MUSTH AND MALE-MALE COMPETITION IN THE AFRICAN ELEPHANT

by

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No animal in the world is so dangerous as an elephant in musth.

Charles Darwin
The Descent of Man and Selection
in Relation to sex (1890).
Repr. from the 2nd English ed.

SUMMARY

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The phenomenon of musth in male Asian elephants, Elephas maximus, has long been recognized and in this study I have documented the occurence of musth in African elephants, Loxodonta africana, in Amboseli National Park, Kenya. The most obvious manifestations of musth are a sharp rise in aggressive behaviour, copious secretions from and enlargement of the temporal glands, and a continuous discharge of urine. Males in musth show a positive association with female groups. In this thesis I have examined the evolutionary significance of musth from two perspectives: a) which selective pressures have favoured the evolution of musth and b) among males who come into musth, which social and ecological factors influence the timing and duration of musth periods.

Males in musth had higher levels of urinary testosterone and exhibited higher frequencies of aggression than did either sexually inactive or sexually active non-musth males. Musth males increased in dominance above their non-musth rank. Rival males retreated from threats given by musth males at a greater distance than they did from the same threat given by a non-musth male of the same size class. For these reasons males in musth were more successful at guarding oestrous females and obtaining matings than were non-musth males.

Although the reproductive benefits of being in musth in terms of male-male competition were apparent and the primary concern of this study, female preferences have probably also been a selective pressure in the evolution of musth. Observations suggested that females in oestrus purposely outran younger non-musth males and oestrous females were observed to maintain proximity only towards males in musth.

The duration of musth periods appeared to be related to a male's rank relative to other males simultaneously in musth. This pattern appeared to be particularly true among the lower ranking males who could be forced out of musth by older, higher ranking males. Among high ranking males musth duration may also be limited by a decline in body condition. The timing of musth periods in individuals appeared to depend on both the temporal and spatial availability of oestrous females and the temporal patterning of musth in other males.

The phenomenon of musth is compared with the physical and behavioural characteristics displayed by rutting ungulates. I argue that the discharge of urine by rutting males indicates body condition and functions in male-male assessment.

PREFACE

This study was conducted in Amboseli National Park, Kenya from January, 1980 through July, 1981. The long term data presented in this thesis were collected by both Cynthia Moss and myself from October, 1975 through December, 1979. Results based on observations made by Cynthia Moss are explicitly stated as such. Chapter 3, as it appears in this thesis, has since been revised by Cynthia Moss and will appear as a joint paper in Primate Social Structure: an integrated approach edited by Robert Hinde. The text of this thesis does not exceed 80,000 words.

I am grateful to the Office of the President, Government of Kenya for research clearance and to the Ministry of Tourism and Wildlife and Bob Oguya, the Warden, for permission to work in Amboseli National Park. Financial support for the project was provided by a Research Fellowship from the New York Zoological Society and by Smith College. I am also grateful to King's College and to the Sigma Xi Society for their financial assistance. I would like to thank Pat Bateson for use of facilities at the Sub-Department of Animal Behaviour.

I wish to express my gratitude to everyone at the African Wildlife Leadership Foundation all of whom helped me in numerous ways during frantic trips to Nairobi. I would like to acknowledge the assistance of my field supervisors, Harvey Croze and David Western.

Bill Lasley and Lonnie Kasman of the San Diego Zoological Society developed an assay to measure urinary testosterone and analyzed the urine samples that I collected. I am very grateful for their assistance.

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I thank Sandy Andelman for coming to Amboseli and sharing the camp with all of us watu wa-cracked. To Debbie Snelson I wish to express my thanks for wonderful days spent at Gil-gil and for all of the emotional support given to me during the writing of my thesis.

I would like to express my sincere gratitude to all the people of Ol Tukai. In particular I thank Daniel Onina for his companionship and help in the field. He transformed my hateful 2-stroke Suzuki into a dependable vehicle, and taught me much about life in the bush.

Cynthia Jensen has shared in each of my triumphs, disappointments and absurd situations over the last few years. Her letters from Amboseli gave me tremendous encouragment during the last nine months. Without Cyn, dancing, footing, running transects and getting lost in the "very jungle" just wouldn't have been the same. Ashe oling!

My gratitude to Cythnia Moss goes back to October, 1975 when she agreed to have me come to Amboseli to watch the bulls. Since then we have spent many months in Eden watching elephants together. She has laughed at me, organized me, given me encouragment and shared in my excitement over our discovery of "green penis". I am extremely grateful to her for allowing me to use and refer to her unpublished data.

I am very grateful to my supervisor, Robert Hinde, for his helpful critisism on the drafts of my chapters and for his letters and words of encouragment throughout.

My mother provided me with the finances to purchase both my car and my tent. She has shared in my enthusiasm and given me support and encouragment from the beginning. I will be forever grateful to her and to my father for introducing me to Africa and elephants. To her and to my brother and sister, I dedicate this thesis.

Finally, credit for keeping my adrenalin levels high goes to Bad Bull whose RHP far exceeded my own. He viewed my maneuvering Suzuki as another musth male and I am thankful that he never actually managed to flatten me during our escalated contests.

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CHAPTER 1

INTRODUCTION

In 1871 Darwin proposed the theory of sexual selection to explain the elaborate ornaments, weaponry, displays and odouriferous secretions observed in the males of many species. He reasoned that since unadorned males could presumably survive and reproduce equally well except for the presence of better endowed males, these sexually dimorphic characters had evolved either through competition between members of one sex (usually males) for access to members of the opposite sex, or through females preferring males with certain characteristics. These two forms of sexual selection were later termed "intrasexual" and "epigamic" selection, respectively, by Huxley (1938).

The concept of intrasexual selection has not been widely contested, although it has been suggested that sexual dimorphism in many species is a consequence of intersexual competition for resources (Selander, 1972). However, the role of epigamic, or intersexual, selection has been a topic of much debate (e.g. Fisher, 1930; Huxley, 1938; Mayr, 1972; Zahavi, 1975; Maynard Smith, 1976; Halliday, 1978) which focuses on the issue of why females should find some males more attractive than others. Fisher (1930) showed that epigamic selection is possible if the character selected by females is associated with high male fitness. Once females begin to select males with such a character, then a female who chooses this type of male will produce offspring who will, in turn, attract many females. The character selected by females may eventually develop to such a degree that it becomes detrimental to survival and is checked by natural selection (Fisher, 1930).

This thesis aims to examine the role of male-male competition for access to mates as a selective pressure in the evolution of musth in the African elephant. The role of female preferences has been considered elsewhere (see Moss, in prep.) and will be discussed to a lesser extent in the present argument.

The phenomenon of musth in male Asiatic elephants, *Elephas maximus*, has long been recognized (Darwin, 1890; Evans, 1901) and musth in the African genus, *Loxodonta africana*, has been recently documented (Poole and Moss, 1981). Musth refers to a set of physical and behavioural characteristics displayed periodically by adult male elephants (Poole and Moss, 1981). The most obvious manifestations in both genera are a sharp rise in aggressive behaviour, copious secretions from and enlargement of the temporal glands, and a continuous discharge of urine (*E. maximus*: Jainudeen et al., 1972a; *L. africana*: Poole and Moss, 1981). Males in musth are sexually active and show a positive association with female groups (*E. maximus*: Eisenberg and Lockhart; *L. africana*: Poole and Moss, 1981). The possible reproductive advantages accruing from being in musth, and the social and ecological factors that influence the timing and duration of musth in individuals are examined.

1.1 POLYGYNOUS MATING SYSTEMS, MALE-MALE COMPETITION AND SEXUAL DIMORPHISM.

Since Darwin's observations, the theory of sexual selection has been expanded through an increased knowledge of the genetics of sex (Fisher, 1930) and the relative reproductive potential (Bateman, 1948) and parental investment (Trivers, 1972) of males and females. In most species the reproductive potential of males is considerably greater than that of females and reproductive success among males usually varies more widely (Bateman, 1948). Females need only mate once in each cycle to achieve their full reproductive potential while male reproductive success is determined by the number of copulations achieved. Bateman (1948) argued that this would produce "undiscriminating eagerness" to mate among males and "discriminating passivity" in females.

In species with little or no male parental investment the reproductive success of males is highly dependent on the relative reproductive effort of other males; a male's reproductive success is potentially very high, but only if he is able to outcompete other males (Trivers, 1972). Consequently, sexual selection should favour the development of traits in males which enhance successful competition for access to mates.

Many sex differences in body size, weaponry development (antlers, tusks, horns, canines), pelage and behaviour patterns can be explained in terms of individual advantages in male-male competition. Strong correlations exist between sexually dimorphic traits and mating success in many species (Le Beouf, 1974; Trivers, 1976; Davies and Halliday, 1979; Geist, 1971; Howard, 1978; Clutton-Brock et al., 1979) and these traits are predicted to be most marked where competition between males for mates is most intense.

Darwin (1890) realized that in polygynous species, where males mate with more than one female, the competition between males for access to females will be intensified and produce exaggerated development of those secondary sexual characteristics used in male-male aggressive encounters. For this reason sexual dimorphism is expected to be least marked in monogamous species and greatly exaggerated in highly polygynous societies. Under certain conditions these characters may be developed to the point where they act counter to natural selection (Fisher, 1930; Selander, 1972).

Emlen and Oring (1977) have explained mating systems in terms of the ecological and behavioural potential of males to monopolize access to mates. Polygynous mating systems are expected to evolve in situations where environmental conditions enable males to control access to multiple mates or to the resources necessary to attract multiple mates (Emlen and Oring, 1977). They describe several means by which monopolization of mates may occur: resource defense polygyny, male dominance polygyny and female or harem defence polygyny. In the first case, males compete for access to females indirectly by monopolizing the resources crucial to them. In the second, males aggregate during the breeding season to display and females choose males from these aggregations. In female or harem defense defense polygyny, males control access to mates directly.

The intensity of male-male competition in polygynous mating systems will depend on the temporal and spatial availability of receptive females and their predictability in time and space (Trivers, 1972). In a species or population where females become sexually receptive in unison, the level of intermale competition for each individual female will be relatively less intense. When females are slightly asynchronized the potential for an individual male to sequentially monopolize many females increases as does the intensity of male-male competition (Emlen and Oring, 1977). Emlen and Oring (1977) point out that as the degree of asynchrony increases the rate of aquiring mates declines so that a point is reached where the energetic cost to a male of continued resource defence or searching exceeds the reproductive benefits gained, and tendencies towards polygyny decline.

The intensity of male-male competition can be estimated by the operational sex ratio (Emlen and Oring, 1977), or the average ratio of fertilizable females to sexually active males at any given time. The greater the imbalance of the operational sex ratio in a population the greater the expected variance in reproductive success among members of the competing sex for members of the limiting sex (Emlen and Oring, 1977). Continuous long periods of sexual activity by males coupled with short asynchronous periods of receptivity by females will produce a strong skew in the operational sex ratio (Emlen and Oring, 1977).

1.2 THE EVOLUTION OF FEMALE GUARDING BY MALES

Parker (1974a) defines time investment strategies as the optimal allocation of time on particular activities so as to achieve maximum reproductive success. Under conditions of intense male-male competition for access to mates, selection may favour males who invest time in guarding females before and after copulation.

Pre-copulatory guarding functions to monopolize an individual female or group of females while awaiting the onset of receptivity, and appears to have been favoured by selection in species where females are dispersed in space and are therefore encountered relatively infrequently (Parker, 1974a). Pre-copulatory guarding by males has been particularly well documented in the insects (reviewed by Parker, 1970), crustacea and anurans (see Parker, 1974a).

Post-copulatory guarding functions to reduce the loss of reproductive gain by preventing sperm competition from rival males (Parker, 1974a). This form of guarding behaviour has probably evolved in situations where there is high female receptivity. Parker (1974a) points out that where ejaculate size is inadequate or where the energy necessary to reject males exceeds its advantage, females may be receptive to further matings by different males. By becoming fully receptive she then places the burden of repelling mates onto the male and can continue with her activities unhindered. Guarding males will be at an advantage if the receptive period is long enough that sperm from early matings may be inviable by the time that ovulation occurs, or where there is competition between successive ejaculates of different males (Parker, 1974a). The advantage to guarders is increased by a male biased operational sex ratio and has the highest advantage when the last male to mate fertilizes most eggs. In situations where the probability of finding another receptive female is low and the probability of sperm competition from rival males high, there should be intense selection for female guarding by males.

Harem holding ungulates are an example of species in which males guard females both pre- and post-copulation (Parker, 1974a). Elephants do not hold harems and guard only during the receptive period. They can primarily be considered post-copulatory guarders.

1.3 REPRODUCTIVE PATTERNS IN LOXODONTA AFRICANA

1.3.1 Distribution

Loxodonta africana and *Elephas maximus* are the only two living species remaining in the order Probocidea. Both genera originated in sub-Saharan Africa in the early Pleistocene (Maglio, 1973). *Loxodonta* remained in Africa, but *Elephas* expanded into Asia in the late Pleistocene. Formerly, within the last three centuries, *L. africana* inhabited all of sub-Saharan Africa in habitats ranging from tropical and montane forests to open grasslands and semi-arid bush (Laursen and

Bekoff, 1978). In recent years, however, ivory poaching and the ever increasing human pressure for agricultural land have reduced the species range and numbers drastically (Riccuti, 1980), and the majority of remaining elephants exist in small pockets of protected land.

1.3.2 Social Organization

The basic social unit in _L. africana_ is the family group which consists of one or more females and their offspring (Buss, 1961; Laws and Parker, 1968; Douglas-Hamilton, 1972; Moss, 1977). Females born into the group remain with the family, while males leave or are forcibly ejected on reaching sexual maturity (Douglas-Hamilton, 1972). Laws and Parker (1968) and Croze (1974) concluded that groups of adult bulls were loose aggregations of unrelated individuals with weak social bonds. Observations by Hendrichs (1971), however, suggested that there may be social ties between males. The relationships and social structure of African elephants as observed in the Amboseli population have been described by Moss and Poole (in press) and will be discussed in more detail in Chapter 3.

1.3.3 Seasonality of breeding, oestrus and interbirth intervals

The seasonality of breeding in females varies with habitat type and rainfall conditions. Several authors have reported well marked seasonal patterns (Hanks, 1969; Laws and Parker, 1968; Laws, 1969a), while others have reported breeding throughout the year with no distinct seasonal acceleration (Perry, 1953; Buss and Smith, 1966). However, the conclusions of the latter authors were based on material collected from several localities and Laws (1969a) suggested that if seasonal breeding had occurred it might have been obscured by variations between populations, rainfall patterns and habitat differences. Laws and Parker (1968) found well marked seasonal patterns that were different for each population studied.

The gestation period of African elephants is approximately 22 months (Sikes, 1971). Laws et al. (1975) suggested that cows conceiving during the rains will produce calves during the months most favourable for calf survival. The proximate factor stimulating the onset of oestrus is probably the seasonal increase in food quality and availability during and following the rains (Laws et al. 1975; Hanks, 1979).

The duration of behavioural oestrous is variable and may last anywhere from approximately 48 hours (Short, 1966) to as long as 10 days (Moss, in prep.). However, observations made on individually known females, Moss (in prep.) suggest that oestrous usually lasts from three to six days. There are no external signs of oestrus (Short, 1966) and detection by observers rests on the recognition of subtle changes in the posture and behaviour of the female and the increased interest taken in her by males (Moss, in prep.). A female may mate with several males during the receptive period. Short (1966) made observations on one female during oestrus and found that there was little interest paid to her initially, but as oestrus progressed male-male competition increased and the largest male present was eventually able to monopolize her. Short (1966) concluded that ovulation occurred at the end of behavioural oestrus.

Interbirth intervals have been found to vary from 35 months (Moss, pers. comm.) up to 13 years (Laws, 1969a) depending on habitat conditions (Moss, in prep.) and population densities (Laws 1969a). Most of the data collected on interbirth intervals were estimated during culling operations by the percent of cows pregnant or by the percent of individuals with calves under one year of age. These values, however, are time-specific and the number of individuals pregnant in a population is greatly influenced by short term environmental fluctuations. In Amboseli the interbirth interval of individually known animals has been estimated over a period of ten years to be approximately 4.7 years. This figure varies between individuals and between years depending on rainfall and habitat conditions.

Laws (1969a) suggested that the male elephant responds to the same seasonal influences as the female. He supported his hypothesis by showing that the mean diameter of seminiferous tubules collected from a sample of males during a month of peak conception frequency was higher than during a month with low conception frequency. In addition, Laws and Parker (1968) found that seminal vesicle fluid varied between individuals from a thick brown viscous secretion of only a few milliters to a thin clear solution of greater than one liter. They observed males with the latter condition to be more active reproductively.

Somewhat contrary to the hypothesis of Laws (1969a), Buss and Johnson (1967) reasoned that since they had observed no distinct breeding among females in the populations of African elephants that they had studied (Buss and Smith, 1966), any reproductive cyclicity in the male African elephant probably manifested itself on an individual basis. They supported their idea with histological studies of the testes which suggested individual reproductive cyclicity (Johnson and Buss, 1967) and observations in which adult bulls showed varying degrees of interest towards oestrous cows (Buss and Smith, 1966). Their study (Buss and Johnson, 1967) showed no consistent relationship between Leydig cell size, testicular testosterone content and age.

Short et al. (1967) found elephant testicular testosterone concentrations ranging from 3 to 490μg/100g of testis. They speculated that these variations could reflect a male cycle, but they were unable to come to any firm conclusion since the values were unrelated to season, age or behavioural status.

Hanks (1973) pointed out that since male reproductive organs continue to increase in size with age, the relatively small seasonal difference in mean seminiferous tubule diameters found by Laws (1969a) could have been due to a difference in the age structure of the two samples he had collected.

Recent behavioural evidence from Amboseli (Poole and Moss, 1981) has shown that male elephants have heightened periods of sexual activity that are unsynchronized and apparently manifested on an individual basis. This finding does not necessarily contradict any of the work of previous authors. However, the findings of Poole and Moss (1981) apply only to males over the age of 25, while the samples collected by previous authors were largely composed of males well under that age. The failure of previous authors to reach any firm conclusions with respect to a sexual cycle in male elephants may be a reflection of the behavioural complexity of the phenomenon that is the focus of this study.

1.3.4 Age of sexual maturity

Laws et al. (1975) found that the age of sexual maturity in female elephants varied between populations and between individuals within a population from nine to 34 years of age. Laws (1969a) suggested that females are ready to undergo their first ovulation at approximately eleven years old, but that follicular maturation and ovulation can be inhibited by physiological, nutritional and social stress.

Puberty in male elephants has been defined as the first production of sperm and sexual maturity as the production of sperm in quantity (Laws et al., 1975). Puberty was estimated to be 14 years of age and that of sexual maturity to be 17 (Laws, 1969a), although this figure varied between populations over a range of five to six years (Laws et al., 1975).

A post pubertal growth spurt occurs approximately eight years after sexual maturity suggesting that social reproductive maturity is reached after physiological maturity (Laws, 1969b). Laws (1969b) found that the mortality rate of the male elephants increases at around 27 years of age and is correlated with this secondary growth cycle. Although much of the increased mortality may have been a consequence of ivory poaching, Laws (see Laws and Parker, 1968) reported that elephants dying natural deaths showed a similar trend.

1.3.5 Sex Ratio and sexual dimorphism

Laws (1969b) found that the foetal sex ratio, although male biased, did not deviate significantly from 1:1, while the secondary sex ratio showed a significant excess of females (55.7%), indicating higher male mortality. The sexes begin to diverge in height from about four years of age onwards but, between 20 and 30 years of age, there appears to be an acceleration in the male growth rate which produces the marked sexual dimorphism in this species (Laws 1969b). The maximum height reached by the male is some 21.8% taller than the maximum height for females (Laws et al., 1975).

Sexual dimorphism in body weight is even more pronounced; fully grown males weigh almost twice that of adult females (Laws, 1966).

Primary growth curves (ages 1-20) predict that males should be only 367Kg heavier than females, but the secondary growth spurt results in males actually weighing over 2,000Kg heavier than females at age 60. (Laws et al., 1975).

In the Asiatic genus sexual dimorphism in tusk development is pronounced; females are tuskless while most males have tusks (Laursen and Bekoff, 1978). In the African genus both males and females have tusks although tusklessness occurs in approximately 10% of females (Hanks, 1972; pers. obs.) and very rarely in males (Hanks, 1972). The rate of tusk growth is sexually dimorphic; in females the rate of growth is linear, while in males the growth rate increases progressively throughout life (Laws, 1966).

Laws (pers. comm.) has found that the temporal glands show a post-pubertal growth spurt in males. The rate of growth in weight is similar for both sexes until about the age of 24 when the growth rate in the male increases dramatically. The temporal gland in males weighs almost three times the weight of the gland in females by the age of 30 (Laws, pers. comm.). This age coincides with the age by which most males have come into musth (Poole and Moss, 1981) and supports the idea of a post-pubertal growth spurt and the attainment of social reproductive maturity between the ages of 25 and 30 (Laws et al., 1975).

1.4 MUSTH AND RUTTING BEHAVIOUR

Musth in the Asian genus, Elephas maximus, has been likened to rutting behaviour in ungulates (Eisenberg et al., 1971). Rutting behaviour has been decribed as a "transient annual phenomenon associated with polygynous mating systems" (Wemmer and Murtaugh, 1980) and "a form of hypersexual activity of limited duration that is directly controlled by the level of testosterone" (Lincoln, et al., 1970). The term "the rut" may have originated in reference to the concentrated period of intense breeding activity in Red deer. The term has been used to refer to similar periods of intense breeding in other polygynous ungulates where male-male competition for access to females or groups of females is high. Although "the rut" usually implies a period where males in a population are temporally synchronized in their breeding activities, it may refer to any male(s) of a species showing a period of heightened sexual activity where the time and energy devoted to other activities is subordinated (Clutton-Brock, pers. comm.). In general, rutting behaviour is characterized by high testosterone levels, the appearance of sexually dimorphic traits, a loss of appetite, increased aggression towards members of the same sex and a heightened interest in females. Rutting males tend to advertize their state by making themselves visually, vocally and olfactorally conspicuous.

In some species rutting males advertize their state by emitting loud and characteristic vocalizations (Red deer: Clutton-Brock and Albon, 1979; Reindeer: Espmark, 1964). Males in rut may become visually conspicuous through physiological changes such as an increase in neck musculature (Red deer: Lincoln, 1971; Reindeer: Espmark, 1964) or by changes in pelage colour or length (Caribou: Lent, 1965; Red deer: Lincoln et al., 1972). Rutting males may further make themselves visibly conspicuous by soiling themselves with mud (Red deer: Lincoln et al., 1972; Mountain goat: Geist, 1964; Tule elk: McCullough, 1969) or by adopting a characteristic stance (Bactrian camels: Wemmer and Murtaugh, 1980).

Olfaction also plays an important role in the advertizement of a male's sexual state. Rutting males may secrete from various glands during the rutting period (Bactrian camels: Wemmer and Murtaugh, 1980; Asian elephant: Jainudeen et al, 1972a; African elephant: Poole and Moss, 1981; Black-tailed deer: Müller-Schwarze, 1971; Mountain goat: Geist, 1971) and often wallow in mud soaked with their own urine or alter their pattern of urination so as to mark themselves with it (Tule elk: McCullough, 1969; Caribou: Lent, 1965; Reindeer: Espmark, 1964; Black-tailed deer: Müller-Schwarze, 1971; White-tailed deer: Moore and Marchinton, 1974; Eland: Hillman, pers. comm.; Mountain goat: Geist, 1964; Domestic goat: Fraser, 1980; Bactrian camel: Wemmer and Murtaugh, 1980: Dromedary: Coblentz, 1969; Asian elephant: Jainudeen et al., 1972a; African elephant: Poole and Moss, 1981). The urine of rutting males usually has a strong odour (Lincoln, 1971; Coblentz, 1976). Self marking with urine has been termed "scent-urination" or "urine-marking" and its occurrence in the ungulates has been reviewed by Coblentz (1976) and Shank (1972).

There have been several proposals suggested for the evolution of odours emitted by males during the breeding season. Darwin (1890:530) stated that "when only the male emits a strong odour during the breeding season, it probably serves to excite or allure the female", implying that odouriferous secretions are the result of epigamic selection. Other authors have found that scent urination by males of some species synchronizes the oestrous periods of females (see Coblentz, 1976). Espmark (1964) thought that scent-urination had the effect of congregating females and repelling males and Estes (1969) found that scent-urination was used in male-male aggressive interactions.

McCullough (1969) suggested that scent-urination functions as a transmitter of information concerning the physical condition of an animal through metabolic by-products excreted in the urine. The males of many species show a decline in feeding and consequently a considerable loss of condition during the rut (Red deer: Lincoln, 1971; Moose: Belovsky, 1978; goats: Coblentz, 1976; Uganda kob: Buechner and Schloeth, 1965; Bison: Lott, 1972; Asian elephant: Deraniyagala, 1955). McCullough (1969) argued that the odour of urine changes as body condition declines and he suggested that selection would favour males who could detect, by the change in odour, when a higher ranking male began to metabolize tissues other than fat. However, he stated that this would facilitate "the replacement of spent bulls by fresh ones to carry on the breeding" implying group selection.

Coblentz (1976) pointed out that terminating or continuing urination when in bad condition would be equally indicative of poor condition. He further suggested that if urine only indicated condition, it would be unlikely to smell differently from that of females. He went on to suggest that the strong odour associated with male urine during the breeding season may actually function to mask a male′s declining condition and that dominant individuals with a very strong odour would have a selective advantage.

In light of the recent literature on assessment in animal conflicts (Maynard Smith, 1974; Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976; Parker, 1974b) these arguments are not entirely plausible. In this study I will attempt to explain the functional aspects of the behavioural and physical characteristics of musth in terms of assessment theory.

In conclusion, I must point out that the reproductive patterns of Loxodonta africana vary from population to population. Although the theoretical arguments presented in this thesis may apply to other populations of elephants, the actual observed patterns of musth (e.g.

the age at first onset, temporal and durational characteristics) will be expected to differ depending on rainfall and habitat conditions, the degree of breeding seasonality and the tendency of female groups towards seasonal aggregation.

CHAPTER 2

STUDY AREA AND METHODS

2.1 INTRODUCTION

In this chapter I will describe the study area, the study population and the techniques of data collection. The techniques of data collection and methods of analysis that apply to specific parts of this thesis will be described in the relevant chapters. The study was conducted in Amboseli National Park in the eastern Kajiado District in southern Kenya. The Amboseli ecosystem has been described in detail by Western (1973) and summarized by Western (1975) and Western and van Praet (1973). The topography, geology and hydrology of Amboseli have been described in Western (1973) and Foley (1979).

2.2 THE STUDY AREA

2.2.1 Geology, hydrology and topography

Amboseli once contained a river that flowed towards the south-east, draining the areas to the north and west. During the late Tertiary, what is now Kilimanjaro erupted and lava flowed along the eastern and north-eastern edges of the present basin blocking the river's course. Although the lava flow apparently never blocked the river completely, silting and consequent rechannelling of the river caused the present Amboseli depression to be eroded out. During this period faulting occurred and consequently the river ceased to have an outlet. Continuous drainage into the lake formed the clays that underlie the present basin sediments. The lake clays are impermeable and form the

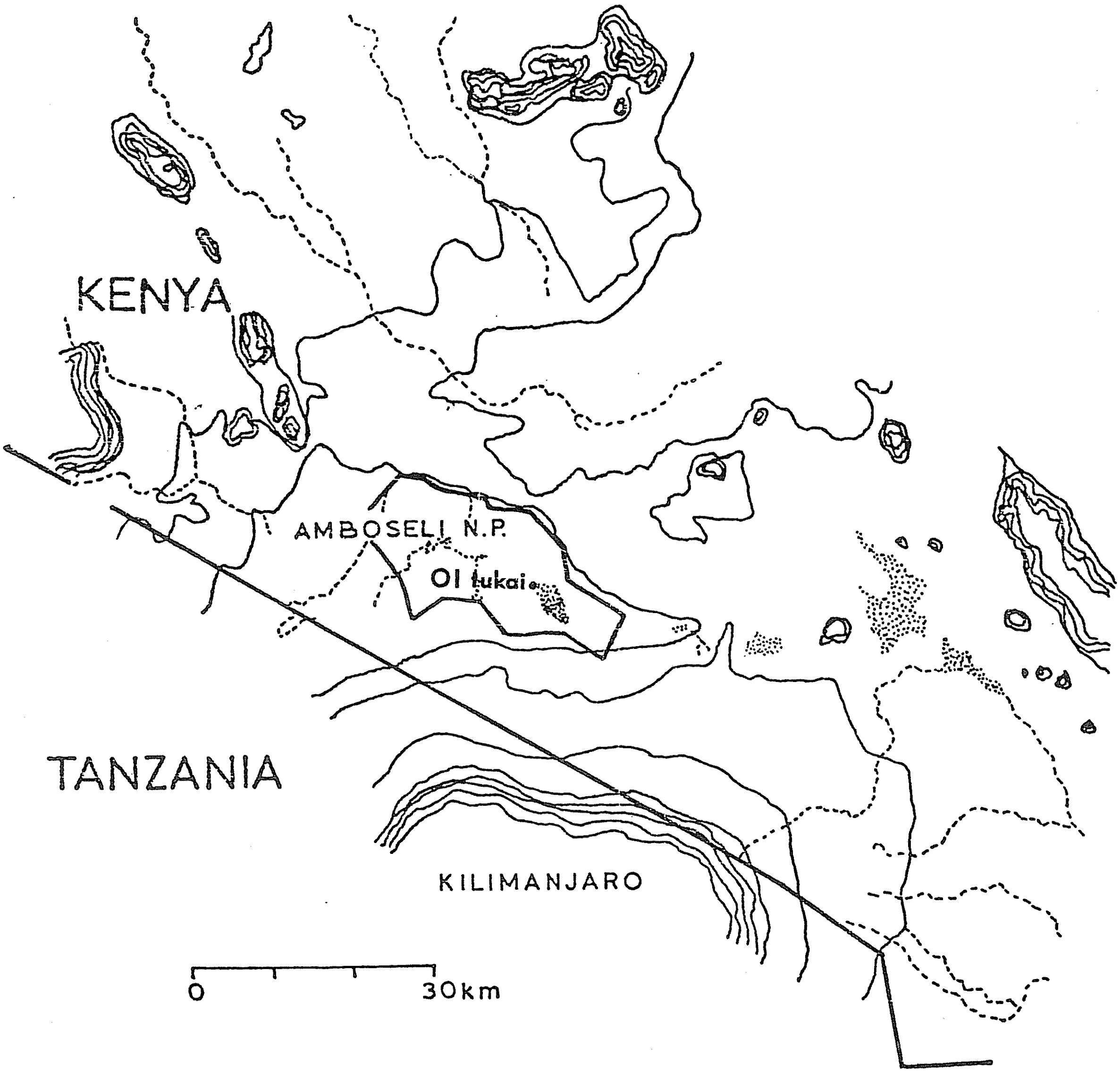


Figure 2.1. Amboseli National Park and surrounding bushlands. The major seasonal rivers are indicated by dotted lines and the principal swamps by stipling. Contour lines represent intervals of approximately 65 meters. The elevation of Ol Tukai is 1170 meters. This figure has been adapted from Lindsay, 1982.

base of an extensive subterranean aquifer (Foley, 1979). Rainfall from the Kilimanjaro watershed now flows underground and emerges at several points around the base of the mountain, forming a series of swamps. Several of these swamps lie in the Amboseli basin and provide the only source of permanent water in the ecosystem. The lake, which in the Pleistocene covered an area of 600 sq.km., is now much reduced and retains water only during periods of high rainfall.

The name "Amboseli" comes from the Maasai word "empusel" meaning open plain. The flat topography of the basin is broken in only a few places by lava outcrops, O-siteti, Kitirua, and Il-mberishari, and transected by two large swamps, Longenye and Enkongo Narok. To the south the land rises sharply towards Kilimanjaro, while to the north the rise in topography is more gradual, although the edge of the basin is marked by a noticeable ridge.

2.2.2 The ecosystem

Western (1975) has described the Amboseli ecosystem as that area covered by the annual dispersal of migratory populations of animals from the basin. This area covers approximately 3,000 sq.km., including the Amboseli basin and the surrounding bushlands. The term Amboseli has recently (Western, 1973 and Lindsay, 1982) been used to refer to the entire ecosystem with the "basin" referring to the Pleistocene lake bed. Amboseli National Park lies within the basin and covers an area of 390 sq.km., constituting the dry season concentration area of the migrating populations. The ecosystem is contained largely in Kenya, although the southern extent of the system lies on the slopes of Kilimanjaro in Tanzania (Figure 2.1).

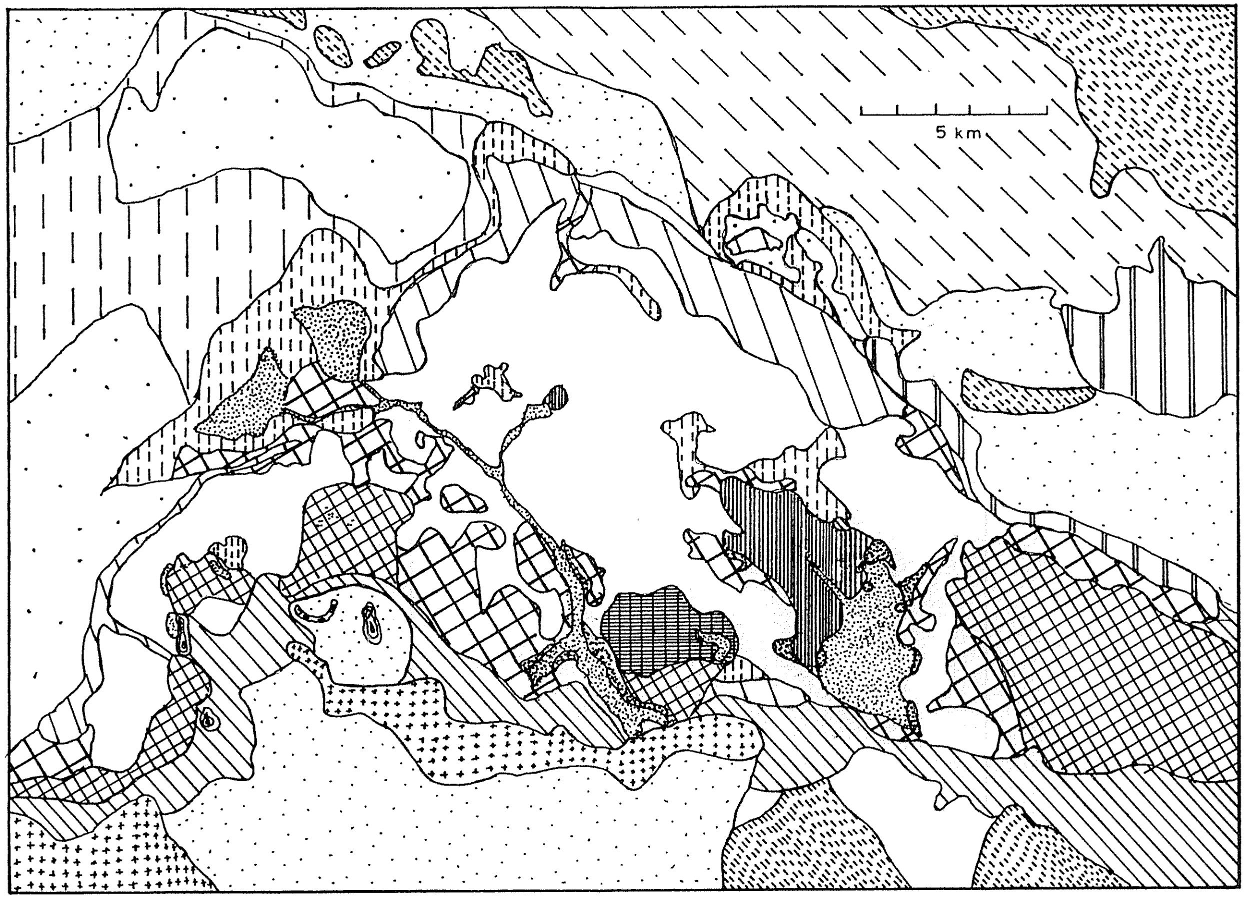


Figure 2.2. Habitat types found in Amboseli National Park and nearby bushlands (adapted from Lindsay, 1982).

- ▨ Dense bushland
- ⁚ Open bushland
- ▧ Bushed grassland
- ✚ *Acacia drepanolobium* dwarf wooded grassland
- ☐ *Sporobolus* spp. short grassland
- ▥ *S. consimilis* tall grassland
- ▥ Mixed spp. grassland
- ▥ Lake grassland
- ⁚ Barren; lake, flood plain
- ▧ *Acacia tortilis* wooded grassland
- ▧ *Acacia tortilis* woodland
- ▩ *Acacia xanthophloea* woodland
- ▦ *Acacia xanthophloea Phoenix reclinata* swamp edge woodland
- ▒ *Acacia xanthophloea* dense young woodland
- ▩ *Salvadora persica Sueda monoica* bushland
- ▥ Swamp edge
- ░ Permanent swamp

2.2.3 Rainfall

Annual rainfall averages less than 350mm (Western, 1975), with most rain falling from November through May. There is usually little rainfall in January, February and early March and these months, the "short dry season", separate the "short rains" in November and December, from the "long rains" in March, April and May. There follows a "long dry season" from late May through October or November, during which very little or no rain falls.

2.2.4 Vegetation

Western (1973) describes 28 plant communities in and around the Amboseli basin and groups these into seven broad vegetation types; lake bed and alkaline plains grasslands, sparse and dense woodlands, swamps, sparse and dense bushlands (Western, 1975). Lindsay (1982) defines "sparse" vegetation types as having a woody cover of 1-2% or less and "dense" types as having 5-20% woody cover. The grasslands, woodlands and swamps are generally confined to the Amboseli basin, while the bushlands occur on the surrounding ridges to the north and the slopes of Kilimanjaro to the south.

The grasslands in the basin are generally of lower nutritional value and respond more slowly to the onset of rainfall than the grasses in the surrounding bushland (Western, 1975). The woody plants also respond to seasonal rainfall, and are productive for longer into the dry season than the grasses (Lindsay, 1982). The swamp edge vegetation, with ground water, remains green and productive except during very dry periods (Lindsay, 1982; pers. obs.). In the deep swamps, vegetation remains productive year round (pers. obs.).

The 28 plant communities described by Western (1973) have been regrouped into 14 habitat types by Lindsay (1982). These are illustrated in Figure 2.2.

2.2.5 Fauna

The Amboseli ecosystem supports a diverse large mammal community (see Williams, 1967). The water dependent species, notably, wildebeest, zebra, Thompson's gazelle and elephant concentrate around the permanent swamps in the basin during the dry season and disperse to the higher quality grass in the surrounding bushlands when there is surface water available during the rains (Western, 1975). Maasai livestock, which in recent years constitute as much as 75% of the large mammal biomass, follow the same seasonal patterns as other water dependent ungulates. Some water dependent species (impala, waterbuck) stay in the vicinity of the permanent swamps throughout the year, while water independent species (e.g. eland, oryx) can be found in low densities throughout the ecosystem in both the dry and wet seasons.

2.3 THE ELEPHANTS

The verbal history of the Maasai suggests that elephants have used the Amboseli region for many hundreds of years (Western, pers.comm.). In 1909, Stigand reported seeing elephants on the slopes of Kilimanjaro and in the Amboseli swamps, and Percival (1924) also spoke of elephants on the slopes of Kilimanjaro. In 1935, Johnson wrote about photographing elephants in the swamps and woodlands of Amboseli.

The presence of the Maasai in this region has meant that elephants in the vicinity of Amboseli have enjoyed a history of lower levels of human disturbance than other populations in Africa. During the 19th Century Maasai warriors prevented Arab slave and ivory trading routes from passing through Maasailand, thereby indirectly providing protection for elephants. In recent years, the presence of the Maasai as pastoralists has meant that, unlike populations elsewhere, the Amboseli elephants have remained unaffected by the increasing demand for agricultural land.

Amboseli was established as part of the Ukamba Game Reserve in 1899 and since that time the area has been protected as a National Reserve and a Maasai County Council Reserve. In 1974 a small portion of the reserve was designated as a livestock-free National Park. The Maasai protested their exclusion from their traditional dry season grazing land by spearing elephants and rhinos. In 1977, during a period of high rainfall, the Maasai were provided with financial compensation, bore holes and alternate grazing land, and agreed to remain outside the Park boundaries.

The lack of compression and relatively low levels of poaching in Amboseli makes the population ideal for gathering baseline data on the ecology and behaviour of free-living elephants. The Amboseli elephant population has been monitored by Cynthia Moss and co-workers (Croze, H., Lindsay, K., Western, D. and myself) since 1972. The population presently numbers 600 individuals. All adults and most juveniles are known individually and young calves can be recognized in the context of their families.

I recognized individuals using the method described by Hendrichs (1971) and used by others since then (Douglas-Hamilton, 1972; Croze, 1974; Moss, 1977). Elephants have ear veination patterns that, like human fingerprints, are unique to each individual, and do not change through time. In addition, most individuals have tears, holes and notches of different shapes and sizes in one or both ears, and although animals may gain new tears through time, the original tear is usually still recognizable. The presence, absence, shape and size of the tusks also help to indentify individuals.

A recognition file of the bulls was begun in 1972 by H. Croze and C. Moss. Each identification card includes two pictures; one taken of each ear. Each male is given an identification number (i.e. M126 - male number 126). There are now 231 adult males on record, although only 162 of these animals are living. Most of the males were lost between 1972 and 1977 as a result of political spearing by the Maasai and poaching.

During the 19 months that I was in Amboseli there were only four deaths among the adult males. A young male was shot by poachers, one died of spear wounds, another badly wounded, was shot by the rangers, and the fourth died of unknown causes. However, only one of these males (M127) was from the Amboseli population. The other three had not been seen in Amboseli previously and I assume that they came to the Park for protection from neighbouring areas. During this period two males were wounded, one by a poisoned arrow (M112) and the other by a spear (M28). Since my departure another large male (M46) died as a result of spear wounds.

Female and calf mortality has also been low in recent years (Moss, in prep.) and under the recent favourable habitat conditions recruitment has increased dramatically. Presently, approximately 18% of the population is under four years old (Moss, in prep.). However, the long term data (see Chapter 5 and Moss, in prep.) reveal how misleading it can be to draw conclusions about population trends from the proportion of calves in a particular year. The age structure of the population suggests that there was a similar increase in recruitment after the heavy rainfall in 1968, followed by a dramatic decline in reproductive activity during the dry years prior to 1977 (Moss, in prep.).

2.4 MALE AGE CLASSES

Shoulder height has been found to correlate closely with age in elephants (Laws, 1966; Hanks, 1972). In Amboseli, Western et al. (in prep.) have found a highly significant relationship between shoulder height and hind footprint length where footprint length=0.158 (height)+3.088. The soils of Amboseli are finely textured clays (Western and van Praet, 1973) and a clear print leaves a wrinkled impression bordered by a smooth narrow margin (Western et al., in prep.). Measurements were made from the rear edge of the wrinkled impression to the middle of the central toenail.

Footprint measurements were taken whenever possible. Measurements were difficult to obtain from males who were moving in large groups and I did not attempt to obtain measurements during the rains when the soil was muddy.

Class 1 males (n=73) include those individuals who have become independent from their original family groups but are smaller than the largest adult females in the population (footprint length 36.0-41.9cm). The remaining males in the population range in footprint size from 42.0 to 53.9cm. These individuals have been divided into three size classes: Class 2 (n=45, footprint length=42.0-45.9cm); Class 3 (n=25, footprint length=46.0-49.9cm); Class 4 (n=19, footprint length=50.0-53.9cm). The footprint lengths of focal males are given in Appendix 7.

Accurate ageing is impossible for all except the Class 1 males who were known as juveniles. I have estimated the ages of older individuals in the population through various means. Shoulder height calculated from footprint measurements (Western et al., in press) can be used to estimate the ages of individuals (Laws, 1966). The ages of individuals in the population can also be estimated from tooth eruption (Laws, 1966). Two males died and I was able to obtain both footlength and tooth eruption measurements from them. Photographs taken in the early 1960s of presently known males (Norman Myers, pers. comm.) also helped to estimate the ages of individuals. Known ages of the younger males give an indication as to the minimum ages of older males. The ages of the four classes of males, based on Laws (1966) and my own estimations are given in Table 2.1.

Table 2.1. Age estimates of the four size classes of adult males

Size Class	number of individuals	Footprint length	Shoulder height	Estimated age Laws	Poole
1	73	36.0-41.9cm	208-246cm	10-13	12-20
2	45	42.0-45.9cm	246-271cm	13-19	20-25
3	25	46.0-49.9cm	272-296cm	19-30	25-35
4	19	50.0-53.9cm	297-320cm	30-60	35+

2.5 DATA COLLECTION

I began research on the Amboseli population in 1976. I spent three months watching elephants during that year and returned to Amboseli for several months in both 1977 and 1978. The results presented in this thesis are primarily from those data I collected during the period January, 1980 through July, 1981. However, some of the questions I will be attempting to answer in this thesis require long term knowledge of individual behaviour patterns and for these analyses I will rely on the complete set of data. When I have used data collected by Cynthia Moss I have specified what proportion of these data are my own. Those results based on focal sampling (e.g. frequency of behaviours, activity budgets, female guarding) and focal scan sampling (e.g. frequency of temporal gland secretion) are all based on data that I collected during the 1980-1981 study period.

2.5.1 Long term monitoring

Since 1972 specific data have been collected from each group encountered in the field. These data are recorded directly onto computer compatable data sheets and include: date; time; location; quality of the count (3-an exact count, 2-a good count, 1-a fair estimation, 0-no count); total number of cows and calves and independent adult bulls; if males present, the number from each of the four size classes; general activity of the group; quality of recognition (3-all recognized, 2-greater than 50% recognized, 1-less than 50% recognized, 0-no recognition); identity of every family unit and/or adult male recognized; identity of any musth male present; identity of any oestrous female present; births; mortalities; matings.

Since 1972, 3,587 records have been made of female groups. Of these 2,007 contained associating males. During the same time period 889 records have been made of bull groups and 868 of lone males. My own observations account for 23.5%, 25.8%, 58.2% and 63.4% of these records, respectively.

2.5.2 Focal sampling

i Selection of focal animals

During the period I spent in Amboseli prior to January, 1980, I recognized musth in ten large adult males (Poole and Moss, 1981). Since the aim of the present study was to provide an explanation of musth in socio-ecological terms, I selected these ten animals and an additional 20 of the largest males as focal individuals. I hoped that some of these additional males would come into musth during my study so that my sample would include some males who had been observed in musth for several years, some of whom had come into musth for the first time during my study and still others who had never come into musth. In this respect I was very lucky; an additional 16 of my focal animals came into musth during my study period, providing an excellent opportunity for comparisons of this sort. M127, one of my focal animals died from a spear wound early in the study period and I replaced him with another male, M175.

ii Selection of individuals for watches

In the field I had to be somewhat opportunistic about which focal males I watched on a particular day. Since the probability of finding a particular animal was extremely low, I could not randomly select a focal male, nor could I work my way through the list of males. Even under my "opportunistic" sampling technique I spent close to 80% of my time searching for focal individuals.

I watched focal males in the order that I located them, but once I had obtained a watch on a particular male I did not watch him again until I began a new focal sample series. If I found several focal individuals in one group, I went through them in consecutive order starting with the male with the lowest identification number.

I had hoped to be able to locate and watch each focal animal once every two weeks so that I could monitor individual changes in sexual state. However, in practice this was not possible. Some males utilized the region to the south of the Park boundary, an area that is very thick bush and in some areas covered with lava rocks. Here, visibility was low and maneuvering a vehicle usually impossible. Following musth males on foot was not a practical solution.

On average I obtained one hour of focal sampling to four hours of searching. Since I was unable to locate some individuals for long periods of time, I began a new sample series after several days of lower than average accomplishment. When I eventually located missing males, these animals had sampling priority over other males in a group.

The approach I used for gathering data from males in musth was necessarily different. Since musth duration is highly variable between individuals and some males only remained in musth for a few days (see Chapter 4) it was often necessary to obtain several watches in a short space of time. Unless I had already gathered a substantial amount of data on a particular musth male, males in musth had sampling priority over non-musth males. The number of watches obtained on each male when in musth or not in musth, with females, with males or alone are presented in Appendix 1.

iii Data collected

I used 30 minute focal samples (Altmann, 1974) during which time all interactions were recorded on a continuous basis. The activity of the focal animal and the distance and identity of two nearest adult neighbours were recorded on-the-dot every five minutes. I recognized eight different activities:

Feeding - handling time, ingestion and mastication of food while standing in one place.

Moving while feeding - when the animal was starting to move but was still either handling or ingesting food.

Walking - when the animal was moving and was neither handling nor ingesting food.

Interacting - when the animal was involved in reciprocal physical or visual contact with another individual.

Standing - when the animal was alert (ears tense) but not engaged in any other activity.

Resting - when the animal was standing, but not alert (ears relaxed).

Comfort - when the animal was involved in some comfort providing activity; mud splashing, wallowing, swimming, rubbing, scratching.

Drinking - when the animal was either swallowing or taking water up into its trunk.

iv Sampling quarters

The day was divided into four sampling quarters: 06:30-09:30; 09:30-12:30; 12:30-15:30; 15:30-18:30. I had originally intended to spend an equal proportion of mornings and afternoons watching elephants. However, I found that the mornings were far more successful than the afternoons. The elephants often spent the nights outside the basin and in the mornings they could be found moving in towards the swamps. At this time an observer could approach to within a few meters. By the afternoon the elephants were usually in the swamp edge habitats, where an observer might have to watch from a distance of several hundred meters. Often the elephants, particularly the males, disappeared completely in the deep swamp. In addition, I found that I was more likely to be disrupted by tourists during the late afternoon game drive between 15:30 and 18:30.

Although the activity patterns of elephants do vary throughout the day (Guy, 1976; Barnes, 1979), I do not feel that the excess of morning samples affected my results significantly, since sexually active and inactive males would have been subjected to the similar morning bias. Of the 752 half hour watches accomplished, 24% were in the first quarter, 44% in the second, 17% in the third and 15% in the last quarter.

2.5.3 Focal scan sampling

The focus of this study is on musth and therefore aimed primarily at large adult males. To look at the difference in the frequency of temporal gland secretion between males and females and between males of different ages I did "focal scans" on selected adult males and females (24 males and 20 females). I selected animals that were highly visible in a group and that used the basin frequently. The first time a focal scan individual was observed on a particular day I immediately recorded the presence or absence of temporal gland secretion.

2.5.4 Monitoring sexual state

For each of my focal animals I recorded information on sexual state on every day that each individual was sighted. The details of this information are described in Chapter 4.

2.5.5 Definitions

I have referred to several different types of elephant groupings in this thesis:

Female - a group of elephants including at least one family unit with or without accompanying adult males. A group is considered any number of elephants moving together with no individual further away than the distance that is equal to the diameter of the coordinated body of the group at its greatest point.

Cow/calf - a group of elephants including at least one family unit but without accompanying adult males. The definition of a group is as above.

Male - an all male group of elephants containing at least two individuals. Individuals were defined as belonging to a group if they were separated by less than 100 meters and were moving in a coordinated manner.

Other terms that I have used throughout this thesis are:

Socially mature male - a male who has been observed in musth at least once.

Socially non-mature - an adult male who has never been observed in musth.

Sexually active - any adult male in association with females or, for socially mature individuals, any male in musth regardless of association.

Sexually inactive - any male in association with males unless in musth.

Study period - will refer to data collected from January, 1980 through July, 1981.

2.5.6 Statistical analysis of data collected

With the exception of the long term data on group size and urinary testosterone analysis, nonparametric statistics (Siegel, 1956) have been used throughout this thesis. The following nonparametric tests have been used. One sample tests: Binomial test; Chi-square one-sample test. Two sample tests: a) related samples: Sign test; Wilcoxon matched-pairs signed-ranks test (T); b) independent samples: Fishers exact probability; Chi-square test for two independent samples; Mann-Whitney U test (U). Nonparametric measure of correlation: Spearman rank correlation. Parametric tests used include t-tests (t), one-way analysis of variance, and the Scheffé test for multiple comparison of means. All probabilites are two-tailed unless otherwise specified. Those results that are recorded as "n.s." are not significant at $p>0.05$.

CHAPTER 3

SOCIAL STRUCTURE OF THE AMBOSELI ELEPHANTS

3.1 INTRODUCTION

Social behaviour can be examined on three levels: interactions, relationships and social structure (Hinde and Stevenson-Hinde, 1976). The social structure of elephants is composed of a multi-tiered network of relationships between closely related and unrelated individuals who interact with one another on a variety of levels. Elephants are born into stable groups of related females. These social groups, known as family units, consist of one or more related adult females and their offspring (Buss, 1961; Laws and Parker, 1968; Douglas-Hamilton, 1972; Moss, 1981). Family units are matriarchal in structure and strong bonds are formed between female members. Females born into a family unit remain there upon reaching sexual maturity, while males leave or are forcibly ejected shortly after reaching puberty (Laws and Parker, 1968; Douglas-Hamilton, 1972; Moss, in prep.). Long-term studies on elephants in Manyara (Douglas-Hamilton, 1972) and in Amboseli (Moss, 1981) reveal levels of organization above the family unit consisting of "kin" or bond groups, clans, sub-populations and populations. Studies have shown that, as adults, males have very different patterns of distribution, association and interactions than do females and calves (Hendrichs, 1971; Croze, 1974).

In many areas, the tendency for elephants to aggregate is seasonally variable (Leuthold, 1976; Moss, 1981; Lindsay, 1982). In Tsavo, Leuthold (1977b) found that during drier periods family units utilized small dry season home ranges. During the wet season elephants left these areas, and there was a tendency towards aggregation

(Leuthold, 1976), so that animals from quite different dry season home ranges might come into contact (Leuthold, 1977b). Elephants were seen to travel long distances in response to localized rainfall and the subsequent new growth of vegetation (Leuthold and Sale, 1973).

In Amboseli, elephants respond to ecological variation similarly; the frequency with which members of the population come into contact and interact with those outside their family unit depends upon rainfall and subsequent food availability (Moss, 1981). Within this ecologically dependent framework of possibilities exists an intricate network of relationships.

3.2 THE AMBOSELI POPULATION

In the Amboseli population family units average 9.4 individuals (range 2-29) and are typically composed of two to three adult females (range 1-9) and their offspring (Moss, in prep.). There are 48 such families in Amboseli, accounting for approximately 451 individuals. Another 162 animals are independent adult males who have left their natal family units. As adults males may be found singly, in all male groups and in association with females. Groups consisting of two or more adult males (mean group size 3.88; range 2-25) are short-lived and relatively unstable in composition. Whether a male associates with males or females depends on his age (see Chapter 5; Section 3.6) and sexual state (see Chapter 4; Section 4.4). The older males, who are the focus of this study, alternate between extended periods of sexual activity and inactivity. When sexually active males search out and associate with females, while during sexually inactive periods they associate with other males (Poole and Moss, 1981). Both sexually active and inactive males may be observed on their own.

In this Chapter I will briefly review how resource availability affects the patterns of distribution and aggregation, and then, within this ecological framework, I will attempt to explain the existing social structure in terms social interactions and relationships.

3.3 DISTRIBUTION AND ASSOCIATION

3.3.1 The females

The females may be divided into two sub-populations based on the way they utilize the available resources during the dry season (Moss, 1977). Members of the "central sub-population" concentrate around the swamp system during the dry season, while members of the "peripheral sub-population" utilize the grass in the surrounding bushland and come to the swamps at night to drink. In the wet season these two sub-populations abandon their dry season home ranges and mix freely in large aggregations, moving between areas where food is abundant (Moss, 1981).

