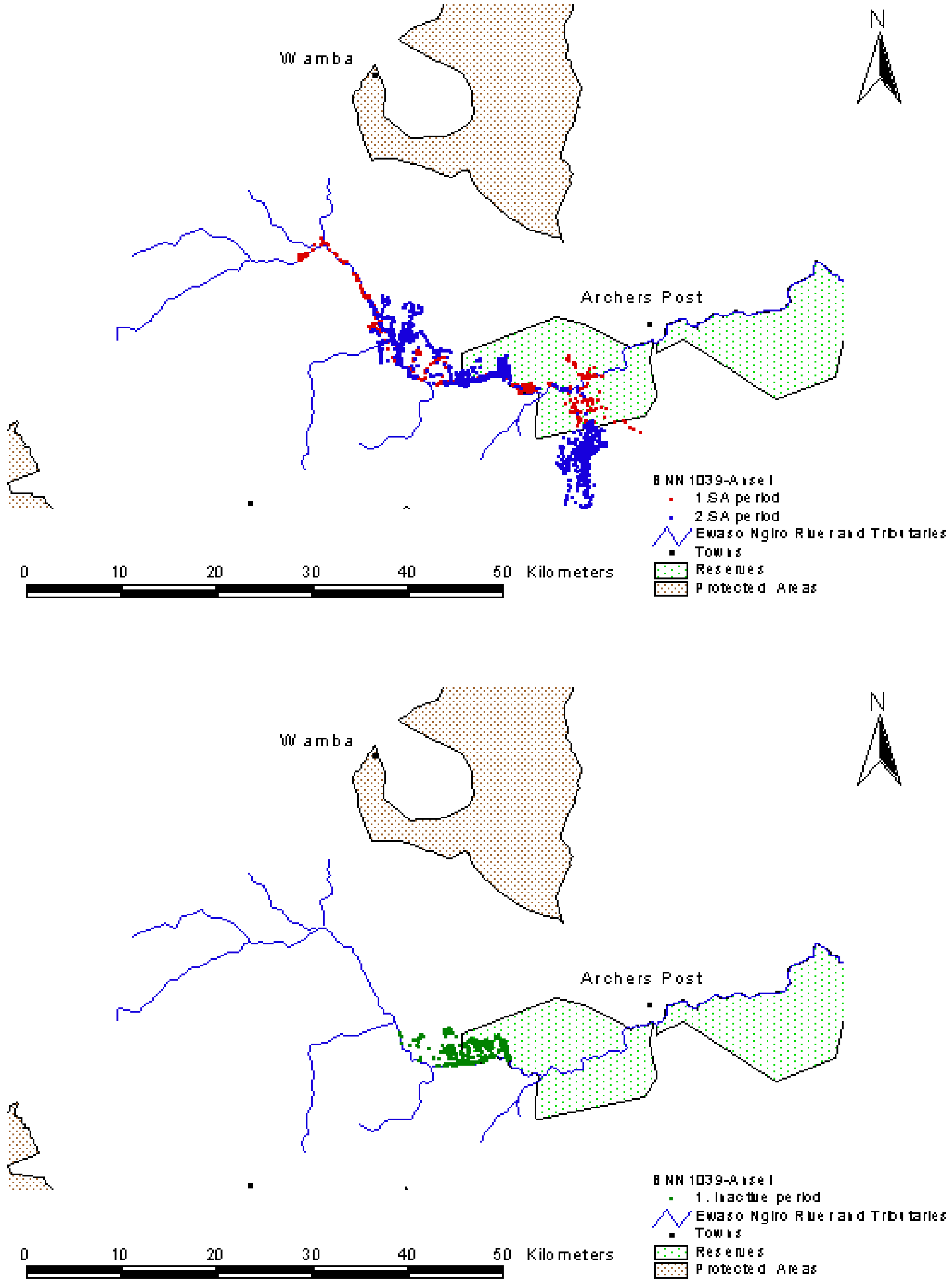

Wamba
Archers Post
N
BNN1026-W history
1. SA period
Unknown
Ewaso Ngiro River and Tributaries
Towns
Reserves
Protected Areas
0
10
20
30
40
50
Kilometers
Wamba
Archers Post
N
BNN1026-W history
1. Inactive period
2. Inactive period
Ewaso Ngiro River and Tributaries
Towns
Reserves
Protected Areas
0
10
20
30
40
50
Kilometers