Within each sub-population a further level can be discerned based on the home ranges used each dry season by individual family units (Moss, 1977 and 1981). Seven dry season home ranges have been distinguished and family units that share a dry season home range have been referred to as members of a "clan" (Moss, 1981). The central sub-population of 27 family units consists of four clans: Longinye, Il-mberisheri, Ol-odo Are, and Southern, of 9, 8, 5, and 5 family units respectively. The peripheral sub-population of 16 family units is still unresolved on the clan level. Agonistic behaviour between adult females from different families is rarely observed (Moss, in prep.), but long term records may reveal that high ranking families are utilizing the optimal habitats during the dry season and excluding the peripheral

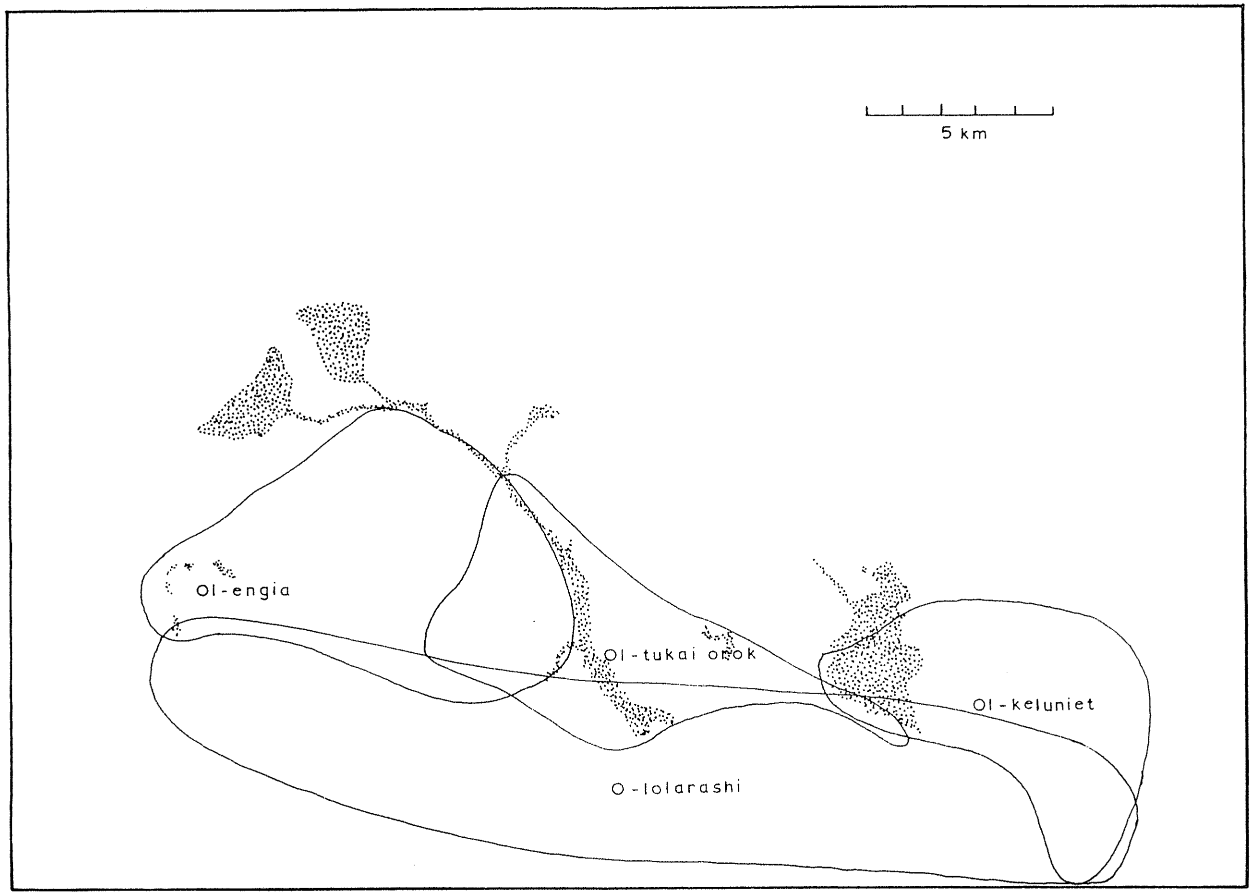


Figure 3.1. Areas used by sexually inactive males when in association with other males.

families (Moss, pers comm.; Lindsay, pers comm.).

The distribution and degree of aggregation of female groups are patterned in response to temporal and spatial fluctuations in food availability. The quantity of social interactions between members of the population are limited during the dry season by nutritional requirements, while during the rains and early dry season these constraints are lifted and families aggregate. As the dry season progresses and the quantity of food in higher quality habitats declines, groups of females appear to try to maintain social groupings by moving to areas where the absolute quantity of food remains high and evenly distributed through the dry season (Lindsay, 1982).

3.3.2 The males

The ranging patterns of individual males when in all-male groups reveal four bull or "retirement" areas: Ol-keluniet, Ol-tukai Orok, Ol-engia, and O-lolarashi (Figure 3.1). These areas overlap and there is no indication that they are defended. During sexually active periods males leave their retirement areas and may be found wherever there are female groups (Figure 3.2). However, the records collected over six years show that each male always returns to the same retirement area after his period of association with females.

Sexually inactive males in their bull areas may distribute themselves so as to efficiently use seasonally changing food resources and they can choose either to move and feed alone or in association with other males. When they are sexually active, their movement patterns depend on the degree of female aggregation and mobility, and they will travel from group to group in search of oestrous females. In doing so, they meet with males from other bull areas. The quantity and quality of interactions between a pair of males and the relationship that they

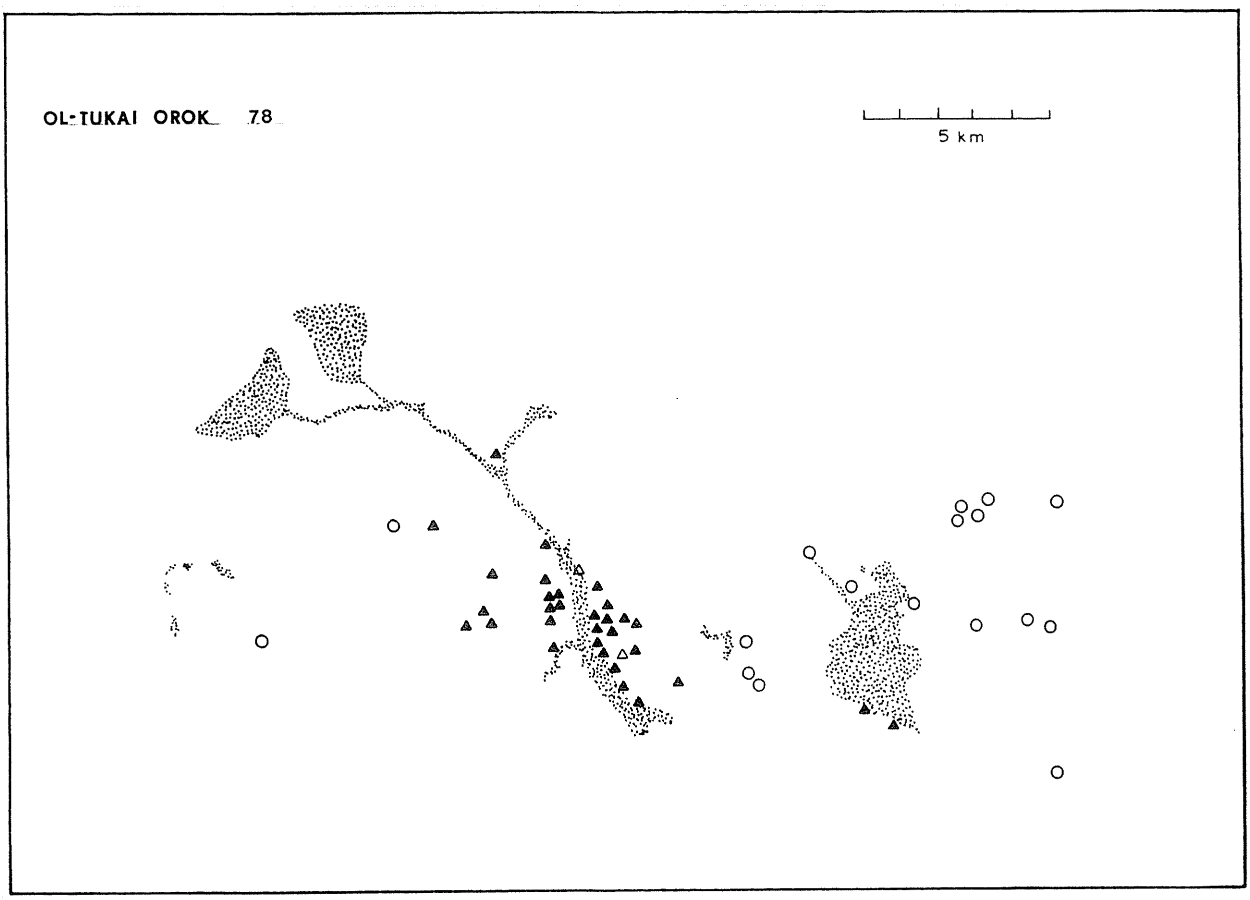
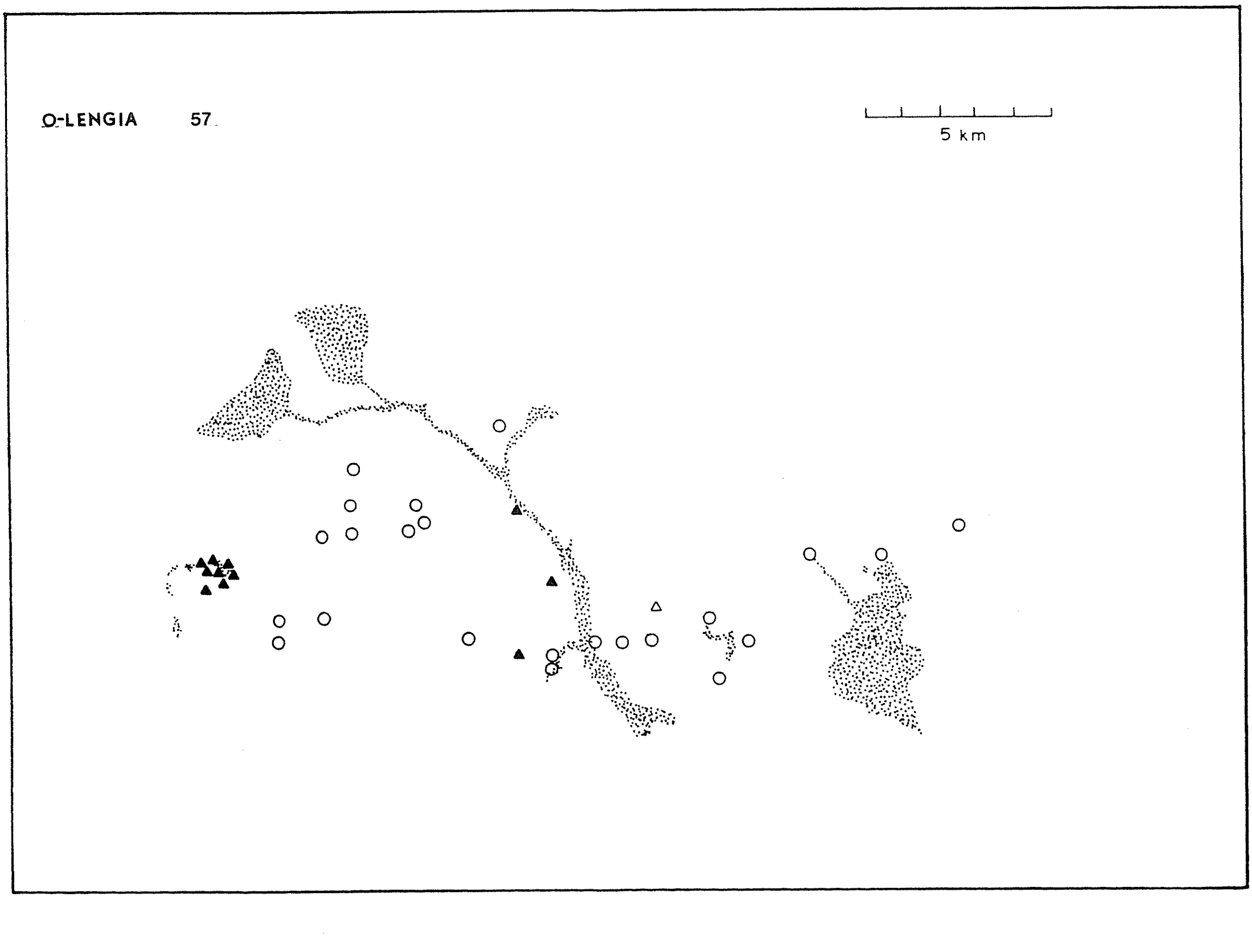
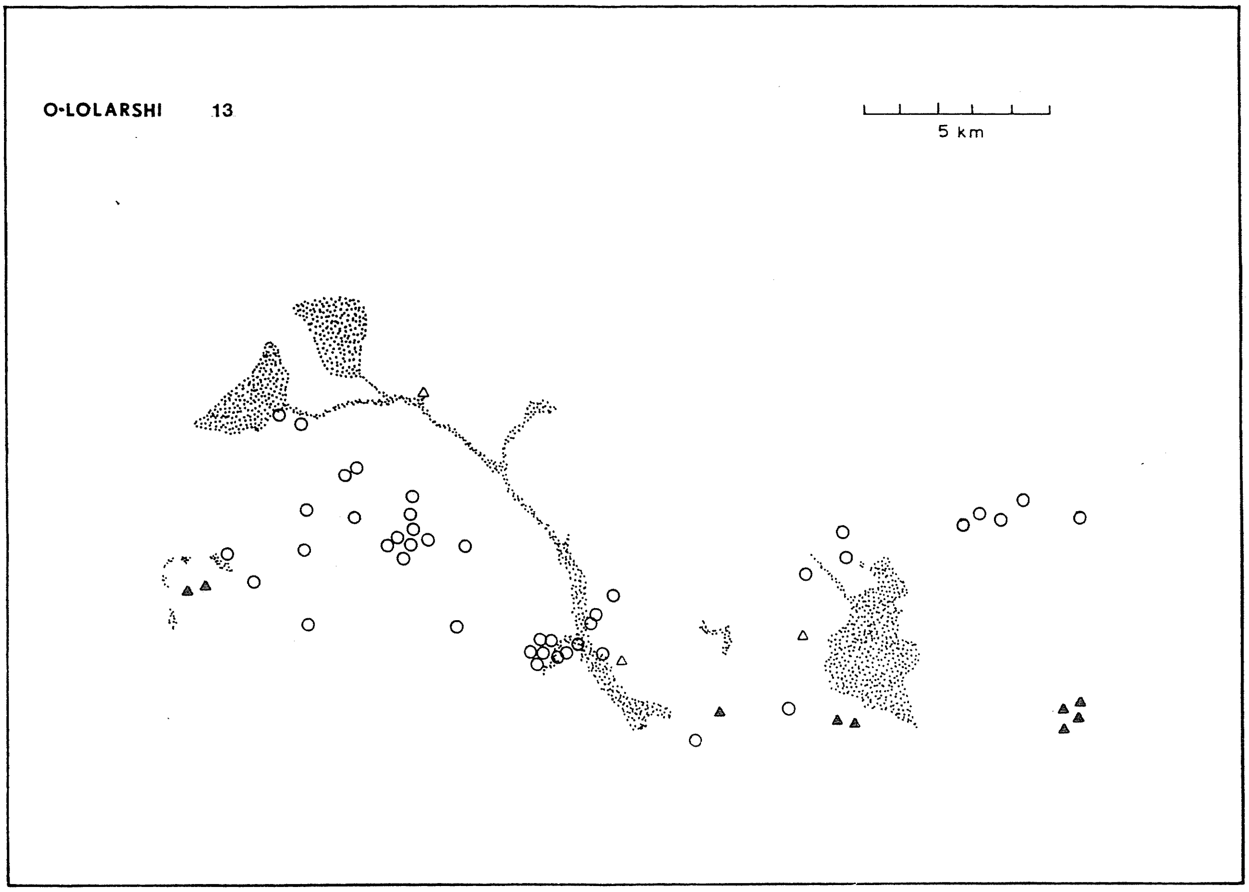


Figure 3.2. Ranging patterns of four males during the study period. Open circles indicate association with females, open triangles indicate association with other males but in musth and closed triangles indicate association with other males not in musth.

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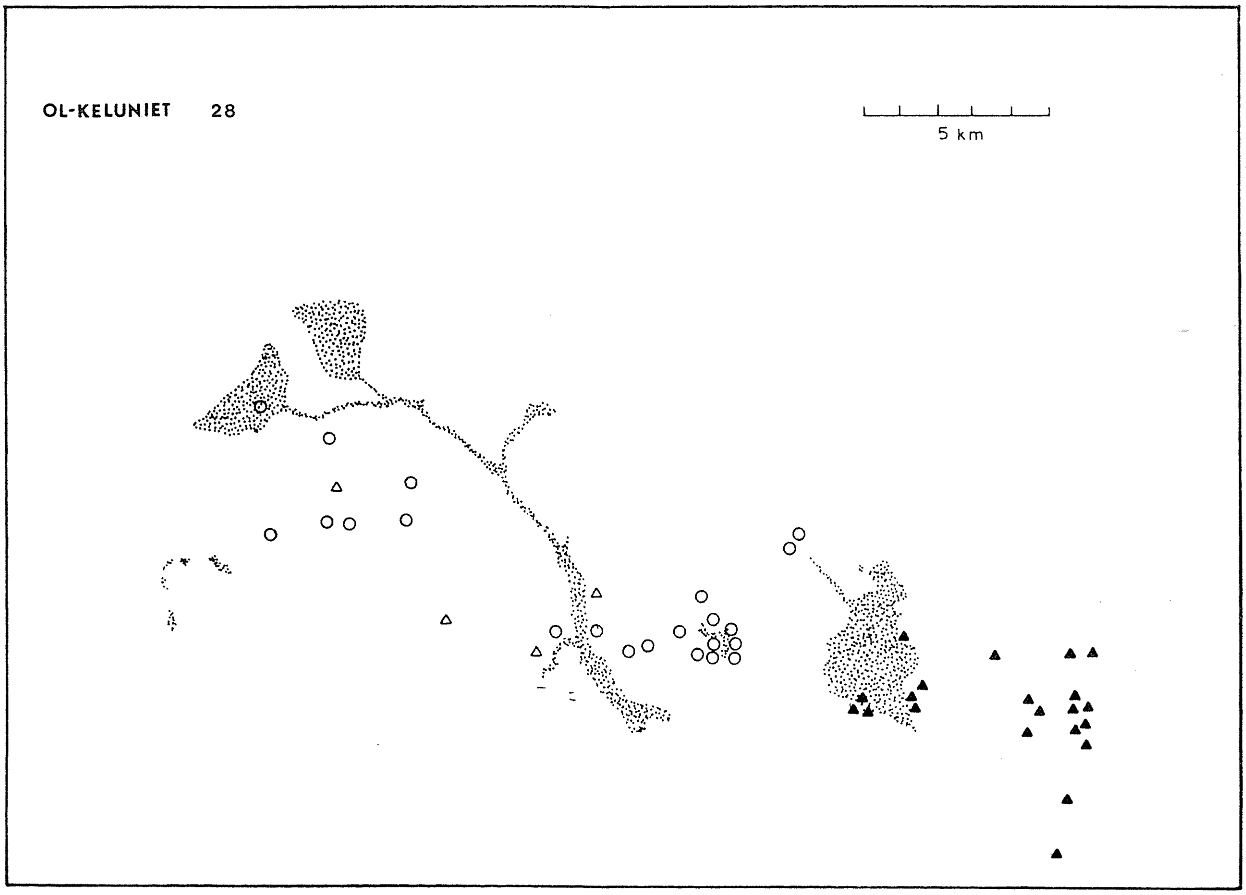
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5 km

share depends on the social context of their interactions.

3.4 SOCIAL INTERACTIONS AND RELATIONSHIPS

3.4.1 The females

In a social system where units aggregate and disband with varying degrees of frequency and duration, one would expect to see the evolution of specific interactions which reflect the importance of reunion to individuals and which maintain and reinforce the types of bonds that these social units share. Among female elephants, reunions are marked by specific greeting behaviour and the form that a greeting takes indicates the strength of the social bond between individuals (Moss, 1981).

All elephants may greet one another but the nature, frequency and intensity of the greeting will vary depending upon the age, sex and relatedness of the elephants involved (Moss, 1981). Greetings between some individuals may occur rarely and will involve at most a reaching of trunks into each other's mouths, while other members of the population will always greet one another in an excited performance even when members may have been separated for less than an hour (Moss, 1981). These individuals will run together and upon meeting raise their heads and ears, turn and back into one another, entwine trunks, while urinating and defecating. This behaviour is accompanied by deep rumbling, trumpeting and screaming and loud ear flapping (Moss, 1981). With rare exceptions only those animals belonging to the same family unit or bond group greet in this way (Moss, 1981).

Examining the association patterns of one family unit in the population reveals the structure of its relationships. The TC family unit, a Longinye clan member, has been observed by Moss (in prep.) on

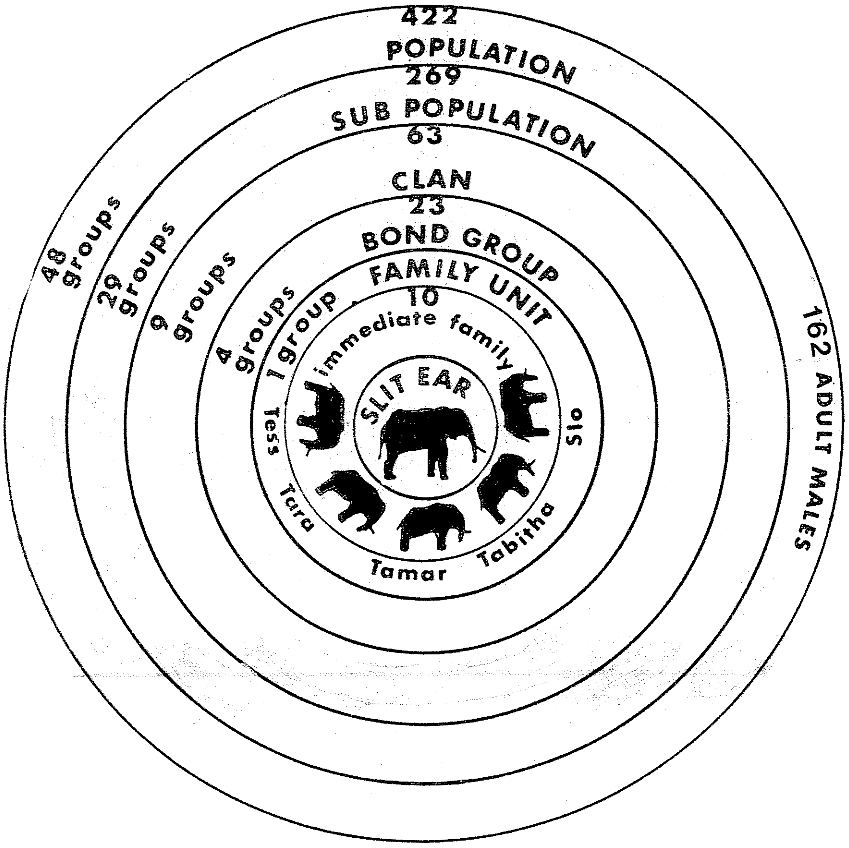


Figure 3.3. Slit Ear lives in a multi-tiered network of relationships. First are her immediate offspring, second the other adult females in her family and their offspring, and third the members of her bond group. The fourth level includes members of her clan, the fifth her sub-population and finally sixth which is the whole population including the peripheral sub-population and all of the adult males (Figure from Moss, 1981).

309 occasions. Moss found that the TC unit associated with most families in the population relatively infrequently, while the levels of association with some individuals were much higher. The TC unit was seen with each of 13 other family units on greater than 10% of the total sightings of this group. All of these were central sub-population families and include at least one family unit from each of the central sub-population's four clans (Moss, in prep). The TC family unit has close associations with all of its own Longinye Clan members, but it has significantly stronger bonds with some of these families than it does with others. In particular, the TC family has strong bonds with the TA, TB, and TC family units, with which it spends 36.2%, 32.0% and 84.8% of its time respectively (Moss, in prep). These four families always greet one another in the excited ceremony that distinguishes bond group members from non-bond group members (Moss, 1981). Their social bonds are obviously strong; when in association they move, feed and rest as a cohesive unit (Moss, 1981). Most families in the Amboseli population are members of a bond group which may be composed of up to five families and all of these bond groups may be distinguished by the quality and quantity of their interactions with one another.

Taking a single adult female, Slit Ear the matriarch of the TC family unit, as the centre of a network of relationships, illustrates that a female lives in a many-tiered social system (Figure 3.3). These relationships change in content and quality as they radiate out through each level. First are her immediate offspring, second the other adult females in the family unit and their offspring and third the members of her bond group. With these first three levels she has strong social bonds which are renewed through frequent contact and greeting ceremonies. The fourth level includes other members of her clan, the fifth the sub-population and finally the peripheral sub-population and the adult males. The type of interactions she has with the adult males will depend on the male's age and sexual state and her own reproductive condition. Both oestrous and anoestrous females often respond to the arrival of a musth male with loud ear flapping and rumbling, and by spinning around and urinating. Females will take an interest in the urine trails left by males in musth and may, as a group, stop to test the urine.

3.4.2 The males

Interactions between individuals are context specific and the quality and quantity and of interactions between male elephants changes dramatically depending upon their sexual state. Interactions between sexually inactive males in bull groups are very different from those occurring between sexually active males in association with cows. Sexually inactive individuals associating with other males exhibit low rates of aggressive interactions, while sexually active males interact aggressively more frequently (see Chapter 6). The older, higher ranking males have a period of heightened sexual activity, known as musth (Poole and Moss, 1981). The musth periods of different males are not synchronized, but occur throughout the year (Poole and Moss, 1981 and see Chapter 4; Section 4.7), and the relative ranks of males in the population change depending upon the temporal and spatial occurrence of individual males' musth periods (see Chapter 6; Section 3.4). Consequently, the types of relationships formed between male elephants are dynamic and highly dependent upon the temporal and spatial occurrence of the musth periods of individual males. Males who only associate with one another when they are sexually active and in association with females will form different relationships from males who associate with one another only when they are in all male groups and sexually inactive.

Males who share a similar bull area associate with one another frequently in small all male groups. They greet one another by reaching their trunks into one another's mouths. This greeting is often extended to smelling each other's temporal glands and genitals, presumably to test each other's sexual state (Plate 3.1). Greetings between males may lead to gentle sparring (Plate 3.1). Males sometimes rumble to one another but they do not greet in the excited manner exhibited by female bond group members. Interactions between sexually active males are more aggressive (Poole and Moss, 1981 and see Chapter 6) and greetings are rarely observed.

Most authors (e.g. Laws and Parker, 1968; Croze, 1974) have concluded that male elephants associate with other males in a random fashion, and that they do not form any long term bonds with other individuals. It is certainly true that males do not form temporally and spatially stable groups, but some individuals do have strong associations with one or more other males. Several pairs of males were observed in association greater than 30% of the time that each were observed in the company of other males (Figure 3.4).

Males who form close associations when in bull areas are rarely seen together when in the company of females, while those from different bull areas are unlikely to come into contact until they are sexually active and in association with females (Figure 3.4). Bulls who come from the same bull area have physiognomic similarities in head, ear, and tusk shape and may be more closely related than they are to bulls from outside their own area.

Male elephants live in a complex social world where the interactions and relationships between individuals are dependent upon

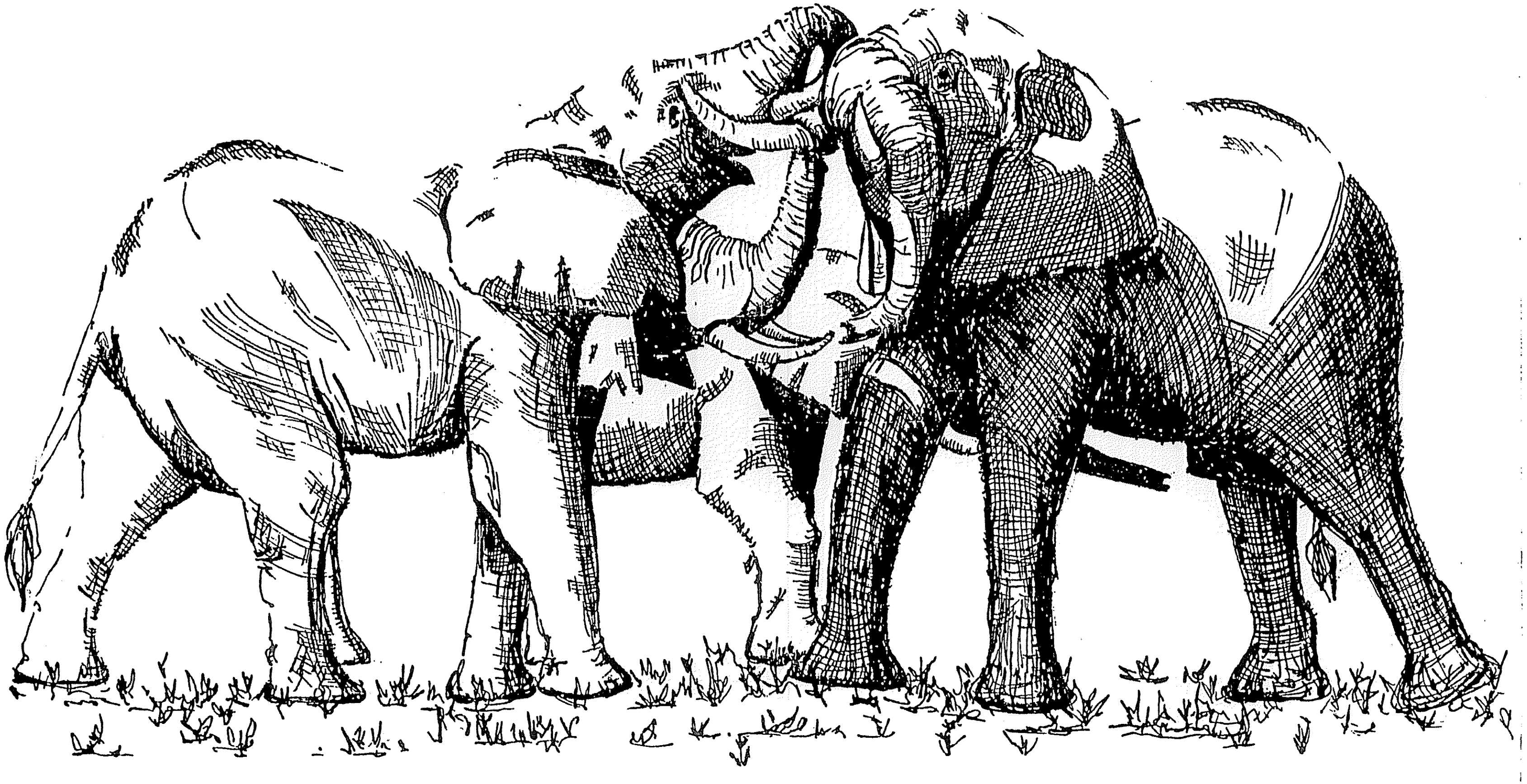


Plate 3.1. Greeting males often smell one another's temporal glands and genitals. Greeting may lead to gentle sparring.

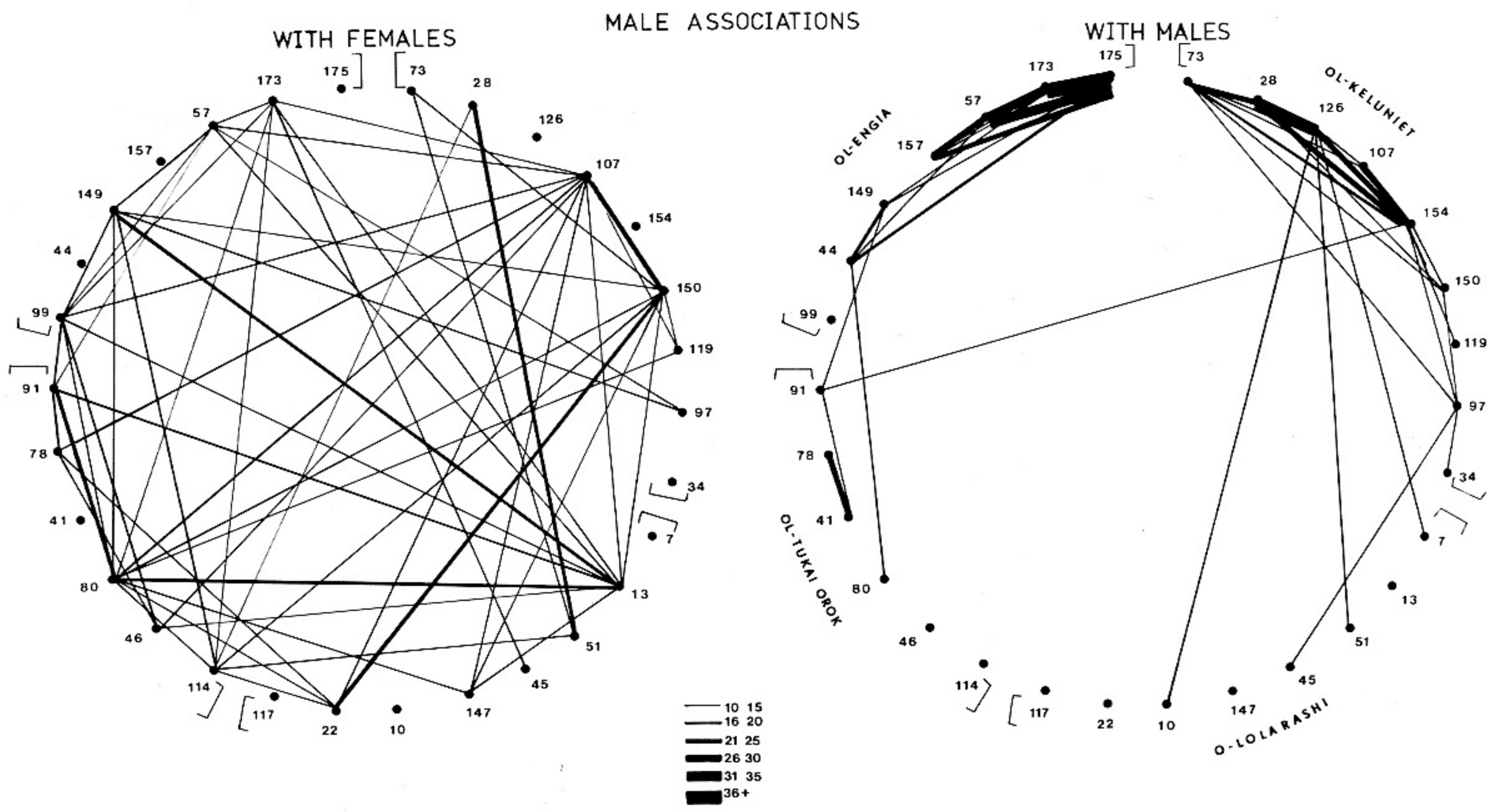


Figure 3.4 Association patterns among the largest adult males when with females and when with males. Lines indicate the percent of observations seen together when with males (or with females) out of the total number of sightings that each was observed in the company of other males (or with females).

their habitat use, their sexual state and possibly their degree of relatedness.

3.5 CONCLUSION

Elephant social organization is dynamic. The spatial occurrence and size of social groups is highly flexible, patterned in response to ecological conditions. Relationships among both male and female elephants are based on a hierarchy of social and spatial interactions. Among the females we find complex greeting ceremonies, the nature and frequency of which distinguish between closely associated and usually closely related individuals and those less so (Moss, 1981). Family unit and bond group members have strong social ties which are maintained throughout the year through frequent contact and greeting ceremonies. Between other clan members social bonds are less strong; although they share the same dry season home range and come into contact regularly, they do not greet one another in the excited manner exhibited by bond groups. Relationships between groups who utilize different dry season home ranges are relatively weak; they come into contact only when ecological conditions permit, and when in association they interact infrequently.

The spatial separation of bull areas and the temporal separation of sexually active periods (Poole and Moss, 1981 and see Chapter 4) means that an individual male will interact with other males on two very different levels. Interactions between males in bull groups are relaxed and amiable, while those between sexually active males are competitive and aggressive. The temporal pattern of musth periods and the spatial distribution of musth bulls changes with the season and through time (see Chapter 4) and the dynamic nature of male interactions, relationships and social structure is a reflection of these fluctuating patterns.

CHAPTER 4

MUSTH

4.1 INTRODUCTION

The phenomenon of musth in male Asian elephants, Elephas maximus, has long been recognized (Darwin, 1890; Sanderson, 1882). Musth, which has been likened to rutting behaviour in ungulates (Eisenberg et al., 1971; Kurt, 1974) refers to a set of physical and behavioural characteristics displayed periodically by adult male elephants. The most obvious manifestations are a sharp rise in aggressive behaviour, copious secretions from and enlargement of the temporal glands and a continuous discharge of urine (Jainudeen et al., 1972a; Gale, 1974). Males in musth show a positive association with female groups (Eisenberg and Lockhart, 1972). For many years there was speculation as to whether musth occurred in the African genus, Loxodonta africana, most researchers contending that it did not exist (Eisenberg et al., 1971; Sikes, 1971; Hanks, 1973; Buss et al.,1976; Hanks, 1979). Recently, Poole and Moss (1981) have shown that musth does occur in L. africana and that it is similar to the phenomenon in the Asian elephant.

In this chapter I will introduce the subject of musth in the African elephant by discussing the phenomenon as it has been described in E. maximus (Fernando et al., 1963; Eisenberg et al., 1971; Jainudeen et al., 1972a; Kurt, 1974; Gale, 1974). I will then discuss some of the reasons that may explain why musth was overlooked in the African genus for so many years. Finally I will describe the physical and behavioural characteristics of musth in African elephants and present data on the age distribution, timing and duration of musth periods in the Amboseli population. This chapter provides the background data for subsequent chapters on the relationship between musth and male elephant ecology (Chapter 5), dominance and aggression (Chapter 6) and mate competition (Chapter 7).

4.2 MUSTH IN ELEPHAS MAXIMUS

4.2.1 Physical and behavioural characteristics of musth

Musth in the domesticated male Asian elephant has been described in detail (Fernando et al., 1963; Eisenberg et al., 1971; Jainudeen et al., 1972a; Kurt, 1974; Gale, 1974). The first stage of musth is characterized by a gradual enlargement of the temporal glands, increasing irritability (Fernando et al., 1963; Eisenberg et al., 1971; Jainudeen et al., 1972a) and the loss of appetite (Fernando et al., 1963). Erection of the penis is frequent during this period (Fernando et al., 1963; Jainudeen et al., 1972a). At the end of this stage, which lasts approximately two to three weeks, a slight discharge from the temporal glands may be observed (Eisenberg et al., 1971; Jainudeen et al., 1972a).

During the second stage the animal becomes extremely aggressive, secretions from the temporal gland flow in a wide stream down the side of the face, and there is a frequent dribbling of urine that is mixed with an odourous discharge (Jainudeen et al., 1972a). This stage may last from a few weeks up to three months (Fernando et al., 1963). As soon as the urine discharge ceases the animal may be handled, and within a few days the temporal gland stops secreting (Jainudeen et al., 1972a). Fernando et al. (1963) report that "the popular belief is that in the wild state the animal in "musth" roams away from the herd leaving a trail of destruction behind".

Similar observations were made by Gale (1974). He spoke of musth as occurring in four stages. In the initial stage the temporal glands begin to swell, the animal loses appetite and becomes indifferent to his mahout's commands. In the second stage the temporal glands appear larger and exude a thick oily substance that runs down the sides of the animal's face. This is termed the "upper musth" phase. Gale (1974) describes the animal as having frequent erections at this time. In the third stage the animal begins to discharge urine and is said to be having his "lower musth". With both the upper and lower musth in evidence the animal is said to be in "full" or "complete" musth (Gale, 1974).

In the fourth or "musth drinking stage" (Gale, 1974), temporal gland secretions flow down to the corners of the mouth. The frequency of urine dribbling increases, leaving the inside of the legs "stained". Gale (1974:46) states that at this time the animal is "at the height of his midsummer madness and will, if only set free, charge and kill anything in sight".

Although the descriptions by Gale (1974) are more dramatic in their presentation than those described by Fernando et al. (1963), Eisenberg et al. (1971) and Jainudeen et al. (1972a), his observations are similar.

Particular behaviours are described as being associated with each musth phase. Jainudeen et al. (1972a) report that during the first stages of musth males may rub the temporal gland area, and they suggest that the swelling may cause some irritation. Eisenberg et al. (1971) also report seeing similar behaviour among free-living musth elephants. During the second stage of musth males are often seen oscillating the head in a rhythmic fashion with the trunk raised high (Jainudeen et al., 1972a). Gale (1974:54) reports an elephant "who suddenly went on "full musth", and at the height of his madness, he stood on his head, his tusks in the ground and his hind legs kicking the air...". Free-living male Asian elephants were seen to rub the temporal gland area against trees and in the vicinity of waterholes more often when in musth than when out of musth, suggesting that the gland may be used in marking (Eisenberg et al., 1971; Kurt, 1974). Although males usually attain a partial erection at micturition, during musth this pattern is altered and the penis is retained in the sheath (Jainudeen et al., 1972a).

4.2.2 Age distribution of musth

Domesticated male Asian elephants under ten years of age were never observed in musth (Eisenberg et al., 1971; Jainudeen et al., 1972a). Jainudeen et al. (1972a) found a gradual increase in the proportion of males observed in musth with age, until by 30 years old almost all males had been observed in musth at least once. Gale (1974) reports an elephant as old as 70 years of age in musth.

4.2.3 Seasonality of musth

In Ceylon, musth among domesticated elephants was observed throughout the year, with peak occurrences coinciding with the months of maximum rainfall (Eisenberg et al., 1971; Jainudeen et al., 1972a). Among free-living elephants in Ceylon, Kurt (1974) also observed musth throughout the year, but he found no particular relationship between the frequency of musth and rainfall. In Burma, Gale (1974) observed males in musth year round with peaks coinciding with the months of highest conception frequency.

4.2.4 Duration of musth periods

Gale (1974) reports that the range in duration of musth periods was from three to 80 days with modes of 23 to 27 days (n=210). Jainudeen et al. (1972a) also found musth periods to be highly variable between individuals, ranging from two weeks up to nine months (n=80). However, the duration of musth periods for individual males was relatively consistent from year to year (Jainudeen et al., 1972a). The length of musth periods appeared to be related to the age of individuals; in young males musth lasted for two to three weeks, while among older individuals musth periods were closer to two to three months in duration (Jainudeen et al., 1972a). Kurt (1974) found that musth periods among free-living elephants lasted from one to 34 days (n=13), decreasing among very old animals. However, his ageing criteria were based on measures such as split toenails, hairless tails, and hollow cheeks and temples, and thus his conclusions are, in my opinion, speculative.

4.2.5 The recurrence of musth periods.

Jainudeen et al. (1972a) found that individual males showed a cyclical pattern in the timing of musth periods. In their study 90% of the males (n=80) were observed to come into musth every year. Irregularities in this pattern were observed among the younger males and those in poor condition (Jainudeen et al., 1972a). Gale (1974) reported that musth occurred at least once a year in healthy animals.

4.3 POSSIBLE EXPLANATIONS AS TO WHY MUSTH WAS OVERLOOKED IN L. AFRICANA.

The above descriptions indicate that the symptoms of musth in elephants are unmistakable and highly visible, so it seems surprising that musth in the African genus could have gone undetected for so many years. There are several possible explanations for this.

In most of the early studies elephants were not individually recognized, so that individual behaviour patterns went largely unnoticed. Those studies in which animals were recognized individually either concentrated on females (Douglas-Hamilton, 1972) or on males in habitats not normally utilized by females (Croze, 1974). In either case sexually active males may have been seldom observed.

However, the main reason that musth was overlooked was probably due to confusion over secretions from the temporal gland. In the Asiatic elephant the most important indicator of musth is the onset of temporal gland activity which, with rare exceptions, occurs only in males in this condition (Eisenberg et al., 1971; Jainudeen et al., 1972a). In the African genus, however, temporal gland secretions of short term duration occur frequently in both sexes. In fact, females have been shown to secrete from the temporal gland more often than males (Douglas-Hamilton, 1972 and see below). Previous authors found no relationship between such secretions and sexual activity (Perry, 1953; Short et al., 1967; Sikes, 1971; Hanks, 1973; Hanks, 1979) and therefore refuted the idea that musth occurs in this genus. This view has been supported by observations that males without secretions were observed mating oestrous females (Short, 1966).

The discussion of musth in L. africana has been further confused by the incorrect use of the term, which in the African genus is often used to refer to temporal gland secretions (Osman Hill, 1953; Kurt, 1974; Buss et al., 1976) rather than to a behavioural syndrome as was originally intended in Asia (Sanderson, 1882; Evans, 1901). Thus, males, females and juveniles are often referred to as being "in musth" (Buss et al., 1976) or "having musth" when they are observed with temporal gland secretions. Secretions from the temporal glands may either be associated with musth in males (Poole and Moss, 1981) or it may be involved in non-sexually related olfactory communication (Short et al., 1967; Eisenberg et al., 1971; Sikes, 1971; Buss et al., 1976;). Eisenberg (pers. comm.) has suggested that there are two different secretions that differ in viscosity and this conforms with my own observations (see below). The non-musth related secretion is watery and dries rapidly, while the secretion associated with musth is much more viscous in nature. To avoid such confusion in future, Poole and Moss (1981) have suggested using the term "temporin" (Sikes, 1971) to refer to both types of secretion from the temporal gland.

The unusual pattern of urination which, in the African genus, is the single most important indicator of musth (Poole and Moss, 1981), was observed previously in _L. africana_ but it was not thought to be connected with the phenomenon of musth (Croze, pers. comm.; Douglas-Hamilton, pers. comm.). Douglas-Hamilton (1972) reported that when a cow is in oestrus associating males may show a "copious secretion from the penis" which may last for several days.

4.4 METHODS

4.4.1 Physical characteristics of musth

Throughout the study I recorded the musth state of each focal male on every occasion that the individual was sighted. Six physical characteristics were recorded as either present or absent or on a scale of increasing amount. The degree of inter-observer reliability is given as the proportion of observations in which the two observers ranked the variable equally:

1) Temporal gland secretion - the presence or absence of temporin was noted. There were several categories related to the freshness and amount of the secretion (Plate 4.1). Temporin was classified as being either "fresh", "congealed" or "old". When it appeared as a very dark oily looking liquid on the animal's face it was defined as fresh. Temporin was termed old when it was detectable only as a light brown stain. The term congealed was used to refer to temporin of a more viscous nature. Congealed temporin dried at varied rates leaving a mottled appearance on the animal's face. (Inter-observer reliability on a scale of 1 (no secretion) to 4 (fresh): 62% agreement; 38% disagreement by score of one; n=13).

The amount of temporin, when present, was classified in four categories depending upon the distance that it flowed from the gland oriface (Plate 4.1): 1 - from the orifice to the lower extent of the eye; 2 - extending to the top of the upper jaw bone; 3 - extending to the corner of the mouth; 4 - extending to the base of the lower jaw. (Inter-observer reliability on a scale of 1 (no secretion) to 5 (degree 4): 77% agreement; 8% disagreement by score of one; 15% disagreement by score of two; n=13).

2) Temporal gland swelling - the degree of swelling was classified in four categories (Plate 4.2): 0 - no swelling; the gland area remains sunken relative to the skull. SL - slight swelling in evidence; the gland area lies flush with the skull. 1 - swelling is obvious; the gland area swells beyond the skull. 2 - the temporal gland is extremely swollen and rounded; puffiness begins immediately behind the eye and extends well beyond the skull. (Inter-observer reliability on a scale of 1 (no swelling) to 4 (extremely swollen): 69% agreement; 23% disagreement by score of one; 8% disagreement by scores of two; n=13).

Plate 4.1. Illustration of the type (fresh, congealed, old) and amount of secretion from the temporal glands. See text for explanation.

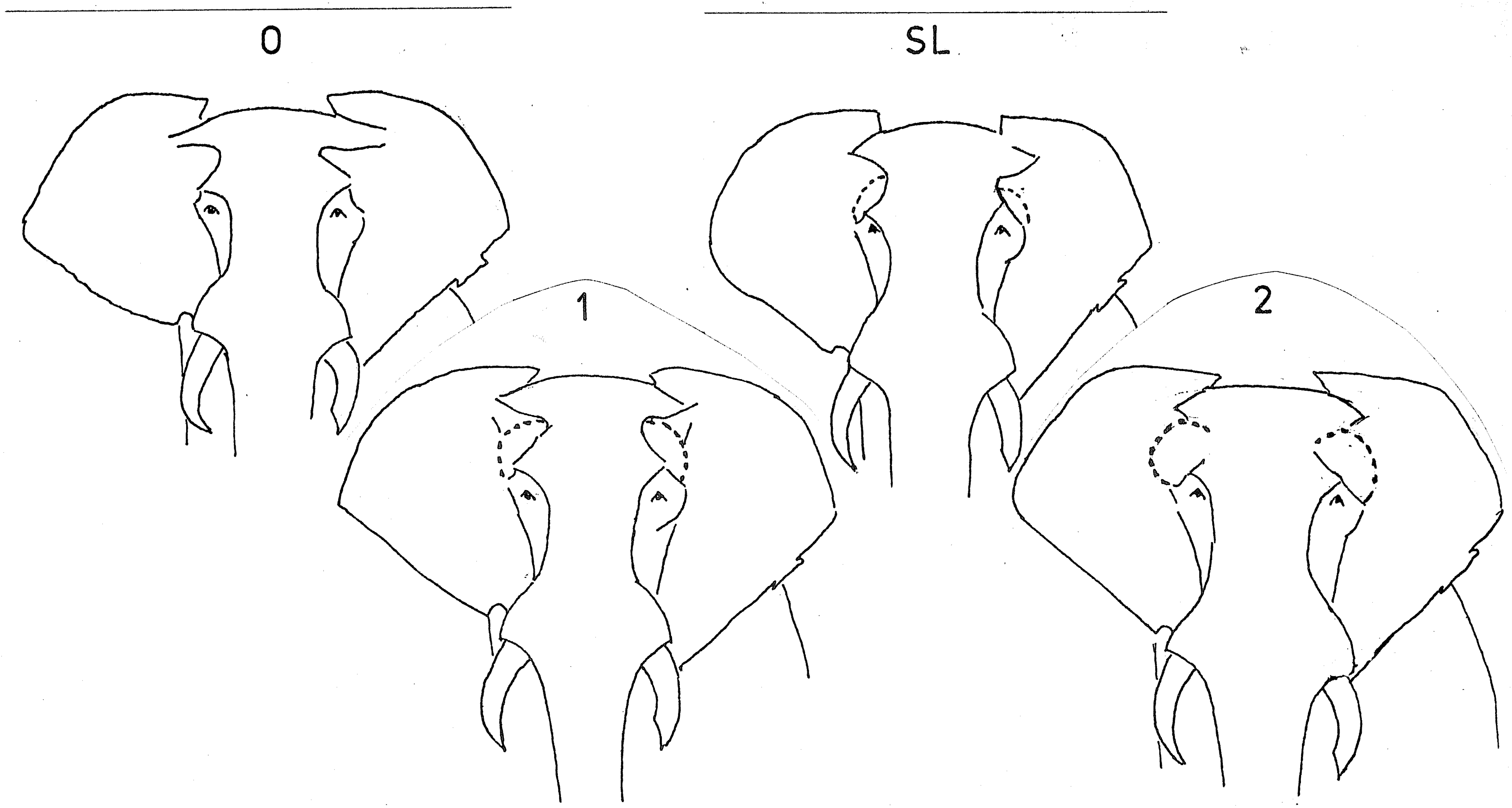


Plate 4.2. Illustration of the degree of temporal swelling during musth. See text for explanation.

3) Urine discharge - urine dribbling was categorized according to the amount that was being discharged: 0 - no evidence of urine dribbling; 1 - no discharge of urine, but the inside of the hind legs are wet from recent urine dribbling; 2 - urine is discharged in a series of discrete drops (Plate 4.3); 3 - urine is discharged as a continuous stream; 4 - urine is expelled in a large spurt. This final category was used in agonistic encounters and was never in evidence for more than a few seconds. It was distinguished from actual urination by the force with which the urine was expelled and by the lack of a subsequent erection (see below). (Inter-observer reliability on a scale of 1 (no dribbling) to 5 (degree 4): 77% agreement; 23% disagree by score of one; n=13).

4) Green penis - when an animal had been discharging urine for a period of time the distal part of the sheath/proximal portion of the penis developed a greenish colouration (Plate 4.4). This was termed green penis or "GP" and was recorded as present or absent (Inter-observer reliability: 92% agreement; 8% disagreement; n=12). In this thesis the term GP, unless specified, will refer to urine discharge and/or the associated colouration.

5) Odour - the discharge of urine, particularly when associated with GP, was accompanied by a strong odour. This characteristic odour was often helpful in identifying whether an animal had recently been in musth (Inter-observer reliability, present or absent: 100% agreement; n=12).

4.4.2 Behavioural characteristics of musth

There are several behaviours, postures and vocalizations that are performed either primarily or exclusively by males in musth. Since I became aware of some of these behaviours only gradually through the course of the study, I have analyzed only those data collected during

Plate 4.3. Illustration of urine dribbling. In this photograph urine is being discharged in a series of discrete drops (degree 2). See text for explanation.

Plate 4.4. Illustration of "green penis"; a greenish colouration developed on the distal part of the sheath/proximal portion of the penis when a male had been dribbling urine for a period of time. Note the wet legs from urine dribbling.

the last year of the study (539 half-hour watches). I have analyzed these data by merely scoring whether a particular behaviour was observed in a watch, but not the frequency with which it occurred. For each behaviour I have compared the proportion of watches in which that behaviour occurred for musth and non-musth state for each male that was observed in musth during my study period (n=26).

I have recognized eight behaviours that appear to be associated with musth (see Section 4.4.9). These behaviours have not previously been described for the African elephant and two have yet to be described for the Asian elephant (ear wave and musth rumble).

1) Ear Wave - elephants have many ear postures: ear flap (social excitement), ear fold (threat), ear flap-slide (a signal of intention to change activity or direction) to name a few. In contrast to other ear postures, the ear wave is accomplished by moving one ear at a time. The upper and inner portion of the the ear is thrust vigourously forward allowing the lower and outer portion of the ear to follow behind. This motion creates a "wave" or undulation diagonally across the ear (Plate 4.5 and may be done once (low intensity) or more than once (high intensity). The ear wave is used in agonistic interactions with other males (see Chapter 7) and individuals usually wave with the ear closest to the male being threatened.

2) Musth rumble - elephant vocalizations are many and varied, even among those described as "rumbles". Moss (pers. comm. and 1981) has described several (i.e. contact and greeting rumbles) and she is able to distinguish the rumbles of different individuals. The musth rumble is unlike any other elephant vocalization. It is a very low and gutteral undulating noise: whooaoo-whooaoo-whooaoo and is often

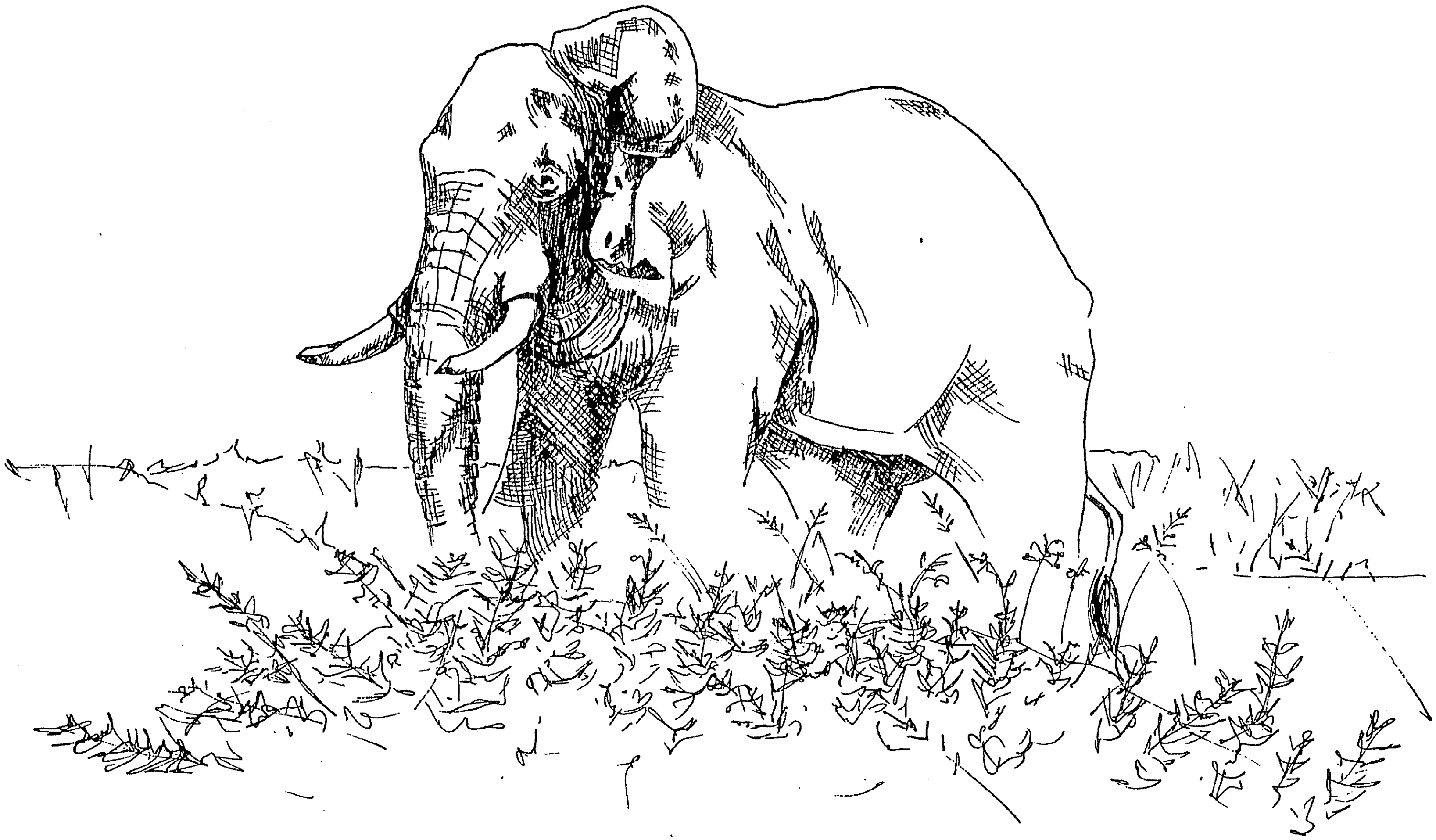


Plate 4.5. The ear wave (M41). This behaviour is performed only by males in musth and probably functions to waft the scent of the temporal gland secretion towards other males.

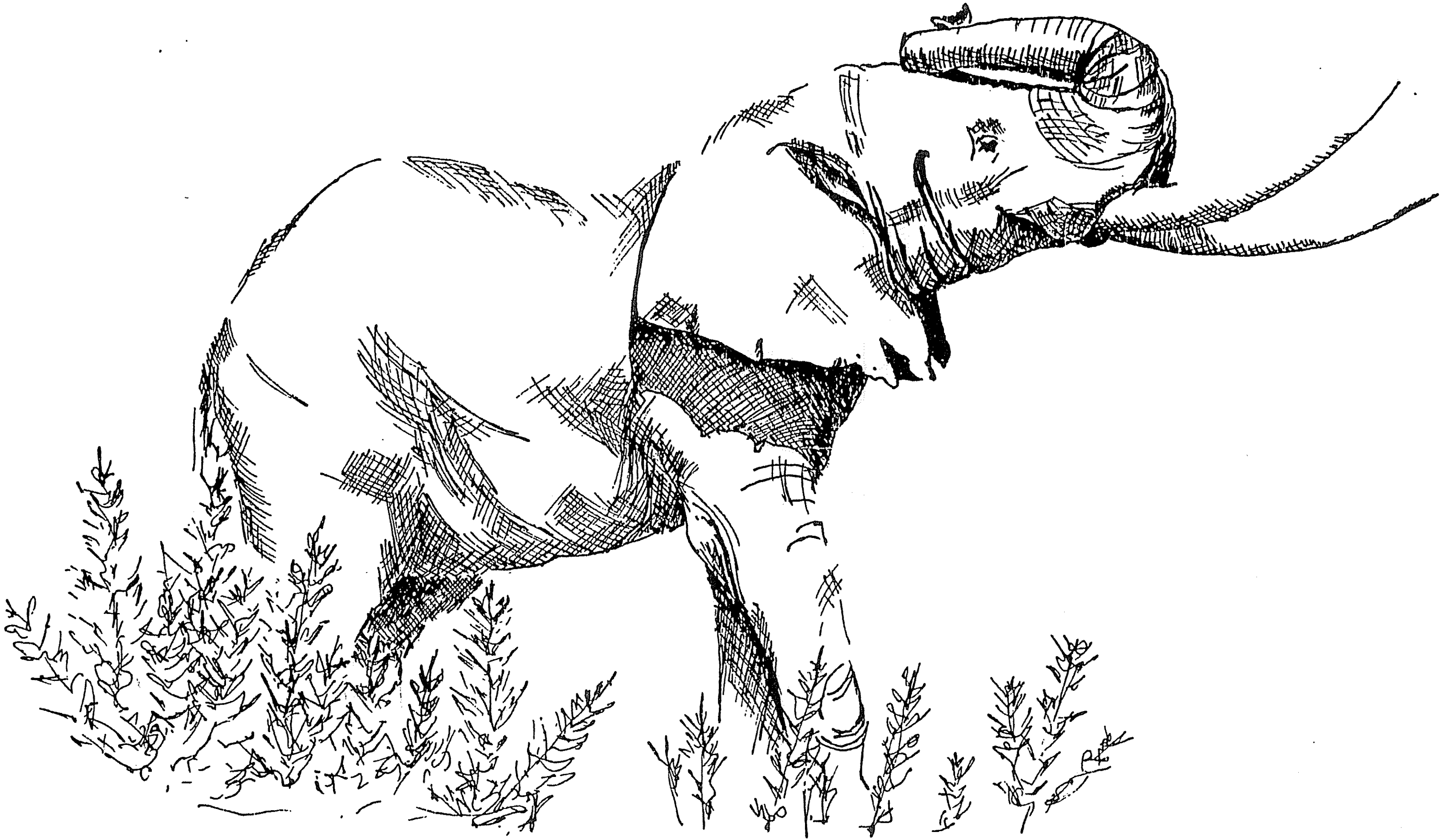


Plate 4.6. The trunk to head (M80). This behaviour is performed only by males in musth.

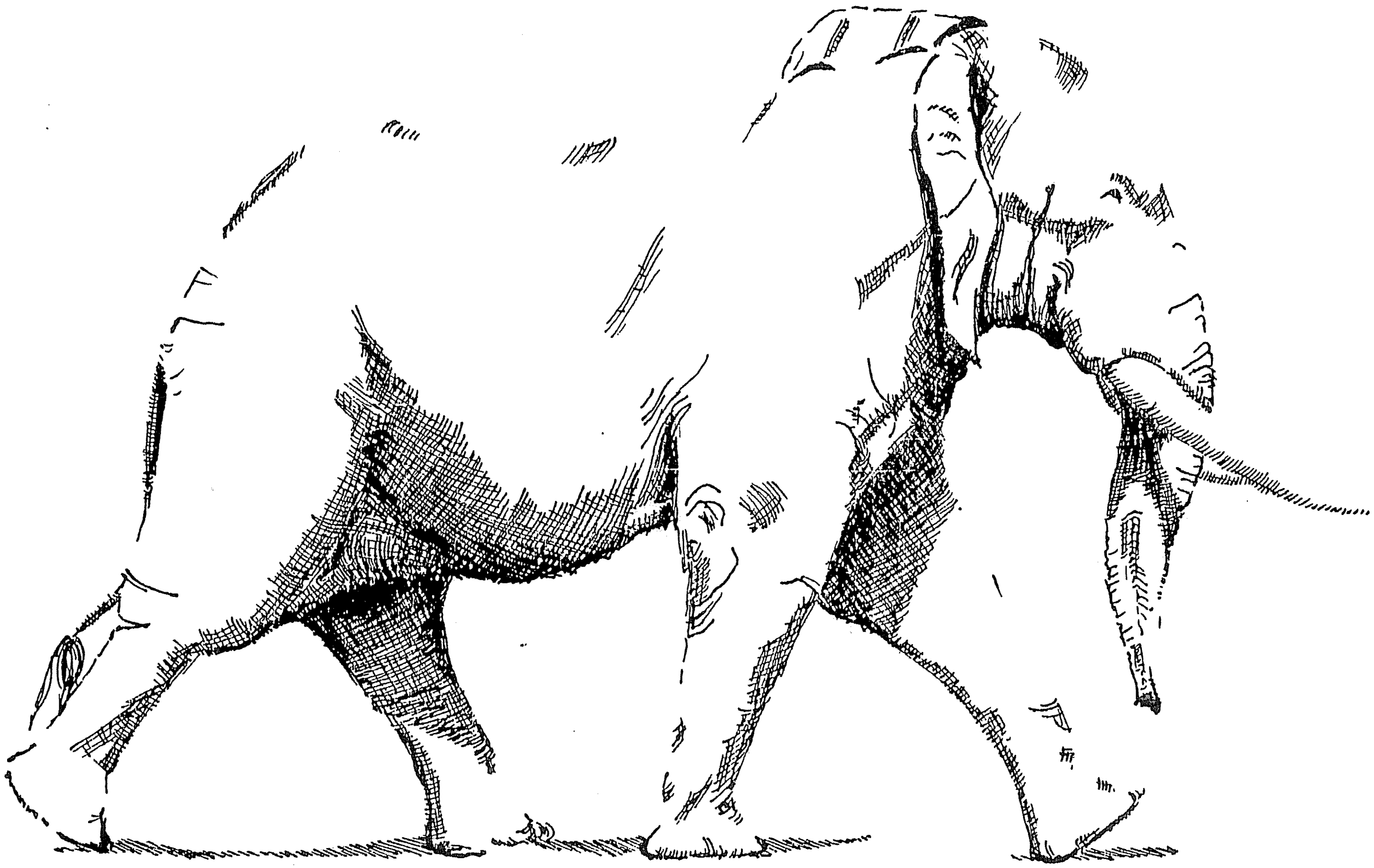


Plate 4.7. The musth walk (M13). Males in musth have a characteristic posture, particularly when moving. The head is carried well above rather than below the shoulder blades ("head high") and held at an angle such that the chin looks tucked in ("chin in"). The ears are carried high, slightly spread and held tensely.

performed in conjunction with the ear wave.

3) Trunk to head - this behaviour is performed by lifting the head high and with the mouth open, reaching up with the trunk to rub the forehead and temporal gland area (Plate 4.6).

4) Head oscillation - during this behaviour the head is rythmically swung in a figure of eight motion. It is done with vigour and the animal often lifts a foreleg off the ground to retain balance.

5) Tusking - the animal may get down on his knees and tusk the ground, lifting up clods of dirt and grass. Tusking vegetation, throwing bushes, logs and other objects at cars or other elephants may also be observed.

6) Marking - the animal is seen to rub the temporal gland area on trees.

7) Micturition without partial erection - urination is usually accomplished with a partial erection; males stand with their legs apart allowing the stream to be directed out between their hind legs. During musth, males will urinate with the penis still in its sheath allowing urine to spray onto the insides of their legs. Musth males may or may not attain a partial erection following micturition.

8) Musth walk - males in musth have a characteristic posture, particularly when moving. The head is carried above rather than below the shoulder blades ("head high") and held at an angle such that the chin looks tucked in ("chin in"). The ears are carried high, slightly spread and held tensely. This posture (Plate 4.7) allowed me to recognize males in musth from a distance of 300-400 meters.

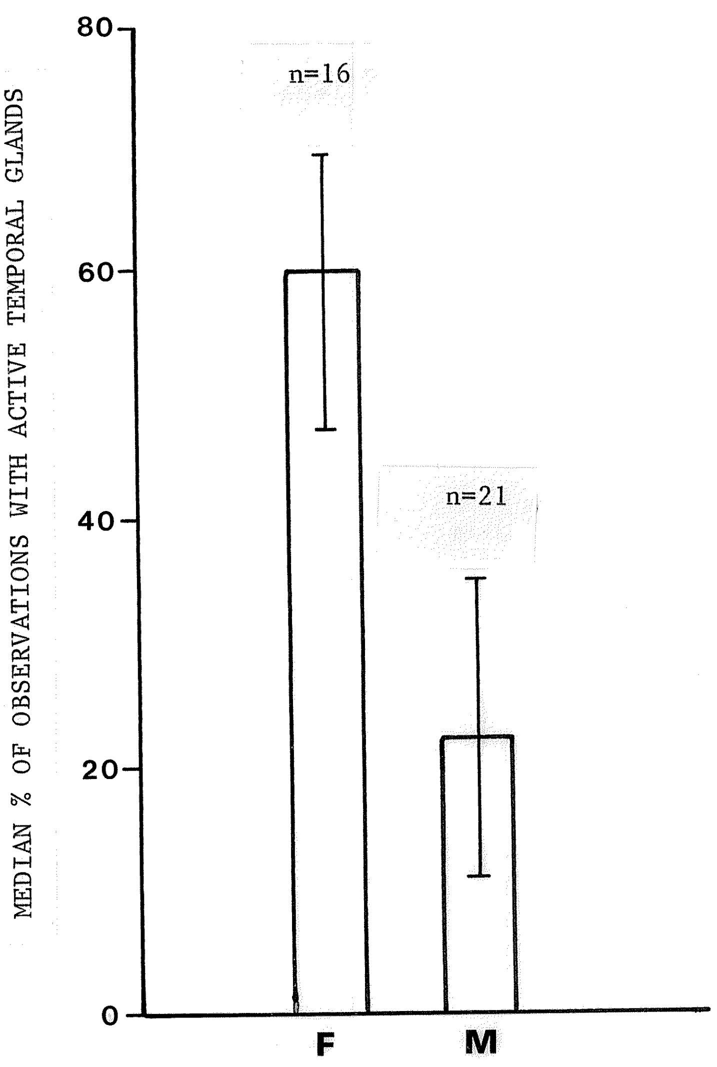


Figure 4.1. Percent of observations of individual males and individual females with secreting temporal glands. Medians and interquartile ranges are shown.

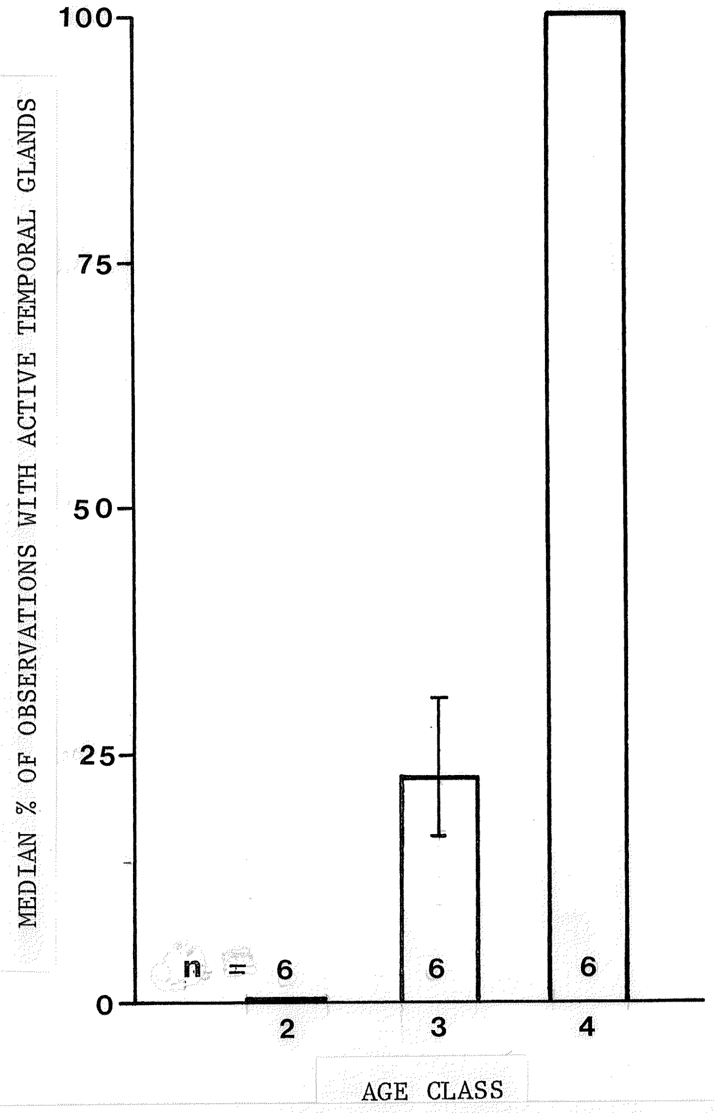


Figure 4.2. Percent of observations of individual males (Classes 2, 3 and 4) with active temporal glands when in association with females. Medians and interquartile ranges are shown.

4.5 RESULTS

4.5.1 The frequency of temporal gland secretions in males and females

Using those data collected through focal scan sampling (see Chapter 2), I have examined the percent of observations in which individual males and females secreted temporin. I have analyzed only those elephants for whom I have at least 11 data points. Females (n=16) were observed with temporin significantly more often than were males (n=21) (U=32.0, z=-4.2, $p<0.001$; median for females=60%; median for males=22%; Figure 4.1).

4.5.2 Age and the frequency of temporal gland secretion observed among males in association with females

Using those data collected through focal scan sampling, I examined the percent of observation in which males of different ages were observed with temporin when they were in association with females. I have analyzed only those elephants for whom I have at least 11 data points. Analysis reveals that gland activity changes with age. When in association with female groups the younger males (Classes 2 and 3; the data were too few for Class 1) were all observed without temporin significantly more often than with temporin (T=0, n=6, p=0.05; T=0, n=6, p=0.05, respectively). Class 4 males showed the reverse pattern when in association with females; these males were more often observed with than without secretions (T=0, n=6, p=0.05), suggesting that among the older males there is a relationship between temporal gland secretion and sexual activity. Figure 4.2 shows the median percent of observations in which individual males from Classes 2, 3 and 4 were observed with temporin when with females.

4.5.3 Determination of musth in L. africana

The occurrence of musth in the genus E. maximus is determined primarily by the onset of temporal gland activity (Jainudeen et al., 1972a). As shown above, the temporal gland in L. africana may be active in males and females of all ages and is therefore not a reliable indicator of musth. Poole and Moss (1981) found the presence of GP to be the most reliable means of determining musth in this genus.

Here I have used the data collected on Class 4 focal bulls to examine the coincidence between the occurrence of GP and temporin. Each of the 19 Class 4 males was sighted at least 15 times. Out of a combined total of 509 sightings of these males (Table 4.1), 40.3% (n=205) showed GP in conjunction with temporin, 51.3% (n=261) exhibited neither, 7.8% (n=40) showed only temporin and only 0.6% (n=3) were observed with GP and but without temporin. These results clearly show the coincidence of temporin and green penis (urine dribbling) in the largest males, indicating that musth does occur in L. africana (see also Poole and Moss, 1981), but that its occurrence cannot be determined by temporal gland activity alone.

Table 1. Observations (n=509) on 19 Class 4 males (each male was observed at least 15 times) showing the coincidence of GP and temporin.

	GP Present	GP Absent
Temporin Present	205	40
Temporin Absent	3	261

4.5.4 Musth and sexual activity

Using the musth data collected on eight of the largest Class 4 focal males (M13, M126, M22, M28, M41, M117, M73, M99) I have examined

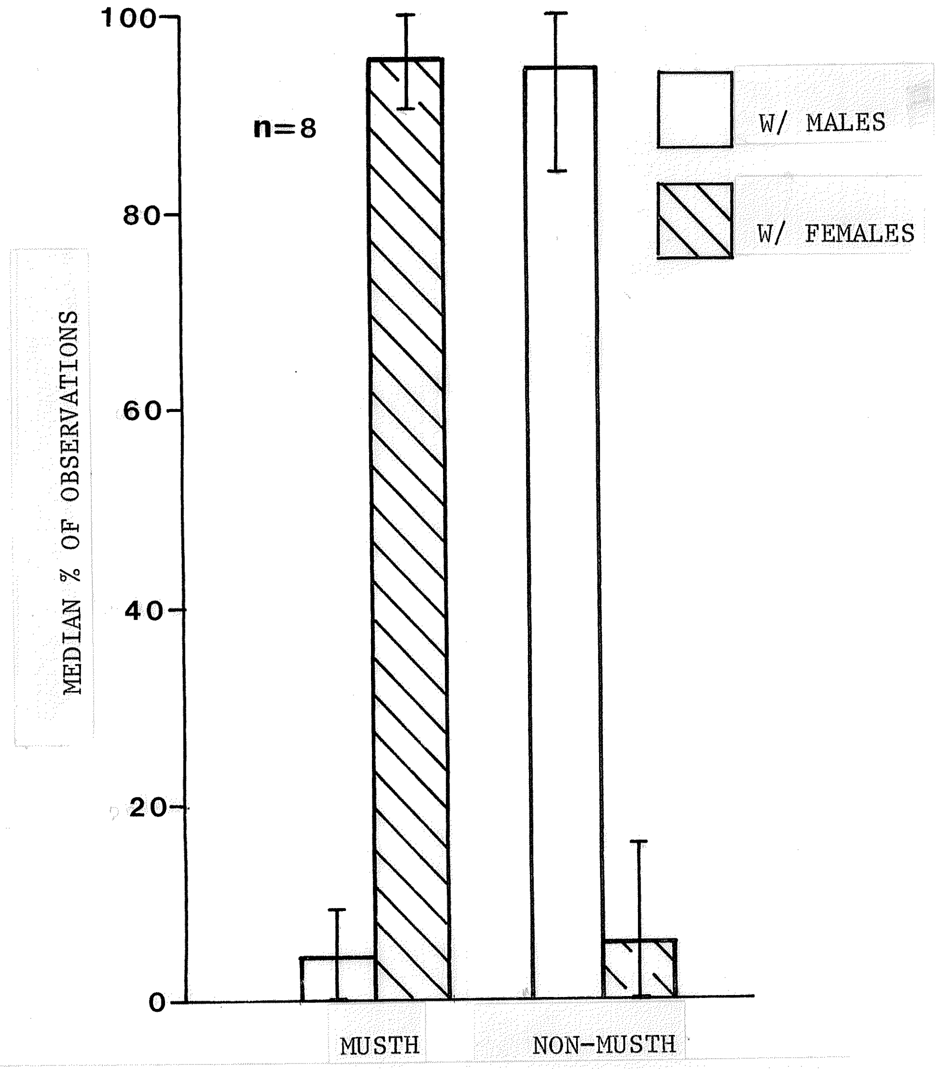


Figure 4.3. Percent of observations with males and females when in musth and when not in musth. Medians and interquartile ranges are shown.

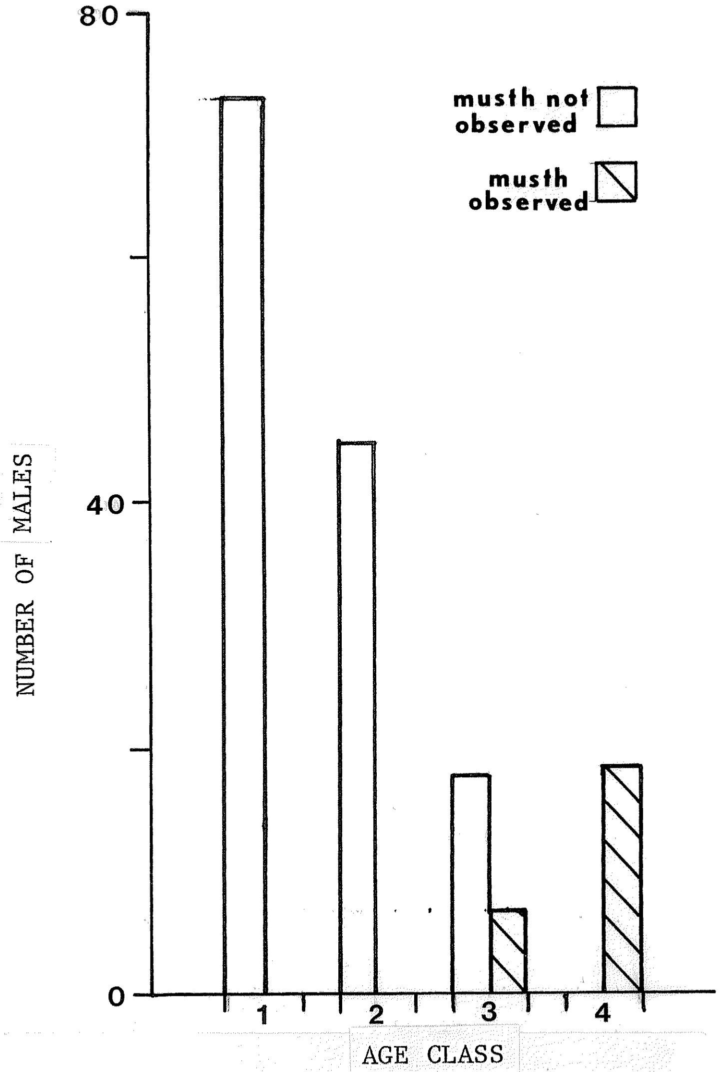


Figure 4.4. Age distribution of musth in the Amboseli population

the proportion of non-musth and musth sightings that each male spent in association with males or females (Figure 4.3). Males in musth were significantly more likely to be found in association with females than in association with other males (T=0, n=8, p=0.01). The same males, when in non-musth state, were significantly more likely to be observed in the company of other males than with females (T=0, n=8, p=0.01), indicating that musth is a sexually related phenomenon.

4.5.5 Age distribution of musth in the Amboseli population

All Class 4 males (n=19) come into musth and seven of the 25 Class 3 males have been observed in musth. The remaining 136 adult males have never been seen in musth (Figure 4.4). No males under twenty-five to thirty years of age have ever been observed in musth.

4.5.6 Duration of musth periods

The date given for musth onset is the first day the animal was seen in musth. Likewise, the date given for musth termination is the last sighting of an individual on which musth could be detected. The figures given for the duration of musth periods are minimum durations since males were not observed everyday.

The duration of musth periods was highly variable between individuals. Males were observed to stay in musth for as short as one day or for up to at least 127 days (Figure 4.5). Although the duration of musth periods was highly variable between individuals the lengths of musth periods for individual males were, in general, similar from one period to the next (see those animals for whom the dates of musth periods were known to within a week: M99, M80, M57, M119; Figure 4.5). The duration of musth periods were closely correlated with age and dominance (see Chapter 6).

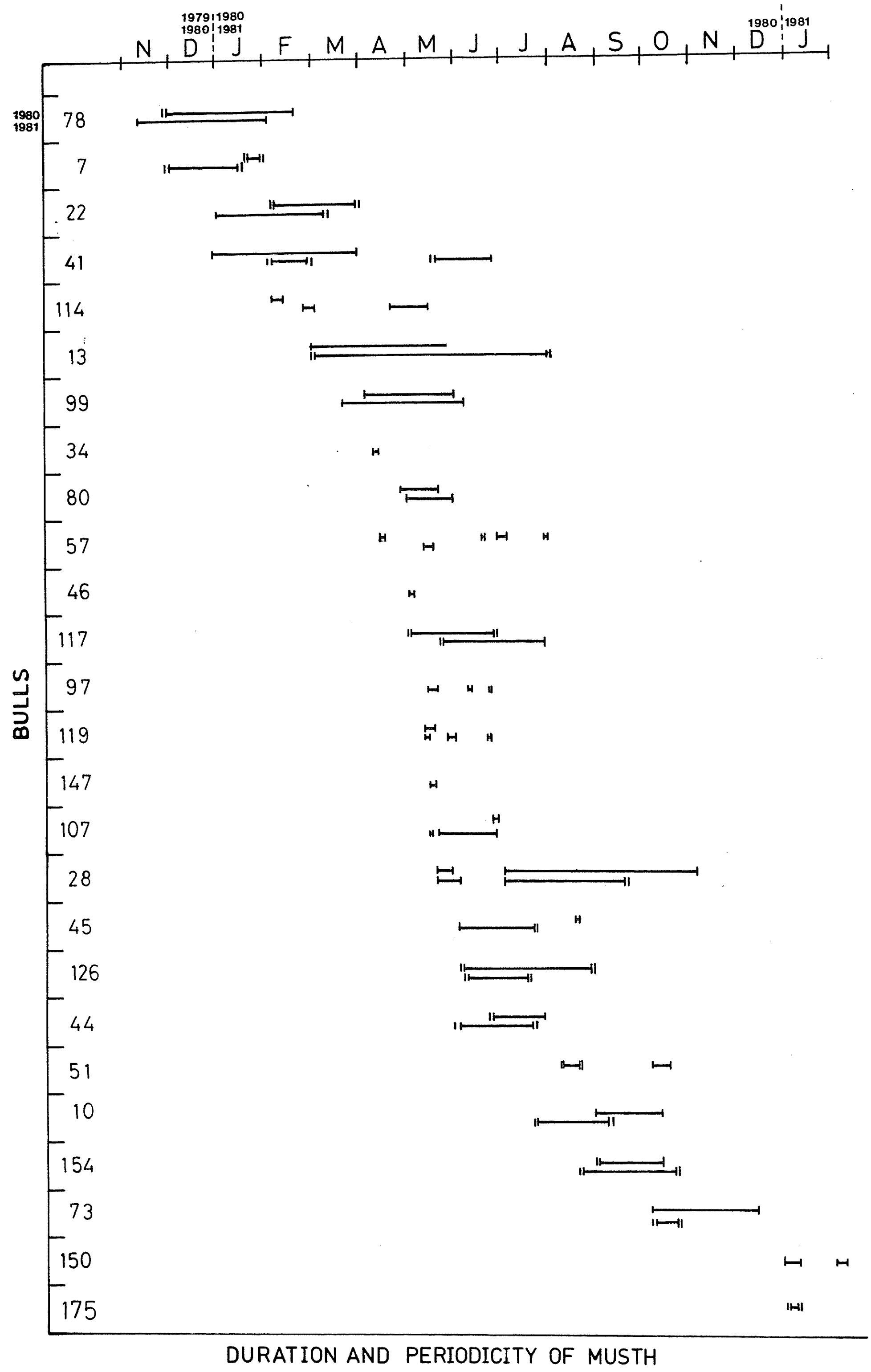


Figure 4.5. Musth duration and timing for all males observed in musth during the study period (n=26). Dates of onset and termination of musth are given as the first and last date that an individual was seen in musth. |—| indicates that musth onset and/or termination were known to within one week. ||—|| indicates that musth onset and/or termination were not known to within one week.

4.5.7 Timing of musth periods

Males were observed in musth throughout the year (Figure 4.5) with peak occurrences during the first six months, during and following the two rainy periods (see Chapter 5). Among those males for whom there are musth records for at least four years in succession, the onset of musth periods are usually closely synchronized from one year to the next (Figure 4.6). Of the 19 males that were observed in musth during both years of my study (Figure 4.5), eight came into musth within two weeks, and 13 males within three weeks, of the recorded date of musth onset for the previous year.

4.5.8 Patterns of musth onset and termination

In the Amboseli population three patterns of musth onset and termination could be distinguished among males. These patterns changed with age and I have divided males into three groups (independent of the size classes described in Chapter 2) according to which pattern they were observed to follow during their 1981 musth period.

Group 1 - the oldest males (n=10; all individuals from Class 4) came into musth before they were seen associating with female groups. They remained in complete musth for the full time they associated with females and only dropped out of musth when they had returned to their "retirement" areas (see Chapter 3).

Group 2 - these males (n=6; all individuals from Class 4) joined female groups and were sexually active but did not show signs of musth until they had been in association with females for several weeks. The temporal glands of this group became swollen as did those of the Group 1 males. This group usually dropped out of musth several weeks before they were seen to leave females.

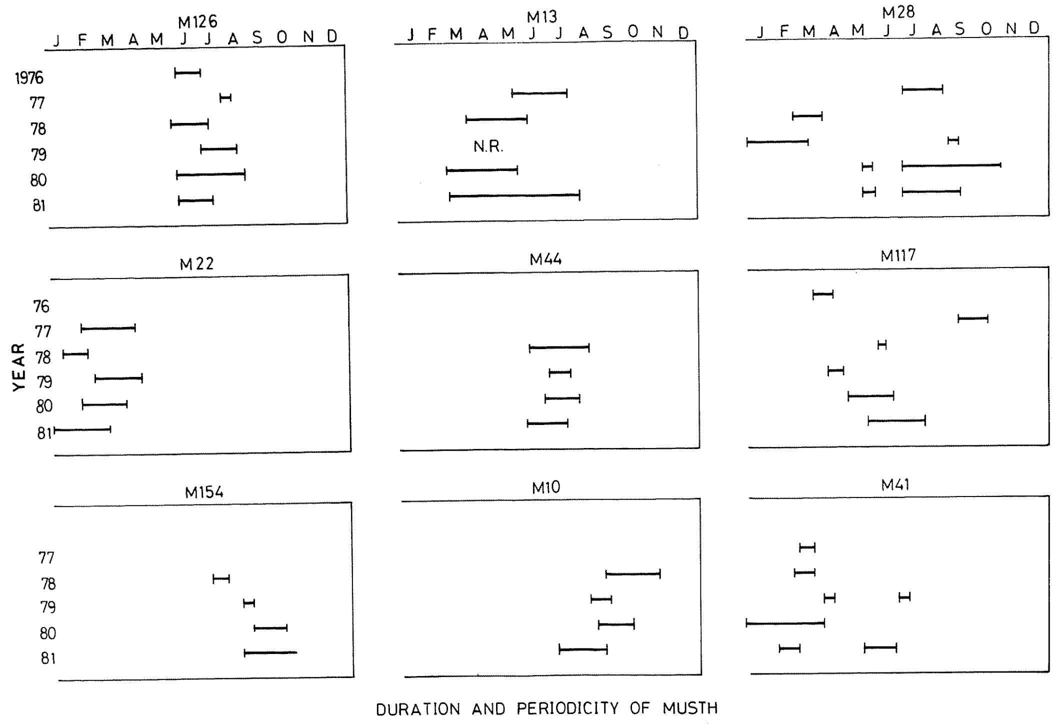


Figure 4.6. Musth timing and duration for males (n=9) for whom there are musth records for at least four years. Dates of musth onset and termination are given as the first and last date that an individual was seen in musth.

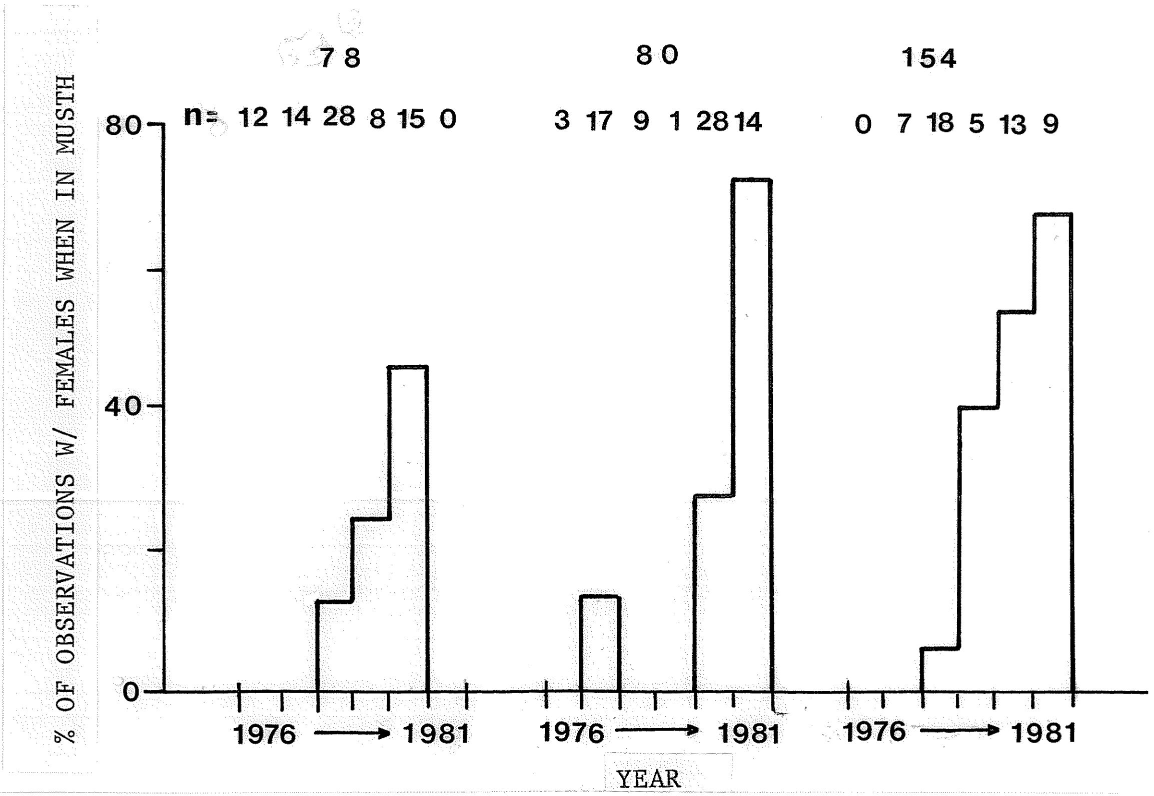


Figure 4.7 Age related increase in the percent time spent in musth when with females for males M78, M80, M154. The numbers of observations of each male with females from 1976 through 1981 are given.

Group 3 - these males (n=10) came into musth after having associated with females for approximately one month. They were rarely observed to stay in musth for more than a day or two at a time and would come into musth several times during a sexually active period. The temporal glands of males in this group became only slightly swollen. These males could be forced out of musth by higher ranking males (see Chapter 6). Three of these males belonged to Class 4 and the remainder to Class 3.

The long term records reveal that males attain longer musth periods as they age (Figure 4.7).

4.5.9 Postures and behaviours of males in musth

a) Ear wave - All males ear waved during a higher proportion of musth watches than non-musth watches (low intensity ear wave: T=0, n=20, $p<0.001$; high intensity: T=0, n=12, $p<0.01$; Table 4.2) and with the exception of two watches, both on male M99, males were observed to ear wave only when in musth.

b) Musth rumble - this vocalization was never heard by non-musth males (T=0, n=9, $p<0.01$; Table 4.2).

c) Trunk to head - with the exception of two non-musth watches, this behaviour was observed only in musth males. Again both of the non-musth watches were on male M99. At the time I suspected that he was coming into musth (he was not in his bull area; he joined females for several days; and he behaved aggressively towards other males), but he did not show the more overt signs of musth until several months later. Otherwise all trunk to head behaviour was performed by males in musth (T=3.5, n=16, $p<0.01$; Table 4.2). My impression is that this behaviour is usually performed by males that are either in the initial stages of a musth period or by the younger males who periodically come into musth.

d) Head oscillation - the sample size was too small to test statistically (n=4; Table 4.2), but ad libitum data do suggest that this occurs primarily during musth.

e) Tusking - the sample size was too small to test statistically (Table 4.2). However, this behaviour was observed in all 5 fights that occurred between musth males during the study period.

f) Marking - males were observed rubbing their temporal gland areas against trees both in and out of musth, but this behaviour occurred more often during musth than non-musth (T=2, n=7, p=0.05; Table 4.2). On several occasions I collected the secretion left on trees following "marking". The secretion had what I would describe as a musky odour. A Maasai, D. Onina, described the secretion as smelling like a male goat. On one occasion I watched a male in musth rub his temporal gland on several trees in succession and then return later to smell where he had "marked".

g) Micturition without partial erection - males were only observed to urinate in this fashion when they were in musth (T=0, n=14, p<0.01; Table 4.2).

Table 4.2. Percent of musth and non-musth watches in which particular behaviours were observed. See Appendix 1 for the number of watches done on each male during the study period. EW li=Ear wave low intensity; EW hi=Ear wave high intensity; MR=musth rumble; TrH=trunk to head; HO=head oscillation; T=tusking; M=marking; Uw/oE=urination without partial erection. M=in musth; Nm=not in musth.

Percent of musth and non-musth watches

	EW li		EW hi		MR		TrH		HO		T		M		Uw/oE	
male	M	Nm	M	Nm	M	Nm	M	Nm	M	Nm	M	Nm	M	Nm	M	Nm
7	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	40	0	20	0	20	0	5	0	5	0	5	0	0	0	5	0
13	41	0	35	0	0	0	0	0	0	0	0	0	0	0	6	0
22	36	0	9	0	9	0	0	0	0	0	0	0	0	0	0	0
28	25	0	10	0	3	0	0	0	0	0	0	0	18	0	5	0
34	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0
41	30	0	10	0	0	0	30	0	0	0	0	0	0	0	10	0
44	20	0	0	0	20	0	20	0	0	0	0	0	20	0	0	0
46	0	0	0	0	0	0	100	0	0	0	0	0	0	0	100	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0
57	0	0	0	0	0	0	20	0	0	0	0	0	0	0	20	0
73	57	0	43	0	7	0	0	0	0	0	0	0	7	0	0	0
78	15	0	8	0	8	0	54	0	8	0	0	0	0	0	15	0
80	20	0	20	0	0	0	60	0	0	0	0	0	0	0	20	0
97	20	0	0	0	0	0	20	0	0	0	0	0	0	0	60	0
99	67	11	44	22	0	0	11	22	0	0	0	0	0	0	0	0
107	22	0	11	0	11	0	22	0	0	0	0	0	22	0	56	0
114	30	0	0	0	10	0	10	0	0	0	0	0	0	0	10	0
117	69	0	0	0	23	0	0	0	0	0	0	0	31	0	8	0
119	33	11	0	0	11	0	11	0	11	0	0	0	0	0	0	0
126	7	0	0	0	0	0	0	0	0	0	0	0	12	0	7	0
147	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0
150	28	0	28	0	0	0	14	0	14	0	0	0	0	0	0	0
154	27	0	9	0	0	0	27	0	0	0	0	0	0	0	0	0
175	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

4.6 DISCUSSION

The relationship between musth and sexual activity in elephants has been a subject of controversy for many years. As recently as 1971 Sikes said of the Asian elephant, "recently the popular idea that periods of rage or musth in bull elephants had a connection with the sexual cycle was firmly refuted". However, the studies by Jainudeen et al. (1972a), Eisenberg et al. (1971), and Kurt (1974) on *E. maximus* and my own study on *L. africana* clearly indicate that musth is a sexually related phenomenon. Eisenberg et al. (1971) suggested that the phenomenon of musth should be viewed as similar to rutting in ungulates. The physical and behavioural characteristics of musth in elephants of both genera are similar to those described for rutting ungulates (see Chapter 1). The significance of self-marking with urine will be discussed in Chapter 8.

In most ungulates males are temporally synchronized in their rutting behaviour. Rut, or musth, among elephants differs on this issue; individuals of both genera may be observed in musth throughout the year. However, in areas where there is a single peak in breeding activity among the females, as in southern Africa (Hanks, 1979), musth among males is likely to be more closely synchronized.

The phenomenon of musth in the two genera is remarkably similar, not only in the physical characteristics of musth, but also in the behaviour and postures of musth males. All of the behaviours and postures described for the Asiatic genus were present in *L. africana*. There were several behaviours that I observed, the musth rumble and the ear wave, which have not so far been described for the Asiatic elephant.

The only difference that I was able to detect between the two genera with respect to musth is that males of *E. maximus* appear to come into musth at a much earlier age than do males of *L. africana*. However, the data collected on the age distribution of musth in Asia were from captive males. In this study, dominant males were able to "force" subordinate males out of musth (see Chapter 6), so it seems reasonable to suggest that older males may be able to suppress the onset of musth among younger males. If this is so, then the age difference in the onset of musth could reflect differences between free-living and domesticated elephants rather than to a genus difference. There are very few male African elephants in captivity, but Eisenberg (pers. comm.) observed a fifteen year old captive male elephant exhibiting what he thought were the signs of musth. This is at least 10 years younger than any of the males observed in musth in the Amboseli population, but very similar to those data collected on captive Asiatic elephants (Eisenberg et al., 1972; Jainudeen et al., 1972a).

Jainudeen et al. (1972a) noted that when two elephants meet they will smell one another's temporal gland region, suggesting that the gland is used in communication. The same behaviour occurs in both males and females of the African genus (see Chapter 3) during greetings. Males may also smell the genitals of another male during greetings (see Chapter 3; Plate 3.1), indicating that they may be attempting to gain information about the sexual state of the other individual.

Studies of the temporal gland in the African elephant have suggested several functional possibilities. Laws (1970) suggested that the gland may secrete in response to a massive release of adrenalin in the blood stream, and may often be indicative of alarm or aggression. Buss et al. (1976) found individual differences in the chemical composition of the gland among five adult males, and they suggested that the temporal gland may have a pheromone producing function which serves in individual recognition. They found that the gland was more active during the dry season than during the wet season, and they were led to conclude that the gland may also secrete in response to stress. Sikes (1971) thought that the gland secreted in response to several different stimuli such as the approach of a potential rival or mate and as a consequence of stress, pain or disease. She also suggested that the temporal gland could function in communication, such as in marking, individual recognition and perhaps as an indication of "acceptance or rejection". Short et al. (1967) and Hanks (1979) found small pieces of wood in the temporal gland suggesting that the gland is employed in marking. Elephants secrete temporin during moments of intense social excitement such as during greeting ceremonies (Moss, 1981), the birth of a calf (pers. obs.) or at the scene of a mating (pers. obs). Dying elephants secrete copiously (pers. obs.), indicating that the gland may function in response to pain.

In conclusion, it would seem that the temporal gland may secrete in response to several stimuli, but ultimately the function of the gland is probably communication. In this particular study I am interested in the function of the gland with respect to the phenomenon of musth. It seems that secretions from the gland during musth communicate the identity and sexual state of the individual both to rival males and to potential mates. There are several behaviours of males in musth which support this idea. Males of both genera were seen rubbing the temporal gland area against trees more often during musth than non-musth periods (_E. maximus_: Eisenberg, et al., 1971). Musth males of both genera were observed to lift the head high and rub the temporal gland area (_E. maximus_: Eisenberg et al., 1971) and Eisenberg et al.(1971) have suggested that this behaviour may function to disperse the scent, communicating to other elephants the presence of a musth male. Finally, it has been suggested to me (N.B. Davies, pers. comm.) that the ear wave probably functions to waft the scent of the secretion towards rival males. Since males usually only wave the ear closest to the animal that they are threatening, this is a very likely explanation.

It would seem that the phenomenon of musth is not functionally different from rutting behaviour in ungulates. In elephants a superficially different system has evolved due to the relatively lower degree of breeding seasonality of the female compared to seasonally breeding ungulates.

CHAPTER 5

ECOLOGICAL VARIATION AND REPRODUCTIVE PATTERNS

5.1 INTRODUCTION

Sexual dimorphism in body weight is pronounced in elephants, fully grown males weighing almost twice that of fully grown females (Laws, 1966). In many species larger males gain access to females and have a higher mating success (Le Boeuf, 1974; Trivers, 1976; Davies and Halliday, 1979; Howard, 1978). In species where there is competition for females and large males gain a competitive advantage, selection will favour an increase in male body size (Darwin, 1890). In elephants, large males rank higher than smaller males (Croze, 1974 and see Chapter 6) and gain access to oestrous females (Short, 1966; Laws and Parker, 1968 and see Chapter 7).

Barnes (in press.) found that during the wet season males traveled long distances each day apparently in search of oestrous females. The number of family units encountered by a male per hour was significantly correlated with the time spent travelling, suggesting that males who traveled furthest and fastest would have an increased probability of finding oestrous females (Barnes, in press). Barnes (1979) speculated that since the energy per unit weight expended during locomotion decreases with increasing body size (Taylor et al., 1970; Taylor, 1977), large males expend less energy per unit weight travelling than do smaller males and may be able to travel for longer distances without foraging. The speed of locomotion has also been found to increase with increasing body size (Pennycuick, 1979). For these reasons larger males may have a higher probability of locating an oestrous female than smaller males (Barnes, 1979).

However, large body size in males may also be associated with costs. In some species larger males have been found to suffer increased mortality and greater suceptibility to disease (Clutton-Brock et al., in press; Selander,1965 and 1972; and see Laws and Parker, 1968) and they may lose fat reserves faster than small males (Searcy, 1979). In sexually dimorphic species the difference in body size and metabolic requirements may mean that males and females exploit food resources differently (Red deer: Clutton-Brock et al., in press and Staines and Crisp, 1978; baboons: Demment, 1979; Post, 1981; Red kangaroos: Newsome, 1980; moose: Belovsky, 1978) often resulting in the spatial segregation of the two sexes outside the breeding season (Red deer: Clutton-Brock et al., in press).

Several authors have noted that groups of male elephants utilize areas removed from female groups (Percival, 1924; Laws and Parker, 1968; Hendrichs, 1971; Croze, 1974; Martin, 1978). If the nutritional requirements of large males cannot be met in areas used by females, it may mean that larger males are not able to devote as much absolute time to reproductive activities as smaller males. In redwing blackbirds, Searcy (1979) found that larger males had less energy available for displays and territorial defense than had smaller males; large males who were provided with food displayed more. In some other species large males spend less time in association with females than do smaller males (Walia ibex: Dunbar and Dunbar, 1981; Red deer: Clutton-Brock et al., in press) suggesting that there may be an upper limit to male body size imposed by energetic costs.

It has been observed that older male elephants spend very little time in association with females. As early as 1890, Darwin noted that adult males of the genus Elephas maximus spend much of their time alone. Early hunters in East Africa observed that male elephants (Loxodonta africana) with heavy ivory were unlikely to be found with female groups, and the commonly held opinion was that the younger males were responsible for paternity (Percival, 1924). However, Wanderobo hunters believed that although the large males spent little time with females they still fathered most offspring (Percival, 1924). Since that time researchers have continued to report that large males are found with female groups only infrequently (Croze, 1974; Laws et al, 1975; Martin, 1978) and Martin (1978) observed that large bulls appeared to show little or no interest in females. Laws et al. (1975) noted that the age distribution of males in bull groups was older than that with cows, and they suggested that either bulls tend to remain with their families for several years after reaching sexual maturity, or that there is a tendency for young adult bulls to spend more time in association with females. This pattern of behaviour has led people to assume that older males are not reproductively active. However, recent evidence from the Amboseli study (Poole and Moss, 1981 and see Chapter 4) has shown that the older males are sexually active.

If, large body size confers some energetic (Barnes, 1979) and reproductive advantages (see Chapters 6, 7, and 8), but larger males spend less absolute time with females than smaller males, then there may also be energetic costs associated with large body size. In this chapter I will discuss the response of elephants to ecological variation in Amboseli, particularly as it relates to reproduction. The questions posed in this chapter require detailed and precise data on size and sex differences in foraging and energetic requirements to be answered properly. I do not have these data, but, the long term records on ecological fluctuation and the elephants' patterns of response to this variation do provide some insights.

This chapter is necessarily based on long term data that have been collected by several different people working in Amboseli during the past ten years. Those results based on data that were collected by persons other than myself are explicitly stated as such. The dynamics of vegetation biomass and quality in Amboseli is the work of Western and co-workers (see Lindsay, 1982; Western and Lindsay, in prep.). The pre 1980 data on group size and the seasonal occurrence of oestrus were collected by C. Moss.

5.2 METHODS

5.2.1 Rainfall records

The rainfall records I have used in this study were taken in the centre of the Amboseli basin at the National Park Headquarters, in Ol Tukai. Rainfall records have been made in Ol Tukai on a daily basis since 1974. Although rainfall in Amboseli is highly localized and the amount of rain on a particular day may vary markedly from place to place, over a longer period the amount of rainfall in different habitats tends to be similar (Lindsay, 1982).

5.2.2 The wet and dry season

The rainfall pattern in Amboseli has been described in Chapter 2. There are two rainy and two dry seasons. The two rainy periods are separated by a short dry season or "mid-rains" in January and February. Western and Lindsay (in prep.) have shown that the biomass of vegetation increases dramatically following the short rains in November/December and remains relatively high until several months after the end of the rains in May. Since elephants are not responding to rainfall, but to the subsequent growth of vegetation, I have defined the wet season as December through June inclusive, and the dry season as July through November.

5.2.3 Woody Vegetation Density

To estimate woody vegetation density I used a modification of the Bitterlich stick or "occlusion quadrat". The technique has been described in Cooper (1957). Briefly, the observer sights along a calibrated stick with a crossbar, as it is swung around 360 degrees, recording all individuals of each species that appear wider than the crossbar. I ran seven transects each including six points separated by 0.5km.

5.2.4 Long term records

The collection of these data has been described in Chapter 2.

5.2.5 Activity budgets

The proportion of time that individuals spent engaged in various activities were estimated from data collected through focal sampling (see Chapter 2; Section 5.2 for a description of the activities and methods of focal sampling). The data collected for a particular individual were used only if I had obtained at least four half-hour watches under the particular social and sexual state in question.

5.3 RESULTS

5.3.1 Rainfall, vegetation biomass and nutritional quality

Western and Lindsay (in prep.) have found that, with the exception of those areas with permanent ground water, herb layer vegetation biomass production is significantly related to wet season rainfall. The herb layers of the swamp edge habitats are less affected by seasonal rainfall and these areas consistently provide the most abundant, but lowest nutritional value (crude protein content) source of food (see Lindsay, 1982). The herb layers in the basin woodlands and outlying bushlands, without permanent water, are only seasonally abundant, but are of higher protein content throughout the year (see Lindsay, 1982). As a population, the elephants respond to the fluctuating pattern of vegetation productivity by utilizing the woodlands and bushlands in the wet season and returning to the swamps and swamp edge grasslands in the dry season (Western, 1975; Moss, 1977; Lindsay, 1982).

Individual families follow this same general pattern (Moss, 1981). Family units belonging to the Central sub-population have dry season home ranges near the permanent swamps and migrate to the surrounding bushland during the rains.