Figure 5 C


Wamba
N
Archers Post
BNN 1039-Ansel
1 SA period
2 SA period
Ewaso Ngiro River and Tributaries
Towns
Reserves
Protected Areas
0
10
20
30
40
50
Kilometers
Wamba
N
Archers Post
BNN 1039-Ansel
1. Inactive period
Ewaso Ngiro River and Tributaries
Towns
Reserves
Protected Areas
0
10
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Kilometers

Chapter 6: Implications for conservation

6.1 Introduction

Often, information collected by either wildlife management or scientists have relevance for the other part. Unfortunately, a lot of that information is often buried “in the drawer” of one part, inaccessible for the other. Data useful for applied conservation were likely to emerge from the general data collection. Although conservation and management related issues are not the main focus of this thesis, questions relevant for local wildlife management were included in the general objectives.

Information on the relative area use and possible travel corridors between areas of importance is needed to optimise decisions on expansions or reductions in areas with protected or reserve status or in order to make decisions on changes in future land use that will minimise conflicts between the elephant population and local communities. As mentioned in the introduction, many of the questions relating to management and conservation are key questions for Save the Elephants’ ongoing research program in Samburu. The following sections are based on a combinations of the data made available by Save the Elephants and data already presented in the chapters 2-5 as well as an aerial count of wells in the Ewaso Ngiro River further to the west of the area described in chapter 2. Furthermore, additional GPS tracking data on females, collected by Dr. Iain Douglas-Hamilton’s tracking project has kindly been made available and used for identification of some of the travel corridors.

6.2 Area use and travel corridors

The areas far outside the two national reserves were not covered in a regular and equal manner. Therefore, observations of elephants in these areas could not be used directly to evaluate the importance of these areas. By combining information on the movements of the collared elephants, the count of wells in the Ewaso Ngiro River (chapter 2), on-ground observation of heavily used elephant trails as well as the direction from which elephants arrived to the reserve, some information on travel corridors and the importance of different areas could however, be obtained.

Both the count of wells in the river and the information from the GPS collars indicate that the area west of the two reserves is heavily used by elephants (Fig 6.2.1 area 2). The area stretches for approximately 25-30 km along the river. Especially the 10-km on each side of the river is heavily used and the riverine vegetation of *A. tortillis* and *A. eleator* shows a clear impact from elephant browsing. This impact was not quantified but the majority of the canopy reaching trees showed signs of debarking and many were dead or dying. The area approximately 50 km west of the reserves along the north south going escarpment have been used by 3 of the collared elephants and had elevated numbers of wells in the river count (Figure 6.2.1 area 1). This indicates, that the area either is used directly for foraging or is part of a North - South going corridor between the Mpala area and the Karisa Hills. The region between area 1, 2 and the Mpala area has been passed by four of the collared elephants. However, none-of the 4 elephants stayed in that area. Furthermore, all the river segments counted in that area either had no, or very low number of wells. This indicates, that the area is mainly used for travelling between other more important areas.