5.3.2 Rainfall and female group size

Elephants respond to the increase in food availability during the rains by aggregating into larger groups. Figure 5.1 illustrates the pattern of rainfall and mean monthly female group size through six years (October, 1975-October,1981; those data recorded from October, 1975 through December, 1979 were gathered by Cynthia Moss; see Appendix 2 for mean group sizes, standard deviations and numbers of groups for data collected by me during the study period). Although the variance in group size each month is very high, the general trend of larger groups during seasons and years of high rainfall is still apparent. Mean monthly group size peaks following periods of high rainfall and remains high until the biomass of vegetation begins to decline during the dry season. During the years of low rainfall and biomass (1976 and early

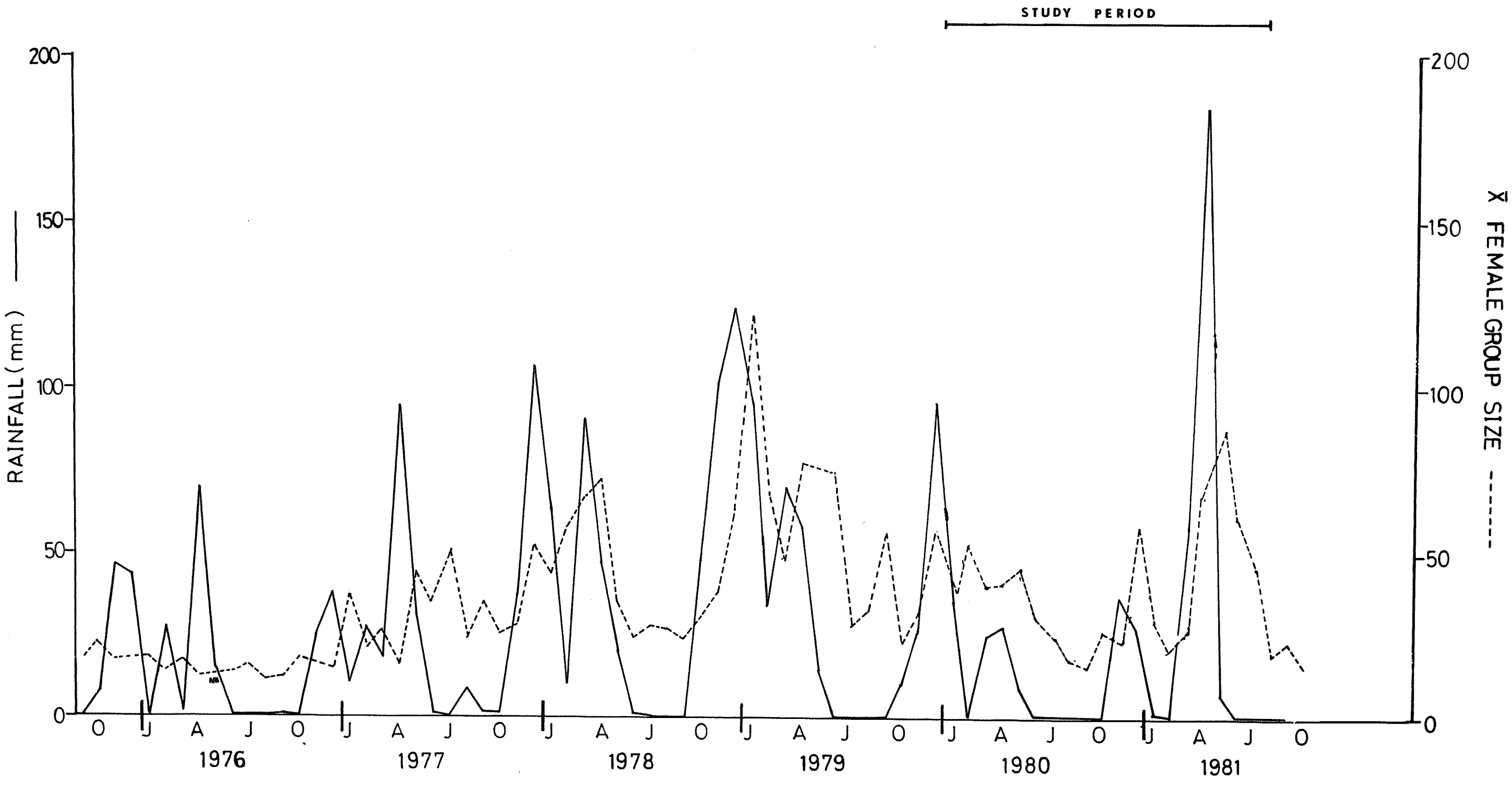
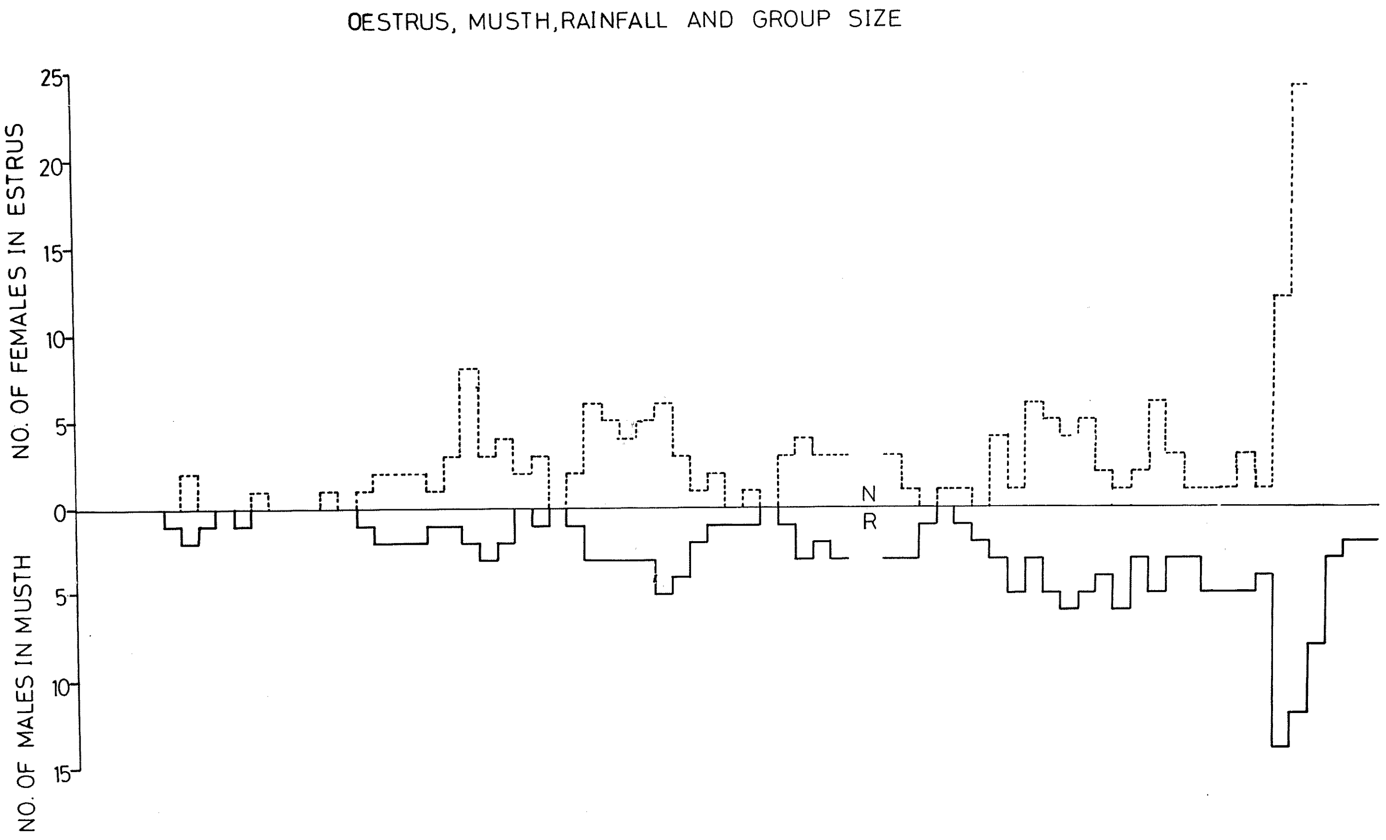


Figure 5.1. The relationship between rainfall and mean monthly female group size. Solid line indicates rainfall (mm.) and dotted line indicates mean female group size.

Figure 5.7. Monthly frequency of oestrous females and musth males from September, 1975 through June, 1981. NR=no record of that month.



OESTRUS, MUSTH, RAINFALL AND GROUP SIZE

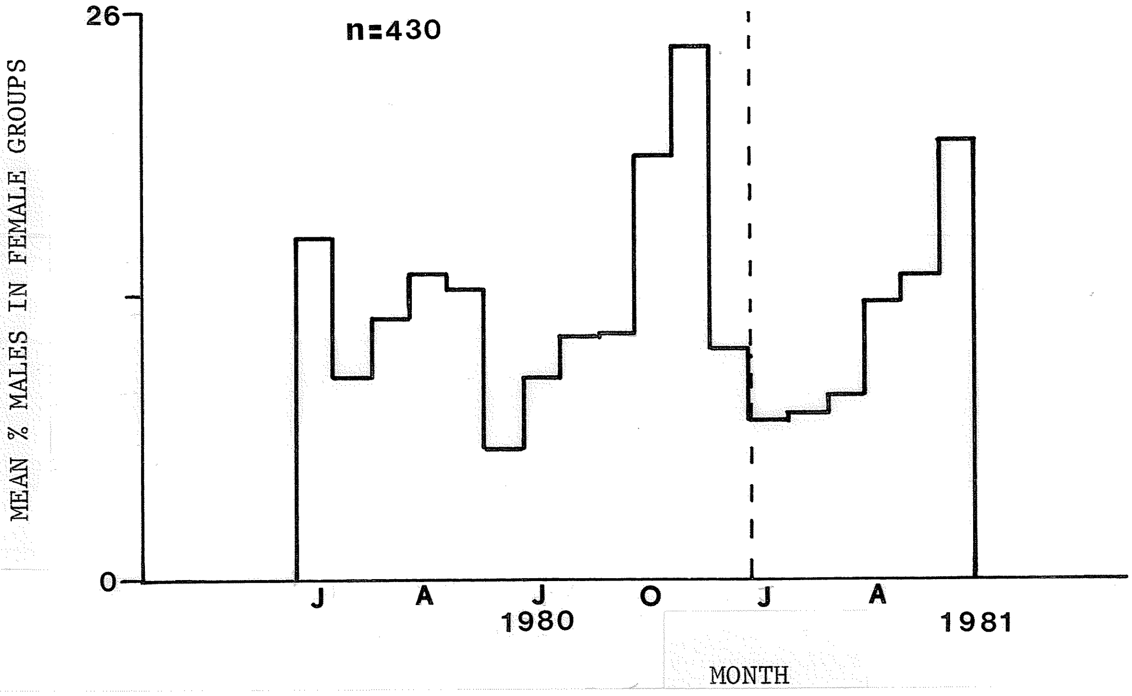


Figure 5.2. The mean monthly percent of males in female groups.

1977) mean group size remained low throughout the year.

Systematic ground counts (Lindsay, 1982) and aerial counts (Western, 1975; Western and Lindsay, in prep.) show the same pattern. Lindsay (1982) found that the proportion of female groups with more than 50 members dropped off after the height of the rains and then continued to decline gradually through the dry season. Concurrently, the total number of female groups in the basin steadily increased, such that during the rains elephants tended to move in several large groups while during the dry season there were many more smaller groups (Lindsay, 1982). Monthly aerial counts by Western (1975 and Western and Lindsay, in prep.) show the same pattern of group dynamics both seasonally, and from periods of drought to years of higher than average rainfall.

On an individual level, particular family units tend to associate with large aggregations in the wet and early dry season, but move in smaller groups in the mid and late dry season (Moss, in prep.). During severe droughts, such as in 1976, even family units have been known to break up to feed for short periods of time (Moss, 1977). The smaller group sizes seen in the dry season indicate that the decline in abundance of nutritious food and profitable foraging may limit group size (Lindsay, 1982; Moss, 1977).

During my study period the mean monthly proportion of males in female groups fluctuated seasonally, indicating that the absolute number of sexually active males varied through the year (Figure 5.2).

5.3.3 Habitat use: males versus females

Lindsay (1982) found that bulls, in Amboseli, preferred the wet swamps and open woodlands in the dry season, while female groups utilized the open woodlands in the wet season and the swamp edge grasslands in the dry season. He observed that the larger female

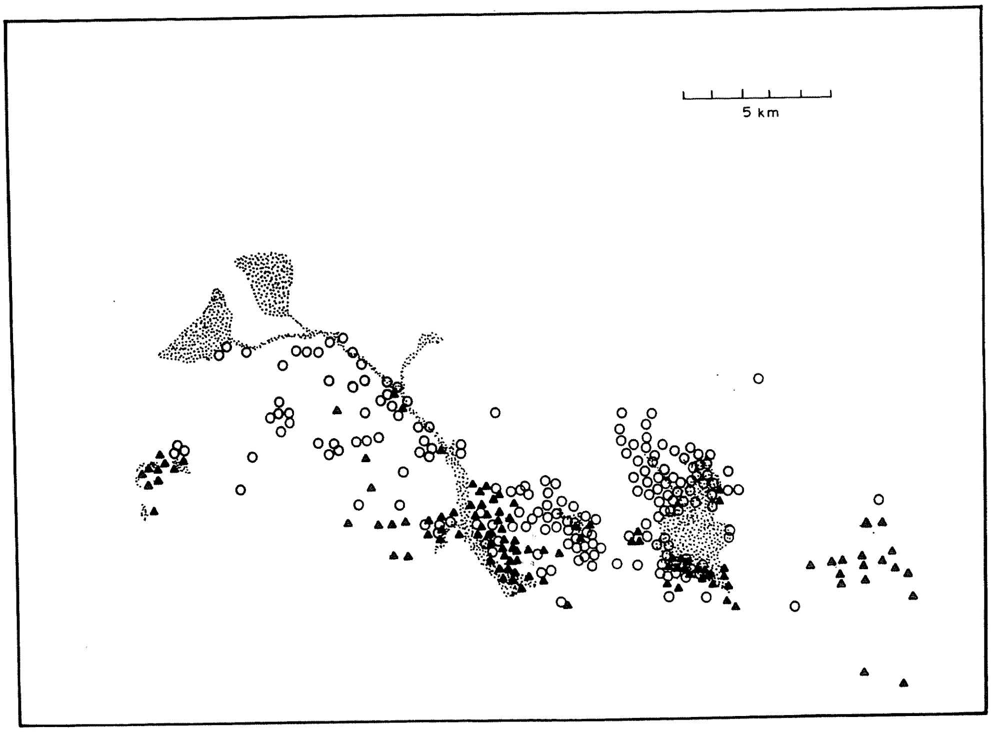


Figure 5.3. Areas utilized by groups of cows and calves (○) and males (▲) when feeding. Only those groups of males with at least one Class 4 or socially mature male present are included. Each symbol indicates one group.

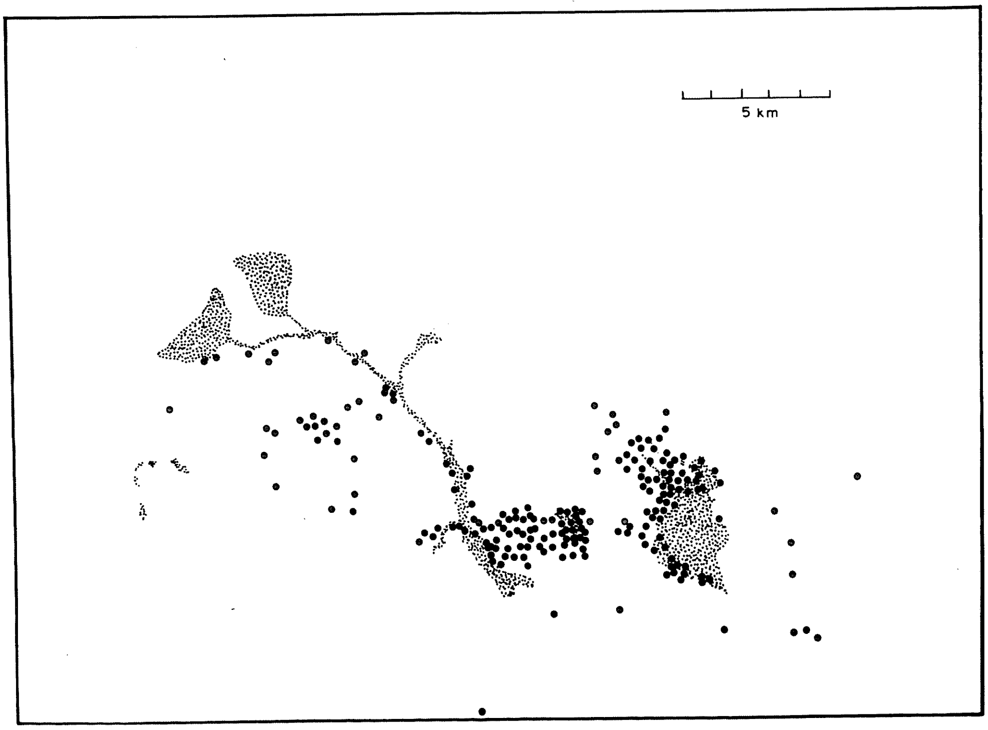


Figure 5.4. Areas utilized by groups of females with accompanying males. Each symbol indicates one group.

aggregations tended to form in the more open habitats with little woody cover. Lindsay (1982) suggested female groups in Amboseli were able to form large aggregations when food was abundant. He found that as the dry season progressed and the biomass of habitats containing high quality vegetation declined the larger groups tended to shift habitats. These shifts, although to areas of lower nutritional quality were to habitats supporting a high and evenly distributed biomass of vegetation. Since the large groups shifted habitats rather than breaking down and remaining in the highest quality areas, Lindsay (1982) reasoned that elephants were attempting to sustain a larger group formation for reasons other than foraging efficiency.

I found similar sex differences in habitat utilization although my data on seasonal variation are too few for statistical analysis. Figure 5.3 shows the areas where bull groups (with at least one Class 4 or mature male present; lone males not included) and cow/calf groups (female groups without accompanying males) were observed foraging. These distributions indicate that certain areas are preferred by cows/calf groups while others are preferred by groups of bulls. The areas used by females with accompanying bulls (Figure 5.4) are similar to those utilized by cow/calf groups, indicating that males leave their foraging areas to search out females and not vice versa. This pattern has also been observed on an individual level (see Chapter 3).

My data suggest that bulls are foraging in habitats that support more woody vegetation. I ran transects through those areas most often utilized for feeding by each sex (Figure 5.5) to obtain an estimate of the proportion of woody vegetation in areas used by males and females. Those areas utilized by males were significantly higher in woody vegetation density (median=12.0%) than the habitats used by female

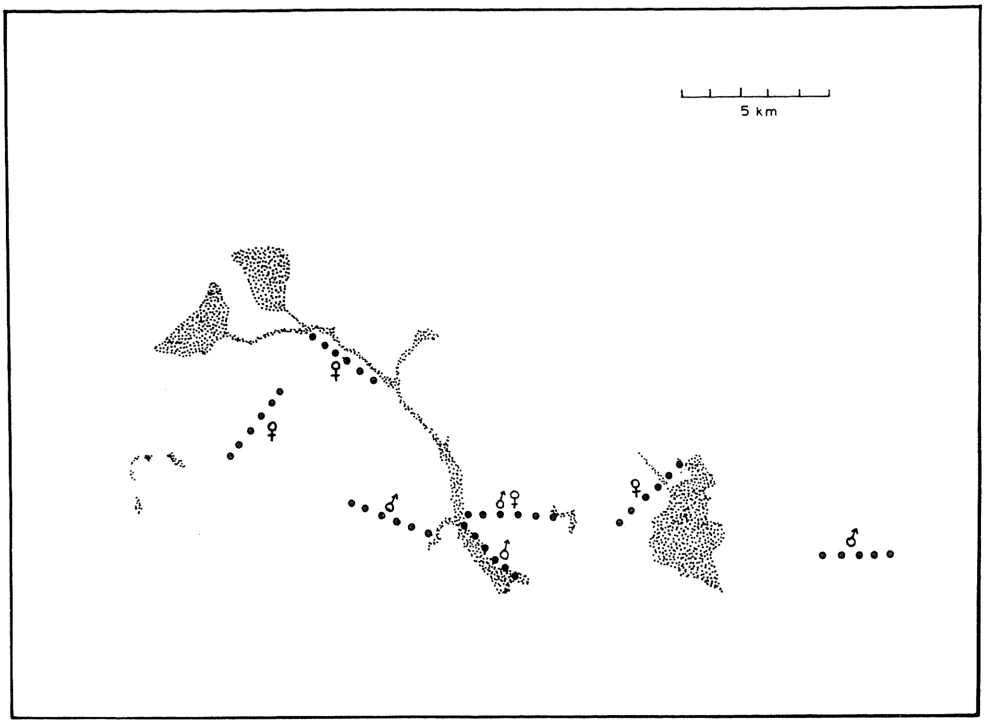


Figure 5.5. Transects run through habitats used by males and females for feeding to estimate the percent of woody vegetation.

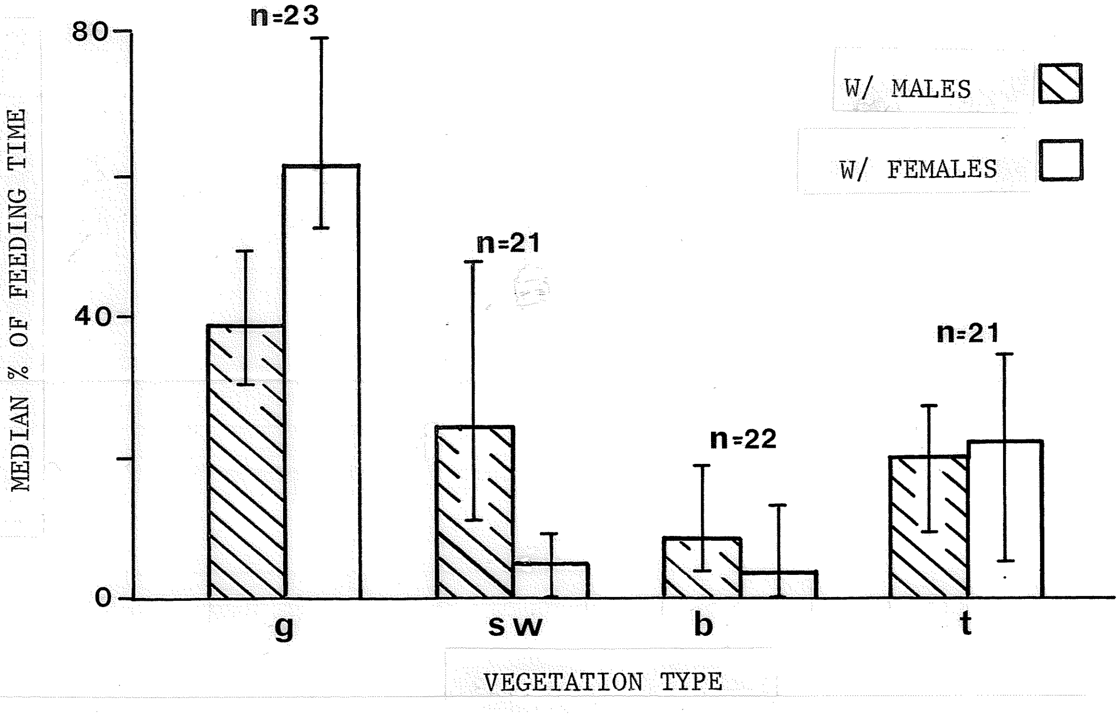


Figure 5.6. Median percent of feeding time spent consuming grass, swamp vegetation, bushes or trees when in association with other males versus that with females. g=grass; sw=swamp; b=bushes; t=trees. Medians and interquartile ranges are shown.

groups (median=5.9%) (U=39.50,n1=18, n2=19, $p<0.002$). Ol Tukai Orok, utilized heavily by both males and females had an intermediate density of woody vegetation (median=8.5%) and was not significantly different from the predominantly bull areas (U=29.00, n1=6, n2=19, $p>0.05$) or from the cow areas (U=29.5, n1=6, n2=18, $p>0.05$).

These results suggest that males may have to select different vegetation when they are in association with cows than when they are with bulls. When males were in association with females they spent a significantly higher proportion of their feeding time, consuming grass (T=13.5, n=23, $p<0.01$) and significantly less time feeding in the swamp (T=7, n=21, $p<0.01$) than males in bull groups (Figure 5.6). There was a tendency for males to spend more time feeding on bushes and less time on trees when with other bulls than when with cows (T=93, n=22, $p>0.05$, n.s. and T=95.5, n=21, $p>0.05$, n.s., respectively; Figure 5.6).

5.3.4 Seasonality of oestrus

In Amboseli, oestrous females were observed throughout the year, but the frequency of oestrus fluctuated with seasonal and yearly patterns of rainfall, the subsequent increase in vegetation biomass and female group size (Figure 5.7; see Chapter 7; Section 2.2 for a description of detection of oestrus). This pattern is particularly evident when comparing the drought years (late 1975 through mid 1977) with the following years of higher than average rainfall. In 1976, only four females were observed in oestrus and these females either did not conceive or aborted, as no calves were born until November, 1978 (Moss, in prep.). Under the more favourable habitat conditions since late 1977, the frequency of oestrus has been high, and presently approximately 18% of the population (n=600) are under three years of age. Figure 5.8 shows the total number of females observed in oestrous

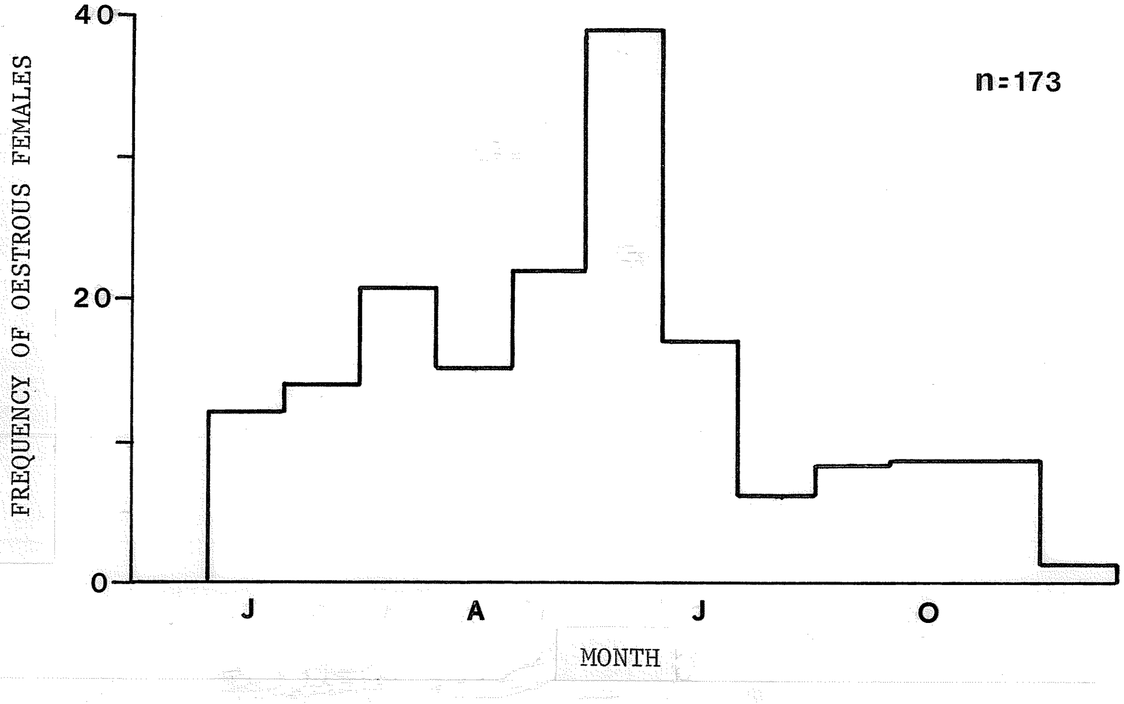


Figure 5.8. Total monthly frequency of oestrous females from September, 1975 through June, 1981 showing breeding throughout the year with a distinct peak in the first half of the year.

in each month since October, 1975. Elephants usually leave the Park at the onset of the rains (particularly in December and March/April) and have been observed as far as 40km outside the Park boundaries (H. Croze, pers. comm.). As a consequence, the number of females recorded in oestrus in December and April is low.

During my study period there was a similar seasonal pattern. Significantly more females were observed in oestrus from December through June than during the remaining five months (Chi-square=6, df=1, p<0.05; Table 5.1). During 1981 the frequency of oestrous females was unusually high (Figure 5.7). The cohort of females born as a result of the high rainfall in 1968 reached sexual maturity (Moss, in prep.) resulting in a sharp increase in the frequency of oestrous females during May and June 1981. Since there was low recruitment in the mid 1970s and most sexually mature females are either pregnant or lactating, reproductive activity is expected to decline over the next few years.

Table 5.1. The frequency of oestrous females during the wet and the dry seasons.

	Number of oestrous females		Number of months
	Observed	Expected	
wet season	69	59.04	13
dry season	13	22.96	5
Total	82	82.00	18

Chi-square=6.00, d.f.=1, p<0.05

The social excitement that occurs in the large groups may facilitate the onset of oestrus (Moss, 1981). My own data from 1980 show that the mean group size containing oestrous females was

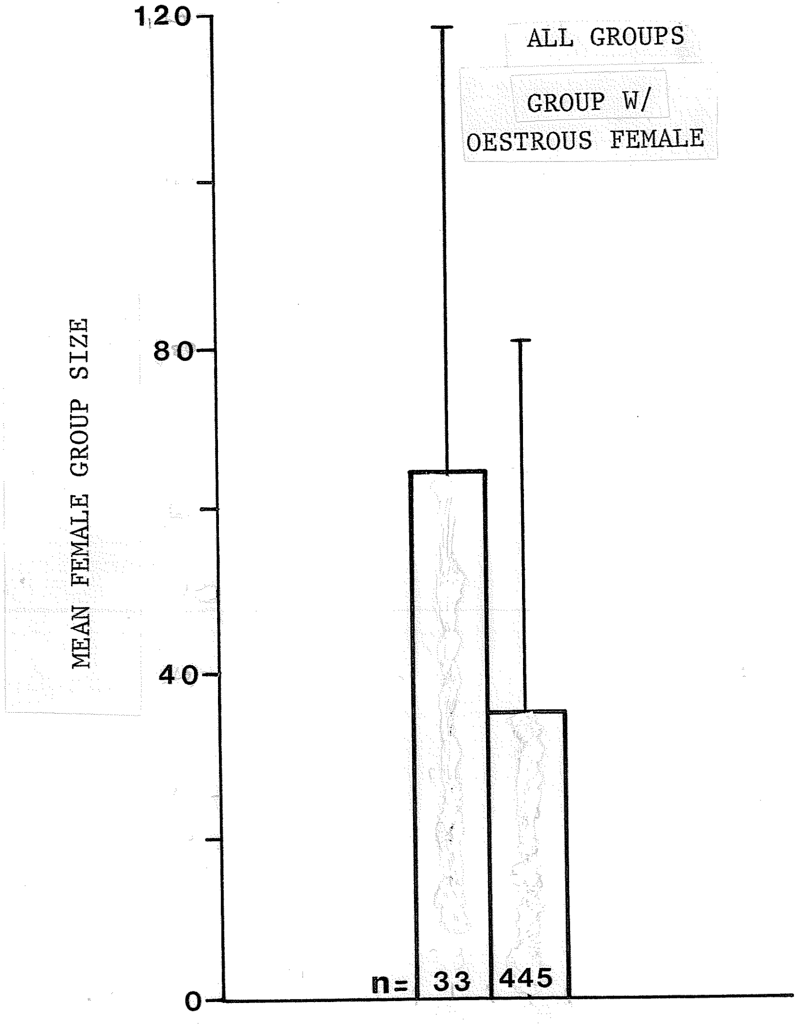


Figure 5.9. Mean female group size containing an oestrous female versus the overall mean female group size(1980 -during the study period). Means and standard deviations are shown.

significantly larger than the overall mean female group size for 1980 ($t=3.5$, d.f.=477, $p<0.002$; Figure 5.9). However, since large groups form when vegetation biomass is high and females are presumably in better condition, it is difficult to tell how important social facilitation of oestrus is.

5.3.5 Seasonality of musth

The seasonal occurrence of musth followed a similar pattern to the occurrence of oestrus, particularly in the pre-1980 years of the study (Figure 5.7). Males were observed in musth throughout the year (see Chapter 4) but, on a monthly basis, there tended to be more males in musth during the wet season than during the dry season. However, some of these males were in musth for up to five months while others were in musth for only a few days. Taking into account the number of days each male was observed in musth during 1980 and 1981, there were significantly more "musth male days" during the wet than during the dry season (Chi-square=3.95, df=1, $p<0.05$; Table 5.2, these results take account of the difference in the length of each season).

Table 5.2. The number of "musth male days" during the wet and dry seasons of 1980 and 1981 is given (November, 1981 not available).

	Number of "musth male days"		Total no. days
	Observed	Expected	
wet season	1082	1040.6	422
dry season	641	680.6	276

Chi-sguare=3.95, d.f.=1, $p<0.05$

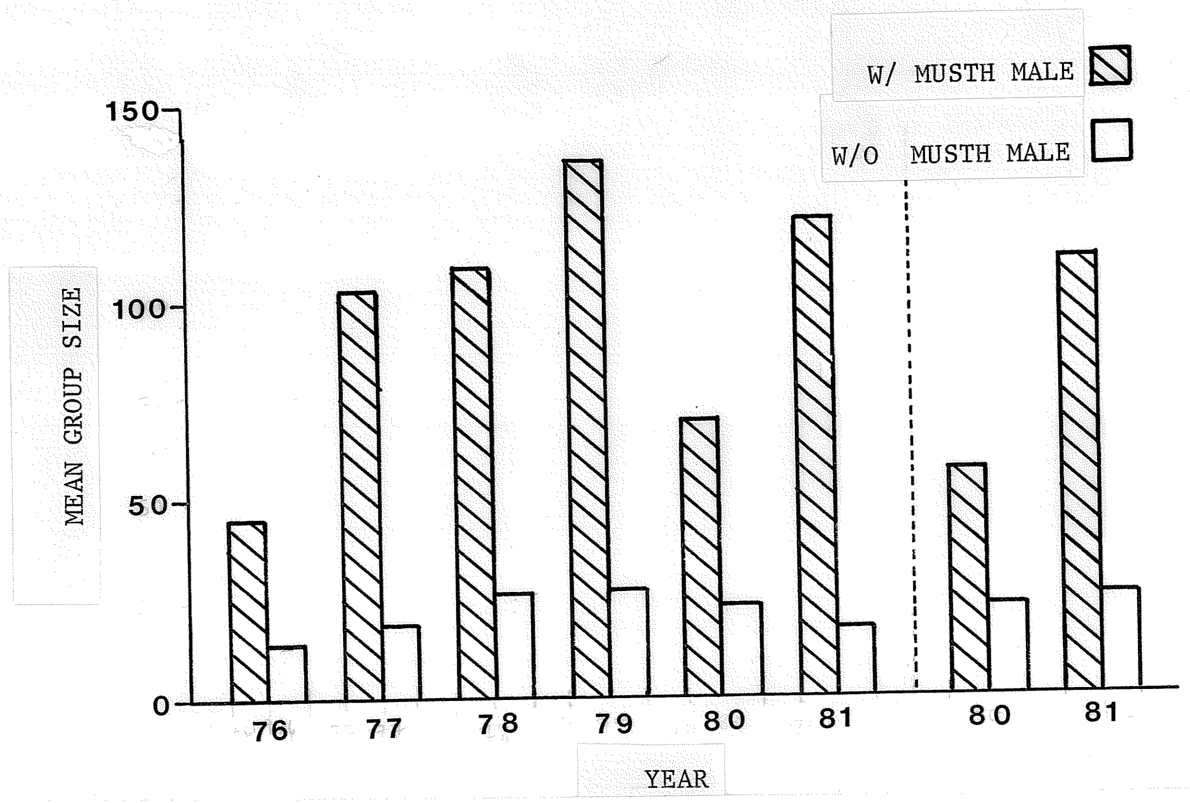


Figure 5.10. Mean yearly female group size with and without accompanying musth males.

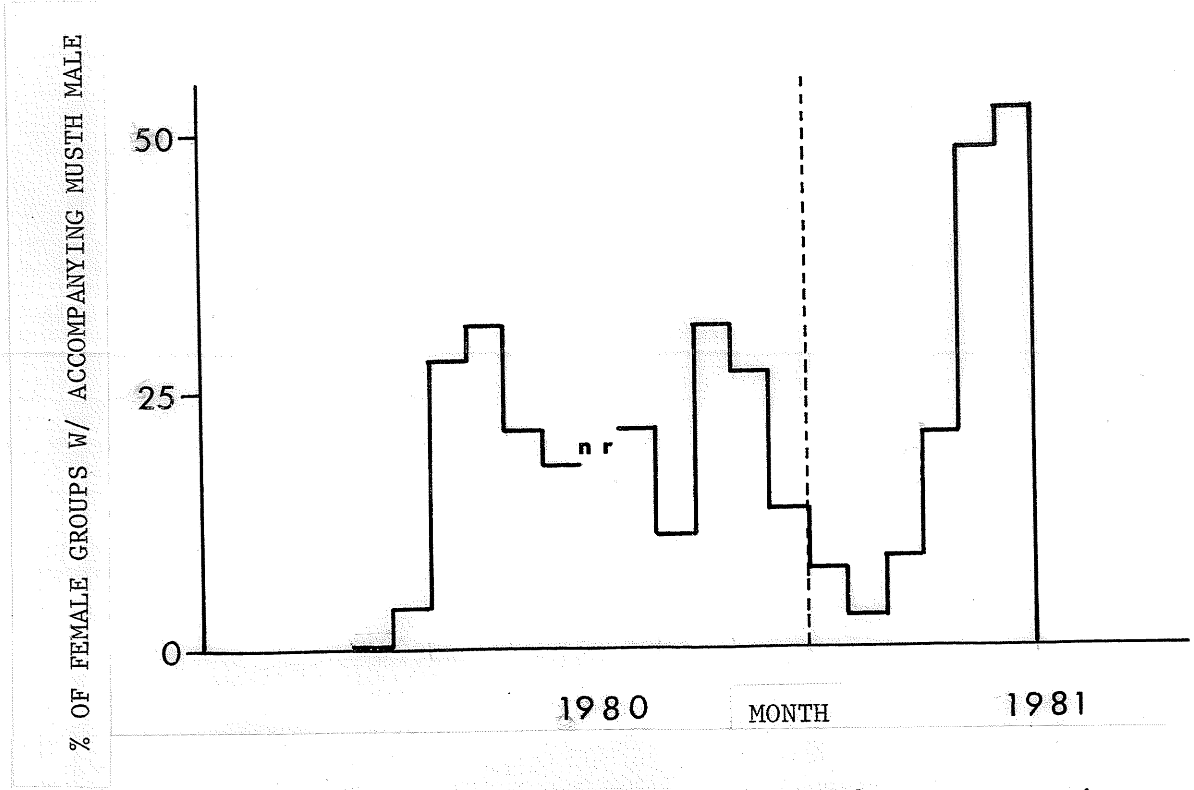


Figure 5.11. Monthly percent of female groups with an accompanying musth male. NR=no record.

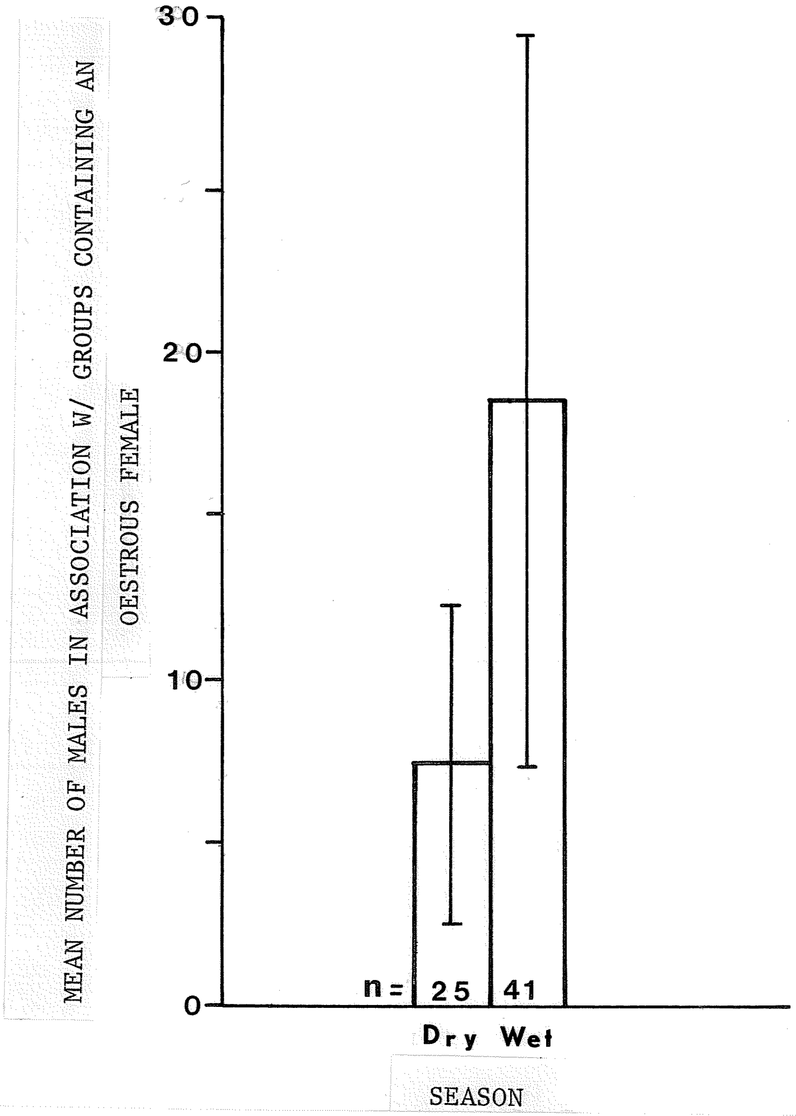


Figure 5.12. Mean number of males in association with groups containing an oestrous female during the dry versus during the wet season. Means and standard deviations are shown.

The mean female group size with associating musth males was significantly higher than the mean female group size without associating musth males (Figure 5.10; for data collected during my study: 1980; t=3.98, df=118, p<0.01; 1981: t=5.96, df=65, p<0.01; see Appendix 3 for the means, standard deviations and numbers of groups for all years). Most males came into musth when females were in large groups and when the absolute number of females likely to come into oestrus was higher. Since the probability of locating an oestrous female is higher in a large group than in a small group (since there are more females), males presumably put more time and energy into searching for and associating with larger groups than smaller groups. Males who came into musth during the first half of the year presumably spent less time and energy searching for mates as more oestrous females were available and most females could be found in one of several large groups (or all in the same group as on 5/5/81).

During the wet season the number of "musth male days" was higher than during the dry season and, due to group aggregation during this period, the absolute number of female groups declined, such that the monthly proportion of female groups containing musth males fluctuated seasonally (Figure 5.11).

Although males who were sexually active during the rains could expect to locate more oestrous females, they could also expect more competition from other males for access to females. During my study the mean number of males in association with a group containing an oestrous female during the wet season was significantly higher than during the dry season (t=2.81, df=51, p<0.01; Figure 5.12).

Assuming that males, overall, associate with females approximately 40% of the time (see below) then, excluding the Class 1 males (n=73) who

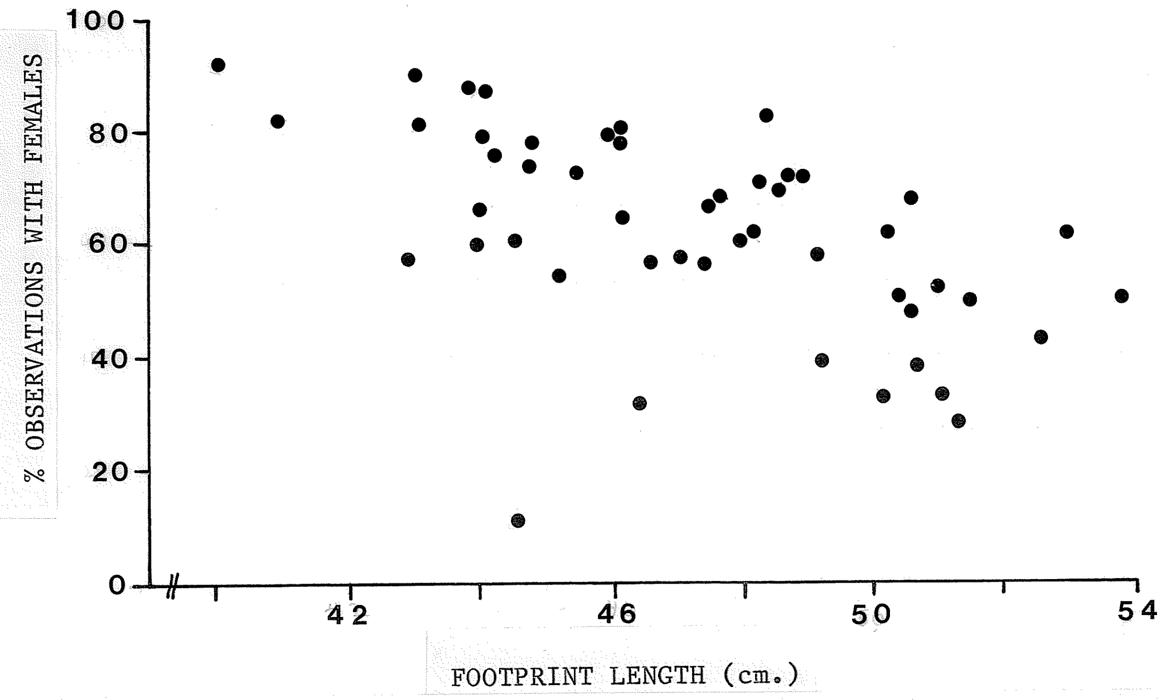


Figure 5.13. Relationship between body size (footprint length) and the percent of observations with females; includes data gathered from 1976 through 1981.

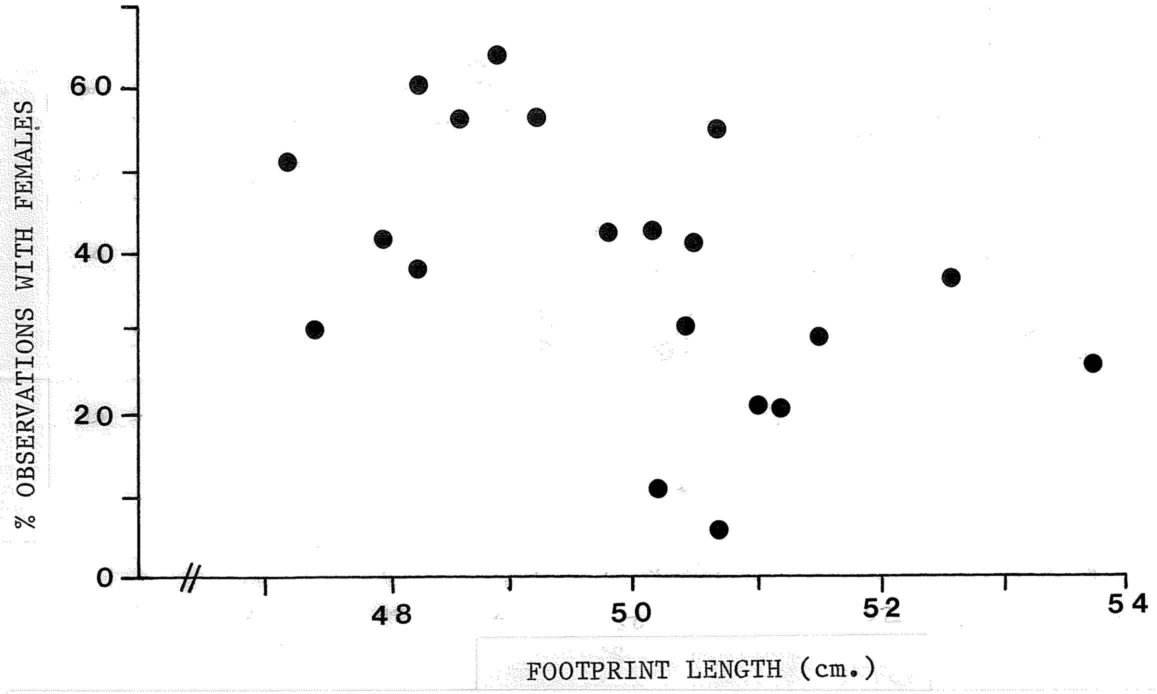


Figure 5.14. Relationship between body size (footprint length) and the percent of observations with females; includes data gathered on focal males who were seen with bulls at least twelve times during the study period.

have little reproductive success (see Chapter 7), there are, on average, approximately 35 sexually active males each day of the year. Assuming a 4.7 year interbirth interval, 170 adult females and oestrus lasting 4.5 days there is only a 45% chance of one female being in oestrus on any given day. Competition between males for access to females is expected to be intense.

5.3.6 Male body size

In Amboseli older males spent less time with females than did younger males (Spearman rank correlation=-0.51, df=47, p<0.002). Figure 5.13 shows the proportion of total observations since 1976 in which males of different ages were observed in association with female groups (all males were observed at least 30 times). This estimation of time spent with females has several biases. Large males are more easily recognized in a group of females than are small males and, for those males who have bull areas outside the Park boundaries and who only utilize the basin when in association with females, this gives an over estimation. In addition, I have very few footprint measurements from the youngest adult males (those with footprint measurements under 44 cm). All of these biases work against the point I am trying to make (i.e.. that large males spend less time with females than small males), therefore I feel that the results I have found are not due to sampling error.

To avoid some of these biases I have done the same correlation using those focal males who I had seen in bull groups at least twelve times during the study period. Although this limits males to those over 25 years old the relationship is still significant (Spearman rank correlation=-0.53, df=18, p<0.02; Figure 5.14), indicating that, even among Class 3 and 4 males, larger males spend less time with females

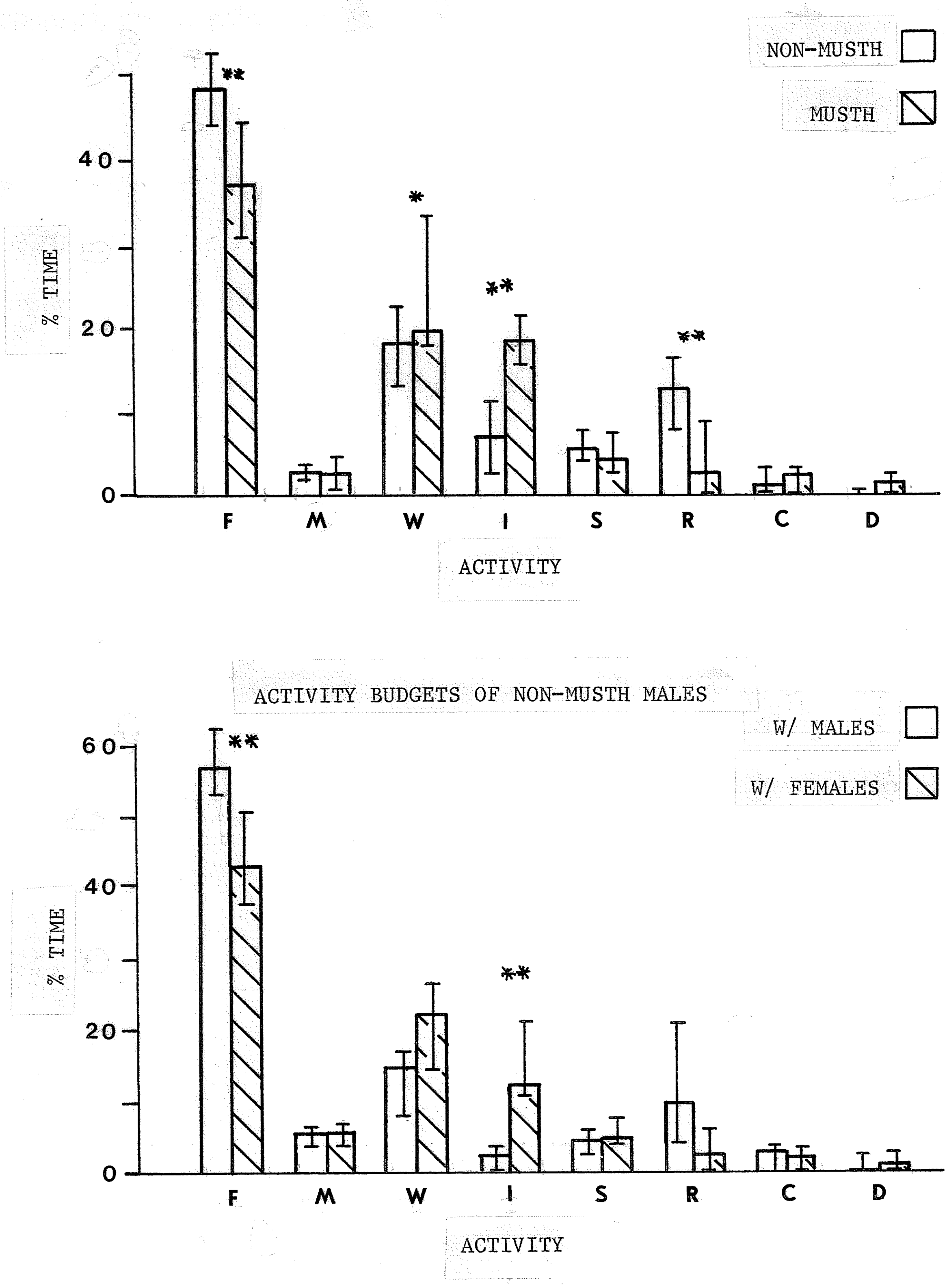


Figure 5.15. Percent time engaged in various activities in different social (with males, females or alone) and sexual (in musth, not in musth) contexts. F=feed; M=move; W=walk; I=interact, S=stand, R=rest, C=comfort, D=drink.

** $P < 0.01$ * $P < 0.05$

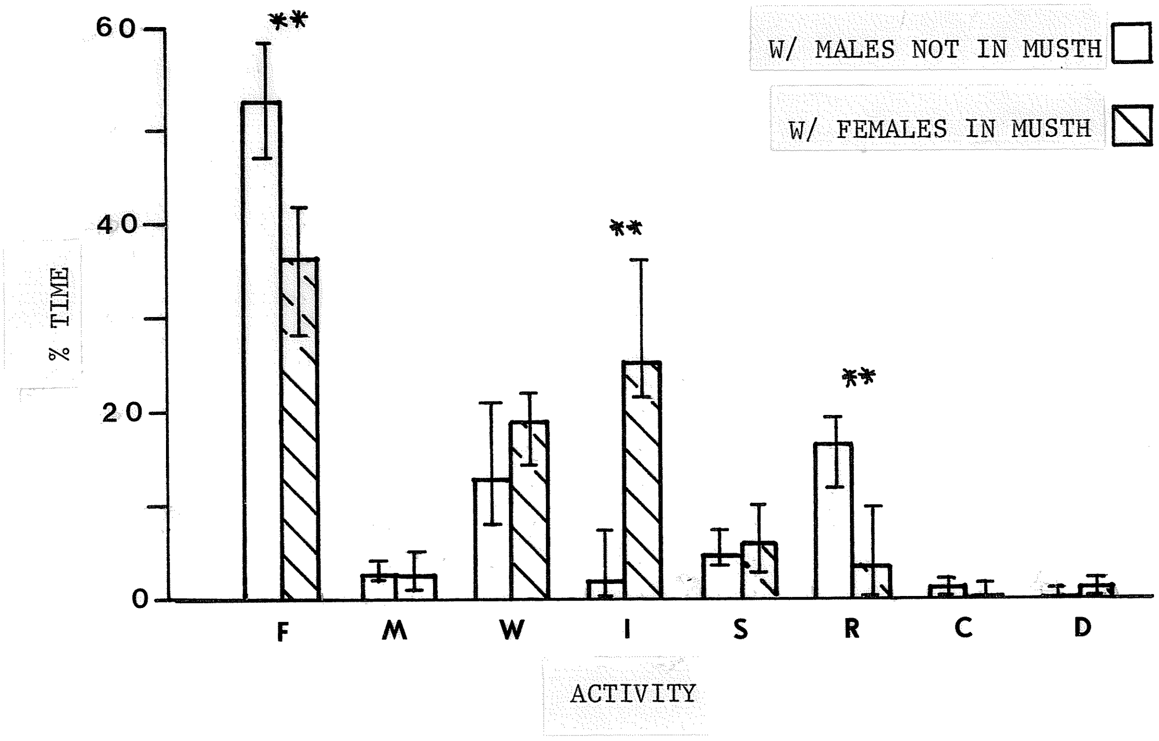
than do relatively smaller males.

5.3.7 Activity budgets: musth and non-musth

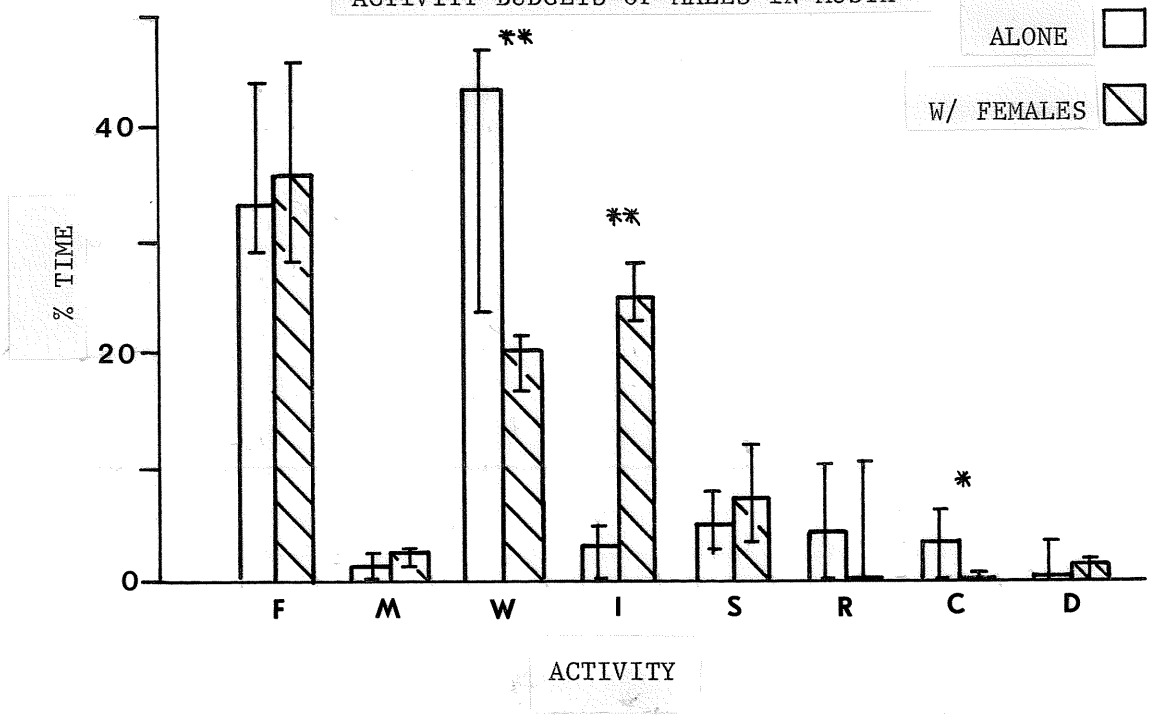
Males were observed and sampled under a variety of circumstances: either in musth or not in musth; with females, with other males or alone. Obviously, the activities of males vary depending on who they are with (see Figure 5.15 for all data on activity budgets). For example, males in association with other males or with females will spend more time interacting than lone males. Comparing musth samples with non-musth samples without regard to association shows that males in musth spent less time feeding (T=21, n=22, $p<0.01$) and resting (T=12, n=22, $p<0.01$), and more time walking (T=44, n=21, $p<0.02$) and interacting (T=5, n=22, $p<0.01$) than when not in musth. There was no significant difference in the time spent engaged in other activities between musth and non-musth state (moving while feeding: T=126.5, n=22, $p>0.05$; stand: T=105, n=22, $p>0.05$; comfort: T=78.5, n=18, $p>0.05$; drink: T=56, n=19, $p>0.05$). Although the difference in time spent drinking was not statistically significant, this was due to one male (M45) on whom I had very few hours. I suggest that the continuous dribbling of urine requires males to drink more often when in musth than when not in musth.

Non-musth males in bull groups budgeted their time differently than did non-musth males in association with cows. When with females males spent less time feeding (T=0, n=8, $p<0.01$) and more time interacting (T=0, n=8, $p<0.01$). There was no significant difference in the time devoted to other activities (moving while feeding: T=14, n=8, $p>0.05$; walk: T=17, n=7, $p>0.05$; stand: T=16, n=8, $p>0.05$; rest: T=7, n=7, $p>0.05$; comfort: T=9, n=6, $p>0.05$; drink: T=12.5, n=7, $p>0.05$).

Similarly, when in musth with females, males spent less time



ACTIVITY BUDGETS OF MALES IN MUSTH



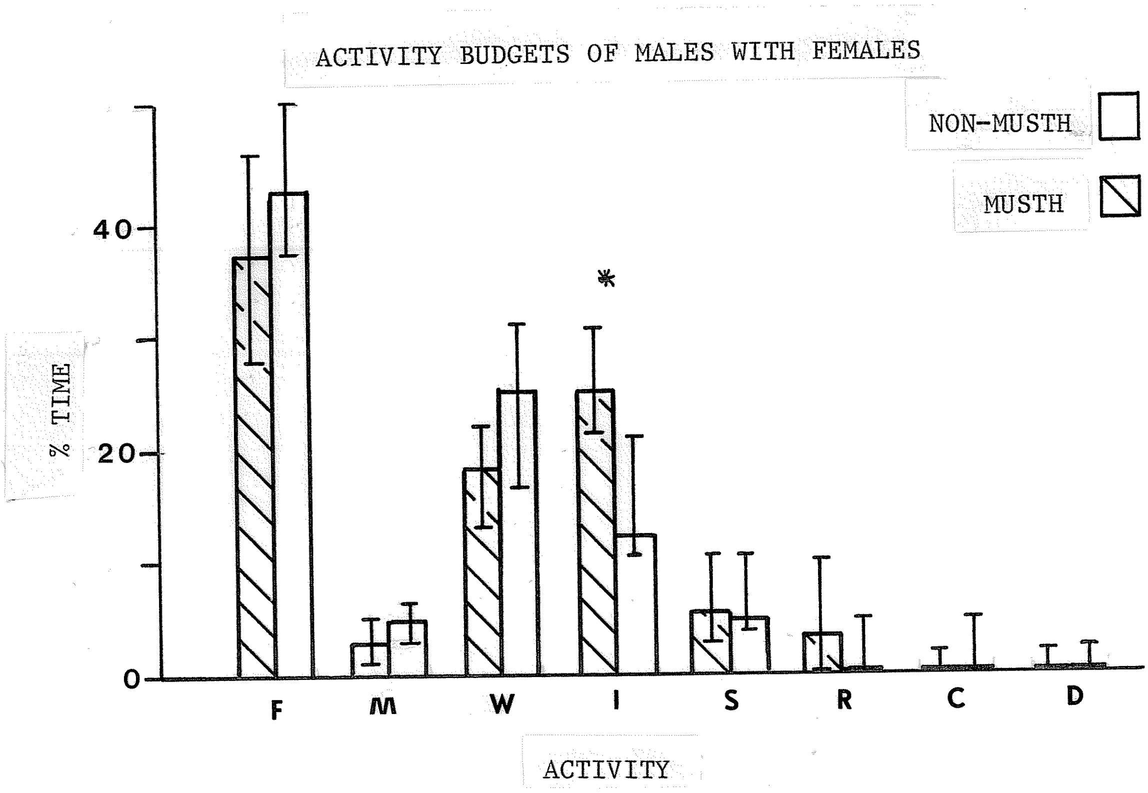
feeding ($T=3$, $n=17$, $p<0.01$) and resting ($T=4$, $n=15$, $p<0.01$) and more time interacting ($T=2$, $n=17$, $p<0.01$) than when with males and not in musth. There was no statistical difference in the amount of time spent moving while feeding ($T=57$, $n=16$, $p>0.05$), walking ($T=40.5$, $n=17$, $p>0.05$), standing ($T=54$, $n=17$, $p>0.05$), comfort ($T=27.5$, $n=15$, $p>0.05$) or drinking ($T=32.5$, $n=14$, $p>0.05$).

Males in musth spent their time differently depending upon whether they were in association with females or alone. Lone musth males spent significantly more time walking ($T=2$, $n=9$, $p<0.01$) and involved in comfort activities ($T=0$, $n=6$, $p=0.05$) and less time interacting ($T=0$, $n=9$, $p<0.01$) than did musth males in association with females. I suggest that the increase in walking time was spent in search of female groups while the increase in comfort behaviour may have been due to wallowing and marking. There was no significant difference in the amount of time spent feeding ($T=18$, $n=9$, $p>0.05$), moving while feeding ($T=13$, $n=7$. $p>0.05$), standing ($T=14$, $n=9$, $p>0.05$), resting ($T=16$, $n=9$, $p>0.05$) or drinking ($T=14$, $n=7$, $p>0.05$).

Among sexually active males (those in association with females) musth males spent more time interacting than did non-musth males ($U=24$, $n1=9$, $n2=16$, $p<0.02$). None of the other activities were statistically different.

5.4 DISCUSSION

In Amboseli, female groups aggregate during periods of vegetation abundance, and split up as vegetation decreases in quality and quantity (Lindsay, 1982; Moss, 1977). Elephant studies elsewhere also suggest that groups of elephants break up as competition for food increases (Douglas-Hamilton, 1972; Leuthold, 1977b). Since foraging efficiency


ACTIVITY BUDGETS OF MALES WITH FEMALES
NON-MUSTH
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is likely to decline in large groups, there must be benefits to group membership that outweigh this cost (Leuthold, 1977a; Post, 1981).

In some areas elephants reportedly aggregate in direct response to human disturbance and poaching pressure (Eltringham, 1977). In Amboseli, pressure from poaching has been extremely low and when it has occurred, adult males, who do not aggregate into large groups except for reproductive purposes, have been most affected. Therefore, in Amboseli, poaching cannot be seen as an important reason for the formation of large groups. Moss (1981 and pers. comm.) and Lindsay (1982) have suggested several possibilities for the aggregation of elephants in Amboseli.

Elephants have been hunted by man for many thousands of years (Monod, 1964) and juveniles and calves are vulnerable to attacks by lions. Adults and juveniles may have suffered fewer risks of predation by remaining in large groups.

The aggregation of large groups may provide arenas for young males to meet and spar with other young males (Moss, 1981). This early assessment of one another's strengths may be important for judgements made during contests in adulthood (see Chapter 6).

Individuals may use these aggregations as an opportunity to exchange information about food availability, thereby increasing the foraging success of individual members (Lindsay, 1982; Moss pers. comm.).

Large groups may also form for breeding purposes (Moss, 1981). Moss (1981) suggests that aggregations of females may attract adult males and that social stimulation may facilitate the onset of oestrus. Additionally, certain behaviour by oestrous females suggests that they may be attempting to incite male-male competition (Moss, in prep and pers. obs.). Although all of these benefits have probably interacted to favour group aggregation, I am primarily interested in this final consideration.

Several authors have reported that African elephants breed throughout the year (Perry, 1953; Buss and Smith, 1966), while others have found distinct peaks in breeding during and following the rains (Laws and Parker, 1968; Laws, 1969a; Hanks, 1969). Hanks (1969) reported that 88% of all conceptions took place in November through April, when 96% of the rain fell. Laws and Parker (1968) suggested that the change in diet during the rains might stimulate ovulation and fertile mating. In Amboseli the quality and quantity of grass increases following the onset of the rains (Western and Lindsay, in prep.). Moss (in prep.) found that 76% (n=135) of conceptions (as estimated by births 22 months later) occurred in December through June in the years 1976 through 1979. During these same years, 61% (n=54) of the females observed in oestrus occurred in these months. These figures (Moss, in prep.) indicate that a higher proportion of the females observed in oestrus during December through June were successful (actually conceived or did not abort) than during the latter half of the year. During my study period the frequency of oestrus was also higher in the months December through June than during the latter period. Both my own data and those of Moss (in prep.) show that although oestrus was observed throughout the year, there was an increase in breeding activity during the first seven months of the rainfall year.

In this chapter I showed that females tend to aggregate into large groups during and following the short and long rains. During this time the absolute number of oestrous females was higher than during the latter half of the year. Data show that there were more males in association with female groups and, more importantly, there were more males in association with oestrous females during these months than at other times of the year. In addition there were more males in musth at this time than at other times of the year. In several months close to 50% of the groups encountered had accompanying musth males. These data suggest that competition between males for access to females is likely to be higher at this time of the year than from July through November. Oestrous females who aggregate will contact more males than those oestrous females who do not aggregate. More importantly, oestrous females are more likely to be mated by a musth male (see Chapter 7) if they aggregate. The implications of this will be discussed further in Chapter 8.

Large males spend significantly less time with females than do smaller males. It may be that the energetic costs during the time spent with females are more significant for large males than for small males. Sexually active males, particularly the large males who come into musth, expend more energy (increase in time spent walking and interacting) and assimilate less energy (less time spent feeding) than sexually inactive males. There was an indication that musth males had to spend more time drinking, than non-musth males, presumably because of the constant dribbling of urine. This may indicate a physiological cost above that experienced by non-musth males. In addition, males in musth have very high levels of testosterone (see Chapter 6) which has in other species been found to be associated with an increase in metabolic rate (Bell et al., 1977). Domesticated Asian elephants, who are chained during musth, reportedly become emaciated and take some time to regain condition following a musth period (Deraniyagala, 1955), indicating that being in musth may have substantial energetic costs.

The energetic cost for sexually active males may also be related to the difference in habitats utilized by the two sexes. All-male groups tend to forage in habitats that are both spatially and vegetationally distinct from those utilized by female groups. Several other authors have reported distinct bull areas (Laws et al., 1970; Croze, 1974; Martin, 1978).

Females may have different priorities than males. The habitats utilized by females tend to be open grasslands and may be selected so that individuals can remain in close proximity and yet still obtain an adequate intake of food (Lindsay, 1982). Selection of foraging habitats by females may be contrained by calves and juveniles whose handling and processing of woody foods may be inefficient. Large males, on the other hand, have higher absolute intake requirements than females half their size, and they are able to utilize fiberous vegetation more efficiently than smaller animals because of their larger gut capacity (Demment, 1978). Therefore, when not sexually active, males may select areas where they can maximize their energy intake.

Elephants are highly sexually dimorphic in body weight (Laws, 1966). The data presented in this chapter suggest that there may be some energetic costs associated with large body size. However, the benefits of increased body size in terms of obtaining access to oestrous females are obviously important and are discussed in Chapters 6, 7 and 8.

CHAPTER 6

DOMINANCE AND AGGRESSION

6.1 INTRODUCTION

The function of aggression and dominance in animal societies has commonly been explained in terms of group selection. Lorenz (1962:22) suggested that aggression "fulfils a species-preserving function" and Wynne-Edwards (1962) believed that dominance hierarchies functioned in population regulation. Hierarchies have commonly been viewed as a behavioural trait rather than the summation, over all individuals, of the costs and benefits to an individual of contesting or submitting to another individual over a given resource (Williams, 1966; Parker, 1974b). "Hierarchies occur because competitive ability inevitably varies between individuals and because less successful animals learn not to contest access to encounters where they are unlikely to win thus saving time and energy" (Clutton-Brock and Harvey, 1976:216).

Among males of many species dominance is related to body size (Bouissou, 1972; Appleby, 1981; Croze, 1974; Le Boeuf, 1974) or some other sexually dimorphic characteristic (horn size: Geist, 1971; Bouissou, 1972) and high ranking males gain access to receptive females and achieve a higher mating success than lower ranking males (Le Boeuf, 1974; Trivers, 1976; Clutton-Brock et al., 1979; Packer, 1979; Davies and Halliday, 1979; Lott, 1979).

Dominance is context specific. In species living in complex social groups (e.g. primates), the relative rank of an individual may change depending upon its ability to form coalitions, its sexual state and the nature of the resource (see review by Bernstein, 1976). In many ungulate species there is a clearly defined and heightened sexual period, or rut, and the costs and benefits of contesting or submitting to a particular individual during this period may be very different from the costs and benefits outside the rut (see Appleby, 1981). Changes in testosterone levels have been shown to be associated with changes in rank (Lincoln et al, 1972), indicating the importance of distinguishing between sexually active and inactive individuals when considering the social context of interactions.

In species where males exhibit external signs of high testosterone levels, such as those ungulate species in which males alter their behaviour and physical appearance during the rut (see Chapter 1), changes in rank in relation to sexual state will be more easily assessed. Among most rutting species there is a well defined breeding season; males are usually active simultaneously and therefore there is little contact between sexually active and inactive males.

Elephants are perhaps unique in this respect. "Rutting" males may be seen throughout the year, and the changes in interactions between particular males as they come into and go out of musth provide a means of assessing the importance of the sexual state of individuals in relation to rank. Jainudeen et al. (1972b) found that plasma testosterone levels vary markedly in relation to musth in _Elephas maximus_ and it has been suggested that being in musth may increase a male's dominance status (Eisenberg et al., 1971; Maynard Smith and Price, 1973).

6.2 METHODS

6.2.1 Urine collection and testosterone analysis

I attempted to collect urine samples early in the morning, before the elephants had reached the swamp to drink. Urine was aspirated from the ground, usually within one minute after micturition, using a 20 ml syringe. The time it took for urine to soak into the ground depended upon soil type. This method of collection meant that the urine was often contaminated with debris and samples were filtered whenever possible. Urine samples were then stored frozen in 20ml glass containers. In July, 1981 the urine was sent on dry ice to San Diego where L. Kasman and W. Lasley developed an assay for analyzing urinary testosterone. Details of their assay are presented in Appendix 5 and in Poole et al. (in prep.).

Fifty-two urine samples were collected from 26 different males. In cases where more than one urine sample had been collected for a particular male one was randomly selected for between male comparisons. A study by Jainudeen et al. (1972b) showed that testosterone levels increase dramatically with the onset of musth in *Elephas* maximus, therefore I feel justified in using one-tailed tests for this particular analysis.

It must be remembered that this study is, to my knowledge, the first time that an attempt has been made to obtain levels of urinary testosterone from free-living animals and, as such, this study should be viewed as preliminary. The conditions under which urine was collected were not ideal. Since I was not certain whether the technique would produce results, samples were collected opportunistically and although I made every attempt to have the samples frozen within four hours of collection, focal sampling received first priority. Therefore, although

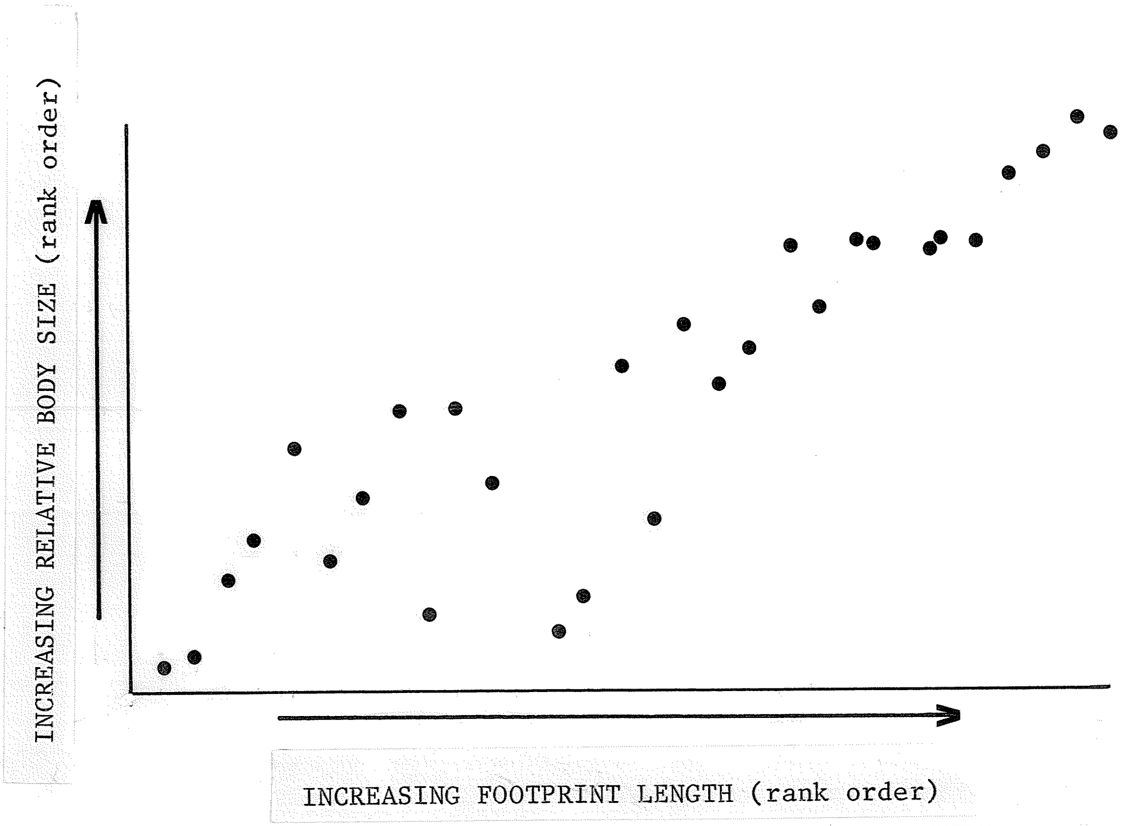

Figure 6.1. Relationship between footprint length and relative body size.

the conclusions drawn from these data are unlikely to be misleading, the precise figures obtained must be viewed with caution.

6.2.2 Estimation of shoulder height

The relative shoulder height of individuals was recorded whenever two males were standing sufficiently close to one another to determine which was the taller individual. The 34 largest animals have been ranked according to their relative shoulder heights. When two or more animals appeared to be the same height I have assigned them equal ranks. Obviously, this system of measurement is open to subjective biases; an animal with a large head or tusks appears taller than one with a relatively small head or tusks. In addition, if I knew one individual to be higher ranking than the other, I may unconsciously have ranked that individual as taller. For this reason I have used footprint measurements (described in Chapter 2, Western et al., in prep.) as a second and independent measurement. Footprint measurements proved useful both as a measure of the relative heights of individuals and as an estimate of the approximate ages of males in the population.

I was able to obtain footprint measurements for 30 of the 34 largest males in the population. Footprint size was found to correlate closely with relative body size (Spearman rank correlation=0.90, n=30, df=28, $p<0.001$; Figure 6.1).

6.2.3 Threat and avoidance categories

A behaviour was considered a threat if the receiving individual usually withdrew:

Threat 1 - while standing in place an elephant raises its head vertically and lifts and slightly spreads its ears. The chin is held in; extending the lower jaw indicates apprehension.

Threat 2 - an individual behaves as above while walking towards another elephant.

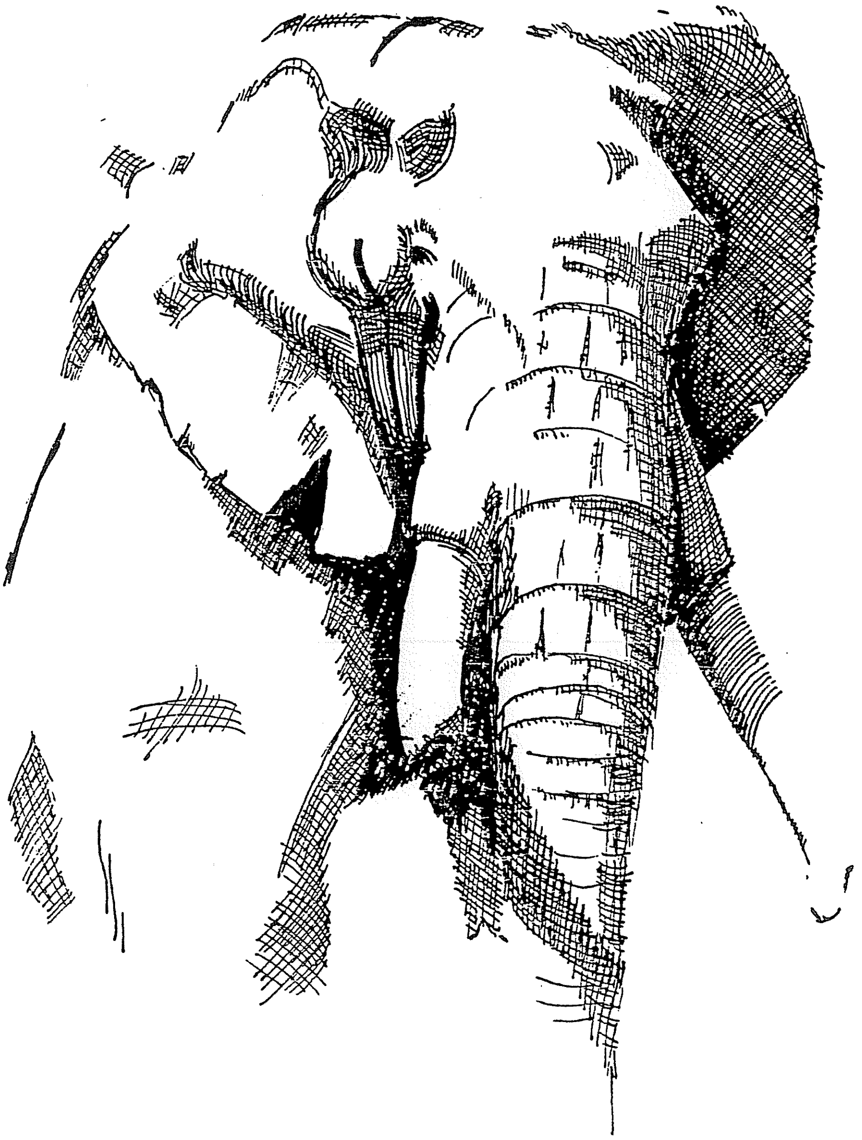

Plate 6.1. Ear fold threat (M126). The lower half of the ears are bent backwards creating a noticeable ridge that runs across the ears parallel to the ground.

Threat 3 - an individual behaves as above while at a run.

Ear fold - the lower half of the ears are bent backwards creating a noticeable ridge that runs across the ear parallel to the ground (Plate 6.1). This behaviour may be done alone or in combination with any of the above behaviours.

Ear wave - this behaviour has been described (see Chapter 4). Ear waves were scored as either low intensity (1 wave) or high intensity (>1 wave). Similar to the ear fold, this threat may be made alone or in combination with any of the above threats.

Head shake - an individual threatens another by shaking its head.

Animals usually responded to these threats by avoidance behaviour:

Avoid 1 - an individual responds by facing away from the threatening male.

Avoid 2 - an individual responds by facing and walking away from the threatening male.

Avoid 3 - an individual responds by facing and running away from the threatening male.

Threats were categorized as being directed towards other elephants or towards non-elephant objects. The latter instances involved threats towards vehicles, usually my own.

6.2.4 Determination of agonistic dominance rank

Interaction rates between non-musth males are usually low (see below), therefore I have used the agonistic interactions observed since 1977 by both Cynthia Moss and myself to determine the relative ranks of individuals. Interactions observed on a single day were not scored as independent so that the figures given are the number of days when particular pairs of males were observed interacting ("interaction-days"). Of these, 87.5% (n=831) were my own observations. The outcomes of interactions include only those that were initiated by the behaviours that I have described as threats. Instances where an approach without a threat caused an animal to move a few steps are not included in this analysis.

Based upon the outcome of interactions between males when neither animal was in musth, I have assigned relative ranks to individuals from the matrix in which the highest number of points fell on one side of the line. For those dyads in which non-musth reversals were observed, the male who won the higher proportion of total interactions was considered the higher ranking of the two.

Definitions:

Aggression - the behaviour of attack or threat.

Dominant (of a pair) - the individual who, when threatening, causes the other male to avoid him.

Subordinate (of a pair) - the individual who responds to a threatening male by avoidance behaviour.

Rank - A dominant animal is said to have a higher rank than the subordinate (Deag, 1977).

Reversal - during a particular time interval or sexual state male A dominates male B; later male B dominates male A.

6.2.5 Retreat distance

For agonistic interactions between individuals I recorded the inter-individual distance (in meters) at which a subordinate animal chose to retreat from a male threatening by walking toward him (Threat 2). Only bouts involving one interaction were used in this analysis. I have selected the first interaction recorded between any two individuals during the study period, so that each pair of males has been counted only once.

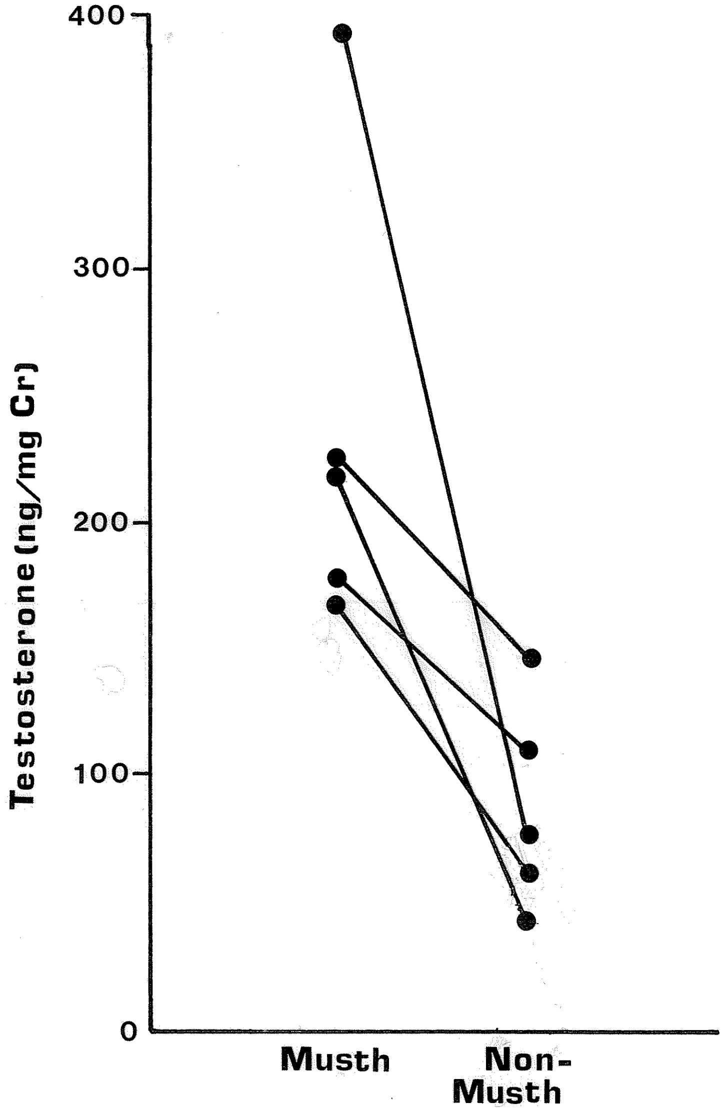

Figure 6.2. Musth and non-musth urinary testosterone levels (ngT/mgCr).

6.3 RESULTS

6.3.1 Musth and urinary testosterone

The samples collected fell into five major categories:

A) Musth - samples from males who showed the physical signs of musth at the time of collection.

B) Non-musth males in association with females - these samples were collected from males who had never been observed in musth and were in association with females at the time of collection.

C) Non-musth males in association with other males - these samples were collected from males who periodically came into musth but who did not show the signs of musth and who were in association with other males at the time of collection.

D) Pre-musth - males who were neither in musth nor in association with females at the time of urine collection, but who came into musth within one month of that date.

E) Borderline - non-musth males who were in association with females at the time of collection, had recently been in musth and came into musth again within one week from the date of collection.

For five of the males under study (M80, M107, M99, M78, M97) I was able to collect urine samples both in and out of musth. All five individuals showed higher levels of urinary testosterone during musth periods than during non-musth (Sign test p=0.031, one-tailed; Figure 6.2).

A one way analysis of variance indicates that the urinary testosterone levels in the first three behavioural groups (A, B and C) differ (F=16, df=2,19, $p<0.001$; Table 6.1). To test where these differences lie, I have used the Scheffé test for multiple comparisons of means (Pollard, 1977). Urinary testosterone levels of males in musth (A) were significantly higher than those of both sexually active non-musth males (B) ($S_{a,b}=4.13$; n=7,5; df=2; $p<0.05$) and sexually inactive non-musth males (C) ($S_{a,c}=16.01$, n=7,9; df=2,19; $p<0.01$). The difference between sexually active non-musth males (B) and sexually-inactive non-musth males (C) was not statistically significant ($S_{b,c}=2.20$; n=5,9; df=2,19; $p>0.05$). This result may, however, be due to the small sample size of group B. The difference between these two groups would be statistically significant if group B were to have an n of 12 and group C were to be held constant.

Table 6.1. Urinary testosterone levels (ngT/mgCr) collected from males in behavioural groups A,B and C.

A		B		C	
Musth		Sexually active non-musth		Sexually inactive non-musth	
male	ngT/mgCr	male	ngT/mgCr	male	ngT/mgCr
119	313.6	147	205.5	45	99.2
78	181.4	149	76.0	126	80.0
99	164.7	132	214.6	41	67.3
13	193.5	91	141.8	28	47.1
114	264.2	97	95.6	44	77.9
107	226.0			10	162.4
80	393.3			51	41.1
				22	41.5
				154	69.9
n=7 mean=248.1		n=5 mean=141.8		n=9 mean=96.4	

The remaining samples come from groups D and E and are too few to analyze statistically. However, it is interesting to note that the urinary testosterone levels for both groups were high (Table 6.2).

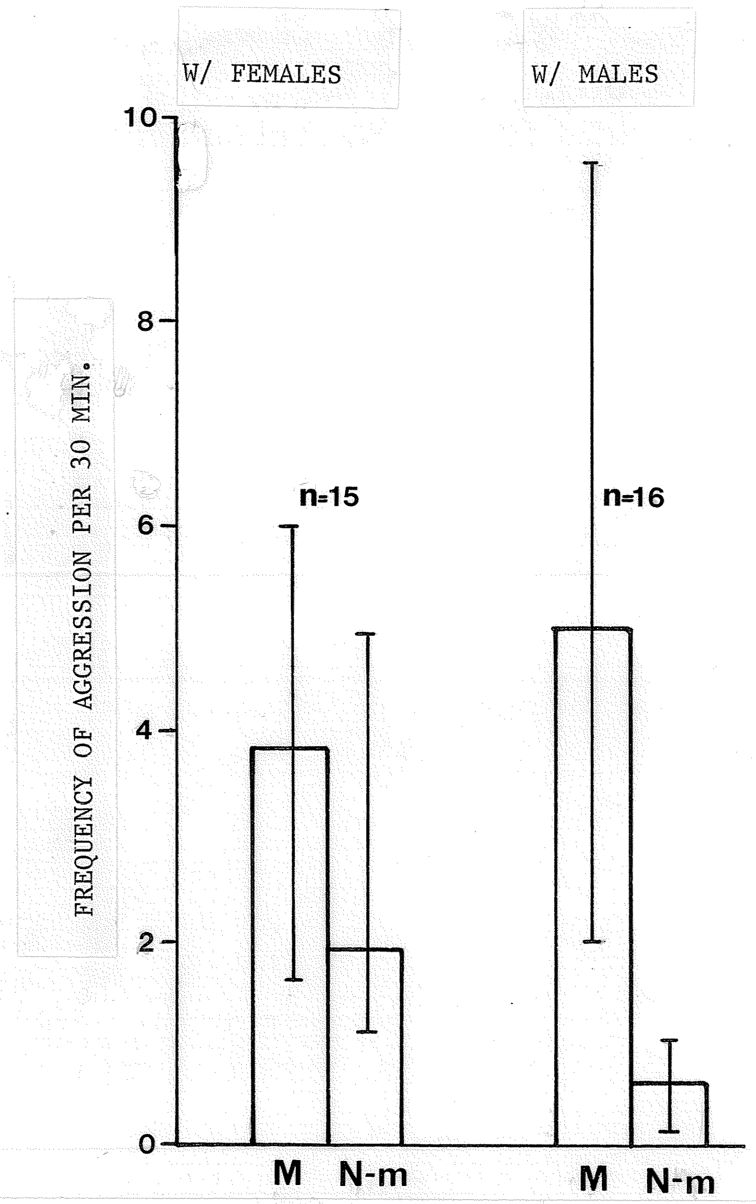

Figure 6.3. Frequency of aggressive interactions directed at other males by musth and non-musth males when in groups with females and in groups with other males. Medians and interquartile ranges are shown.

Table 2. Urinary testosterone levels (ngT/mgCr) collected from males in behavioural groups D and E.

D Pre-Musth male	 ngT/mgCr	E Borderline male	 ngT/mgCr
114	361.3	150	223.0
57	303.6	46	91.9
44	176.2	80	248.5
107	181.7	57	142.3

6.3.2 Frequency of aggression: sexually inactive and sexually active and musth and non-musth males

I have looked at the frequency of aggression (including all behaviours defined above as threats) for sexually inactive and sexually active musth and non-musth males, dividing the data into whether threats were directed at elephant or non-elephant objects, and into whether threats occurred between males in association with females, between males in bull groups, or by lone males.

The rate of aggressive interactions towards other elephants increased from non-musth to musth state both when in association with females ($T=19$, $n=15$, $p<0.02$) and when in association with other males ($T=13$, $n=16$, $p<0.01$; Figure 6.3). The rate of threats towards non-elephant objects also increased from non-musth to musth state when in association with females ($T=0$, $n=7$, $p<0.02$) and when in association with other males ($T=3$, $n=11$, $p<0.01$; Figure 6.4). In addition, lone musth males threatened non-elephant objects more often than did lone non-musth males ($T=6.5$, $n=17$, $p<0.01$; Figure 6.4).

Urinary testosterone levels were found to be low among males who were in association with males, higher among non-musth males in

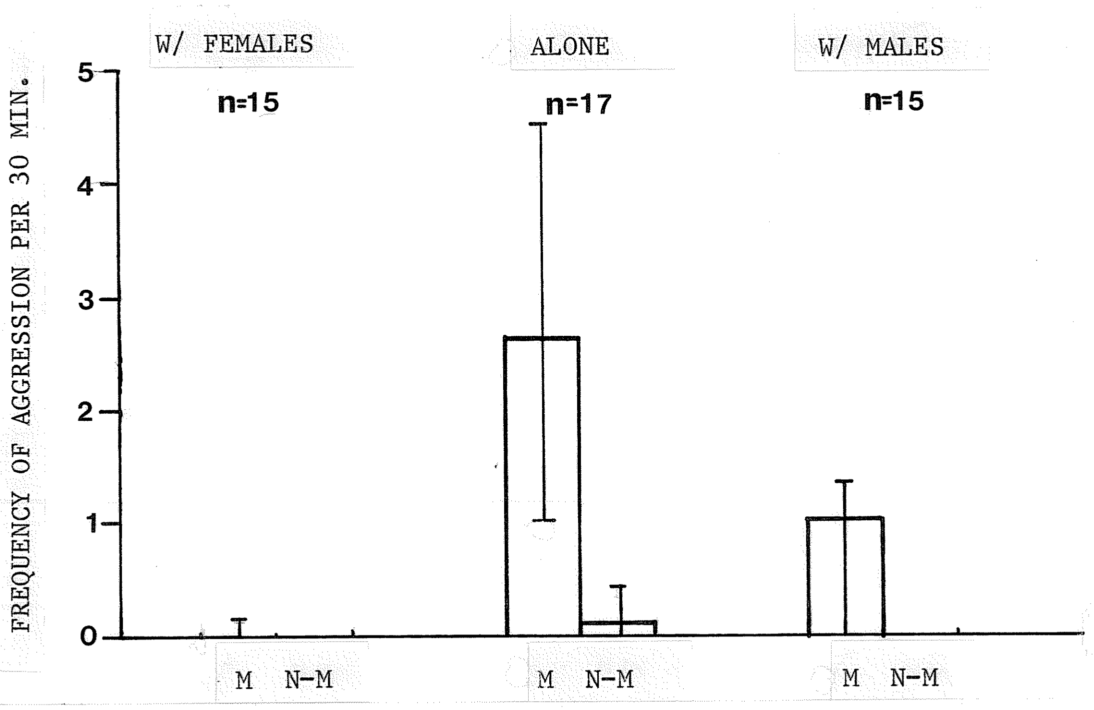

Figure 6.4. Frequency of aggressive interactions directed at non-elephant objects by musth and non-musth males when in groups with females, alone or in groups with other males. Medians and interquartile ranges are shown.

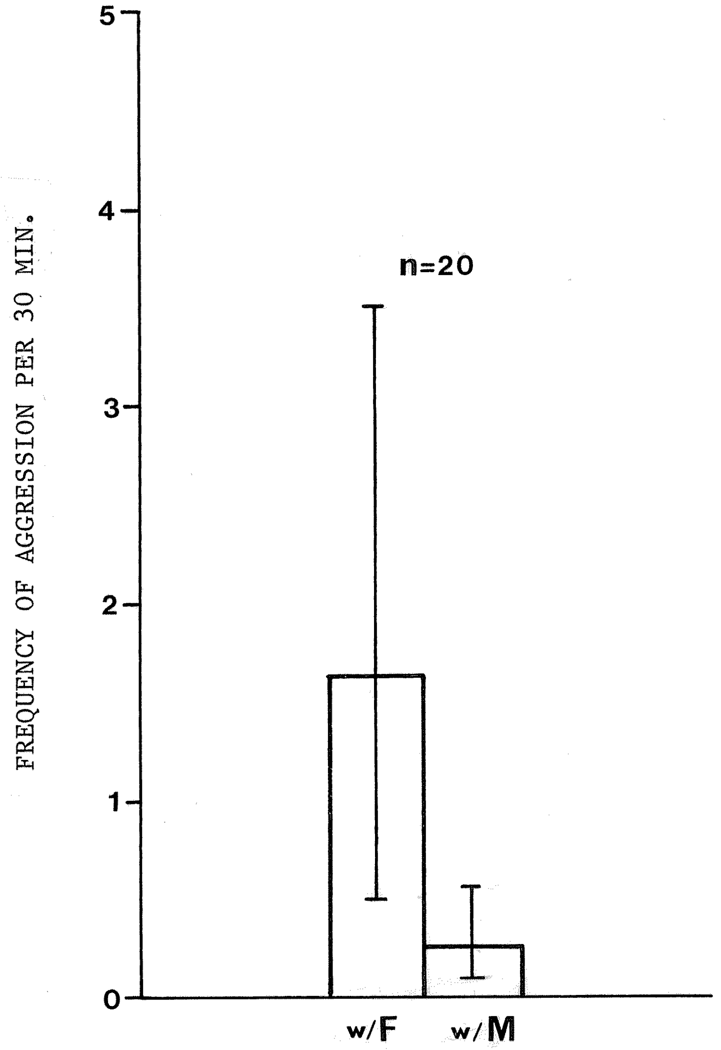

Figure 6.5. Frequency of aggressive interactions for non-musth males; with females versus with males. Medians and inter-quartile ranges are shown.

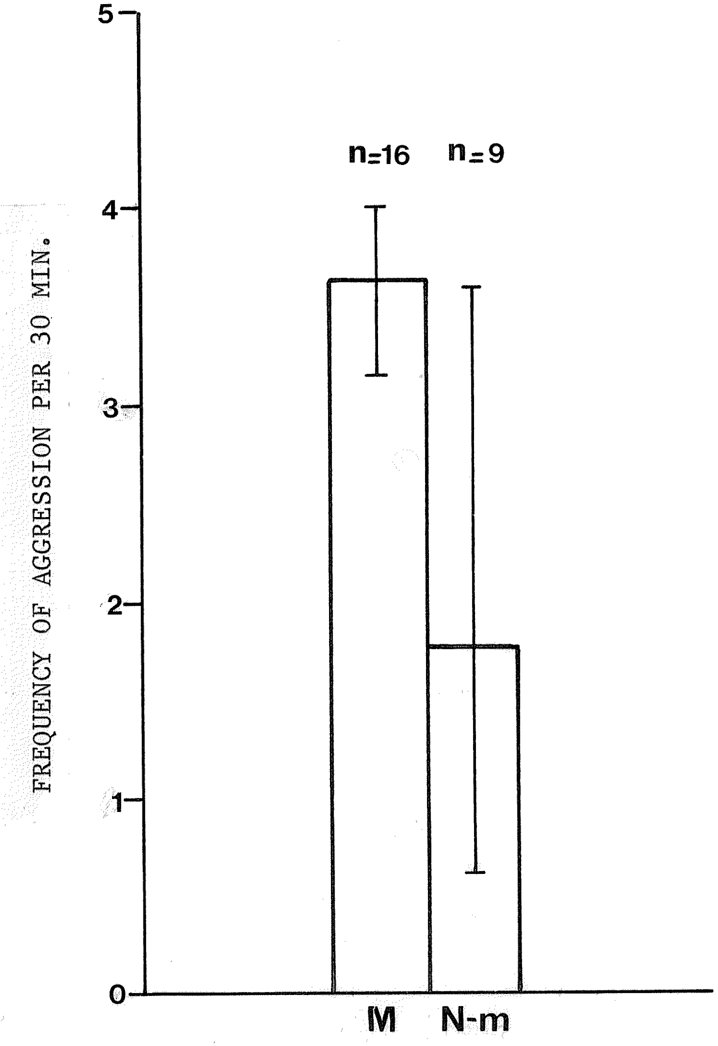

Figure 6.6. Frequency of aggressive interactions for musth and non-musth males with females. Medians and inter-quartile ranges are shown.

association with females and highest among males in musth (see above). Correspondingly, the rate of aggression among non-musth males was higher when they were in association with females, than when they were in association with males ($T=20$, $n=20$, $p<0.01$; Figure 6.5) and among males in association with females, males in musth had higher rates of aggression than did non-musth males ($U=43.00$, $n1=9$, $n2=16$, $p<0.05$; Figure 6.6).

6.3.3 Non-musth rank

Male elephants do not live in permanent groups and individuals meet and interact under highly varied social contexts (see Chapter 3). Perhaps for this reason the relationships between males do not result in a strictly linear non-musth agonistic dominance hierarchy (Figure 6.7). For instance, during the course of the study, M97 dominated M51, M51 ranked above M150, but M150 was able to dominate M97. Similarly, M57 ranked above M150, M150 above M51, M51 above M114, but M114 was dominant to M57. Ideally, I should restrict interactions to those occurring between non-musth males only when they were in association with bulls. However, since the level of association between members from different bull areas is so low (see Chapter 3), I would only be able to rank individuals against males from within their own bull area. Since I wish to make comparisons between non-musth and musth rank, this would not be a satisfactory solution.

Although the rank order I have presented may not be a perfect solution, it correlates closely with both relative body size (Spearman rank correlation=0.98, $n=30$, $df=28$, $p<0.001$; Figure 6.11) and footprint size (Spearman rank correlation=0.88, $n=30$, $df=28$, $p<0.001$; Figure 6.12). Before analyzing these data I made note of which animals I thought had relatively large heads. It is interesting that these

Figure 6.7. Non-musth non-musth agonistic dominance matrix. For this and all other dominance matrices the figures given are the number of days on which individuals were observed interacting. *=serious interaction involving a chase; F=an escalated contest involving physical contact; _=reversal observed between a pair of males; u=conflict unresolved.

Subordinate - Non-musth

Dominant - Non-musth	13	28	126	22	41	117	73	44	99	78	107	80	45	119	10	114	7	51	97	154	150	57	175	174	147	91	173	46	79	49	149	34	157	125	132	137	145
13		$\underline{1}$	2				1				1									2				1	1	1			1								1
28	$\underline{1}$		$\underline{2}$				3				3			1	1					2																	
126		$\underline{2}$					2			1	4	1			1			1		2					1	1			1			1					
22					2	$\underline{1}$				1	1		2											1				1	1	1							
41						1		3	2			2	1	1			1			1								1		1							
117				$\underline{1}$						1	1		1	1														1	1		1						
73											5			1					2	2	2			2		1		1	1		1					1	
44										1		2						1				1	1			1			1	2	1		1				
99										1		1		1				1								1			1			1	1				
78											$\underline{2}$	$\underline{1}$		1		3					1				1			2	1				2				
107									1	$\underline{1}$		1		$\underline{4}$	$\underline{1}$	1				3	1	1		1	2			1	1	1	1			2			2
80										$\underline{1}$				2	1							1	1					1	3	1	1	1	1				
45														1		1		1		1					1			1	1		1						
119											$\underline{1}$					1			1		2	2		1	2	5	1	2	1	3				1	1		2
10											$\underline{1}$					1					2		1					1	1		1		1				
114																	1	$\underline{1}$	1		2	2		2	3	2		1	2		1		1		1	3	1
7																		2				2	1			1							1	1	1		
51																$\underline{2}$			*$\underline{1}$		1			2		1											
97																		F$\underline{1}$		1					1	1		1	1	1	1	1	1		2	1	2
154																									1							1				1	
150																				1				F3					3		2			1	3	2	1
57																					1		1				1	1	1		1		1				
175																										1	1		1		1		1		1	1	
174																									1	2			2		1				1	1	
147																										2			2						2		1
91																											1	2		1	1		1	1			
173																												1						1			
46																									1					1	1			2			1
79																														2		2		1	2	1	
49																																					
149																																1	1	1	2		
34																																			1		
157																																				1	
125																																			6		
132																																				1	1
137																																					
145																																					

Figure 6.8. Musth non-musth agonistic dominance matrix.

Subordinate - Non-musth

Dominant - Musth

	13	28	126	22	41	117	73	44	99	78	107	80	45	119	10	114	7	51	97	154	150	57	175	174	147	91	173	46	79	49	149	34	157	125	132	137	145
13			1			1	3	1		1	8	2	1	5		4	1		2	1	2	5			2	3	4	4	1	4	5		1	3	4	1	4
28					1		1			2	2	2		3		3	2	3	1		1	2	1	1	1	1		1	2		1		1	1	1	1	
126				$\underline{1}$		1	2	1		4	4		2	9			1		3		4	4		2					1	2					2		
22			$\underline{1}$								1	2		1		1					3							1					2	1			
41									$\underline{1}$	2	4		1	1					1		1	2	1		1					2	1		2	1	1		1
117				1			1					2		5	1	2	1		2		3				2	2					2		4	1	4	1	3
73														3	1			3	1		2					1			2						1	1	
44										$\underline{3}$	3			3	1	1			1		$\underline{3}$	1	1		1	1	1		1			1	1	1	1	1	
99					$\underline{1}$		1			3	2					3			6		1	2	1		3			2			5		1	1	1	3	1
78							1	$\underline{1}$													2		1	1		2			3	1					2		
107														1						1	2	2				2	2	3	1	3	2			2	2		
80										2	2										1	1				1	1	2			2		2	1	2		1
45																			1							1	2				1		1		2		
119																*1					1			1							1						
10			*1									1	*1						1			1														1	
114																								1			1			1	2		1		1	1	1
7																																					
51												2				2			1										2								1
97																																				1	
154																1		1							1												
150								*$\underline{1}$								*1																					
57																1										1					1					1	
175																																					
46																			1							1											
34																																					

Figure 6.9. Musth musth agonistic dominance matrix

Subordinate - Musth

Dominant - Musth	13	28	126	22	41	117	73	44	99	78	107	80	45	119	10	114	7	51	97	154	150	57	175	147
13			*1		3	*2		*2	4		5	6	2	2		1			1					1
28					F1										1			1				1		1
126								*3										1						
22	*1						1												1					
41																								
117								F1																
73																								
44						F1							1											
99								1			3	*3										1	1	
78																	1				1			
107													*2						1					
80					F1						2													1
45					F2			F1				F1			1									
119																								
10																								
114																								
7																								
51																								
97																								
154															*1			1						
150																								
57																								
175																								
147																								

Figure 6.10. Non-musth musth agonistic dominance matrix.

Subordinate - Musth

Dominant - Non-musth	13	28	126	22	41	117	73	44	99	78	107	80	45	119	10	114	7	51	97	154	150	57	175	147
13																								
28																								
126																								
22												1												
41															1									
117																								
73																1								
44												1												
99																1								
78																				1				
107																							2	
80																								
45																								
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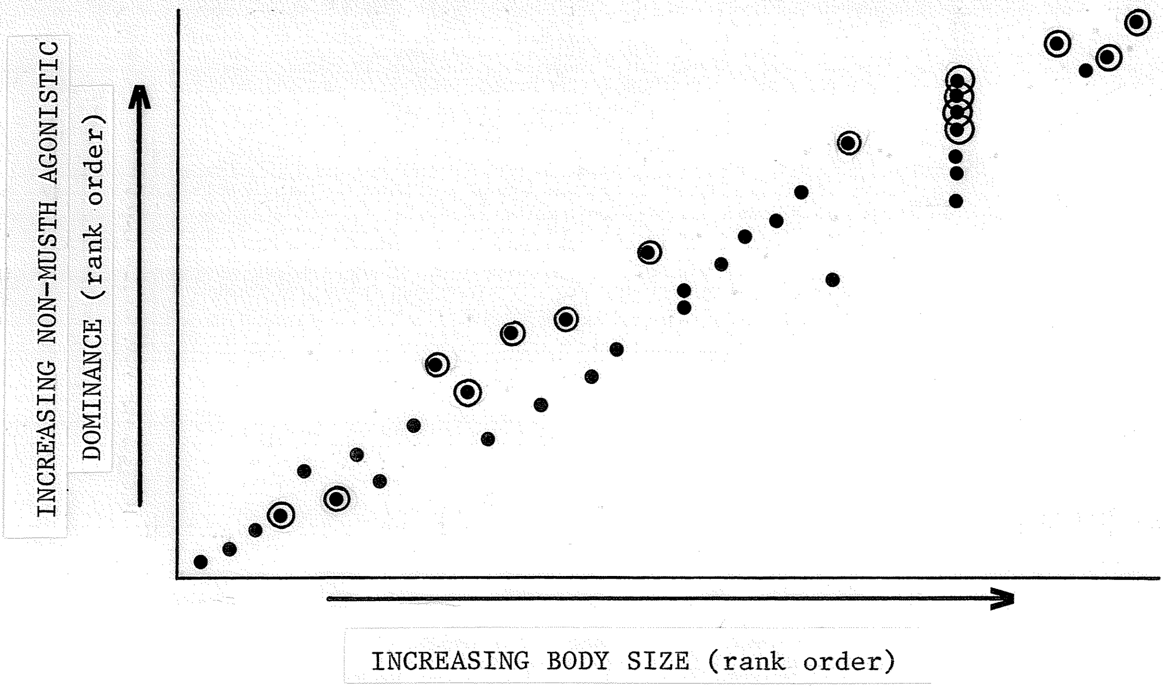


Figure 6.11. Relationship between body size and non-musth agonistic dominance rank.

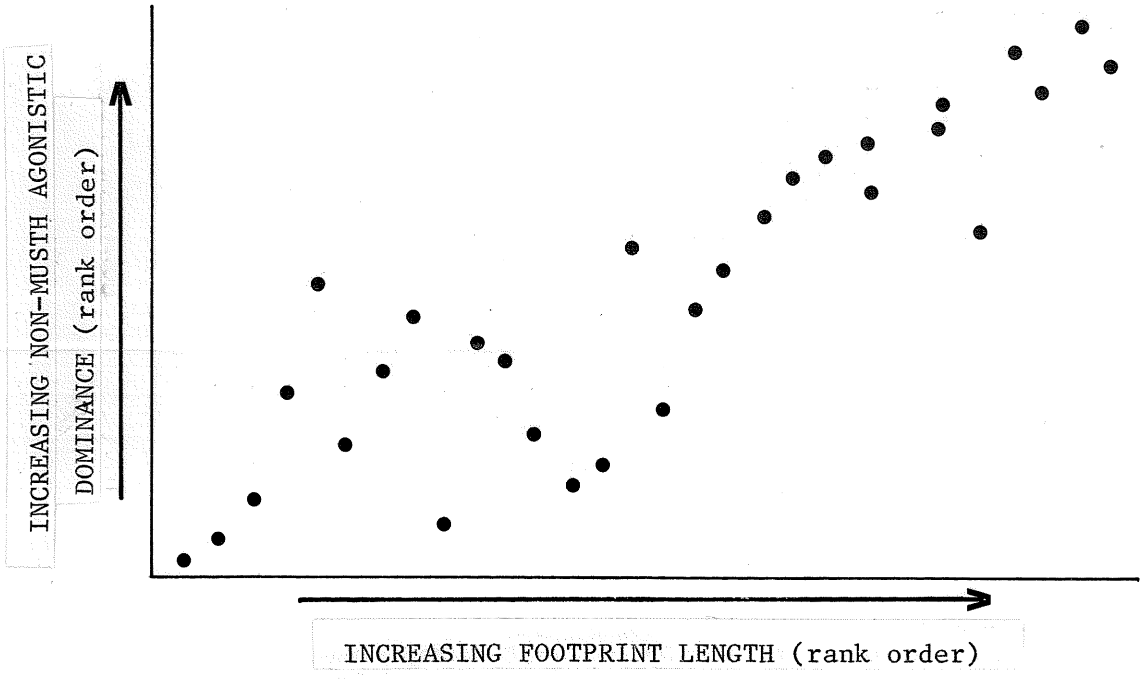


Figure 6.12. Relationship between footprint length and non-musth agonistic dominance rank.

animals rank above those animals of a similar body size who have relatively smaller heads, indicating that head size may be of importance in male-male agonistic interactions (Figure 6.11). During musth the heads of males with swollen temporal glands appear larger still.