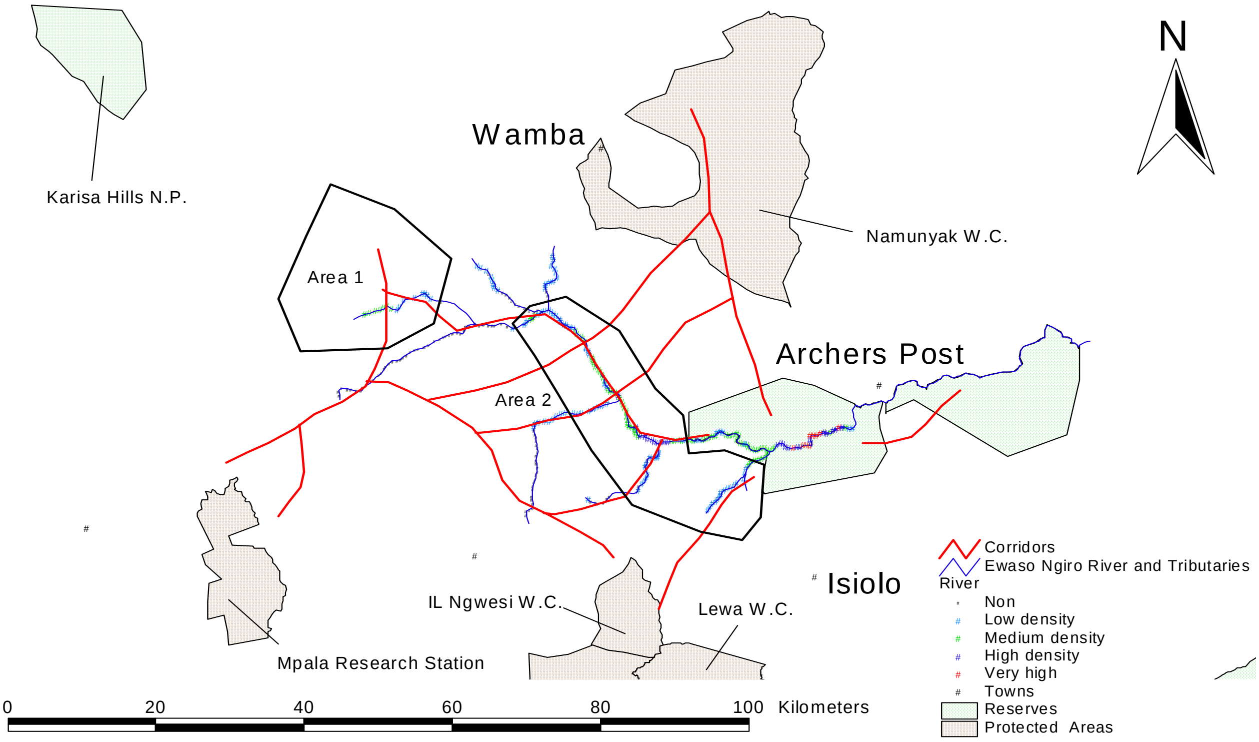

Figure 6.2.1 Map of travel corridors and areas outside protected areas highly utilised by elephants (area 1 and 2)

For the last two years, wildlife scouts from IL Ngwesi have reported large congregations of elephants within the wildlife conservancy just following the November/December rainy season. In January 2001, I visited the area in response to the reports and found a congregation of elephants in the southern part of the conservancy estimated to number around 400 individuals. After spending two days in the area, none of the elephants seen was identified as known within the study area, indicating that these elephants had arrived from elsewhere. Most likely, these elephants are from the Laikipia plateau south and west of Il Ngwesi and are recurrently migrating northeast as a response to rainfall on the low-lying areas. This corresponds both in terms of number and movements to the "Ewaso Ngiro subpopulation" described by Thouless (Thouless 1996). Later that month a similar number, probably the same group was spotted from the air between the conservancy and the Ewaso Ngiro River. This time two older known bulls were seen within the congregation (BNN 1027 Esidai, BNN1038 Roosevelt) indicating some mixing, at least of bulls between the study population and the elephants occurring further to the Southwest.

When looking at the GPS collar data in combination with on ground observations of elephant trails, several routes or corridors could be identified (Figure 6.2.1). From the Mpala area one route goes to the Northeast, branching off to the north along the escarpment towards Karisa Hills. From the branching point, it continues to the west, with two routes branching off to the Northeast towards Namunyak. Elevated numbers of droppings and wells were observed during the river count at the two points where the Northeast going corridors intersect the Ewaso Ngiro River. After the two routes branches to the Northeast, the route bends Southeast towards Il Ngwesi and Lewa. Another two routes goes from the two national reserves north towards Namunyak and south towards Il Ngwesi/ Lewa. Furthermore, one short route is going from the eastern part of Buffalo Springs N. R. to Shaba N. R. crossing the lava areas south of Archers Post.