6.3.4 Musth and dominance rank

Using the same rank order that I determined for non-musth males I have looked at how being in musth affects an animal's rank. Of the 25 rank reversals that I have recorded, only seven reversals took place when both males were not in musth. Of these seven reversals three took place in bull groups and four occurred when the males were in association with cows. The remainder of the reversals occurred when at least one of the males was in musth. Table 6.3 gives the types of reversals observed (and see Figures 6.8,6.9, and 6.10).

Table 6.3: The types of rank reversals observed and the individuals involved in them. R=ranks above; nm=non-musth; m=musth; A=male A; B=male B; "="=tied ranks.

Type of reversal

Anm R Bnm but Bnm R Anm		Anm R Bnm but Bm R Anm		Am R Bnm but Bm R Anm		Anm = Bnm but Bm R Anm		Anm R Bnm but Bm R Am		Am R Bm but Bm R Anm	
A	B	A	B	A	B	A	B	A	B	A	B
13	28	114	57	126	22	22	117	41	45	45	10
126	28	107	80	41	99	78	80	41	80		
107	78	126	10	44	78	51	114				
107	119	80	10	44	150						
107	10	114	150								
51	114	97	46								
51	97	91	46								

Several reversals involved relatively large "jumps" in rank and individuals were seen to dominate males much larger than themselves (e.g. the reversal between M44 and M150; M126 and M10). These large

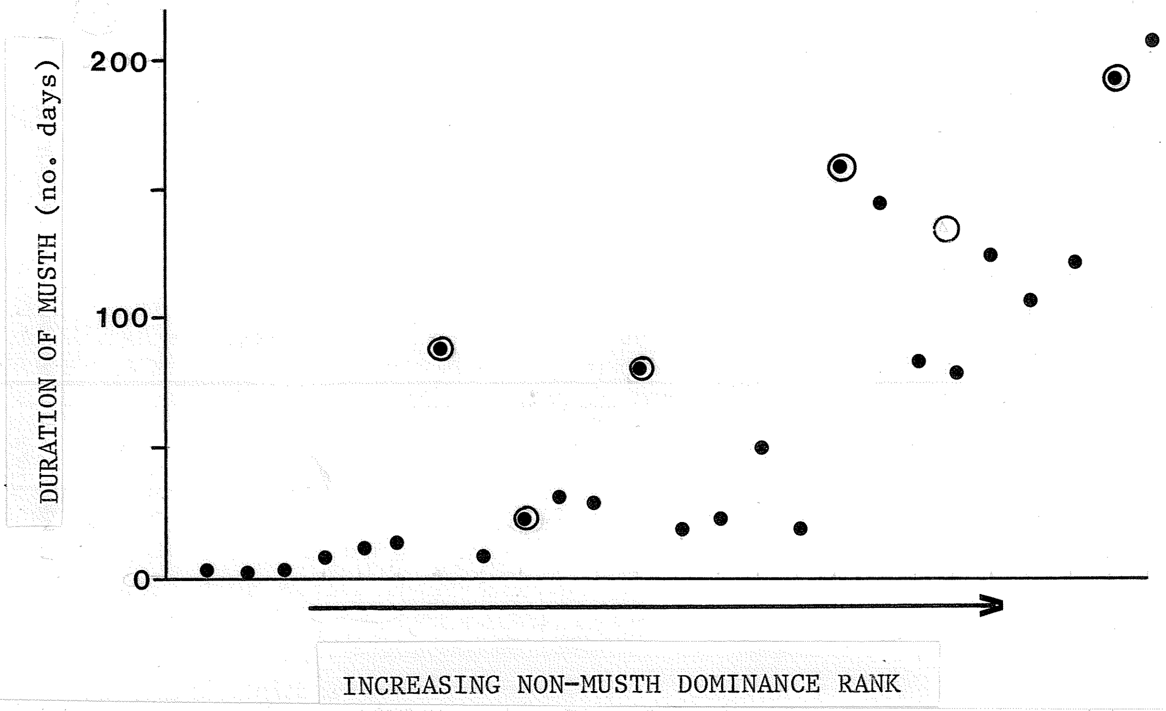


Figure 6.13. Relationship between non-musth rank and musth duration during 1980-81. See text for method of calculation of musth duration.

changes in rank occurred when the usually subordinate male came into musth when the usually dominant was out of musth.

6.3.5 Factors affecting the duration and spacing of musth periods

While being in musth may increase an male's rank relative to other individuals, non-musth rank appears to be related to the length of time a male is able to stay in musth. Non-musth rank correlates closely with the number of days (1980 and 1981 combined) that each male was observed in musth (Spearman rank correlation=0.87, n=25, df=23, $p<0.001$; this includes all individuals who periodically come into musth except M73, for whom I was unable to obtain 1981 data; Figure 6.13).

Since the duration of musth periods correlates closely with rank, duration is obviously also correlated with both relative body size (Spearman rank correlation=0.80, n=25, df=23, $p<0.001$) and footprint size (Spearman rank correlation=0.73, n=22, df=20, $p<0.001$). Although the duration of musth periods correlates closely with height and dominance, body condition may also be important.

To examine the role of body condition more closely it may be helpful to look at those males (n=5) whose onset of musth was during the latter part of the year and before the start of the short rains (August-November). These males seem to have longer musth periods (see those circled in Figure 6.13) than males of similar rank who come into musth during the earlier part of the year. During the latter half of the year females are in smaller groups, there are few females in oestrus and fewer males are sexually active so that there is less competition for access to females (see Chapter 5). Are these males able to stay in musth for longer periods because a) they have built up fat reserves during the wet season, b) because when they are in musth there is more time available for feeding and they are therefore able to stay in better

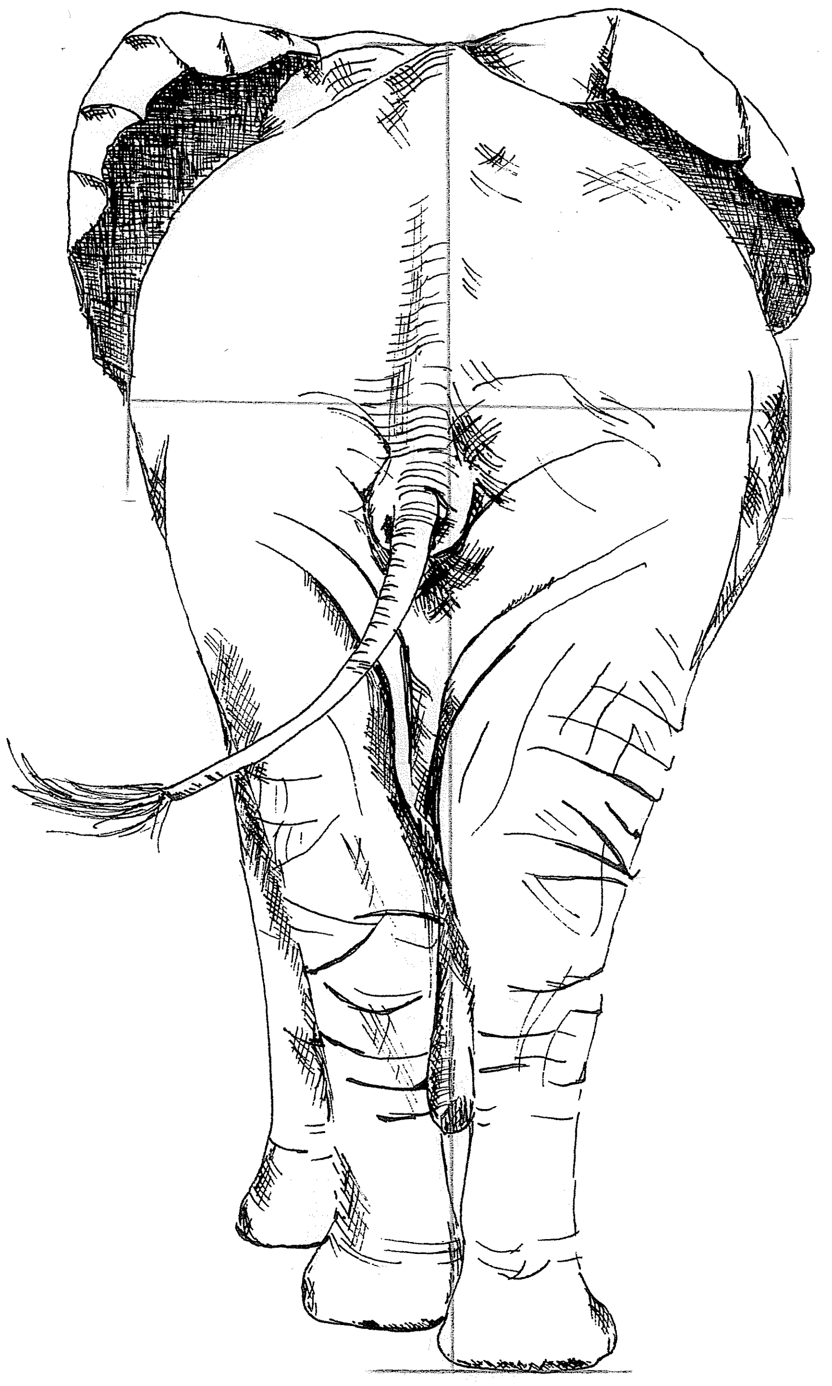


Plate 6.2 Illustrates the measurement of midriff to back height ratio as a method of estimating body condition from photographs.

condition for longer, or c) because their musth periods are not inhibited by higher ranking males?

I have attempted to estimate whether males lose body condition during musth by comparing photographs of individuals taken pre and post musth. I have estimated body condition by calculating the midriff width to back height ratio from photographs taken immediately behind the male (Plate 6.2). Males whose photographs were taken in mid to late musth and up to one month post musth had significantly lower ratios than males who had been out of musth for at least 3 months and those in early to mid musth ($U=0$, $n1=4$, $n2=6$, $p<0.005$; Figure 6.14). Although this result is highly significant, I do not attach any particular reliability to it. It is likely that males in musth lose weight: they spend more time walking and interacting and less time feeding (see Chapter 5), but this measure, if valid at all, would mean more if it were taken of the same individual through time. Unfortunately, when I was in the field I decided that this method was not worthwhile and I stopped taking photographs. In four cases I have two values for the same individual and all showed a decrease in body condition (as estimated by this ratio) late in the musth period or immediately post musth (Figure 6.15). For two bulls I took two photographs within a week and in both cases the ratio does not vary (Figure 6.15).

Although the loss of body condition may be an important determiner of musth termination among males who stay in musth for long periods, musth duration among low ranking males is probably limited by their rank relative to other males who are in musth simultaneously. I saw several instances where, following a long chase between two musth males, the defeated male immediately ceased dribbling urine and temporal gland secretion subsequently dried up. Although I did not often witness the

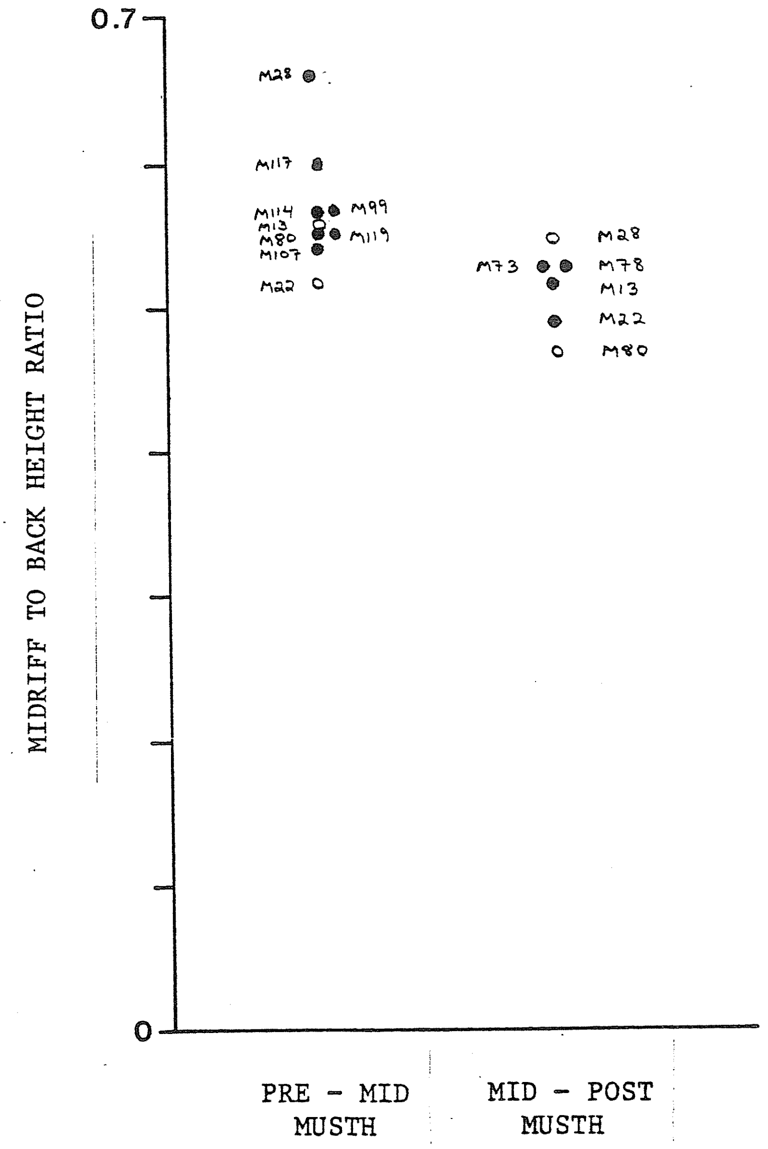


Figure 6.14. Midriff to back height ratio as an estimate of body condition of males photographed during pre to mid musth and mid to post musth, showing possible weight loss during musth. Since for some males ratio scores were available for both pre- and post-musth (see Fig 6.15) males were randomly selected such that the two groups remained independent. Open circles indicate males whose scores were not included in the analysis for this reason.

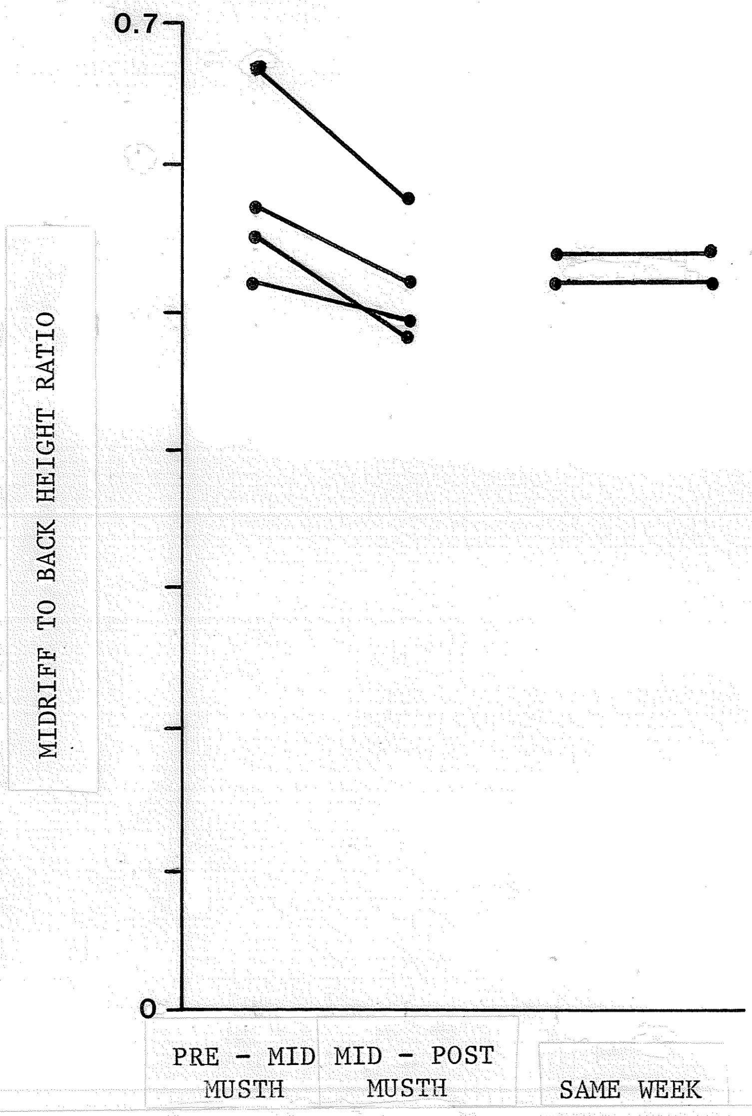


Figure 6.15. Midriff to back height ratio of four males photographed both during pre to mid musth and mid to post musth, showing possible weight loss during musth. These are compared to the ratios from two males whose pictures where taken within one week and show no change.

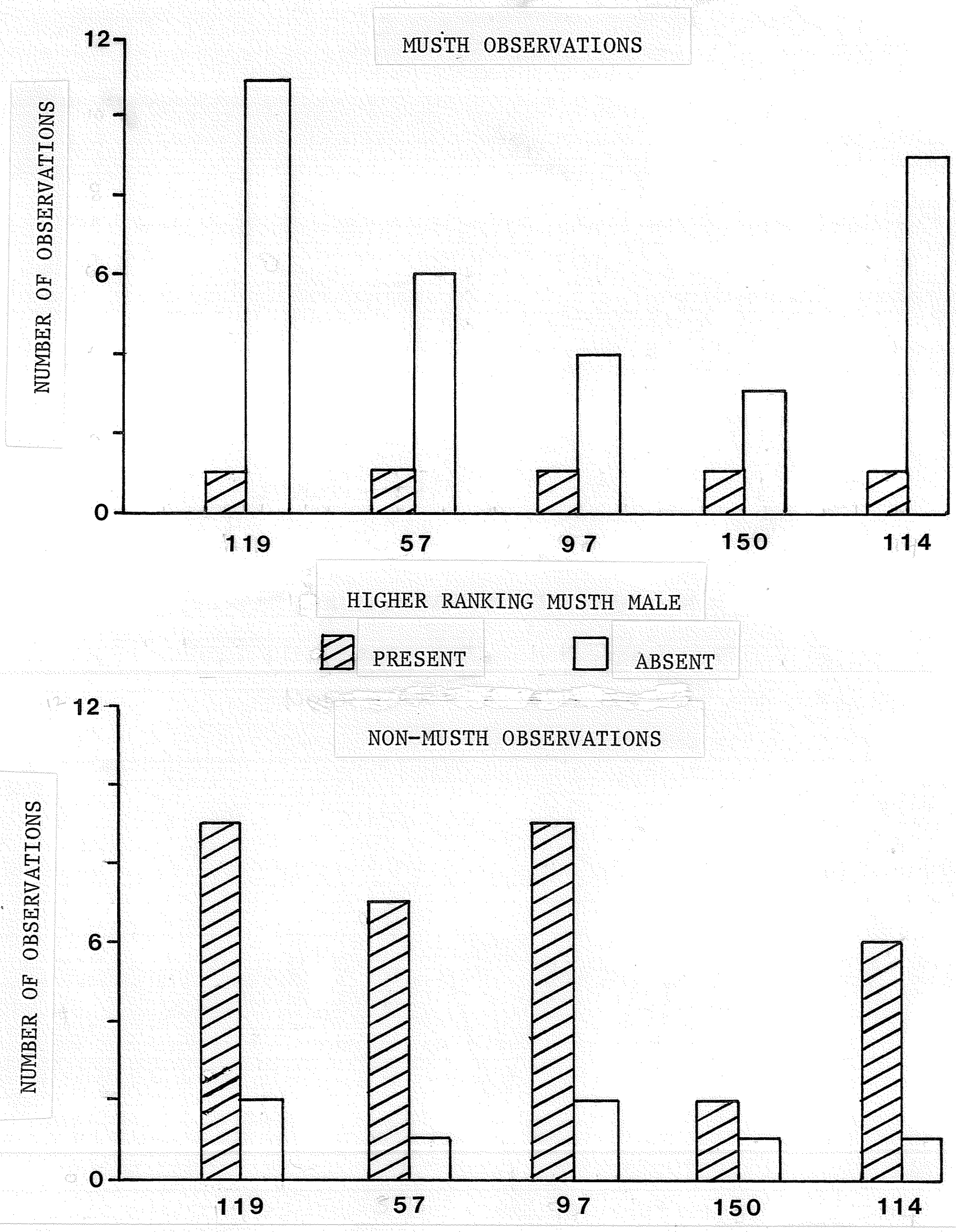


Figure 6.16. The effect of the presence or absence of a higher ranking musth male on the occurrence of musth in five low ranking individuals.

actual interaction and subsequent change from musth to non-musth state (n=10 approximately), I frequently observed what I interpret as the result of such interactions. Younger musth males were often observed to come into and go out of musth several times within one sexually active period (see Chapter 4) and this pattern appeared, in the field, to be related to the presence or absence of a higher ranking musth male. For the males who showed this pattern repeatedly (M114, M119, M150, M97, M57), I have looked to see whether their alternating non-musth and musth states had any connection to the presence or absence of a higher ranking musth male. For each male I have looked at those observations from the first day musth was observed to the observation following the last date that musth was seen during a particular sexually active period. If high ranking males are able to inhibit musth in lower ranking individuals, I would expect to find low ranking males in musth when they are not in association with a higher ranking musth male, and not in musth when they are in association with a higher ranking musth male. This is exactly what I have found (Figure 6.16). I feel that this is strong evidence in support of the theory that the duration and perhaps the occurrence of musth among the lower ranking individuals is determined by the relative ranks of individuals with overlapping musth periods. Among older males relative dominance may affect the spacing more than the duration of musth periods.

For the males who come into musth before they join females and stay in musth for the full time that they are with females (Group 1 males, see Chapter 4: M13, M28, M126, M22, M41, M117, M73, M44, M99, M45) I have tried to examine whether their musth periods are timed to avoid one another (see Figure 4.5 for the temporal patterning of musth periods for individual males). Table 6.4 shows the number of days that each male was in musth from January, 1980 through October, 1981.

Table 6.4. The total number of days that each Group 1 male was in musth from January, 1980 through October, 1981 is given. Males are arranged in order of decreasing non-musth rank.

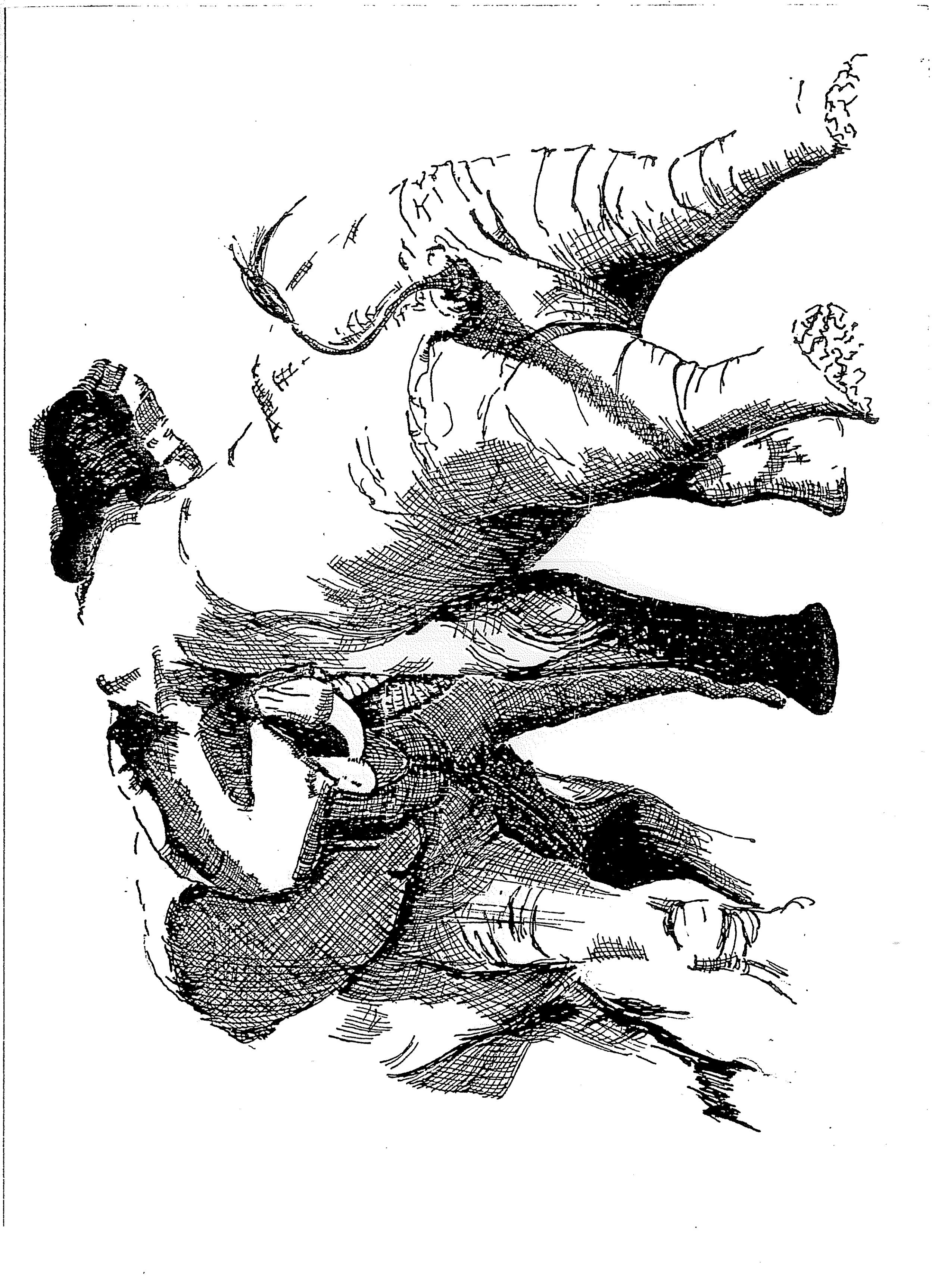
male no.	13	28	126	22	41	117	73	44	99	45	Total
No. of Days	211	193	123	108	128	80	67	86	148	24	1168

I have looked at the percent of overlap of musth periods for each possible pair of males (n=45). The percent of overlap was calculated as the number of days that both males were in musth out of the sum of the number of days that each was in musth. The percent of overlap for each possible pair of males ranges from 0 to 41% with a median overlap of 11% (see Table 6.5).

Table 6.5 Frequency distribution of the percent overlap of musth periods for each of the 45 possible pairs of Group 1 males (n=10).

% overlap	0	1-10	11-20	21-30	31-40	41-50
No. of pairs	12	9	18	3	2	1

However, even when the musth periods of males overlapped considerably they came into contact infrequently. In other words if males were attempting to avoid one another they could do so either by coming into musth at different times of the year or by overlapping with another male(s) but utilizing different sections of the Park. Table 6.6 shows the number of overlap days for each pair of males and the number of days that each pair of males was observed together (when with



females) during that period.

Although these males were observed with females on a total of 136 days (see Appendix 4) they were actually seen together extremely infrequently. It is my impression that males attempt to avoid overlapping with certain other males. When overlap occurs males appear to avoid coming into contact by utilizing different parts of the Park.

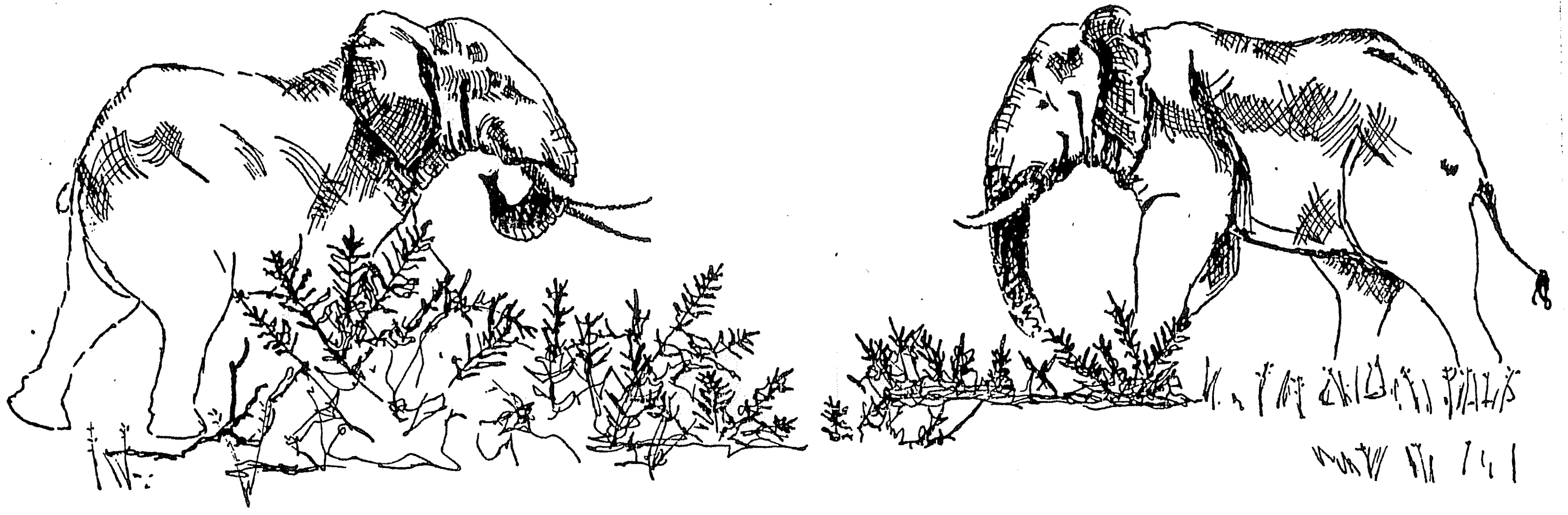
Table 6.6 The number of musth overlap days for each pair of males and the number of days that each pair of males was observed together (in brackets) when with females and in musth is given. See Appendix 4 for the number of sightings of each male with females.

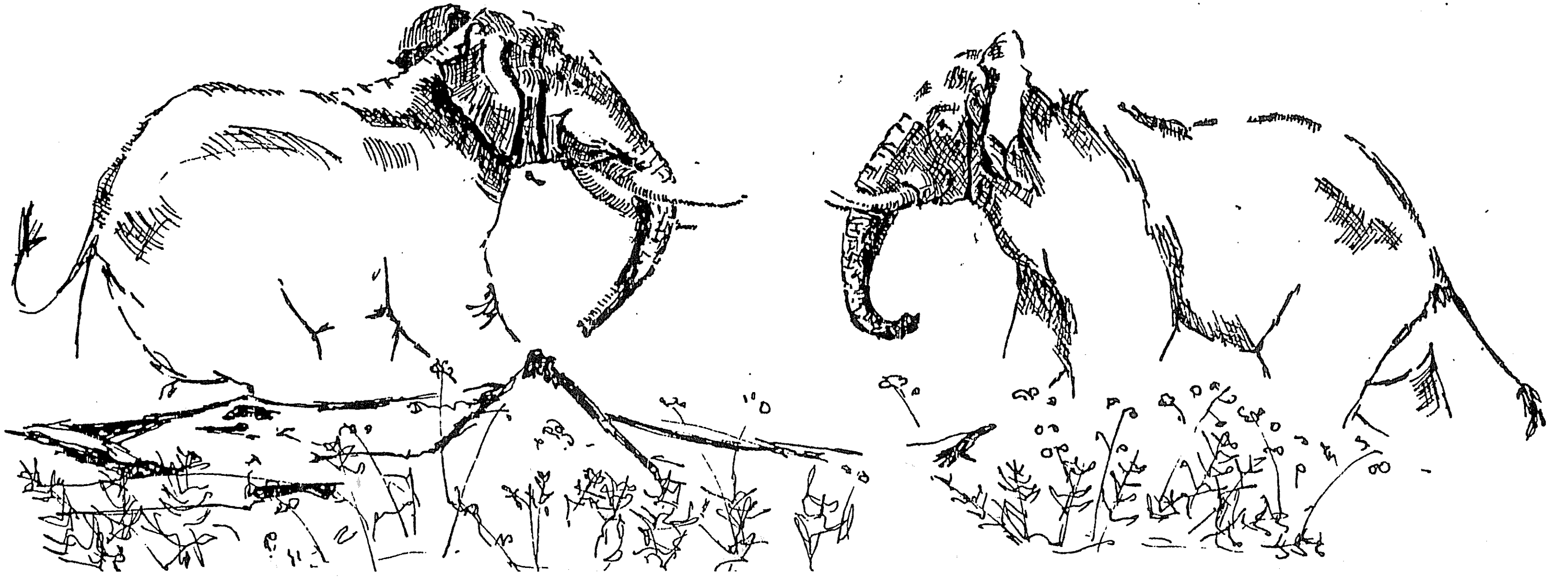
	13	28	126	22	41	117	73	44	99	45
13		70	30	30	66(1)	50(1)	0	38	148(7)	23(1)
28			113	6	35	67	31(1)	53	52	2
126				0	17	34	0	76	11	18
22					44	0	0	0	1	0
41						28	0	25(1)	30	23(1)
117							0	28	37	23
73								0	0	0
44									18(1)	23
99										13
45										

6.3.6 Escalated contests

Fights between male elephants occur rarely. Since the study began in 1972 Cynthia Moss and myself have witnessed only eight fights. Seven of these occurred during my 19 month study, of which five occurred between 3/6/81 and 25/6/81, a period of intense sexual activity. Two of these fights lasted for a minimum of 90 minutes and one lasted for over six hours.

The incidence of fighting was very low between pairs of males neither of whom were in musth. When both males were non-musth only two





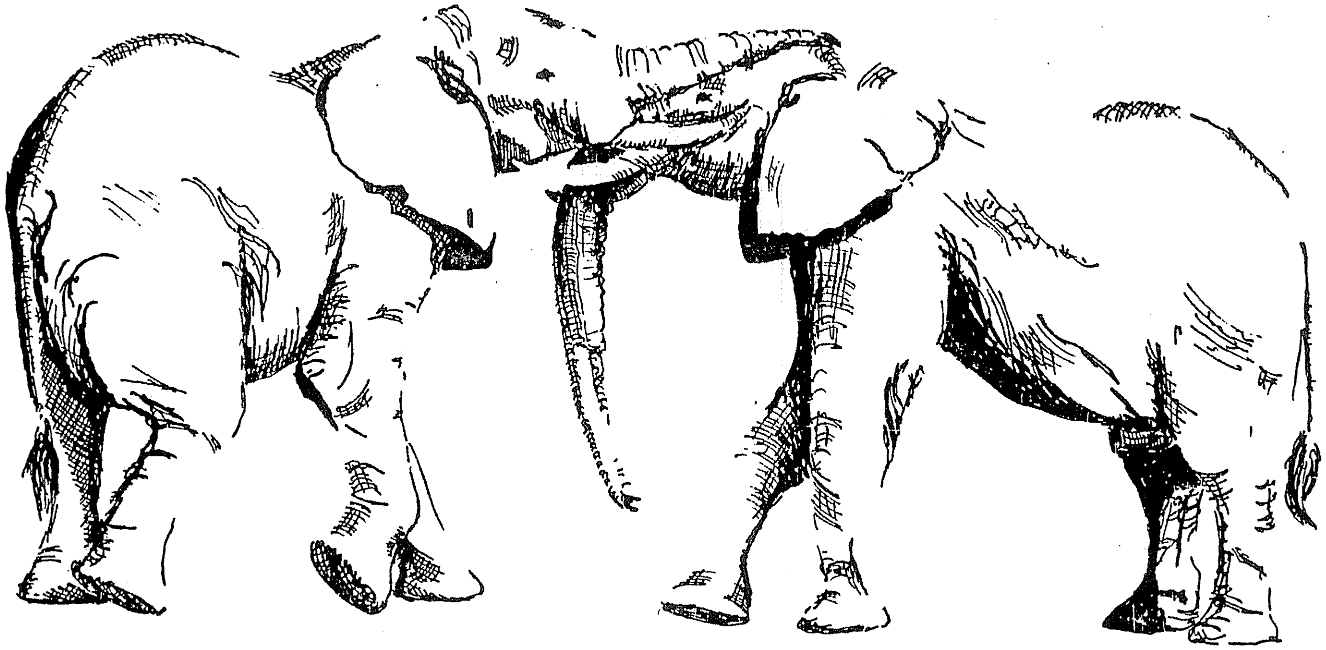


Plate 6.3. Sparring versus fighting.

fights out of 348 interaction-days were recorded and the males involved in these two fights clashed only once. No fights were recorded when either the dominant male was in musth and the subordinate not in musth (n=405; see Figure 6.8) or visa versa (n=8; see Figure 6.9). The incidence of fighting increased substantially when both males were in musth. Out of the 70 recorded agonistic interaction-days between musth males six resulted in escalated contests (see Figure 6.9). During the fight lasting six hours the lower ranking male, M80, used his long asymetrical tusks to hold M41 and almost succeeded in toppling the larger male (with short broken tusks) over. M41 chose at the last second to break away and flee. Presumably once M80 had knocked M41 over he would have had little difficulty goring and perhaps killing him. This observation leads me to believe that tusk length may be important during escalated contests.

The postures of males during fights are very different from those during sparring (Plate 6.3). Sparring often occurs following greetings between males and usually involves tactile and affiliative behaviour. The most obvious difference is that during sparring the trunk is held up and is used to push the opponent, while during fights the trunk is curled tightly under and the combatants lunge sharply at one another using their tusks. The positioning of the ears and head are also very different (see frontispiece).

6.3.7 Factors affecting retreat distance

I found that urinary testosterone levels and rates of aggression of musth males were higher than either sexually active or inactive non-musth males. Here I look at how differential body size and sexual state affect the responses of lower ranking animals receiving a Threat-2 from a higher ranking Class 4 male. Fights and other escalated encounters (e.g. serious chases) occurred between closely matched males in highly competitive situations (see above). What cues are males using to assess the fighting ability of other individuals and are males able to assess the probability that a male will escalate in a particular situation?

When males were in bull groups and neither animal was in musth there was no statistical difference in retreat distance from a threatening Class 4 male by Class 4 (median=2 meters) or Class 3 (median=3 meters) individuals (U=54.00, n1=6, n2=20, p>0.10), but Class 2 males retreated from Class 4 males at a greater distance (median=10 meters) than did Class 3 males (U=0.00, n1=3, n2=6, p=0.02; Figure 6.17).

However, when males were with females in a sexually competitive situation and the probability of escalation was high, then the reverse became true. When animals were close in fighting ability the subordinate male retreated at a greater distance than when the males were less evenly matched. In encounters where the threatening Class 4 male was in musth and the retreating animal not in musth (Figure 6.18), Class 4 males retreated at a greater distance (median=19 meters) than did Class 3 males (median=11 meters)(U=248.50, z=-2.21, n1=16, n2=48, p=0.03) and Class 3 males retreated at a greater distance than did Class 2 males (median=10 meters)(U=605.00, z=-2.44, n1=36, n2=48, p=0.02). There was no statistical difference in retreat distance by Class 2 and 1 males (median=8 meters) from Class 4 males (U=94.00, z=-1.13, n1=7, n2=36, p=0.26, n.s.).

Similarly, when both of the interacting individuals were in musth and in association with females (Figure 6.19) there was a trend for males closer in size (Class 4) to retreat at a greater distance

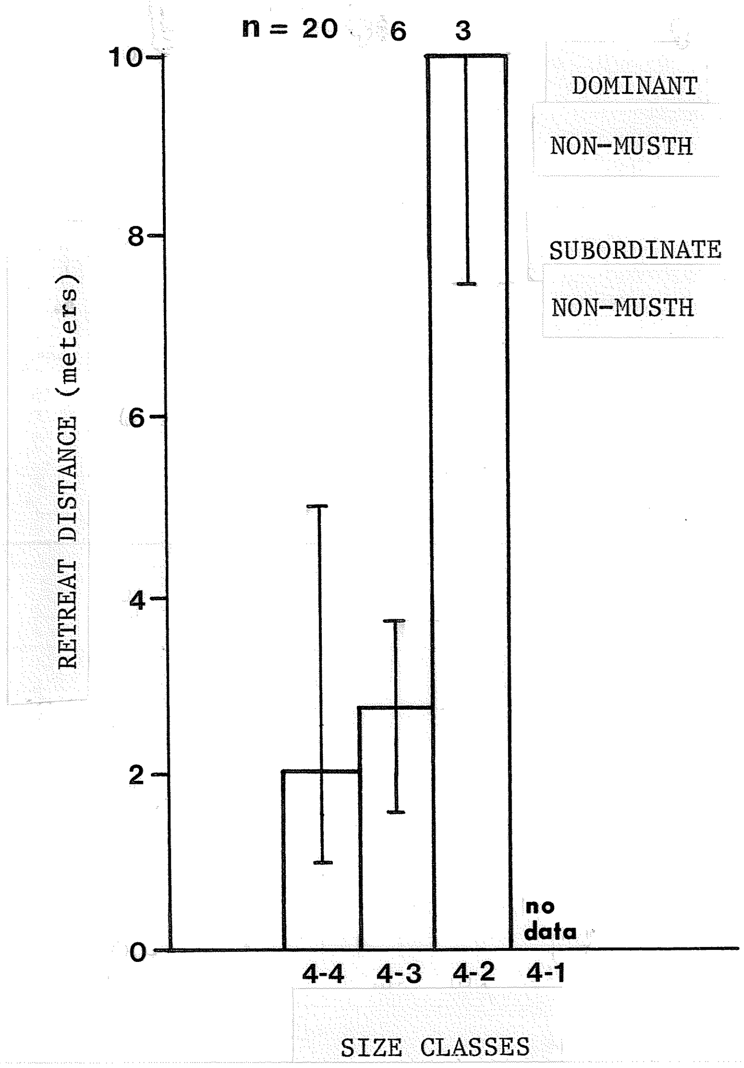


Figure 6.17. Retreat distances by non-musth Class 4, 3 and 2 male from a threatening non-musth Class 4 male when in bull groups. Medians and interquartile ranges are shown.

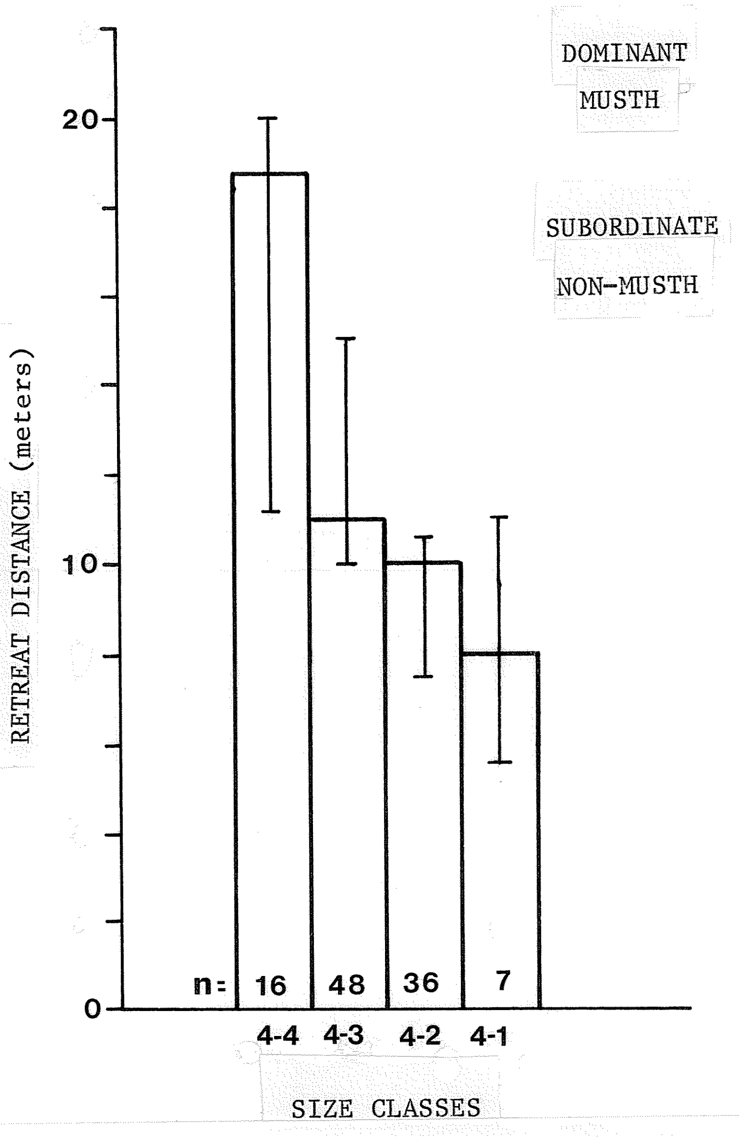


Figure 6.18. Retreat distances by non-musth Classes 4, 3, 2 and 1 males from a threatening Class 4 musth male when in association with females. Medians and interquartile ranges are shown.

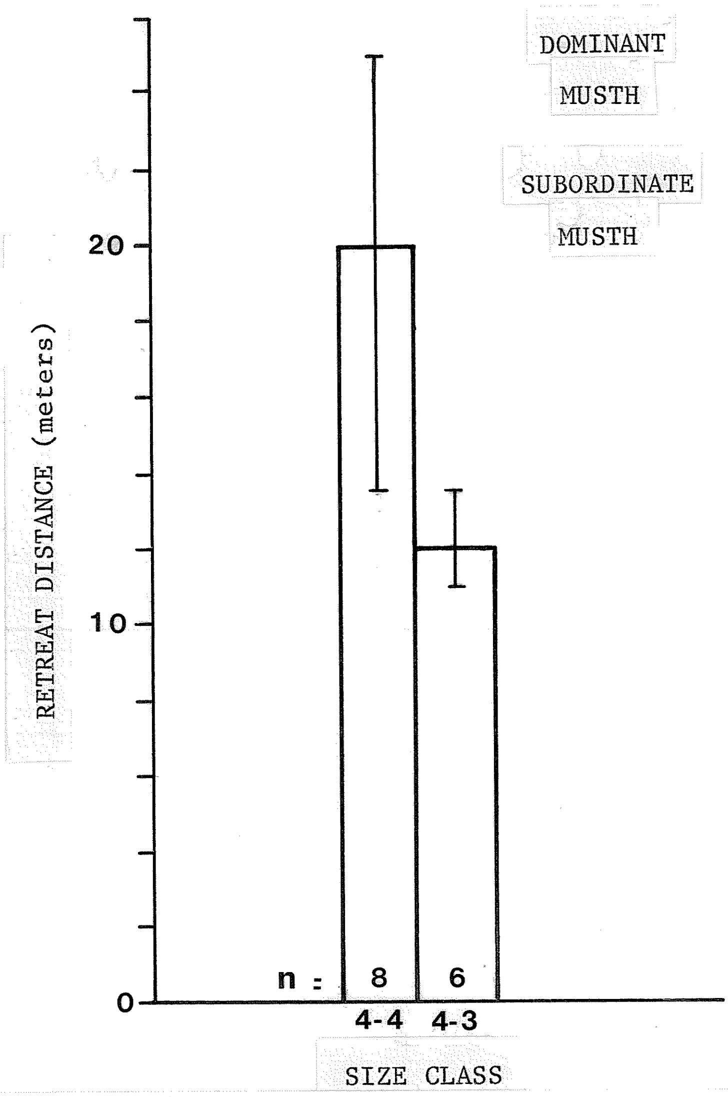


Figure 6.19. Retreat distances by Class 4 and 3 musth males from a threatening Class 4 musth male when in association with females. Medians and interquartile ranges are shown.

(median=20 meters) than smaller males (Class 3, median=12 meters) from dominant Class 4 males (U=11.00, n1=6, n2=8, p=0.11, n.s.). These data may indicate that a male is able to assess both the difference in fighting ability (size, strength disparity) between himself and his opponent and the probability that his opponent will escalate.

This second assessment process can be further examined by looking at how retreat distance changes between sexually active and inactive males. Both Class 4 and Class 3 non-musth males retreated at greater distance from Class 4 non-musth males when they were in association with females (medians=8 and 10 meters, respectively) than when they were in association with other males (Class 4 median=2 and Class 3 median=3 meters) (Class 4: U=7.00, n1=3, n2=20, $p<0.05$; Class 3: U=0.00, n1=3, n2=6, p=0.024; Figure 6.20). The probability of escalation is low among sexually inactive males and males retreat only when the threatening male is very close.

Similarly when in bull groups Class 4 non-musth males retreated from Class 4 musth (sexually active) males at a greater distance (median=10 meters) than from Class 4 non-musth (sexually inactive) males (median=2 meters) (U=6.00, n1=5, n2=20, $p<0.002$; Figure 6.21). The same pattern was true of Class 3 males: when in bull groups Class 3 non-musth males retreated at a greater distance from threatening Class 4 musth males (median=10 meters) than from non-musth males (median=3 meters) (U=1.0, n1=6, n2=7, p=0.002; Figure 6.21).

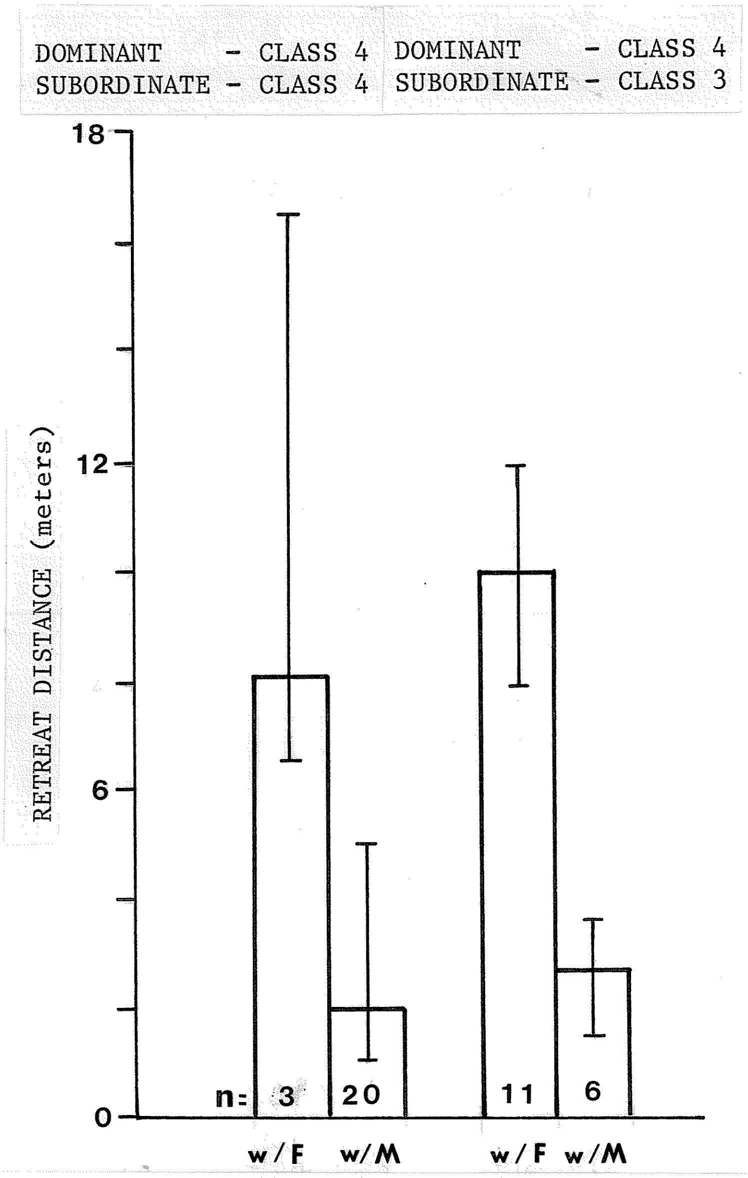


Figure 6.20. Retreat distances by non-musth Class 4 and 3 males from a Class 4 non-musth male when the males were sexually active (with females) versus sexually inactive (with males). Medians and interquartile ranges are shown.

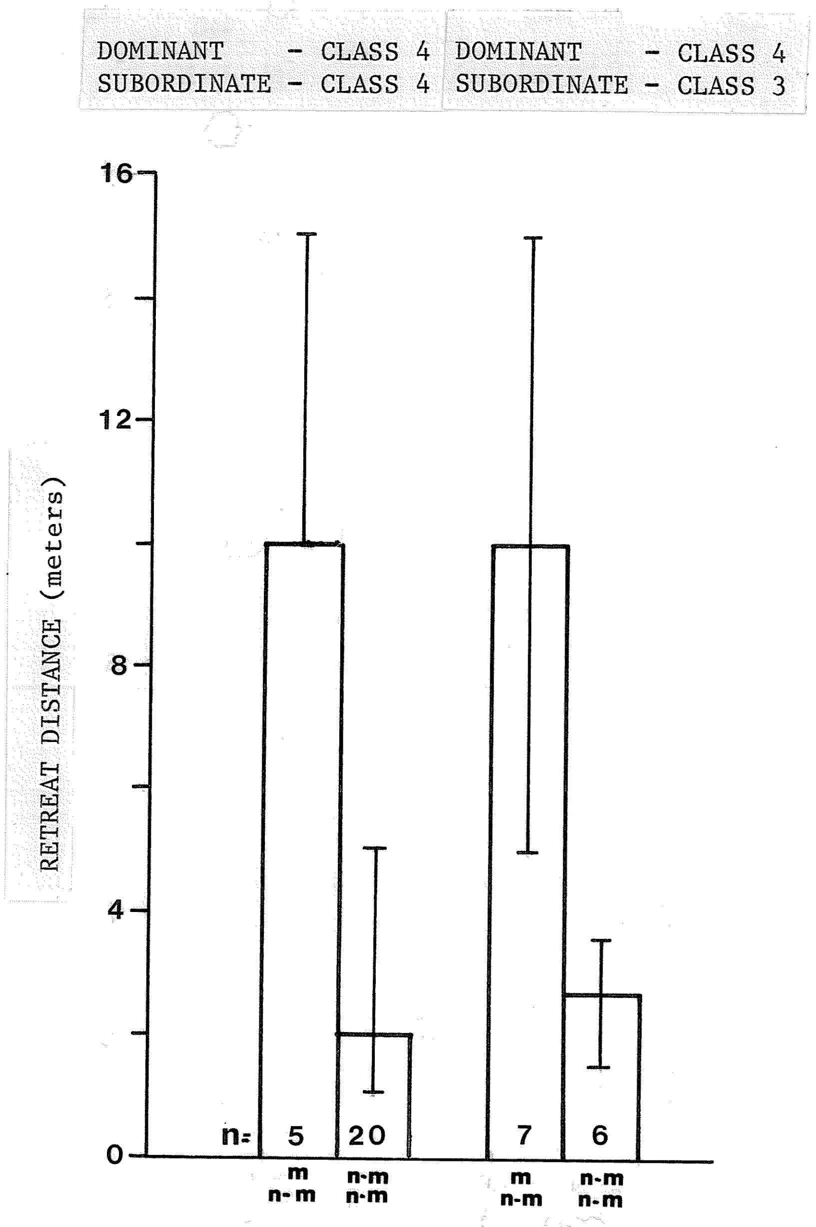


Figure 6.21. Retreat distances by non-musth Class 4 and 3 males in bull groups from Class 4 musth and non-musth males. Medians and interquartile ranges are shown.

6.4 DISCUSSION

In a discussion of animal contests Maynard Smith (1979) makes a clear distinction between the signaling of information concerning intentions (motivation) versus that concerning resource holding potential (ownership, size, strength, etc.). He claims that during contests animals mainly convey information about RHP, because it affects the outcome of an escalated contest and cannot be increased without cost in time or resources. Intentions, on the other hand, can be exaggerated without cost and would be open to evolutionary cheating. The logic of his argument (Maynard Smith, 1979) is as follows: if individuals signaled information about their intentions (the level to which they were willing to escalate), then if an opponent signaled a higher intention it would pay to retreat immediately. However, in this situation an individual who lied and claimed a very high, but untrue, intention would have a selective advantage. Soon all individuals would lie and it would pay to ignore the announced intention.