The area from the two national reserves stretching approximately 25-km along the Ewaso Ngiro River to the west of the two reserves (area 2, figure 6.2.1) is an area of concern. This area has a high density of elephants and is at present not under any kind of protection. The sex ratio in the area is highly skewed toward bulls and the area is especially utilised by many of the older bulls. This makes the area interesting for potential poachers. Even a few incidences of poaching in this area could potentially have large impacts for the whole population, since the loss of only one or two of the bull herds would reduce the number of old bulls in the population significantly. Furthermore, two major corridors between the Mpala and Namunyak region, going from Southwest to Northeast would be cut off if the area became impassable due to either poaching, changed land use, or increased human settlements. Another area of potential concern is the area 50-km west of the reserves (area 1, fig 6.2.1). Less information has been obtained from this area. However, information from both the GPS collared individuals and the aerial river count points towards a relative high utilisation of that area by elephants. Furthermore, the area is most likely part of a north-south going corridor between the Mpala and Karisa Hills region making it important for migration between the regions used by the Laikipia/Samburu population. Several big elephant trails have been observed going east west just south of Archers Post. Furthermore, this route has been used by one of the collared elephants. This corridor may be the main route from the Samburu and Buffalo Springs National Reserves to Shaba National Reserve and maybe further east. Since this corridor is situated close to Archers Post, any town development south of the river could potentially cut this route off, or result in undesired human /elephant encounters. The creation of open “gaps” should be considered in the case of building plans in the area.

Chapter 7: General discussion

In this chapter, a combined discussion of the results presented in the previous chapters will be made and some of the implications and future research plans will be presented. The results from this study will be compared to other studies, especially from the Amboseli National Park. The size of the elephant population in and around the Amboseli National Park, Kenya is similar in size to the Samburu population (170 adult bulls and 500 cows and calves in Amboseli (Poole 1987) and 158 adult bulls and 750 cows and calves in Samburu). Furthermore, the patterns of sexual activity and musth are well known from the study carried out by Joyce Poole and the ongoing Amboseli Elephant Research Project. (Poole and Moss 1981; Moss and Poole 1983; Poole, Kasman et al. 1984; Poole 1987; Poole 1989; Poole 1989; Poole and Moss 1989; Moss 1994; Poole 1994) This makes it possible to compare results between the two areas. The rainfall patterns are similar between the two parks, with the majority of rain falling in November-December and April-May. However, Amboseli generally receives more rain (350 mm (Poole 1987)) than Samburu (200 mm, data from Archers Post weather station). The two-peak oestrus seasons between December- February and April-June observed in Samburu (Chapter 3), are in Amboseli fused into one longer period between February and July where an estimated 2/3 of the oestrus females occur. (Poole 1987; Poole 1989). The Amboseli population generally ranges over a smaller 3500-km^2 area (Moss and Poole 1983) compared to the app. 10.000-km^2 of the Samburu population (Pers. Obs. and GPS Tracking) and is even more confined during the dry season where it mainly resides within the 350 km^2 of the Amboseli National Park (Moss and Poole 1983). Hence, a reduced spatial component exists in Amboseli compared to Samburu. As a result, generally higher densities of elephants are expected in Amboseli.

7.2 Prediction of elephant distribution and number of oestrus females

The method of estimating densities of elephants described in chapter 2 is limited to dry season periods in semi-arid regions where no other water sources are available. However, many free ranging elephant populations do occur in such, often remote, areas. Since the alternative methods of either total or sample aerial counts are both time and resource consuming, aerial counts of drinking wells could prove to be a fast and cheap method to obtain rough relative estimates of the distribution of elephants in large areas. Any development of the method to estimate absolute numbers are likely to run into problems of similar nature as the ones affecting dung counts (Jachmann 1984). Furthermore, since the method is limited to semi-arid regions where direct aerial counts have a high accuracy due to the low vegetation cover, the latter should still be the preferred technique for absolute counts.

The spatial distribution of elephants obtained from the river count of wells and dung boli was used to estimate densities of oestrus females over the entire duration of the study. This could only be defended due to a relative stable number of females observed in the core study area. This stability cannot generally be assumed due to the potentially highly variable local rainfall patterns affecting the ranging patterns of the elephants. Even with the relative stable number of different females observed in the core study area during the present study, the use of a fixed spatial distribution of females is probably one of the main sources of error in the estimate of the spatio-temporal distribution of oestrus females. An investment in regular (minimum one per month) aerial counts of elephants is recommended if a more accurate estimate of the spatial distribution is needed in the future.