However, van Rhijn and Vodegel (1980) point out that if individual recognition and past experience play a role, bluff is unlikely to evolve because exaggerating individuals will be recognized as doing so. In groups of animals in which individuals know one another (and each other's strengths) conflicts may be settled by a means of a "process of heterogeneous summation of the strength-difference (known to individuals) and the interest-difference (indicated by signals)" (van Rhijn, 1980).

Differential body size (RHP) correlates closely with non-musth rank in elephants and may be used by males to assess the absolute fighting ability of other males. Laws (1966) found that male elephants continue to grow throughout most of their lives. Making the assumption that a cohort of males will all grow at approximately similar rates, then differential body size is a measure of fighting ability that may remain relatively constant through time among individuals in a population. In a long lived species such as elephants an individual is likely to recognize most other members of a population and thus might be expected to know his own fighting ability relative to every other member without continual assessment. However, changing levels of testosterone may alter a male's motivation to escalate against a particular male in a given situation.

The data presented in this chapter suggest that males may actually be signaling intentions. Within a particular size disparity the distance at which a male chose to retreat from a threatening Class 4 male varied with sexual state. Do these differences indicate that intentions are being communicated? The problem revolves around whether testosterone levels are considered as affecting motivation (intention) or RHP (absolute fighting ability). Although an increase in circulating testosterone is associated with increased metabolic rate and consequently some physiological cost, this cost, at least in the short term, is unlikely to be substantial (Maynard Smith, pers. comm.). The distinction is not entirely clear, but it seems plausible that in a situation where individuals know one another, intentions in conflict situations may well be signalled.

I found that males in musth had higher levels of urinary testosterone and rates of aggression than did sexually active and inactive non-musth males. Relationships between males did not remain static, but varied in content and quality with changing sexual state. In a species where males are unsynchronized in their periods of sexual activity and where the levels of testosterone and aggression can vary dramatically (this chapter and Jainudeen et al, 1972b) it will be important for males to be able to make accurate and continual assessments of even those individuals they know well. There is evidence that males do make such assessments: during greetings males usually smell one another's temporal glands and penises (Plate 3.1) and they may be attempting to monitor changes in sexual state.

A small male presents little competition to a large male and the cost of escalation, particularly if he is guarding an oestrous female (e.g. possible injury, reduction in reproductive success due to sperm competition from other males, see Chapter 7; energy expenditure), may be substantially greater than the benefits. Class 2 males retreated at the same distance from Class 4 musth or non-musth males whether they were in bull groups or in association with females (10 meters), indicating that they were aware that the likelihood that a threat would be followed by an escalation was low.

Larger males, particularly those closely matched in sexual state, present more competition to a high ranking male and the benefits of escalating may outweigh the possible costs. The Hawk-Dove model incorporating asymmetries (Maynard Smith and Parker, 1976) predicts that for any given value of resource and damage cost, the likelihood of both opponents escalating is expected to increase as the asymmetry between them decreases. The behaviour of male elephants during encounters appears to fit this model. Interactions between two similarly sized males in musth were much more likely to lead to escalation than were encounters where the asymmetries in sexual state and size were pronounced. In other species, Rubenstein (1981b) found that contest length in pygmy sunfish increased as the difference in rank declined and

Clutton-Brock and Albon (1979) found that red deer stags rarely resorted to escalated contests when there were visible discrepancies between opponents.

Plasma testosterone levels have been measured in domesticated Asiatic elephant in relation to musth (Jainudeen et al., 1972b). When males showed no signs of musth, testosterone levels were low (<0.2 to 1.4 ng/ml). During the initial stages of musth testosterone levels rose (4.3 to 13.7 ng/ml) and in full musth the levels of testosterone were extremely high (29.6 to 65.4 ng/ml). They suggested that musth is associated with, and possibly caused by a marked increase in testicular testosterone.

In this study the oldest males came into musth before they left their bull area and began associating with females; they tended to come into musth at the same time each year regardless of the change in the frequency of oestrous females through the year (see chapter 4). This suggests to me that some individuals musth periods are not influenced by the frequency of oestr us so much as by the temporal patterns of musth in higher ranking males. However, in the Asiatic elephant Jainudeen et al. (1972) showed that males can be brought into musth several months early by "teasing" them with oestrous females, suggesting that there may be several factors controlling the onset of musth.

Sexual stimulation either by visual contact or by copulation has been shown to produce rises in testosterone levels in several species (Primates: reviewed by Dixon, 1980; Rhesus monkeys: Rose et al., 1972; rabbits: Saginor and Horton, 1968) while defeat and aggression received from other males has been found to depress testosterone levels (Rhesus: Rose et al., 1972). I found that serious fights or chases in which one of the two musth males was soundly defeated could cause secretion from the temporal gland and urine dribbling to cease. The secretion took some time to disappear while the latter occurred instantaneously. These physical responses to aggression could reflect a decrease in testosterone secretion.

Both the duration and spacing of musth periods appear to be influenced by the temporal patterning of musth in higher ranking males. However, among the highest ranking males who stay in musth for long periods of time, loss of condition may be an important determiner of musth duration. Domesticated Asiatic elephants are often chained up during musth but, even so, they lose condition (Deraniyagala, 1955). High levels of circulating testosterone are associated with an increase in basal metabolic rate (Bell et al., 1977) so that even without the behavioural changes that accompany sexual activity (e.g. increased interaction, increased walking, decline in feeding) weight loss may occur.

CHAPTER 7

MATE COMPETITION

7.1 INTRODUCTION

Jarman (1974) suggested that the varied mating systems observed in ungulates have evolved through the attempts by males to maximize reproduction within the constraints imposed by the varying patterns of female mobility and aggregation. In situations where a portion of the members of one sex (usually males) is able to control the access of others to potential mates, selection may favour the evolution of alternative mating strategies. The typical pattern usually includes males who control access to mates either directly, by physically monopolizing mates and excluding other members of the same sex from these mates, or indirectly, by defending resources essential to the opposite sex (Emlen and Oring, 1977). Alternative strategies are usually less successful than the typical pattern but, the cost of reproductive competition is usually virtually eliminated (Rubenstein, 1981a).

Alternative mating strategies in animal societies has been a topic of recent interest (e.g. Le Beouf, 1974; Dunbar, 1979; Parker, 1978; Wells, 1977; Davies and Halliday, 1978; Clutton-Brock et al., 1979) and has been reviewed by Rubenstein (1981a). However, Rubenstein (1981a) points out that many cases of alternative strategies are probably only the opportunistic behaviour of young males delaying the adoption of the more costly pattern until the chances of successful competition are higher.

The evolution of female guarding behaviour will be favoured in situations where the number of competing males is high, and where a guarding individual can achieve a greater reproductive fitness by maintaining exclusive rights to a particular female than by investing the equivalent time searching for additional females (Parker, 1974a). The proportion of guarders that succeed will be frequency dependent and will largely be determined by the operational sex ratio (Rubenstein, 1981a). Guarding males must contend with "sneaks", who as opportunists attempt to mate whenever the guarding male is unattentive or chasing away other rivals. As a result not all guarded females will be successfully inseminated by the guarding male (Rubenstein, 1981a).

Pre-copulatory guarding apparently serves to establish mating rights with a particular female or group of females while awaiting the onset of female receptivity (Parker, 1974a). Post-copulatory guarding may be seen as a method of maintaining the reproductive gain already achieved by reducing loss due to sperm competition by rival males (Parker, 1974a).

In many species body size is related to the ability of males to gain access to and monopolize females (e.g. Geist, 1971; Le Boeuf, 1974). Observations on both genera of elephants suggest that oestrous females are monopolized by the largest male present (*Loxodonta africana*: Short, 1966; Laws and Parker, 1968; *Elephas maximus*: McKay, 1971).

7.2 METHODS

7.2.1 Sampling methods

The determination of guarding by males of oestrous females and of the solicitation of guarding behaviour by females was derived from 62 focal samples on 19 different males and 30 different oestrous females.

It should be kept in mind that the results from focal sampling apply to Class 3 and 4 males only. The occurrence of oestrus in females, musth in males, matings and guarding behaviour was recorded for each group encountered by both Cynthia Moss and myself. My own observations accounted for 65 of the 85 females observed in oestrus and 44 of the 54 matings recorded during the study period. No male was observed to mate a particular female more than once on any one day.

7.2.2 Description of oestrus and mating behaviour

Oestrous and mating behaviour in elephants have both been described in detail by Moss (in prep.). I will describe only those behaviours relevant to the present discussion. Oestrus can be identified by characteristic behaviour on the part of both the female and accompanying males. These behaviours have been described by Moss (in prep.) as wariness, the oestrous walk, the chase, mounting and consort behaviour.

Males search for oestrous females by testing each female encountered; placing the trunk at the entrance to the urogenital tract, or by smelling or tasting the urine of a micturating cow. An anoestrous female will stand still when she is being tested, while an oestrous female will move rapidly away from the testing male in a characteristic manner decribed by Moss (in prep.) as the "oestrous walk". The female carries her head high, her chin out, and looks over her shoulder at the following male. This posture gives the female the appearance of having arched her back. A male will take an active interest in a female who responds to his approach in this manner.

The oestrous walk may lead into a chase with as many as ten bulls with erections in pursuit. The female usually runs in a wide arc and may cover well over a kilometer before returning to her family (Moss, in prep.). A chase may not culminate in a mount for several reasons: the female may outrun the males (see Moss, in prep.); low ranking males may be chased away from the female by higher ranking males (see Moss, in prep.); large males have disproportionately long penises and have great difficulty running with an erection. The growth rate of the penis appears to increase with age so that among Class 4 males a semi-erect penis often touches the ground. When one of these males attempts to run with an erection his penis swings back and forth interfering with the movement of his hind legs so that he is forced to run with his legs widely spread, often slowing to a walk. On two occasions M13 lost the females he was guarding for this reason. On one of these occasions the female was, as a result, mounted by four different males and successfully mated by two of them. M13 did not locate this particular female again until at least six hours later. The implications of this observation will be discussed in the final chapter.

Once a male succeeds in touching the female with his trunk she usually slows and the male attempts to mount. A mount may be unsuccessful if the female refuses to cooperate (Moss, in prep.) or if a higher ranking male arrives and forces the mounted male down. The male achieves intromission by bending his knees slightly and hooking his S-shaped mobile penis into the female's ventrally located urogenital sinus (Plate 7.1). Moss (in prep.) describes the male as pushing in and up raising the female's genitalia some 30cm or more apparently achieving considerable intromission. A cooperative female stands still or backs towards the male apparently facilitating intromission. An uncooperative female moves forward (Moss, in prep.). The male stays mounted for approximately 45 seconds. After the male has dismounted the female often touches or smell the male's penis and may pick up ejaculate from the ground and throw it onto herself with her trunk.

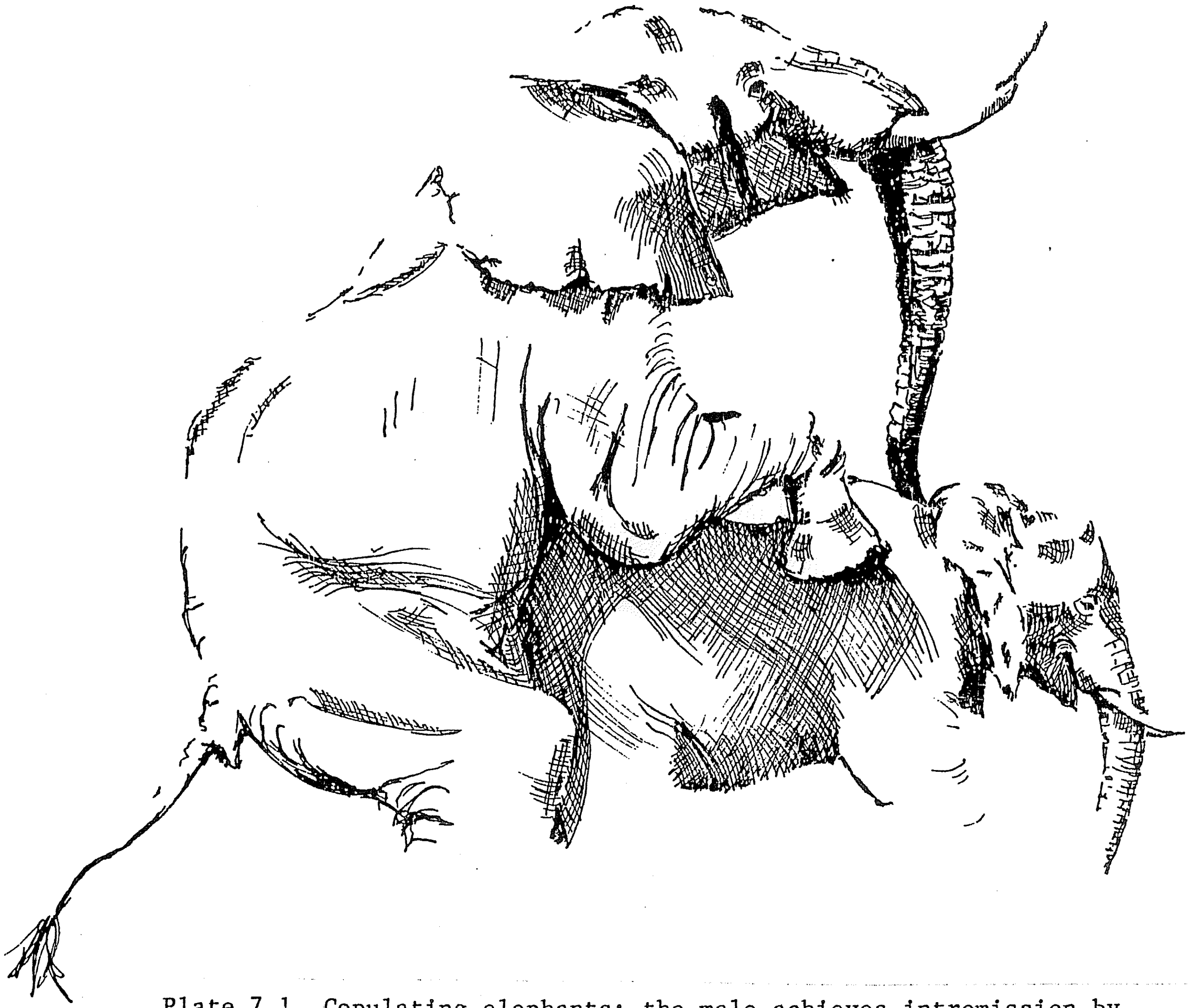
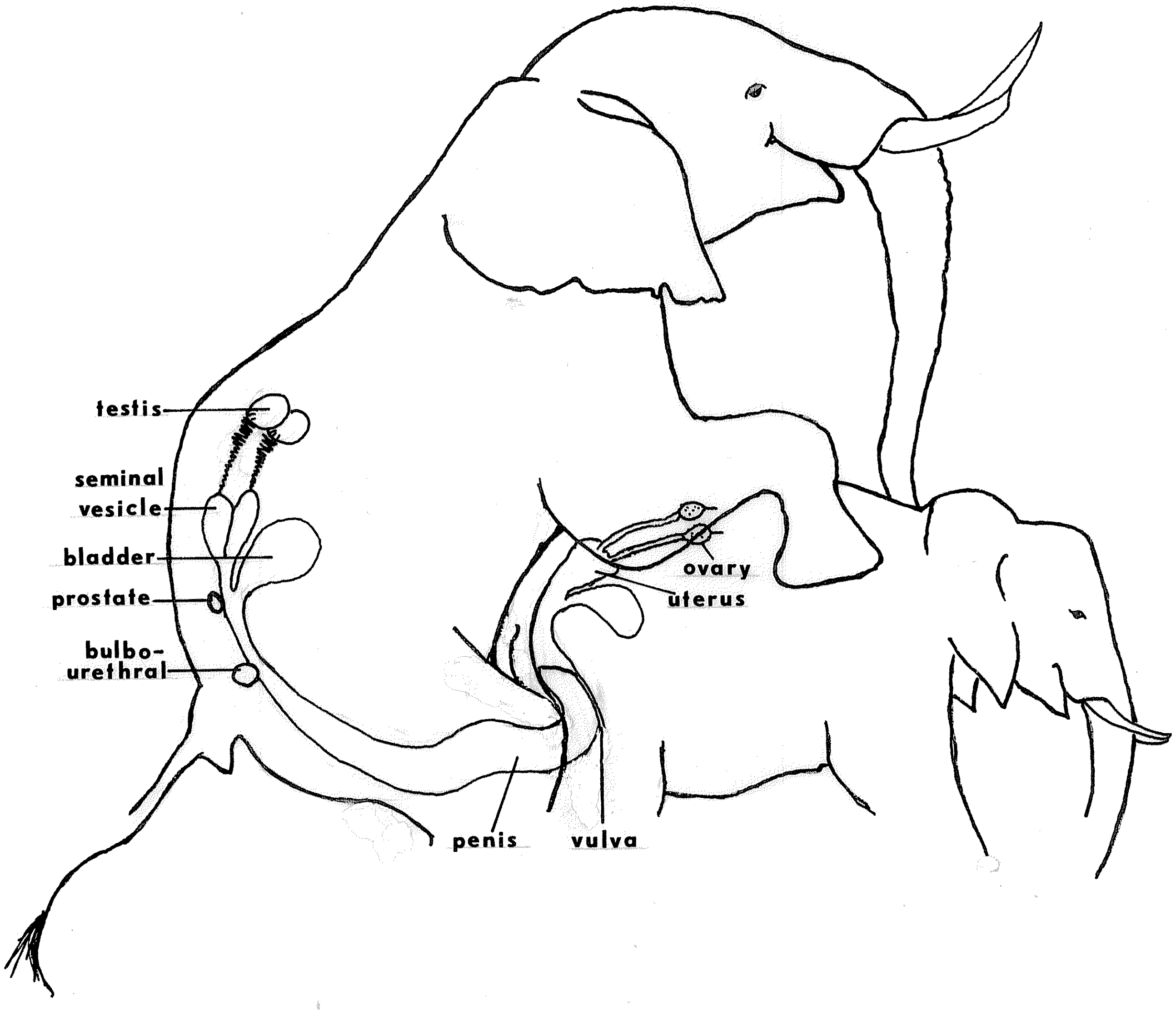


Plate 7.1. Copulating elephants; the male achieves intromission by bending his knees slightly and hooking his S-shaped mobile penis into the female's ventrally located urogenital sinus.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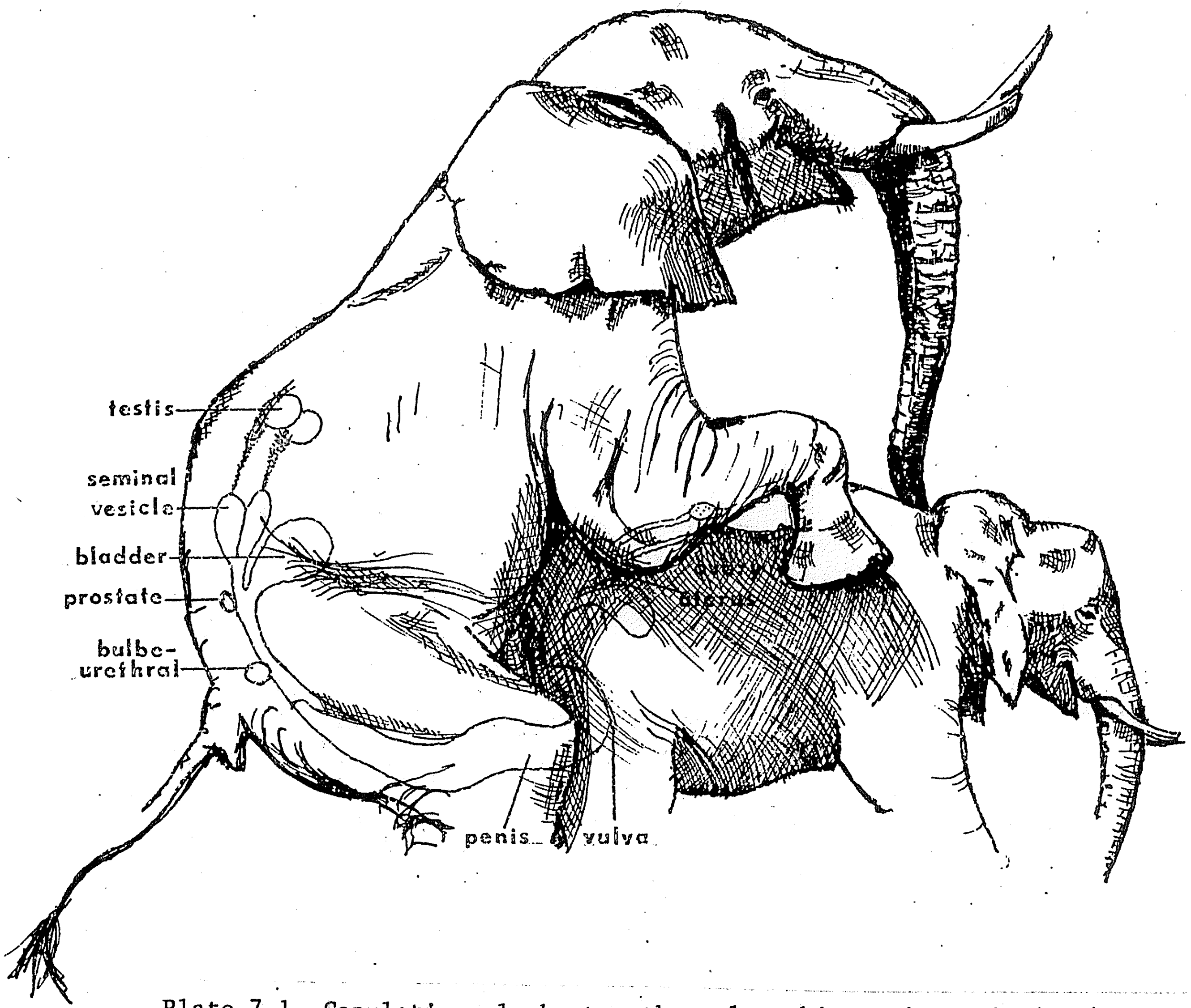

Plate 7.1. Copulating elephants; the male achieves intromission by bending his knees slightly and hooking his S-shaped mobile penis into the female's ventrally located urogenital sinus.

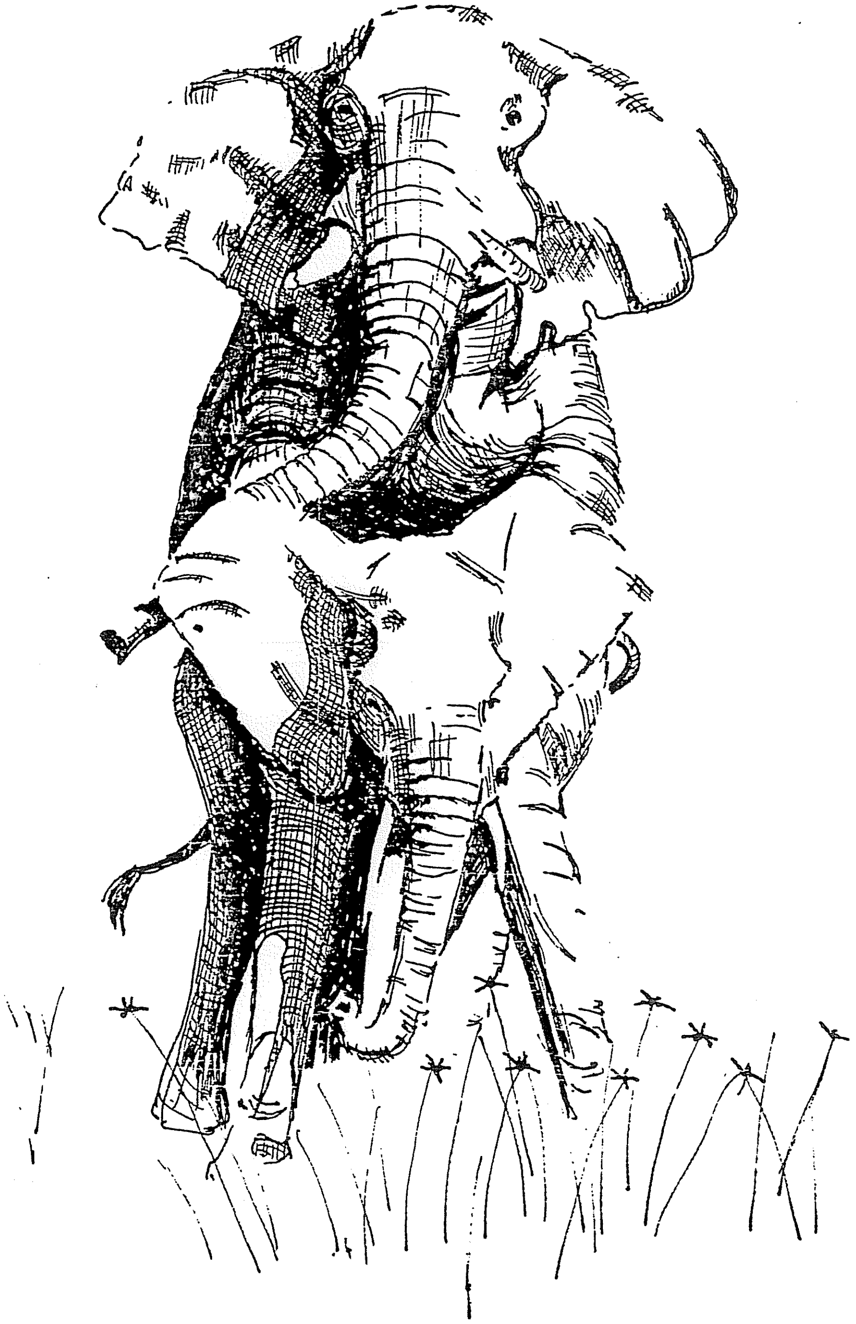

Plate 7.2. Mating elephants.

7.2.3 Determination of guarding

During oestrus female elephants may be monopolized by the highest ranking male present (Short, 1966; Laws and Parker, 1968). Female guarding is defined here as behaviour on the part of a particular male which attempts to prevent rival males from obtaining access to an oestrous female. Guarding is accomplished by maintaining proximity to the female and keeping competing males away from her. By my definition, a male must be shown to be responsible for the maintenance of proximity to the female and must not be observed avoiding any other male present to be considered a "guarder". If a male satisfies the first, but not the second, criterion then he is considered a "non-guarder". When an oestrous female is responsible for maintaining proximity to a particular male, she is defined as "soliciting" guarding behaviour from that male. The highest ranking male present in a group with an oestrous female is considered a "potential" guarder.

To establish the occurrence of guarding behaviour in elephants I have calculated a proximity index for each half hour watch obtained on a focal male when he was found in a group with an oestrous female. This index is the difference between the percentage of approaches due to the female and the percentage of leavings due to the female:

$$\frac{\text{Ap F}}{\text{Ap F} + \text{Ap M}} - \frac{\text{L F}}{\text{L F} + \text{L M}}$$

(Hinde and Atkinson, 1970). When the index is negative the male was mainly responsible for maintaining proximity and when positive the female was responsible. Movements of the focal male and oestrous female were considered as approaches and leaves only when the partners were separated by less than 20 meters. The total number of approaches and leaves made by both male and female were calculated for every watch that

Table 7.1. The proximity indeces are given for each focal male and oestrous female dyad. The behavioural status of the focal male is given. *=musth male.

male #	oestrous female	proximity index	comments
41*	FEL	+ 0.50	female solicits guarding
41*	FEL	+ 1.00	" " "
13*	ECH	- 0.54	guarder
22*	ECH	+ 0.75	female solicits guarding
99*	AME	- 0.75	guarder
114	AME	- 0.90	"
22*	ECH	+ 0.86	female solicits guarding
13*	RAP	- 1.00	guarder
132	INE	- 1.00	non-guarder; avoids guarder 99*
13*	INE	- 1.00	guarder
13*	INE	- 0.55	"
114	INE	- 1.00	guarder of post oestrous female
99*	JEZ	- 0.86	guarder
34	kili.	- 0.38	"
80*	XAL	+ 0.80	female solicits guarding
99*	XAL	- 0.95	guarder
99*	XAL	- 1.00	"
114	XAL	- 0.77	guarder ~ 1 hr while 99* chases 80*
51*	QAS	- 1.00	guarder
51*	QAS	- 1.00	"
51*	QAS	- 0.89	"
28*	ELO	+ 1.00	female solicits guarding
28*	ELO	- 0.67	guarder
79	ELO	- 1.00	"guarder" but female solicits guarding from 28*
114	ELO	- 1.00	non-guarder; avoids guarder 28*
28*	ELO	- 0.60	guarder
28*	ELO	- 1.00	"
28*	ELO	- 0.71	"
28*	ELO	- 1.00	"
73*	VEL	- 1.00	"
73*	VEL	- 1.00	guarder
73*	VEL	- 1.00	"
51	STA	- 1.00	"
28*	ERI	- 1.00	"
132	ERI	- 1.00	non-guarder; avoids guarder 28*
150	TIL	- 1.00	non-guarder; avoids guarder 119*
73*	TIL	- 1.00	guarder
73*	TIL	- 1.00	"
119	TIL	- 1.00	non-guarder; avoids guarder 73*
97	unid.1	- 1.00	guarder
22*	Tb.g.	+ 0.22	guarder
22*	Tgp.	- 0.78	female solicits guarding
13*	BIG	- 0.75	guarder
13*	RAf.u.	- 0.14	"
13*	FEN	- 0.94	"
13*	FEN	- 0.79	"
114*	OLI	- 0.80	"
114*	OLI	- 1.00	"
114*	Zf.u.	- 0.92	"
114*	Zf.u.	- 0.80	"
13*	unid.2	- 1.00	"
80*	unid.2	- 0.83	"
97*	1 tusk	- 1.00	"
97*	1 tusk	- 1.00	"
79	KBf.u.	- 0.82	non-guarder; avoids guarder 114*
97*	unid.3	- 1.00	guarder
41*	PHY	- 1.00	"
114	unid.4	- 1.00	"
80*	ALI	- 0.80	non-guarder; avoids guarder 13*
45*	FIF	- 1.00	guarder
45*	RIV	- 1.00	"

was done on a male in association with an oestrous female (n=87). The median number of total approaches and leaves during a half-hour watch was eight (range 1-36). I selected, for analysis, all those watches in which the total number of approaches and leaves exceeded the lower interquartile range (>4) and I calculated a proximity index for each (n=62).

7.2.5 Definitions

Mount - when a male has succeeded in resting his forelegs on a female's back.

Mating - Intromission and ejaculation occur. This can be determined in three ways: the duration of the mount; the presence of ejaculate; the behaviour of the male and female post-mount. A mount followed by another chase indicated that a successful mating did not occur, while if the pair stood together resting it was assumed that the mount resulted in a successful mating (Plate 7.2).

Female days - the number of days that a male was observed in association with female groups.

Musth (non-musth) female days - the number of days that a male was observed in association with female groups when he was in musth (not in musth).

Oestrous female days - the number of days that a male was observed in association with an oestrous female.

Musth (non-musth) oestrous female days - the number of days that a male was observed in musth (not in musth) when in association with an oestrous female.

7.3 RESULTS

7.3.1 Female guarding by males and solicitation of guarding behaviour by females

Proximity was maintained primarily by the male on 89% of the watches and by the female on 11% (n=62). Eleven different males in musth were the subjects for 48 of the 62 watches and eight non-musth males were the subjects for 14 watches (Table 7.1). In 7 of the 48 watches on musth males the value was positive, indicating that the female was attempting to stay close to the male in musth. By my definition, the females in these cases were soliciting guarding behaviour from these males. In every instance where non-musth males were the focal subject the index was negative, indicating that the male was mainly responsible for maintaining proximity. Females were never observed to maintain proximity to non-musth males.

To differentiate between males who have a positive proximity value and are guarders from those who are non-guarders, I have taken into account whether or not males were observed avoiding another male(s) during the focal sample. In 46 of the 55 cases where the male was responsible for maintaining proximity to the female, the focal male was not observed avoiding any other male present. By my definition these males are termed "guarders". In 9 cases, although the male was attempting to stay close to the female, he was observed avoiding another male(s) present. These males are by definition non-guarders. In only 2 out of the 46 cases of guarding was the male actually not the dominant male present. In one instance the dominant male (M28) was no longer interested in the female, and I suspect that she was no longer in oestrus. In the second case, the female was attempting to solicit guarding behaviour from the dominant male (M28), without success, again indicating that he was no longer interested in her. I feel that this indicates that my criteria for the determination of guarding in elephants are sufficient.

7.3.2 Age related mating success

During the period from January, 1980 to July, 1981, a total of 54 successful matings were observed. These matings were considered in two categories, those where the guarding male was interested in the oestrous female and those where he was no longer interested (Table 7.2). In the latter instances the copulations observed (N=9) have been excluded from the analysis on mating success since I have concluded these females were no longer in oestrus. These copulations were accomplished predominantly by Class 1 and 2 males, while matings that were obtained when the dominant male was still attempting to guard, were performed largely by older males. When the highest ranking male present was attempting to guard 85% (n=20) of the non-guarders matings were obtained by 12 different Class 3 and Class 4 males and only 15% (n=20) were achieved by three different Class 2 males. Class 1 males obtained no matings. When the potential guarder was no longer interested no Class 4 males were seen mating. Two low ranking Class 3 males obtained 33% (n=9) of the matings and 66% (n=9) were obtained by six different Class 2 and Class 1 males.

Table 7.2. The number of matings obtained by guarding and non-guarding males are given for each age class. The reasons why non-guarders were able to achieve copulations when a higher ranking male was present and interested in the oestrous female are given when known. Copulations obtained when the highest ranking male was not interested have been excluded from the subsequent analysis on mating success.

Matings obtained when the highest ranking male was interested in the female

Class	Guarders	Non-guarders			Total matings
		Guarder not alert	Guarder interacting w/ another male	Unknown	
4	22	0	0	1	23
3	3	4	4	8	19
2	0	1	1	1	3
1	0	0	0	0	0
Total	25	5	5	10	45

Table 7.2. cont.

Class	Matings obtained when the highest ranking males was not interested in the female
4	0
3	3
2	5
1	1
Total	9

Age related mating success can be seen by comparing the number of males in each class that were seen mating at least once with those who were never observed mating (Table 7.3). I do not have accurate data on the number of times each of the Class 1 and 2 males were observed with females, so I cannot give probability values for these data. However, since younger males spent more time in association with females than did older males (Chapter 5; Section 3.6), it is likely that I observed the younger males with females at least as often as I did the older two classes. It is clear that males from Classes 3 and 4 are more successful at obtaining matings than are males from Classes 1 and 2.

Table 7.3. The number of individuals in each age class that were or were not observed mating.

	Class 4	Class 3	Class 2	Class 1
observed mating	11	11	3	0
not observed mating	8	14	42	73
Total no. males in each Class	19	25	45	73

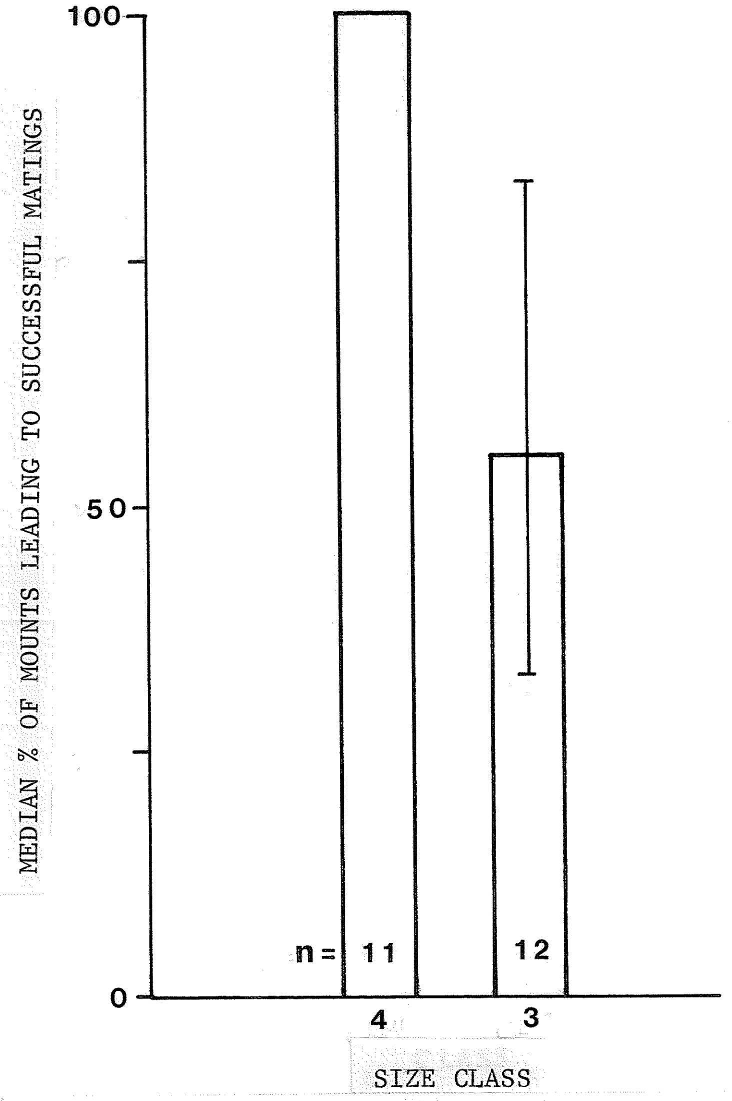

Figure 7.1. Percent of mounts by Class 4 and 3 males that lead to successful matings. Medians and interquartile ranges are shown.

Age related mating success can also be seen by examining the proportion of mounts that result in successful matings for each class. During the study period, a total of 75 mounts were recorded, of which 45 (60%) resulted in successful matings. Among Class 4 males, 23 of the 25 mounts recorded (92%) resulted in successful matings. Class 3 males mated successfully on only 54.9% (n=34) of their mounts. Class 2 males were even less successful; only 3 out of 14 mounts (21.4%) resulted in successful matings. Class 1 males were observed mounting on only two occasions and were never observed to obtain a successful copulation. Class 1 and 2 males were apparently only able to obtain access to post-oestrous females.

Although age related mating success between Class 3 and 4 is not evident when comparing the proportion of males in each group seen mating, there is a significant difference between the success of these two classes in terms of the proportion of mounts that resulted in successful matings (U=26.0, n1=11, n2=12, p<0.02, Figure 7.1). In conclusion, both in terms of the actual numbers of matings obtained, and the proportion of mounts that lead to successful copulations, mating success is closely age (and therefore body size) related.

7.3.3 Mating success of musth and non-musth males; guarders and non-guarders

Of the 45 matings accomplished by 27 different males, 22 were accomplished by males who were in musth and guarding, 20 by non-musth non-guarders, three by non-musth males who were guarding and none by males who were in musth and attempting to mate when the guarding male was not alert. There is obviously a close relationship between being in musth and obtaining matings as a guarding male and not coming into musth and accomplishing matings as a non-guarder.

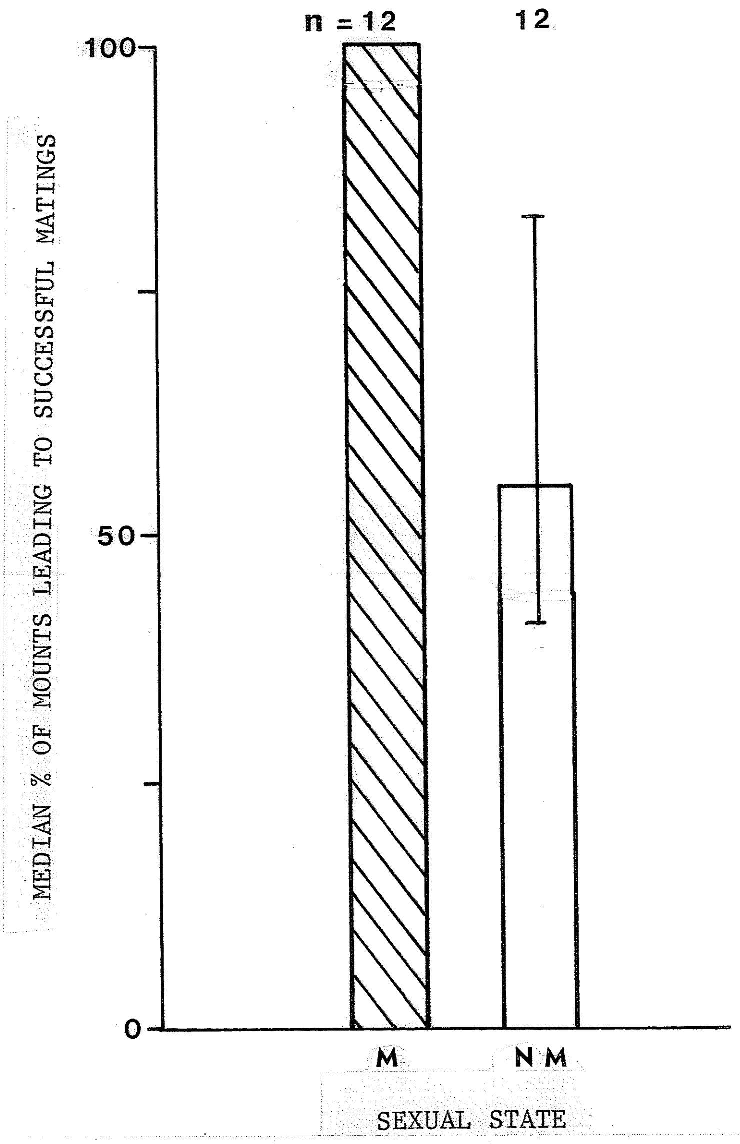

Figure 7.2. Percent of mounts by musth and non-musth males that lead to successful matings. Medians and interquartile ranges are shown.

The success of musth males, in terms of the proportion of mounts that resulted in successful matings, was significantly higher than that of non-musth males (median of musth males=100%; median of non-musth males=55%; U=26.5, n1=12, n2=12, p<0.02; Figure 7.2). Once mounted, males in musth were able to mate successfully upon almost every attempt, while non-musth males were not.

A total of 25 copulations were achieved by guarding males and 20 by non-guarders (Table 7.2). Since a guarding male presumably has access to an oestrous female until a higher ranking male arrives, one might expect guarders to have achieved a larger proportion of the matings than I observed.

There are several factors that may account for this observation. First, of the 25 matings accomplished by guarders, three involved no chase, while all non-guarder matings were preceded by chases. Chases may last over half an hour and are usually accompanied by loud and conspicuous vocalizations. If guarding males are often able to mate without a chase, then some matings may have gone unnoticed by the observer.

Second, if the purpose behind guarding is to prevent sperm competition by rival males (Parker, 1974a), then frequent copulations by guarders may not have any additional advantage. During my study period, M13, the largest and highest ranking male in the population, was observed guarding 27% of all females observed in oestrus (n=85). Although he presumably had access to all of these females he was only seen mating on four occasions (8.9% of all copulations recorded), suggesting that guarders copulate infrequently. However, when the highest ranking male was unsuccessful at guarding, and non-guarding males obtained brief access to the oestrous female, she was often mated

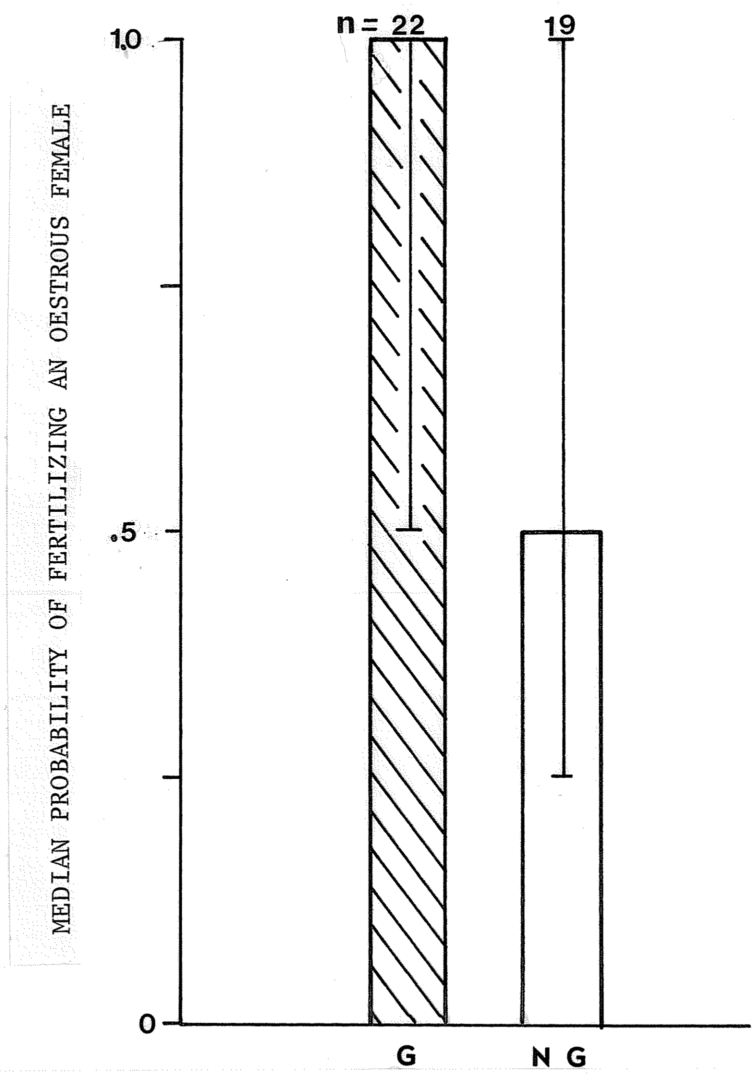

Figure 7.3. Probability of fertilizing an oestrous female for guarders and non-guarders based on the number of males observed copulating with each female (n=28). See text for explantation.

by several males in succession. On one particular occasion five matings and five mounts by six different males occurred within an hour. For non-guarding males, the best option may be to stay as close to the oestrous female as the guarding male will allow, and attempt to mate whenever the opportunity arises.

These data suggest that using the number of observed matings as a measure of reproductive success may significantly underestimate the realized success of guarding males, particularly when, in terms of sperm competition, the temporal patterning of matings is important (Parker, 1974a).

Up to this point I have made the assumption that each copulation observed was an equal measure of mating success, so that although a particular female may have been mated by four different males, each received a score of one. In reality, if the assumption is made that the temporal occurrence of a mating has no effect on the probability of fertilization, each male would only have had a 25% chance of fertilizing her.

With this in mind, I have looked at the 28 females that were seen mated and assigned probability values to each mating. If only one male was observed copulating with a particular female he received a score of 1.0, while if four different males were observed mating her, each would be assigned a score of 0.25, etc. Although I watched oestrous females for a very small proportion of the duration of oestrus (several hours out of three to six days), I am going to assume that the period of observation is indicative of the full period.

The probability values obtained for guarding males (median=1.0) and those for non-guarders (median=0.5) suggest that guarders are more successful at obtaining exclusive matings with females (U=151.50, n1=19,

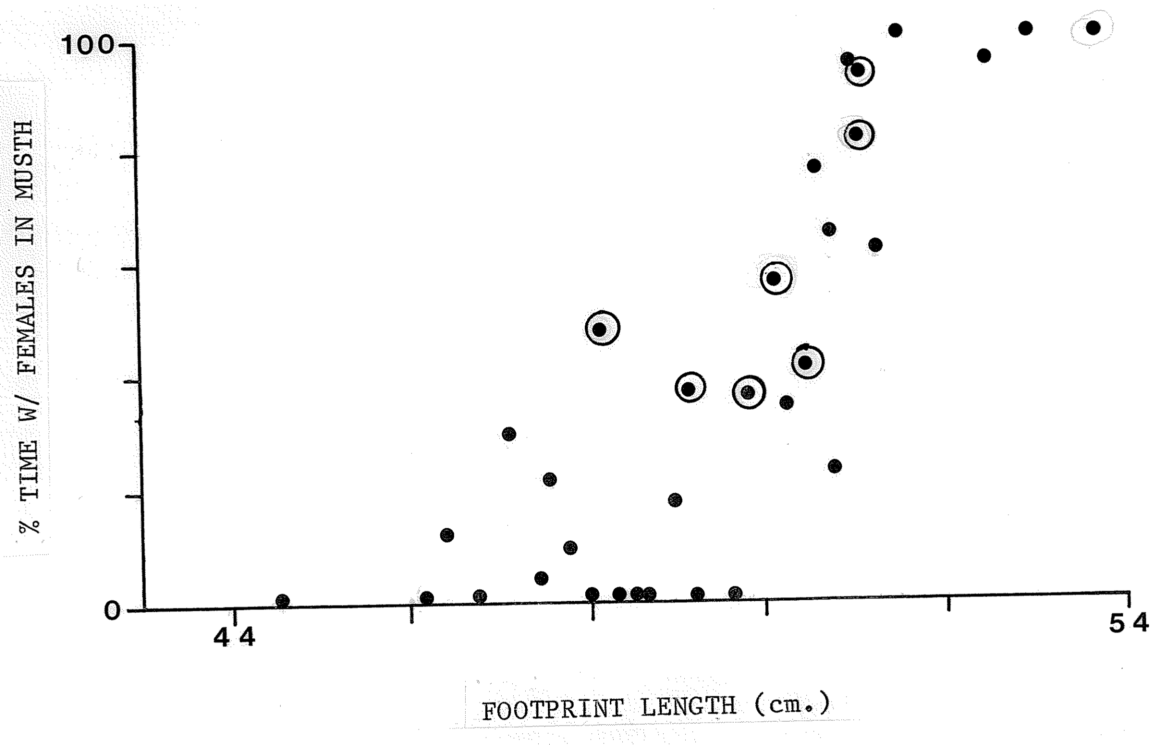

Figure 7.4. Relationship between age (footprint length) and the percent of time with females spent in musth. Individuals circled came into musth during the latter half of the year.

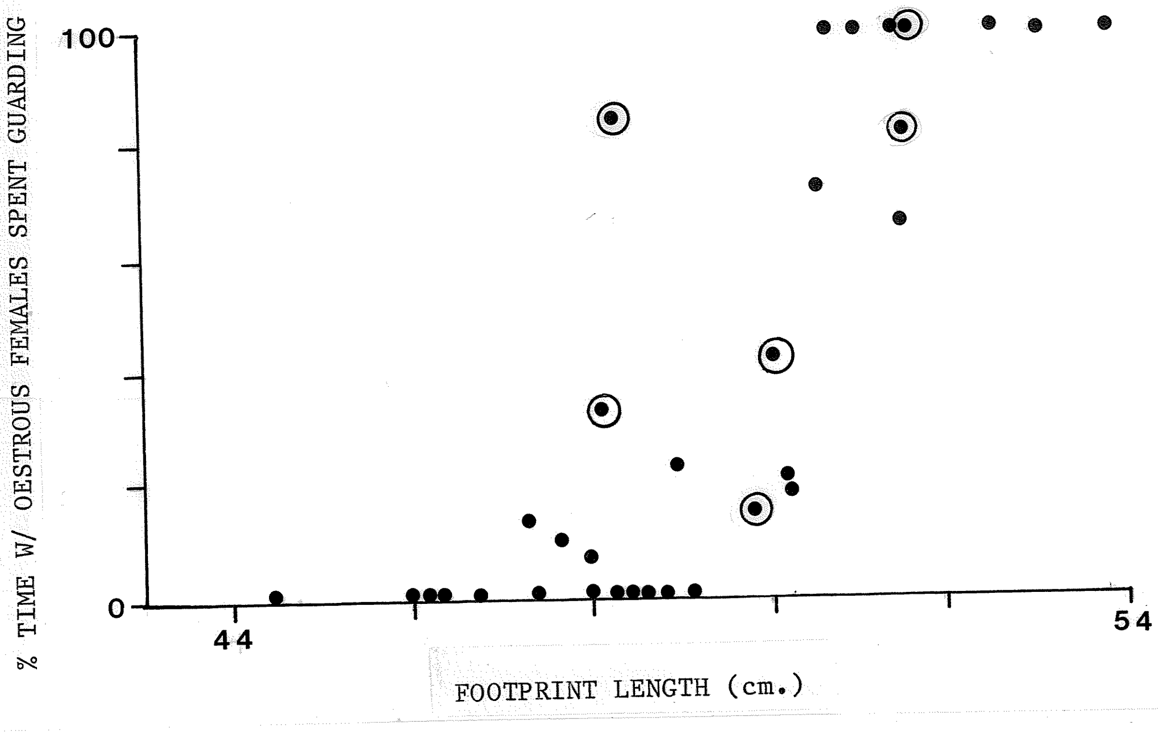

Figure 7.5. Relationship between age (footprint length) and the percent of time with oestrous females spent guarding. Individuals circled came into musth during the latter half of the year.

n2=22, p=0.05; 1 tailed; Figure 7.3). As a further refinement, I have asked whether guarders or non-guarders are more effective at obtaining exclusive matings with a female. Of the 20 females who were observed to mate with only one male, 14 were mated by guarders while only six were mated by non-guarders. The probability that guarders should accomplish 14 of the 20 exclusive matings is low (Binomial Test p(14)=0.04).

In summary, Classes 3 and 4 males have a higher mating success than do Classes 1 and 2 males. The number of mounts that lead to successful matings was significantly higher for Class 4 than for Class 3 males. Those males who are able to guard oestrous females obtain more exclusive matings than do males who are unable to guard, and the proportion of mounts that lead to successful matings is higher for males in musth than for non-musth males.

7.3.4 Age related mating strategies

Some males guard females apparently to maintain exclusive mating rights, while other males mate opportunistically. These two opposing behaviour patterns can be considered age-related mating strategies. The data indicate that being in musth and guarding is more successful than attempting to obtain copulations as a non-guarder. However, the situation is not as clear cut as I have presented so far.