The accuracy of the method using seasonal rainfall to estimate number of oestrus females cannot be judged before data on the number of new born calves become available by the end of next year. However, the very high correlation found between seasonal specific rainfall and number of calves born 2 years later, as well as the ability of the method to mimic the within season distribution of oestrus events are very promising for the use of the method to predict time specific numbers of oestrus females. Rainfall records were only available from one station (Archers Post) during the present study. In order to minimise the effect of the variable rainfall, recording average rainfall from more stations covering a larger geographical area would be preferable. Within the Samburu study area additional stations for recording precipitation is in the process of being installed. Although the vast majority of females probably come into oestrus as a response to rainfall (vegetation growth) and therefore can be predicted using the described method, single females do occasionally come into oestrus “out of season” or faster than the 6 week delay used in the method. These single events are likely to affect the bulls in the local area in a way not predictable by average numbers. As an example, one female, Shel (PO2 67) lost her 6-month old calf around August 1999 and was seen in oestrus already one-two months later on October 16th. This could have triggered the earlier than expected musth in the age group 4 bull, Clint (BNN1007), who came into musth 13 days prior to the first observation of Shel in oestrus. When she was observed, Clint was guarding her and later mated her. Another female, Polycantha (ACA 4) was seen in oestrus on November 24th only 18 days after the first rain, again seen guarded by Clint but only seen successfully mated by two younger 20-25 year old bulls. Despite these unpredictable events, which will put a limit to the accuracy of any model predicting the actual number of oestrus females, this study has shown that the prediction of specific resource value both in time and space is possible. This will provide the necessary foundation for the creation of spatial, individual based models on reproductive decision-making in bull elephants.

7.3 Sexual activity in bulls

In this study, the youngest bulls observed in musth were in their early twenties. However, the musth periods in these individuals lasted only a few days and generally, the occurrence of musth was not seen in the majority of bulls before the age of 30. The medium aged bulls typically had musth periods lasting around one to two months and had prolonged sexually active non-musth periods. Bulls above the age of 35 spend most of their sexually active time in musth, with musth periods lasting up to four months, but more often lasting 2-3 months. This is comparable to the patterns and ages reported from the Amboseli study (Poole 1987; Poole 1994), and is in support of musth being a strategy displayed by older high-ranking bulls rather than among younger bulls as suggested by Hall-Martin (Hall-Martin 1987). It is also in accordance with the predictions that individuals should not engage in a competitive reproductive strategy before late in life in a system with high male-male size-dependent competition for mates (Whitehead 1994). Therefore, the focus of older bulls in musth on the peak oestrus seasons was expected and somewhat not very surprising.

In Table 7.1, the occurrence of musth during the study period is shown in summary, together with comparable data from the Amboseli National Park (Poole 1987; Poole 1989). The figures for the Samburu population are consistently lying below the figures from Amboseli.

	Samburu (2000-2001)	Mean	Amboseli (1980-1985)	Mean
Sum of different musth bulls per month per year	29; 36	32.5	51; 57; 24; 71; 58; 83	57.3
Max. number of musth bulls in a month each year	7; 6	6.5	6; 13; 6; 11; 8; 13	9.5
Number of month with musth bulls per year	9; 8	8.5	12; 11; 12; 12; 11; 12	11.7
Number of different musth bulls per year	19; 16	17.5	20; 25 (1980-81)	22.5

Table 7.3 Summary of the occurrence of musth. (Year =August-July). Data from the Amboseli National Park are shown for comparison (Poole 1987).

Furthermore, in Amboseli, 31 escalated fights have been observed in 14 years (Poole 1989). In Samburu, only 2 fights have been observed in the 4 years since the research program started; One between two age group 2 non-musth bulls when both followed an oestrus female, and one between two age group 4 musth bulls. In the latter, no other elephants were seen in the area and the fight ended after 3-4 hours of continuos threat displays, including uprooting of trees, but without actual physical contact between the contestants. However, the loosing part was observed chased for more than 4 km before the two bulls crossed a river and went out of sight. These data are sensitive to differences in the number of days spent in the field between the two projects. However, during the majority of the months between August 1999 and July 2001 two separate teams collected data in Samburu each logging on average 20 days in the field per month. This level is believed to be comparable to the effort invested in Amboseli and not capable of causing the discrepancies between the two areas seen in table 7.3.

The generally lower number of musth bulls, fewer months a year with musth bulls present and the low number of escalated fights seen in Samburu indicates that the system here is less competitive than in Amboseli. If the density of oestrus females needs to be above a certain threshold before a competitive strategy pays, the distribution of elephants over a larger area, and thus lower general densities in the Samburu population may explain this reduced competition. With an increase in space, the general density of females and thus the density of oestrus females will be lowered, hereby bringing down the total space-time area with a resource value above that threshold. Furthermore, the gain and cost of engaging in a fight should be viewed relative to what can be obtained without fighting. A system with a larger spatial component will offer a larger variety of medium to low quality areas, separated in both time and space. This will make a bull more prone to avoid the cost of a fight and settle with a lower gain but without paying the cost of fighting. Secondly, simply by being larger, such a system will have room for more bulls occurring in non-overlapping areas.

A larger variety of low, medium and high quality areas in both time and space could also explain the variation in strategies among younger medium ranking bulls. In this category a number of options are possible, ranging from musth at times or in areas with low to medium density of receptive females or non-musth in high density periods. Almost all possible combinations of musth/non-musth and one or two sexually active periods per year were observed among bulls between 25 to 35 years. Some bulls of almost similar size had vastly different strategies e.g. BNN1042 Armstrong (aged 29) come steadily into musth once a year for a month around July/August whereas BNN1026 Winston (aged 31) just as steadily seems to have two periods of sexually active non-musth per year during peak oestrus season. This indicates that the payoffs, between the different strategies in medium aged bulls, are probably close and that musth is not always optimal, although available as an option in some areas and at certain times.

Observations from Amboseli, reported by Poole, suggests that size and thus fighting ability is not exclusively determining musth:

“Relative fighting ability is not a satisfactory explanation of musth since, in Amboseli, smaller musth bulls were able to dominate larger, normally higher ranking non-musth bulls” (Poole 1989).

Instead, Poole suggested that differences in the time specific resource value between individual bulls could explain the observations of younger musth bulls dominating larger non-musth bulls:

"The ability of small musth bulls to dominate larger non-musth males may occur when the time specific value placed on winning by the smaller male is great enough and the value placed on winning by the larger male is small enough to override the difference in fighting ability" (Poole 1989).

In this study, evidence also indicates, that larger bulls under certain conditions refrain from musth at the same time where younger bulls do engage in this strategy. A lack of older musth bulls was observed during certain periods with medium to low densities of oestrus females (section 4.2). Especially the April-June season 2000 is interesting since this period during and just following a rainy season was one of the two expected yearly periods with peak numbers of receptive females, normally focused on by the largest bulls. During this specific period the below average rainfall, probably resulted in few females coming in oestrus. Some of the older bulls normally have periods of musth at that time of year but refrained from it during that season hereby missing an entire season. This indicates that musth may not pay for the older bulls during sub-optimal periods and could be due to a threshold in the density of oestrus females where below either the combined cost of signalling musth plus the cost associated with fighting outweighs the payoff, or a higher payoff can be obtained from that investment at a later stage.

In section 4.3, the occurrence of bulls was compared to the distribution of oestrus females in both time and space. A general over dispersal of both sexual active musth and non-musth bulls was seen towards areas with high oestrus densities. Since the accuracy of the estimated spatiotemporal distribution of oestrus females is unknown, the interpretation of these results should be done with some caution. However, a lower ratio seems to exist between sexually active bulls and oestrus females at places with a low density of oestrus females compared to places with high densities. In the case of musth bulls this also points towards a threshold density of oestrus females, however the same effect is seen among sexually active non-musth bulls. In places with high numbers of oestrus females the chance of several females being in oestrus at the same time is higher which may result in a relatively better chance for lower ranking non-musth bulls, thus making them concentrate in these areas.

7.4 Movement patterns and investments in reproduction

The investments in reproduction in terms of reduced feeding and increased daily distance covered, made by sexually active non-musth bulls is contrary to previous belief. Unfortunately, no GPS collared bulls have to date been in musth (without trashing the 8000 US $ collar and loosing all data) preventing a comparison of the changes in daily travelling distance between musth and active non-musth bulls. Musth bulls did reduce feeding more than non-musth bulls. However, since the musth bulls were generally older than the non-musth bulls and therefore at an age with limited continued growth, these bulls are probably capable of reducing their daily energy intake more than younger bulls. Although a bigger individual (older) would be assumed to need more energy to cover the basic metabolic requirements compared to a smaller (younger), the extra energy requirements for a larger body is assumed to be small, compared to requirements for growth. Therefore, the larger reduction seen among musth bulls could at least partly be due to a confounding effect of age. The somewhat similar reduction in foraging together with the comparable number of herd shifts and females encountered, indicate that the two sexual states do not engage in vastly different types of searches or investments. Therefore, if any costs are associated specifically with the state of musth they must, either be due to injuries from fighting, or an energetic cost associated with elevated levels of androgens. The latter could potentially be investigated in captive elephants, by measuring basic metabolic rates, using oxygen consumption, together with measuring androgen levels. This would enable us to differentiate and start quantifying the investments in reproduction.