In the Amboseli population there appear to be three age-related mating strategies used by males when in association with females: always be in musth, always guard; guard when in musth, attempt to mate opportunistically when not in musth; never come into musth, always attempt to mate opportunistically. I will refer to these three developmental stages as "continual musth-guarders"; "conditional musth-guarders" and "continual non-musth non-guarders". Males belonging to the continual and conditional group fall on a continuum that is age

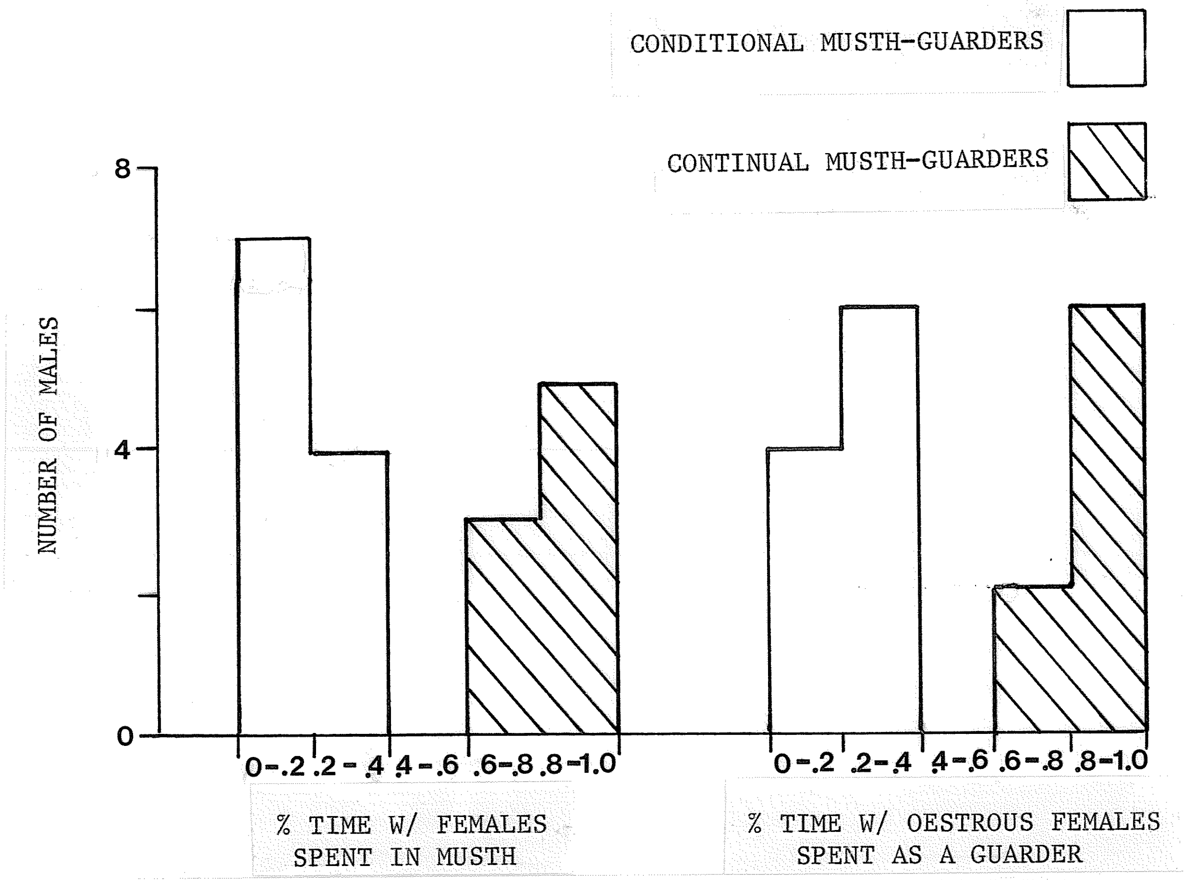

Figure 7.6. Frequency distribution of a) percent time with females spent in musth and b) percent time with oestrous females spent guarding for males who were sexually active during the first half of the year.

and body size related. As males get older they spend a larger proportion of the time that they are with females in musth (Figure 7.4), and they are able to guard a larger proportion of the oestrous females that they locate (Figure 7.5). However, the males who fall in the centre of the distribution on both measures (M154, M51, M10, M78, M7) were sexually active during the latter half of the year. During this period female group sizes were smaller, there were fewer females in oestrus and fewer competing males (see Chapter 5). These males stayed in musth for longer periods than expected based on their relative ranks (see Chapter 6; Section 3.5) presumably because they were less likely to be forced out of musth by a higher ranking musth male (see Chapter 6; Section 3.5). Although they were observed with oestrous females more often as guarders than as non-guarders, the sample sizes are small as there were few females in oestrus during this half of the year. Considering only those males who were sexually active during the first half of the year, males fall into a bimodal distribution on both measures (Figure 7.6). For this reason I have included the above males with the conditional musth-guarder group.

All of the continual musth-guarders (n=10; equivalent to the Group 1 males - see Chapter 4) belong to Class 4. The conditional musth-guarders (n=16) are composed of the smaller Class 4 (n=9) and larger Class 3 (n=7) males. The continual non-musth non-guarder group (n=136) is made up of the remainder of the males from Class 3 (n=18) and all males from Classes 1 and 2 (n=118).

The continual non-musth non-guarders obtained significantly fewer matings (median=0) than did the continual musth guarders (median=1.5) even when Class 1 and 2 males are discounted (U=42.5,n1=10, n2=18, $p<0.05$; Figure 7.7). There is no significant difference between the

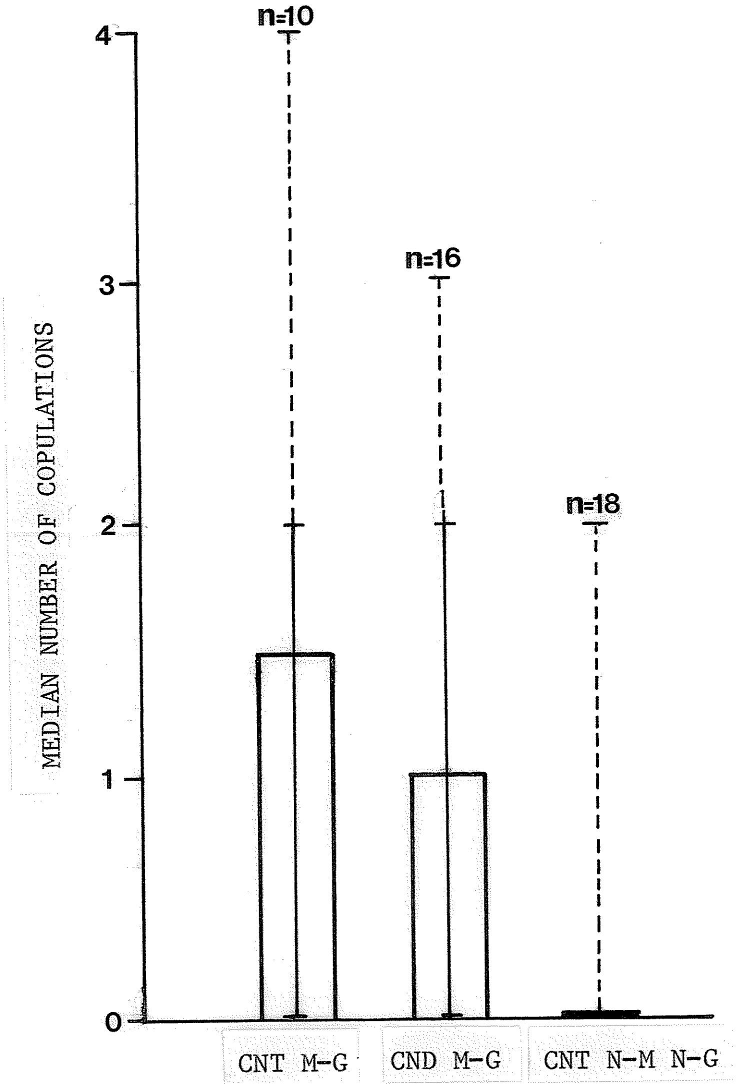

Figure 7.7. Mating success of continual musth-guarders (CNT M-G), conditional musth-guarders (CND M-G), and continual non-musth non-guarders (CNT N-M N-G). Medians, interquartile ranges, maxima and minima are shown.

mating success of the conditional musth guarders (median=1.0) and the continual non-musth non-guarders (median=0) (U=102.50, n1=16, n2=18, p>0.10; Figure 7.7). The mating success of continual and conditional musth-guarders also appears to be similar.

7.3.5 The mating success of continual versus conditional musth-guarders

Continual and conditional musth-guarders were not observed to spend significantly different numbers of days with oestrous females (U=57.5, n1=10, n2=16, p>0.10; Table 7.4). However, continual musth-guarders (n=10) had a higher mating success per day with oestrous females than did conditional musth-guarders (U=49.50, n1=10, n2=16, p=0.05; 1 tailed; Figure 7.8).

Table 7.4. The number of days each male from the continual and the conditional musth-guarder groups was seen in a group with an oestrous female is given.

Musth-guarders			
Continual		Conditional	
Male	oestrous female days	Male	oestrous female days
13	27	114	22
28	11	150	19
99	11	97	14
22	6	107	14
73	6	119	13
41	4	147	13
117	4	51	13
44	3	57	10
45	3	80	10
126	2	46	7
		154	7
		78	7
		7	3
		34	3
		175	2
		10	0
Total days	77		157

Mann-Whitney U=57.5, n1=10, n2=16, p>0.10

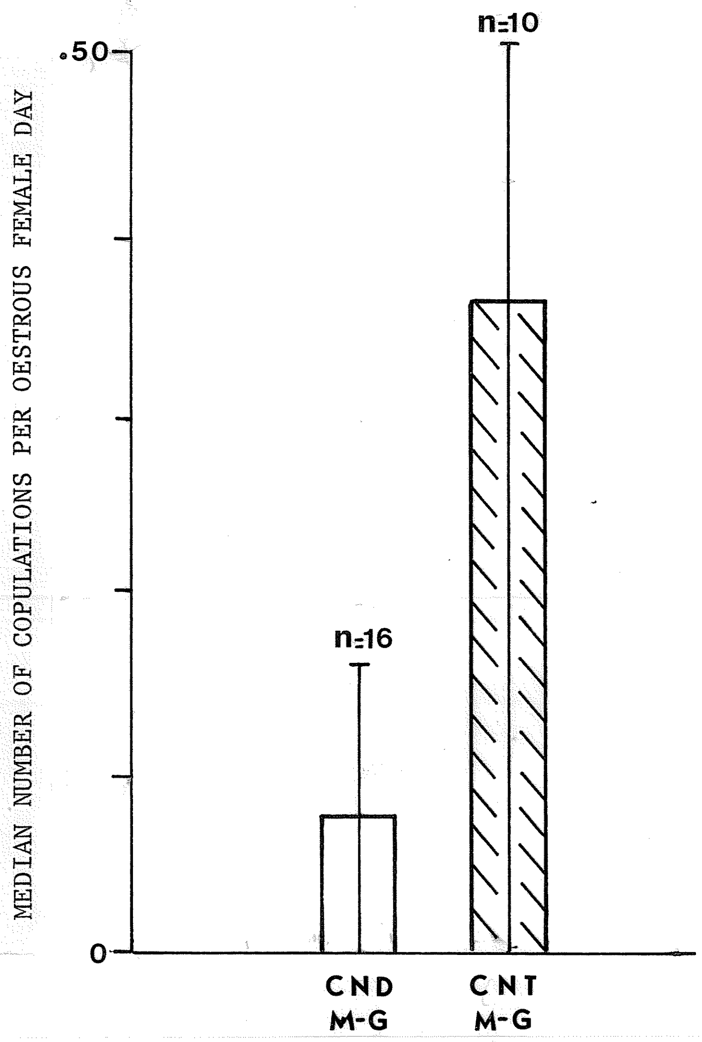

Figure 7.8. Mating success of continual musth-guarders (CTN M-G) and conditional musth-guarders (CDN M-G) per oestrous female day.

Additional support can be made for this argument by examining the proportion of mounts that lead to successful matings. All mounts by the continual musth guarders (n=16) resulted in successful matings, while seven of the 24 mounts made by conditional musth-guarders were unsuccessful.

Continual musth-guarders can presumably select the optimal time at which to mate, while the non-guarder males of the conditional group attempt to mate whenever the opportunity arises. For this reason, the continual musth-guarders are likely to achieve a mating success above that which the data suggest.

7.3.6 Conditional strategies

The conditional musth-guarders (n=16) have the option of following either of two broad behavioural patterns at any given time. My original definition for this group was: guard when in musth; attempt to mate opportunistically when not in musth. This is, however, an over simplification of the situation. Males in this group may find themselves in either of four situations: not in musth and attempting to mate when the guarding male is not alert; in musth and attempting to mate when the guarding male is not alert; not in musth and attempting to guard; in musth and attempting to guard. The question I pose here is whether each option is equally successful, and if not, under which conditions do males choose to adopt each strategy?

For each female observed in oestrus during the study period (n=85), I have scored each male that was present in a group with her as being in one of four categories: musth guarder; non-musth guarder; musth non-guarder; non-musth non-guarder. Although a male might have been seen with a particular oestrous female for two or more days in a row, each day has been scored as independent, since the arrival of another male could change his score from musth guarder on one day to non-musth

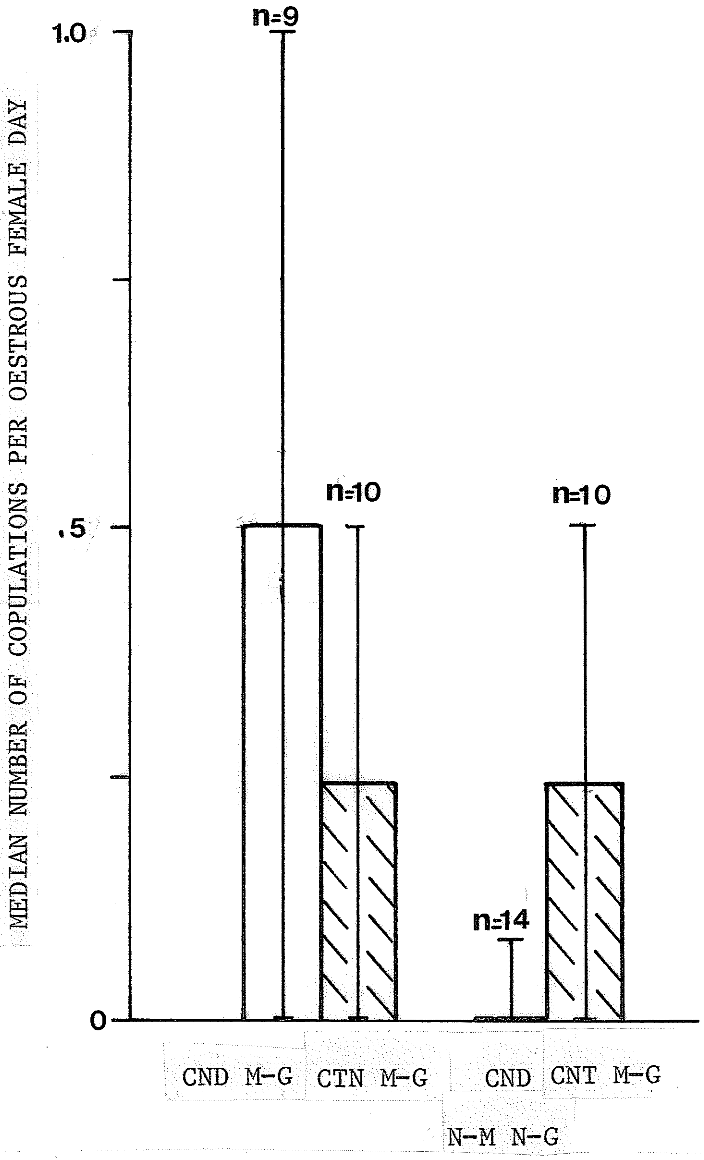

Figure 7.9. Mating success per oestrous female day of continual musth-guarders (CTN M-G) versus conditional musth-guarders when acting as non-musth non-guarders (CDN N-M N-G) or musth-guarders (CDN M-G). Medians and interquartile ranges are shown.

non-guarder on the next. I have examined the number of copulations obtained per oestrous female day for each male as a guarder versus non-guarder and in musth versus not in musth.

Although the conditional musth-guarders were observed in association with oestrous females more often as non-guarders than as guarders (Wilcoxon T=4.5, n=14, p<0.01; Table 7.5), guarding males aquired more matings per unit time than did non-guarders (Wilcoxon T=0, n=7, p=0.02; Table 7.5). Conditional males were observed with oestrous females significantly more often as non-musth than musth males (Wilcoxon T=6.5, n=14, p<0.01; Table 7.5), but there was no statistical difference in mating success between musth and non-musth males per unit time observed with oestrous females (Wilcoxon T=5, n=7, p>0.05 n.s.; Table 7.5). Although I am drawing conclusions from very small sample sizes, it appears that being in musth increases a male's mating success only if he is the highest ranking male present and is therefore able to guard. As a lower ranking non-guarding male attempting to gain access to a female guarded by a musth male, being in musth is a liability. Musth males are more aggressive towards other musth males than they are to non-musth males (see Chapter 6) and will not tolerate another musth male near the guarded female.

7.3.7 A comparison of continual and conditional musth-guarders

The differential mating success of the continual versus conditional musth-guarders as estimated by the number of copulations per oestrous female day varies depending upon which strategy the conditional males adopt (Figure 7.9). Comparing the success of males acting as musth guarders, the conditional males appear to do as well as the older males (U=40.0, n1=9, n2=10, p>0.10, n.s.). However, as non-musth non-guarders the conditional males do significantly less well than the continual musth-guarders (U=33.50, n1=10, n2=14, $p<0.05$).

Table 7.5. Mating success of conditional musth-guarders per oestrous female day when acting as musth-guarders; musth non-guarders; non-musth guarders; non-musth non-guarders. D=number of days observed with oestrous females; M=number of observed matings; M/D=number of matings per oestrous female day.

	Musth						Non-musth					
	Guarder			Non-guarder			Guarder			Non-guarder		
Male	D	M	M/D	D	M	M/D	D	M	M/D	D	M	M/D
7	0	-	-	0	-	-	1	0	0	0	-	-
10	0	-	-	0	-	-	0	-	-	0	-	-
34	0	-	-	0	-	-	1	1	1.0	2	0	0
46	0	-	-	0	-	-	0	-	-	2	0	0
51	2	1	0.5	1	0	0	0	-	-	10	0	0
57	1	0	0	0	-	-	0	-	-	8	0	0
78	2	0	0	0	-	-	1	0	0	4	0	0
80	2	1	0.5	3	0	0	0	-	-	4	0	0
97	1	1	1.0	1	0	0	0	-	-	13	2	0.15
107	1	1	1.0	3	0	0	2	1	0.5	8	1	0.12
114	3	0	0	1	0	0	1	1	1.0	14	1	0.07
119	2	2	1.0	1	0	0	2	0	0	8	0	0
147	0	-	-	0	-	-	0	0	0	12	1	0.08
150	0	-	-	1	0	0	0	-	-	18	3	0.17
154	6	0	0	0	-	-	0	-	-	1	0	0
175	0	-	-	0	-	-	0	-	-	1	0	0
	20	6		12	0		8	3		110	8	

The continual musth-guarders have the highest reproductive success as estimated by the numbers of matings achieved per oestrous female day. The conditional musth-guarders have the option of coming into musth and attempting to guard oestrous females, or not coming into musth and attempting to copulate when the guarding male is not alert. Although the data suggest that the former option confers a higher mating success, males actually spend more time following the latter. Being in musth is costly, not only energetically (see Chapters 5 and 6), but in terms of the increased aggression received from higher ranking musth males (see Chapter 6).

The proportion of guarders who are successful will be frequency dependent and largely determined by the operational sex ratio (Rubenstein, 1981a). At any given time when the ratio of available females to musth-guarders is less than one, the conditional males should act as non-guarders, while when this ratio is greater than one, they should come into musth and attempt to guard any "excess" oestrous females. An example of this can be seen by comparing the behaviour of males in May, 1980 and May, 1981. In May of the first year, when four continual and no conditional musth-guarders were observed in musth, six females were recorded in oestrus. In May, 1981 the number of oestrous females increased to 12 and there was a corresponding increase in the numbers of musth males to 13. Of the 9 additional males over the previous year, only one was a continual musth-guarder, while the remaining eight were the "opportunistic" males of the conditional group.

7.4 DISCUSSION

In elephants the ability to guard oestrous females is closely rank related. The guarding male or the "potential" guarder is always the highest ranking male present in a group with an oestrous female. Females solicit guarding behaviour from guarders or "potential" guarders, but not from lower ranking males.

Male elephants continue to grow throughout life (Laws, 1966) and body size is closely correlated with age in years (Laws, 1966). In the Amboseli population, non-musth rank correlates closely with body size (see Chapter 6). Mating success in the Amboseli population is therefore age/body size/rank related; older, larger, higher ranking males obtain a disproportionate number of the observed matings. Mating success is highest among males who are able to guard oestrous females successfully.

The ability of high ranking males to guard females is enhanced by being in musth.

The typical mating pattern, musth-guarding, is a high cost high benefit strategy, while the alternative, non-musth non-guarding, can be seen as the opportunistic behaviour of younger males. Rubenstein (1981a) suggests that in most species it is unlikely that an individual will be able to switch between two strategies within a single breeding season. However, the conditional musth-guarders were able to switch between two different physiological and behavioural patterns readily.

Musth may increase individual mating success in three ways. First, there is the possibility that odour from the dribbling of urine and secreting temporal gland of a musth male may induce oestrus. In seasonally breeding animals such as sheep and goats adult males stimulate the synchrony of oestrus (see Geist, 1971 and Coblentz, 1976). The arrival of a musth male in a group or merely the smell of urine from a musth male elicits an excited response from females (see Chapter 3), but whether male elephants are able to influence the onset of oestrus remains to be seen.

Secondly, there may be an element of female preference. Females were observed to maintain proximity to musth males but never to non-musth males (see also Moss, in prep.) and the three matings in which the female stood for a male without a pre-copulatory chase were all accomplished by musth males. The role of female preferences is dicussed further in Chapter 8.

Finally, musth males are extremely aggressive (see Chapter 6) and are able to keep rival males at a greater distance from oestrous females than are non-musth males (see Chapter 6). The physiological and behavioural characteristics associated with musth may advertize the male's condition to rivals. Parker (1974b) argues that an individual who is able to use some cue to assess his opponents fighting ability relative to that of his own will have a selective advantage. Maynard Smith and Price (1973) have discussed the phenomenon of musth in Elephas maximus as being a form of aggression that cannot be counterfeited. They suggest that the secretion from the temporal gland gives a visual and olfactory warning to other males and that "the madness of the animal "on musth" causes other elephants to avoid him and thus may give an increase to his dominance status..."(Maynard Smith and Price, 1973)

Undernourished male Asiatic elephants do not come into musth and mahouts have, for many years, practiced underfeeding males as a method of keeping males from coming into musth (Gale, 1974). If the onset and termination of musth periods are closely associated with changes in body condition, then physiological and behavioural characteristics associated with musth may be a form of "honest advertizement" (Clutton-Brock and Albon,1979) of the temporal changes in fighting ability through the "rut" (see Chapter 8).

CHAPTER 8

DISCUSSION

The aim of this thesis was to examine the evolutionary significance of musth from two perspectives: a) which selective pressures have favoured the evolution of musth and b) among males who come into musth, which social and ecological factors influence the timing and duration of individual musth periods?

8.1 THE EVOLUTION OF MUSTH

8.1.1 Male-male competition

In this study males in musth were found to have higher levels of urinary testosterone than either sexually active or sexually inactive non-musth males (Chapter 6; Section 3.1). Males in musth were highly aggressive towards other males (Chapter 6; Section 3.2) and increased in dominance above their relative non-musth rank (Chapter 6; Section 3.4). Rival males retreated from threats given by musth males at a greater distance than they did from the same threat given by a non-musth male of the same size class (Chapter 6; Section 3.7). For these reasons males in musth were more efficient and more successful guarders of oestrous females than were non-musth males (Chapter 7). The mating success of musth-guarders was higher than for non-musth non-guarders (Chapter 7; Sections 3.5,3.6,3.7), and based on the number of females guarded, the actual reproductive success of musth-guarders was predicted to be higher than the number of observed matings suggested.

Female elephants may mate with several males during oestrus (Short, 1966; Chapter 7; Section 2.3) and guarding behaviour by high ranking males appears to function to reduce sperm competition by rivals (Parker, 1974a). Guarding behaviour reduces the time and energy available for locating additional receptive females (Parker, 1974a). However, since available females tended to be dispersed rather than clumped in time (Chapter 5; Section 3.4) and the probability of locating another receptive female at any given time therefore low (Chapter 5; Section 3.5), there should be intense competition for access to each receptive female and strong selection for the evolution of guarding behaviour.

The results from this study suggest that the phenomenon of musth functions primarily in male-male competition and that most characteristics of musth have evolved through intrasexual selection rather than epigamic selection. For example, urine dribbling and ear waving are increased during aggressive encounters with other males (Chapter 4; Section 3.1,3.2 and 4.9, respectively); these are discussed in the following section. Female preferences have, however, undoubtedly been an additional selective advantage favouring the evolution of musth (see Section 1.3.). There is also the possibility that the presence and smell of a musth male brings females into oestrus as has been described in some ungulates (see Geist, 1971 and Coblentz, 1976).

8.1.2 The evolution of musth and urine dribbling

The functional aspects of "scent urination" in rutting ungulates have been addressed by several authors (see Chapter 1), but, the recent literature on assessment theory (Parker, 1974b; Maynard Smith and Price, 1974; Maynard Smith and Parker, 1976) show that the explanations given previously were not evolutionarily stable strategies (Maynard

Smith and Price, 1973).

If, as proposed by Espmark (1964), the function of urine dribbling is to intimidate other males, then selection should favour all individuals adopting this pattern whether or not they are actually capable of winning an escalated contest. In other words, males would "cheat" and claim that they were more prepared to fight than they actually were, and the display would come to have very little meaning to other males.

Assessment theory (Maynard Smith and Price, 1974; Parker, 1974b; Maynard Smith and Parker, 1976) predicts that selection should favour individuals who are able to assess the physical and behavioural traits of rival males and, with this knowledge, adjust their behaviour only to the costs and benefits of fighting and to the probability of winning. Selection should favour responsiveness to traits that are indicative of actual fighting ability. However, for such selection to be effective, the cost of being caught cheating must be very high. The behaviour of musth males appears to fit this model.

Males in musth are highly aggressive towards other musth males (Chapter 6; Section 3.6,3.7) and a very high proportion of the serious chases and escalated conflicts that were observed in this study occurred between two males in musth (Chapter 6; Section 3.6). The cost of fighting is high. Elephants are capable of inflicting fatal wounds with their tusks. There have been numerous reports (see Douglas-Hamilton, 1972 and Leuthold, 1977a) of adult males found dead, their skulls gored by a tusk from another male. A male who cheated habitually would sooner or later be seriously injured. Not only does a cheating individual risk a possible decline in rank, injury or death, but fighting is also costly in terms of energetics and thermoregulation. As body size increases the surface area:volume ratio decreases, and therefore the rate of metabolic heat loss declines (Calow, 1977). All of the escalated contests observed in this study occurred in the middle of the day and the increase in metabolic rate associated with fighting could cause severe thermoregulatory stress. Finally, an elephant's reproductive effort is spread over 20 to 25 years so that males are unlikely to risk an escalated contest unless they are confident of winning. Older males may be prepared to invest more in conflicts than younger males because the reproductive potential of older males is lower (Trivers 1972; Clutton-Brock and Harvey, 1976).

It is to the advantage of individuals to detect and punish cheating males. If a cheater is detected and punished he will be less likely to attempt to cheat against that individual again (assuming he is able to change his behaviour). By detecting and punishing a cheater a male not only increases his reproductive gain relative to the cheater, but he decreases the likelihood that the gene for cheating is passed on to future generations, thereby increasing his inclusive fitness.

In view of these benefits selection should favour those individuals who are able to accurately assess fighting ability in other individuals and who advertize their fighting ability with signals that cannot be faked.

While most morphological traits such as body and horn size (Geist, 1971 and see Davies and Halliday, 1978) are presumably used in assessment, Clutton-Brock and Albon (1979) point out that they are usually not indicative of declining condition through the breeding season or with advancing age (but see Packer, 1979). Declining condition late in the breeding season is typical of many rutting ungulates (see Chapter 1) and for this reason we would expect to find traits exhibited by males which reflect temporal changes in fighting ability (Clutton-Brock and Albon, 1979).

If, as suggested by McCullough (1969), "scent-urination" accurately reflects body condition through changes in metabolic by-products excreted in the urine, then urine dribbling in elephants may function as a form of "honest advertizement" (Clutton-Brock and Albon, 1979). The strong smell associated with urine dribbling may serve to advertize a male's condition to both rival males and to receptive females. It is likely that males who come across a path of urine are able to identify not only which individual it has come from, but what condition that male is in. When musth males are alone and searching for oestrous females it would be to the advantage of a high ranking male to leave a trail of urine wherever he goes, thereby deterring rival males from attempting to follow and compete with him. Lower ranking musth males whose periods of sexual activity overlap with that of a higher ranking male would not be expected to leave an obvious trail as this might be to their disadvantage.

Several studies on the nature of the secretion from the temporal glands have suggested that it aids in individual recognition (Buss et al., 1976). Ear waving wafts the scent of the temporal gland secretion towards other males (Chapter 4; Section 5), suggesting that the secretion from musth males may also function in assessment.

8.1.3 Female choice

Although the reproductive benefits of musth in terms of male-male competition are apparent and the primary concern of this study, the benefits in terms of female preferences cannot be overlooked. Oestrous and anoestrous females became excited by the approach of a musth male and took great interest in the urine trails left by them (Chapter 7; Section 4). Oestrous females were observed maintaining proximity only to musth males (Chapter 7; Section 3.1). Moss (in prep.) found that on 86.8% (n=38) of the occasions that this orienting behaviour was observed the males were in musth and all of the males were socially mature. Females may have been "choosing" these males because musth is, in some way, associated with high male fitness (Fisher, 1930) and because musth males were able to provide them with protection from the continual harassment of younger, less dominant individuals (Parker, 1974a).

Parker (1974a) points out that persistent courtship and continual attempts at mating can have a disruptive effect on the activities of females. By becoming fully receptive during a period of intense intermale competition the female shifts the burden of repelling mating attempts onto the male and can continue her activities unhindered. Females who remain close to a musth male are indeed able to continue with other activities unharassed (Moss, in prep). Older females appear to have learned to stay close to musth males (Moss, in prep.) and as a result are less harassed during oestrus than are younger females and are presumably less energetically costly for males to guard.

Observations suggest, however, that females may actually be actively selecting individuals with whom to mate. Moss (pers. comm.) watched a female run from a Class 2 male for over 30 minutes, covering a distance of several miles, but when she was finally approached by a Class 4 male she immediately stopped and backed into him, facilitating mating. Data collected by Moss (in prep.) suggests that the failure of Class 2 and 3 males to catch females and obtain matings is due more to the females' ability to elude them than to male-male competition.

My impression was that larger males were not able to run as fast as the younger males, particularly when they had erections (Chapter 7; Section 2.2). Since large males obtain many more matings than younger males, females may be purposely outrunning younger males.

If females are actually selecting some males over others, why are they doing so? Male elephants do not begin reproducing until approximately 25 years of age and they do not become successful guarders until they are at least 35 to 40. One explanation for females choosing older males is that in elephants longevity is a highly desirable trait to pass on to one's male offspring. A second possibility is that, with only a few days in which a female is attractive to males, it is important for a female to find a fertile male (Moss, in prep). Since males in musth have the highest levels of testosterone (Chapter 6; Section 3.1), which in some other rutting species corresponds with increased spermatogenesis (Short and Mann, 1966; Lincoln et al., 1970), females may be selecting musth males because they are more likely to be impregnated by them than by non-musth males.

8.1.4 Seasonality, male-male competition and the evolution of musth

Jainudeen et al., (1972a) noted the similarity of temporal gland activity and urine dribbling in elephants to the patterns exhibited by many cervids during the rut. They hypothesized that musth in *Elephas* is a vestige of a truly seasonal rut which may have existed at some point in the evolutionary history of the genus. They further hypothesized that although the physical and behavioural correlates of musth remain, the degree of breeding seasonality in this genus has, in recent history, declined with both sexes now being potentially reproductively active at all times of the year.

Although elephants may once have been highly seasonal breeders, I suggest that seasonality, in itself, need not be invoked as a condition for the evolution of musth. Musth is likely to have been favoured by selection in situations of intense male-male competition, which is not necessarily dependent on seasonality.

Lower degrees of seasonality mean that receptive females are dispersed in time and, particularly when females are clumped in space, predicts a higher intensity of male-male competition (Trivers, 1972; Emlen and Oring, 1977). Contrary to this hypothesis, D. Western (pers. comm.) predicts that sexual dimorphism in body size among present day African elephants should be more pronounced in highly seasonally breeding populations suggesting that intrasexual selection has been more intense.

When several females are in oestrous concurrently intermale competition is expected to decline unless a male is able to monopolize more than one receptive female simultaneously. Since male elephants are unlikely to hold harems except possibly under conditions of very low density (see Barnes, in press), and cannot otherwise monopolize two oestrous females simultaneously (pers. obs.), it is likely that intense male-male competition and increased sexual dimorphism occurs in populations where receptive females are clumped in space but dispersed in time, rather than in areas with highly seasonal breeding (Barnes, in press).

What ultimately affects the degree of male-male competition is the operational sex ratio, or the ratio of sexually active males to fertilizable females (Emlen and Oring, 1977). Continuous long periods of sexual activity among males with short asynchronous periods of receptivity among females produces a strong skew in the operational sex ratio (Emlen and Oring, 1977). Male competition for access to females should be most intense in situations where females form large groups in a predictable way and become receptive sequentially so that many males will be in one place at one time competing for access to one female. In this situation the operational sex ratio will be highly skewed towards males. In Amboseli there are on average 35 sexually active males (excluding the 73 Class 1 males who have very little mating success) each day, but there is only a 45% chance of one female being in oestrus on any given day (Chapter 5; Section 3.5).

It has been suggested that one reason why females get into large groups during the wet season is to incite male-male competition (Moss, in prep.). The mean female group size with an associating musth male was significantly higher than the mean group size without an accompanying musth male (Chapter 5; Section 3.5). Musth males are attracted to large groups of females since the energetic and time cost of searching for receptive female is reduced (i.e.. if all of the 48 family units are in two groups of 240 each rather than 48 groups of ten the time and energy associated with searching will be relatively lower). This suggests that if a female comes into oestrous in a large group she is more likely to be located, guarded and mated by a musth male than if she stays in a small group. The benefits to a receptive female of being guarded by a musth male have been discussed above (Section 1.2). However, for this argument to be plausible one would have to explain why pregnant or lactating matriarchs join large groups. An argument could be made that by having a daughter mated by a musth male she increases her inclusive fitness. Although this may be a factor, it is probably only one of many reasons why elephants form large groups (see Chapter 5; Section 4).

8.2 FACTORS AFFECTING THE DURATION AND TIMING OF MUSTH

8.2.1 Musth duration

The duration of musth periods in individuals appears to be related to a male's dominance rank relative to other males simultaneously in musth (Chapter 6; Section 3.5). This seems to be particularly true among the lower ranking mature males who can be forced out of musth by higher ranking individuals (Chapter 6; Section 3.5). It is more difficult to determine the factors limiting the duration of musth in older, higher ranking individuals. I observed a high ranking male "forced" out of musth on only one occasion and this followed an escalated conflict. Although escalated conflicts are a rare occurrence, they may, in conjunction with loss of condition, be an important determiner of musth duration (Chapter 6; Section 3.5). The loss of condition would not have to be substantial; even a small decline in condition might mean losing a fight to a male who, although usually lower in rank, had recently come into musth and was in peak condition. Olfactory senses in elephants are keen (Laws, 1970; Sikes, 1971) and since musth males leave a trail of strong smelling urine wherever they go (Chapter 4; Section 3.1), other musth males are presumably able to identify who else is in musth and what condition they are in without actually having to come into contact. If a male who has been in musth for several months, and is in poor condition, finds a path of urine or a tree marked with temporin from another male, he may choose to drop out of musth until the following year rather than risk a confrontation that may result in a permanent decline in rank, injury or death.

8.2.2 Temporal patterning of musth

The degree of breeding seasonality in elephants varies from population to population and from year to year within populations depending upon rainfall and food availability (Laws et al., 1975; Moss, in prep.). In Amboseli 60-70% of the females observed in oestrus occurred in the wet season (Chapter 5; Section 3.4). This figure varies from year to year depending upon rainfall and subsequent habitat conditions, interbirth intervals and the number of females reaching sexual maturity. However, during the years of the long term study in Amboseli, there have always been substantially more receptive females available during the wet than during the dry season (see Chapter 5; Section 3.4 and Moss, in prep.). This suggests that there has been intermale competition to come into musth at this time of the year.

The benefits of having a musth period at this time of the year are further enhanced by the tendency of females to form large groups (Chapter 5; Section 3.2). Although the variance in these figures is enormous (i.e. there are also smaller groups), the formation of some large groups, and the consequent decline in the total remaining groups in which to look for females, decreases the energetic and time cost of searching, thereby increasing the probability of locating an oestrous female. Male-male competition for obtaining a musth period at this time might therefore be intense even if the frequency of oestrous females remained constant throughout the year. A further benefit of obtaining a musth period during the rains is that food is both plentiful and of high quality (Chapter 5; Section 3.1) so that the nutritional costs of associating with females may be lower during the wet season than during other times of the year.

However, there are costs to coming into musth at this time. There were more males in competition for oestrous females during the wet than the dry season (Chapter 5; Section 3.5), so that the energetic costs associated with guarding an oestrous female are likely to be higher at this time of year.

With the above knowledge, the predicted pattern of individual musth periods might be that the dominant males come into musth during the first half of the rainfall year and the lower ranking animals wait until the competition is less intense during the latter half of the year, gradually attaining better temporal positions as they age and increase in rank. This pattern has been observed in dragonflies (Camponella and Wolf, 1974). However, in elephants the pattern does not appear to be so straight forward. Although the highest ranking male comes into musth from March through June (M13) (Chapter 4; Section 4.7; Figure 4.5) several other high ranking males come into musth much later in the year (M28 and M126) (Chapter 4; Section 4.7). Males of intermediate rank also come into musth during both times, but appear to be able to remain in musth for longer during the dry season, presumably because of the lower levels of male-male competition at this time (Chapter 6; Section 3.5). The lowest ranking males all come into musth during the wet season (Chapter 4; Section 4.7), but are frequently forced out of musth by higher ranking musth males (Chapter 6; Section 3.5).

The lowest ranking mature males spent most of their sexually active period in a non-musth state and only came into musth for a few days at a time (Chapter 6; Section 3.5). The data show that these males were more successful at obtaining matings as musth-guarders than as non-musth non-guarders (Chapter 7; Section 3.6,3.7). However, in situations where available females were already monopolized by high ranking musth males, lower ranking males were more successful as non-musth non-guarders because they were permitted to remain closer to the guarding male and oestrous female and were therefore in a better position to attempt to obtain a copulation. These lower ranking individuals were most likely to be successful as musth males when there were an "excess" of oestrous females (Chapter 7; Section 3.7), an event that was more likely to occur during the wet season than during the dry season.

High ranking musth males are able to inhibit musth in sexually active low ranking individuals (Chapter 6; Section 3.5) thus determining the timing and duration of musth in these males to a large extent. It is likely that the onset of musth periods of sexually inactive males may be influenced by other males who share the same bull area. Dominant individuals may be able to prevent the onset of musth in animals with whom they spent much of their time.

8.3 SEXUAL SELECTION: SOMATIC AND GENITAL

When Darwin proposed the theory of sexual selection he considered the way in which it affected the development of general bodily characteristics such as body size, colouration, weaponry and odouriferous secretions. Recently, Short (1979) has emphasized that sexual selection should be viewed as having two components: factors determining general body size and factors determining the size of the gonads and external genitalia. He refers to these two forms of sexual selection as somatic selection and genital selection. Somatic selection is related to the mating system and is concerned with the successful competition between members of one sex for access to mates (Short, 1979). Genital selection refers to the evolution of the male and female reproductive tracts and, although influenced by mating type, is ultimately a reflection of copulation frequency and sperm competition. For example, in species where copulation frequency is high, the testis to body weight ratio is predicted to be greater than in species with low copulation frequency. Genital selection has also led to the development of the penis in sexual diplay. Huxley (1938) introduced the concept of the term "psychological penis" to emphasize the role of the male organ in both copulation and intersexual display.

This study has concentrated on the evolutionary forces favouring sexually dimorphic characteristics related to somatic selection, namely body size, odouriferous secretions and behaviour patterns. The results given in this thesis showed that dominance is positively related to body size (Chapter 6; Section 3.3) and that the largest and highest ranking male present always has access to an oestrous female (Chapter 7; Section 3). I have discussed the function of musth and the sexually dimorphic physical and behavioural characteristics associated with it and I have argued that they have evolved primarily through male-male competition.

Whenever studies have been made on the reproductive tracts of elephants authors have made note of the outstanding length and peculiar location and structure of male and female genitalia (e.g. Sikes, 1971; Hanks, 1979): the testes are located intra-abdominally; the mobile penis is extremely long and in large adults may weighs over 45kg; the female urogenital sinus is in an anterior position situated between the female's hind legs, thus necessitating an extremely long urogenital tract; the clitoris is large and well developed. Although the reproductive tracts of elephants have been the subject of numerous studies (e.g. Johnson and Buss, 1967; Buss and Johnson, 1967; Short et al., 1967; Hanks 1973; Laws, 1969a; Laws, 1969b; Laws and Parker, 1968), there has, to my knowledge, been no functional explanation given for their peculiar structure. Although I have not addressed myself to the problem of genital selection, the apparent secondary growth spurt of the penis associated with social maturity and the consequent reproductive cost associated with its large size (Chapter 7; Section 2.2) requires an explanation.

The length and unusual position of the female reproductive tract has been given as an explanation of why the male penis is so long. But why is the female's tract in the position it is? An argument could be made that its location nearer the ground prevents injury to the calf during birth. However, during births in the wild (Leuthold and Leuthold, 1975; Moss, pers. comm.; pers. obs.) females were observed to kneel on their hind legs, so that the fall would be very short even if the vulva were located in the normal mammalian position. A more plausible explanation may be reached by discussing the male genitalia.

In Chapter 7 (Section 2.2) I suggested that there was a reproductive cost associated with the development of a large penis in males. This suggests that there must also be reproductive benefits that outweigh this cost. There is a suggestion in the Asian elephant that the penis may be used in display. Gale (1974;46) gives the following description of a male in full musth: "the whitish discharge continues to drip in a never-ending stream from the penis, which remains, as in the third stage, fully extended, swollen and for several hours, hanging down to the ground between the animal's hind legs." No other authors make mention of this except Fernando et al. (1963) who states that during musth "the penis is capable of protrusion but is limp and intromission is not possible". In the African genus, musth males sometimes extruded the penis slightly (see Plate 4.3), however it was rarely fully extended or erected except when attempting to mount an oestrous female. Unlike non-musth males, musth males did not obtain semi-erections when urinating (Chapter 4; Section 4.9), so they were actually seen with erections less frequently than were non-musth males. Even if the penis is used by musth males in display, this would not explain its large size when erect. A more likely possibility is that extreme size of the penis functions to reduce sperm competition from rival males.

Hanks (1979) comments that the length of the penis that enters the vagina is probably limited. However, having witnessed over 50 matings at very close range (often within 15 meters) I would disagree. I suggest that a large portion of the penis that is free enters the female. Descriptions of matings by Moss (in prep.) agree with this interpretation. Males with longer penises will be at an advantage for two reasons: a) the further up the female's genital tract a male can place his sperm, the less likely it is to fall out (females were observed to pick ejaculate up off the ground after having been mated; Chapter 7; Section 2.2) and b) when several males mate with one female, the male with the longest penis will be at an advantage over other males in terms of sperm competition.

It seems plausible that the extreme length of the female reproductive tract has evolved because females with longer reproductive tracts produced more surviving offspring. I suggest that these females may have produced more surviving offspring because they were more likely to have been fertilized by older, more fit males who had larger penises.

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Appendix 1. The number of musth and non-musth half-hour watches on focal males in association with females, with males or alone is given. w/F=with females; A=Alone; w/M=with males.

	Musth			Non-musth			
Male	w/F	A	w/M	w/F	A	w/M	Total
7	5	1	0	1	2	3	12
10	1	13	2	4	6	12	38
13	20	10	3	0	1	7	41
22	10	7	0	0	4	9	30
28	26	11	4	0	2	14	57
34	2	0	0	1	1	4	8
41	8	5	4	0	2	12	31
44	3	2	2	0	8	11	26
45	4	2	3	2	2	8	21
46	0	0	1	1	8	8	18
51	9	1	1	2	2	4	19
57	4	4	0	1	3	5	17
73	14	0	0	0	3	8	25
78	12	2	2	1	3	12	32
79	-	-	-	7	0	9	16
80	8	3	0	3	8	8	30
91	-	-	-	6	0	11	15
97	3	2	0	6	9	3	23
99	10	9	3	0	8	7	36
107	7	2	0	3	3	11	26
114	7	7	2	12	2	7	37
117	10	3	0	0	2	8	23
119	7	5	1	9	0	9	31
126	12	5	0	0	0	14	31
132	-	-	-	7	2	6	15
147	1	0	0	6	3	7	17
149	-	-	-	3	2	11	16
150	3	2	2	8	4	7	26
154	6	0	5	1	1	10	23
157	-	-	-	3	3	6	12

Appendix 2. Mean female group sizes (including males), mean number of males in association with female groups, standard deviations and numbers of groups are shown for each month of the study period.

	Female group size			Number of associating males		
Month	mean	s.d.	n	mean	s.d.	n
1980	37	45	445	7	9	276
Jan	39	44	5	11	10	3
Feb	54	67	44	13	12	21
Mar	41	43	45	7	8	31
Apr	41	45	55	8	7	38
May	45	48	32	6	7	18
Jun	31	35	36	5	3	16
Jul	24	16	10	4	3	6
Aug	18	15	37	4	3	24
Sep	15	12	42	4	2	21
Oct	26	24	48	5	4	36
Nov	23	30	39	8	17	30
Dec	57	65	52	13	11	32
1981	44	69	271	10	12	154
Jan	30	40	27	7	8	12
Feb	21	21	62	3	3	27
Mar	26	30	69	6	5	30
Apr	67	88	24	9	11	17
May	78	99	45	17	15	33
Jun	61	96	39	13	14	30

Appendix 3. Mean numbers of elephants in female groups with and without an associating musth male present. Standard deviations and numbers of groups are given. Data collected by Cynthia Moss are indicated.

	Musth male present			Musth male absent		
Year	Mean	s.d.	n	Mean	s.d.	n
(C.J.M.)						
1976	45	29	7	11	8	377
1977	101	64	36	19	22	307
1978	106	86	58	26	28	320
1979	133	85	23	27	33	156
1980	69	78	59	24	30	382
1981	118	139	30	18	17	160
(J.H.P.)						
1980	55	56	91	30	40	352
1981	108	110	63	25	31	209

Appendix 4. The total number of times each focal male was seen by the author during the study period. M=musth; Nm=non-musth.

Male	w/females		Alone		w/males		Total
	M	Nm	M	Nm	M	Nm	
7	5	1	1	1	0	8	16
10	3	1	7	13	1	17	42
13	44	0	16	1	1	6	68
22	14	3	7	8	0	14	46
28	14	0	6	5	2	21	48
34	1	5	0	5	0	10	21
41	11	0	8	7	4	22	52
44	2	0	1	17	2	16	38
45	4	3	1	4	2	16	30
46	0	16	1	19	1	18	55
51	6	12	3	10	2	10	43
57	5	15	1	6	0	10	37
73	9	2	1	5	1	12	30
78	8	8	4	7	1	24	52
79	-	27	-	6	-	22	55
80	12	16	4	21	1	11	65
91	-	37	-	4	-	25	66
97	4	32	1	11	0	11	59
99	19	4	8	12	1	12	56
107	10	19	3	9	0	12	53
114	5	26	4	10	1	15	61
117	10	1	2	5	1	10	29
119	10	28	2	4	2	13	59
126	9	0	8	0	0	17	34
132	-	56	-	2	-	12	70
147	3	17	0	10	0	13	43
149	-	30	-	2	-	21	53
150	1	34	3	4	1	15	58
154	6	6	0	1	3	16	32
157	-	14	-	7	-	13	34

APPENDIX 5

HORMONE ASSAY

A major problem concerning the measurement of urinary hormone levels is that of a varying volume of urine relative to the concentration of hormone. Creatinine - a metabolic by-product of endogenous muscle breakdown - is present in urine, throughout a 24 hour period, at a constant level. Therefore all samples were indexed against the concentration of urinary creatinine so that all testosterone values are expressed as ng per mg of creatinine(1).

METHOD: Urine (0.2 ml) was diluted with 0.2ml of phosphate buffer (pH 5.0) and enzyme hydrolyzed with 0.02 ml beta-glucoronidase-arylsulfatase[a]. The samples were then incubated at 37°C for 24 hr. Tritiated testosterone (2000 cpm) was added to the hydrolysates before extraction with 8.0 ml of freshly obtained, anhydrous diethyl ether[b], in order to monitor any losses incurred during the extraction. The ether extractants were decanted and reduced under a stream of nitrogen, to approximately 0.5ml. Afterwards 1.0 ml of isooctane[b] was added to each sample, and the extractants further reduced, in order to evaporate all the remaining ether.

Liquid chromatography was carried out according to the method of Anderson _et al_ (1976)[b], using celite mini columns [ethylene glycol: celite (1:2 w/v[2]]. Testosterone was eluted in 5.0 ml of cyclohexane (95%) and benzene (5%)(2). The solvent eluates were dried under nitrogen, and then reconstituted in 1.0 ml phosphate buffer (pH 7.0). Aliquots were taken for recovery determination and radioimmunoassay (RIA).

0.1ml aliquots for radioimmunoassay were made up to 0.5 ml with buffer (pH 7) and incubated with 10,000 cpm ^{3}H testosterone in 0.1 ml phosphate buffer, and testosterone-3-oxime-HSA directed antiserum (Abraham, S1599 No.3). The antiserum has a maximum cross- reactivity with 5 alpha-dihydrotestosterone of 17%.

The samples were incubated overnight at 4°C. Antibody-bound steroid was separated by adding 0.2 ml of charcoal-dextran (0.625% and 0.0625%, respectively, in phosphate buffer, pH 7.0). After 30 min at 4°C the samples were centrifuged at 2,500 rpm for 10 min. The supernatants were then counted. Unknowns were compared with testosterone standards[d] incubated in duplicate, over a range of 3.9 to 1,000 pg.

Interassay precision (expressed as the coefficient of variation) was ±9% (n=4) and ±7% (n=4) for 15% and 35% bound testosterone respectively.

Assay Validation

Celite column cochromatography samples (n=2) were hydrolyzed and extracted as described previously for testosterone (T) analysis. These samples were submitted to celite cochromatography, and ten 0.5 ml fractions were collected during the elution of T. 0.2 ml of each fraction was assayed and an equal volume was monitiored for the percentage recovery of the added tritiated testosterone.

Selected samples (0.5 ml each) were diluted with 0.5 ml of phosphate buffer (pH 5.0), and enzyme hydrolyzed with 0.02 ml beta-glucoronidase-arylsulfatase. The samples were incubated for 24 hr at 37°C. Before extraction of the hydrolysates, 0.1 ml of ^{3}H testosterone and ^{3}H dihydrotestosterone (DHT) (2000 cpm) were added to each sample in order to monitor methodological losses. The samples were then extracted with 8.0 ml of anhydrous ether, reduced to 0.5 ml under a stream of nitrogen, and then transferred to a conical vial and evaporated to dryness. The samples were reconstituted in 0.5ml of MeOH, prior to injection on a 4.6 x 250 mm column[c] using acetonitrile[b] water (40:60 v/v) as the isocratic solvent. Eluate fractions were collected at 30 second intervals for 15 minutes, and then at 20 second intervals for an additional 21 minutes. The flow rate was a steady 1.0 ml per minute. The fractions were evaporated under nitrogen, reconstituted in 1.0 ml phosphate buffer (pH 7.0). 0.4 ml aliquots were taken for testosterone assay and for monitoring the recovery of labelled hormone.

Results

Celite column cochromatography (Fig. 1) of immunoreactive vs radioactive T indicates elution of T from urine corresponding to tritiated pure hormone.

The HPLC cochromatography of immunoreactive vs radioactive T is shown in Fig. 2. The continuous elution pattern shows well-defined immunoreactive peaks, corresponding to the tritiated T and DHT.

a Boehninger, Mannheim, Germany

b Mallinkrodt Inc., St Louis, Mo.

c Licrosorb C-18, Altex No.254-70, Cole Scientific, Calabasis, Cf.

d Sigma Chemical Co., St Louis, Mo.

(1) Tanssky H.H. (1954) A microcolorimetric determination of creatinine in urine by the Jaffe reaction. J.Biol.Chem., 208: 853-861.
(2) Anderson, D.C., Hopper B.R., Lasley B.L. & Yen S.S.C. (1976) A simple method for the assay of eight steroids in small volumes of plasma steroids. Steroids, 28: 176-196.

Fig.1

Cochromatographic analysis of pure, tritiated T vs urinary testosterone immunoreactivity across the entire eluate normally taken for radioimmunoassay.

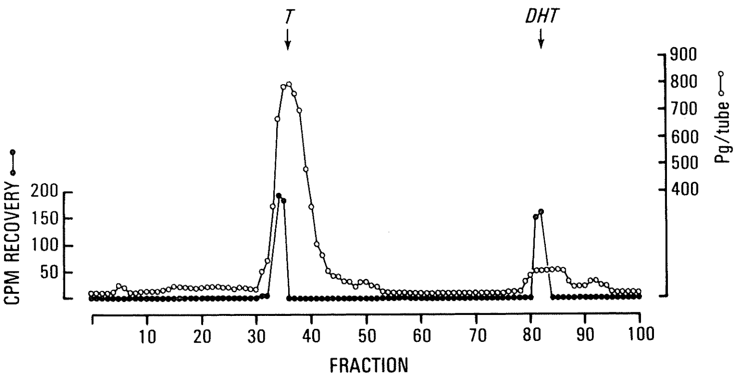
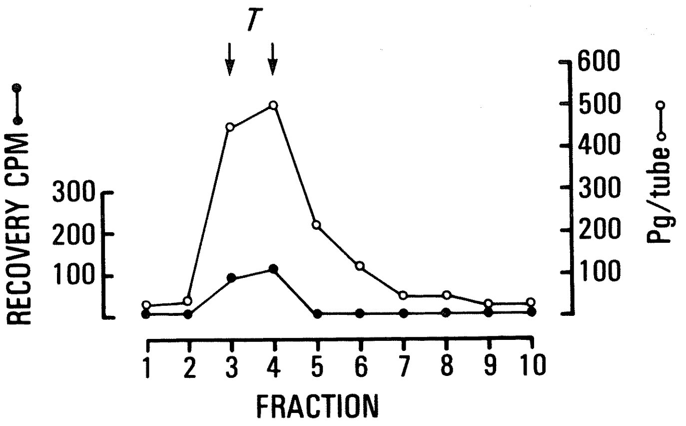


Fig.2

Total testosterone immunoreactivity compared with the recovery of tritiated testosterone after reverse phase high pressure liquid cochromatography of male elephant urine.



dix 6. Scientific names of mammals mentioned in the text.

: Marsupialia

:angaroo	*Megalela rufa*

: Primate

: baboon	*Papio anubis*
ıs monkey	*Macaca mulatta*

: Lagomorpha

ıt	*Oryctolagus cuniculus*

: Carnivora

	Panthera leo

r Proboscidea

:an elephant	*Loxodonta africana*
a elephant	*Elephas maximus*

r Perissodactyla

k rhinoceros	*Diceros bicornis*
hell's zebra	*Equus burchelli*

r Artiodactyla

rian camel	*Camelus bactrianus*
edary	*Camelus dromedarius*
deer	*Cervus elaphus*
elk	*Cervus elaphus*
deer	*Rangifer tarandus*
bou	*Rangifer tarandus*
e	*Alces alces*
k-tailed deer	*Odocoileous hemionus*
e-tailed deer	*Odocoileous virginianus*
son's gazelle	*Gazella thomsoni*
d	*Tauotragus oryx*
a Oryx	*Oryx beisa*
la	*Aepyceros melampus*
da kob	*Adenota kob*
rbuck	*Kobus ellipsiprymnus*

Wildebeest	*Connochaetes taurinus*
Cattle	*Bos taurus*
Bison	*Bison bison*
Mountain goat	*Oreamnos americanus*
Domestic goat	*Capra hircus*
Feral goat	*Capra hircus*
Walia ibex	*Capra waalie*
Mountain sheep	*Ovis canadensis*

Appendix 7. Footprint measurements of focal males. Means, standard deviations and number of measurements are given.

male	mean	standard deviation	n
7	–	–	0
10	50.1	0.3	4
13	53.0	0.0	2
22	52.5	0.6	8
28	51.5	0.8	8
34	46.4	0.6	16
41	51.0	0.8	14
44	50.7	0.5	12
45	51.2	0.8	22
46	47.4	0.4	8
51	49.8	0.5	16
57	47.6	0.5	17
73	–	–	0
78	50.4	0.5	13
79	–	–	0
80	50.2	0.6	13
91	49.2	0.4	13
97	47.7	0.5	7
99	50.5	0.6	24
107	50.7	0.5	9
114	47.1	0.3	14
117	51.0	0.4	12
119	48.9	0.5	15
126	53.8	0.4	11
132	–	–	0
150	48.3	0.6	3
154	48.2	0.4	15

m147
m17[illegible]
[illegible]