The significant investment in reproduction by sexually active non-musth bulls indicate that they do obtain some reproductive success, probably comparable to similar aged bulls engaging in a competitive musth strategy in less favourable areas. However, a measure of actual payoff must be obtained in order to compare the different strategies and tactics. Unfortunately, the only way of measuring the reproductive success and comparing payoff between different strategies is by doing paternity analysis on the calves, a method that was not possible during the present study. However, a genetic study of the entire Samburu population is in the process of being established and will, through paternity analysis of the calves being born in the following 2 years provide us with information on the payoff obtained by the different bulls engaging in various strategies during this study.

The very detailed recordings of movements obtained from the GPS collars made it possible to calculate changes in daily distance travelled as well as changes in ranging area between sexually inactive and active non-musth bulls. However, this new high-resolution data on movements being collected by Iain Douglas-Hamilton and Save the Elephants opens up possibilities for other and novel types of analysis. For example, one could look at changes in shapes of daily movements, depending on factors like sexual state, season, water availability etc. to mention some as well as detailed interactions between individuals. At present, not enough data is available for a proper analysis of this kind due to the large number of factors influencing detailed area and time specific movements. Therefore, this has not been included in this thesis work. However, some preliminary analysis has been made suggesting that bulls changes from a daily perpendicular movement to and from the river (water/forage) during sexually inactive periods to moving along the river during periods of sexual activity. Since the females are dependent on drinking on a daily basis, this may indicate that the bulls patrol a vital resource for the females (water) in a way (along the river) so they maximise the encounter rate of females. The data from the GPS collar combined with the recording of sexual state and activity patterns, herd shifts and number of females encountered will now enable us to create the first generation models on for example, optimal search patterns depending on density and distribution of females.

7.5 Conclusion

In this thesis, it has been shown that it is possible to estimates actual densities of oestrus females in both time and space. Sexually active bulls seems to be able to fine tune their decisions related to reproductive on the basis of the local set of conditions. Therefore, knowing the time specific resource value of an area in terms of number of receptive females as well as the number and relative rank of competitors is vital for the understanding of these decisions.

It has also been shown, that the investment in reproduction in terms of time allocation as well as the type of search for receptive females is comparable between sexually active non-musth bulls and musth bulls. This suggest that sexually active non-musth bulls do obtain an, until know unknown reproductive success although probably lower than older musth bulls. This indicates that the reproductive role of the younger sub dominant bulls cannot be ignored. In terms of investigating strategies depending on varying competition, resource values and trade-offs the medium aged bulls between 25-35 years of age may actually be the most interesting group to study since they are faced with a larger array of constrains and trade-offs compared to the largest bulls.

From the comparison with the elephant population in Amboseli National Park, it is evident that variations in the patterns and frequencies of musth and general reproductive strategies exit between different populations, probably because of variations in densities, distributions and ranging of the elephants. Apart from being scientifically interesting, this could have conservation related implications since many elephant populations throughout the continent faces fragmentation, and confinement due to encroachment from an increasing human populations.

7.6 Future plans

A planned three-year continuation of this study is scheduled to begin in December 2001. The project will focus on following 20 known focal bulls between 25 and 40 years of age. The bulls will be collared with a combination of GPS collars and conventional radio collars. The aim is to obtain better quantitative data on the investment in reproduction made by bulls of various ages and in different sexual states. In a planed collaboration with the DNA lab at University of Makerere, Uganda, the relatedness of the entire Samburu population will be investigated. Regarding the bulls, this will reveal if closely related individuals avoid competition over females. Paternity analysis will be carried out on the calves, hereby obtaining information on the payoff achieved by bulls engaging in various reproductive tactics. Furthermore, in a collaboration with the German Primate Centre, longitudinal data on androgen and cortisol levels in the focal bulls will be measured to compare levels between musth and non-musth bulls and to investigate if the younger musth bulls falsely signal musth, without paying the physiological cost of increased androgen levels.

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