Reprinted from: BEHAVIOUR
102—3/4

LEIDEN
E. J. BRILL
1987

RUTTING BEHAVIOR IN AFRICAN ELEPHANTS: THE PHENOMENON OF MUSTH

by

JOYCE H. POOLE[1)2)]
(Sub-department of Animal Behaviour, Cambridge University, Madingley, Cambridge, CB3 8AA, England)

(With 16 Figures)
(Acc. 28-XI-1986)

Introduction

In 1871 DARWIN proposed the theory of sexual selection to explain the elaborate ornaments, weaponry, displays and odoriferous 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.

The evolution of rutting behavior in male mammals is the result of such selection. In general, rutting behavior in males is characterized by high testosterone levels, the exaggeration of sexually dimorphic traits,

---

[1)] Present address: Department of Biology, Princeton University, Princeton, N.J., 08544, U.S.A.

[2)] This work was funded by the New York Zoological Society, the Guggenheim Foundation and NIMH (5 F32 MH09277-02) and was carried out in affiliation with the Kenya Rangeland Ecological Monitoring Unit and the Sub-department of Animal Behaviour, Cambridge University. I thank them for their sponsorship and support. For permission to conduct research in Amboseli National Park, Kenya, I thank the National Council for Science and Technology, the Office of the President, the Wildlife Conservation and Management Department and the Amboseli Wardens. Katherine PAYNE, William LANGBAUER, David WICKSTROM and Greg BUDNEY (Lab. of Ornithology, Cornell University) helped with some of the recording and analysis of the vocalizations and I am thankful for their assistance. For helpful comments on the draft I am grateful to Phyllis LEE, Keith LINDSAY, Cynthia MOSS, Daniel RUBENSTEIN, and Robert SEYFARTH. Special thanks goes to Cynthia MOSS, Phyllis LEE and Keith LINDSAY for providing me with their records of musth and estrus and for all of their help and support over the years. Finally to Wamaitha NJIRAINI I wish to express my gratitude for her assistance and dedication in the field.

increased aggression towards members of the same sex and a heightened interest in females. In some species rutting males advertise their condition by emitting loud and characteristic vocalizations (red deer, *Cervus elaphus*: CLUTTON-BROCK & ALBON, 1979; reindeer, *Rangifer tarandus*: ESPMARK, 1964). Males in rut may become visually conspicuous through physiological changes such as an increase in neck musculature (red deer: LINCOLN, 1971) or by changes in pelage color or length (caribou, *Rangifer tarandus*: LENT, 1965; red deer: LINCOLN *et al.*, 1972). By soiling themselves with mud (red deer: LINCOLN *et al.*, 1972) or adopting a characteristic stance (Bactrian camels, *Camelus bactrianus*: WEMMER & MURTAUGH, 1980) males may further make themselves visually conspicuous to others.

Olfaction also plays a role in the advertisement of a male's sexual state. Males may secrete from various glands during the rutting period (Bactrian camels: WEMMER & MURTAUGH, 1980; Asian elephants, *Elephas maximus*: JAINUDEEN *et al.*, 1972a; African elephants, *Loxodonta africana*: POOLE & MOSS, 1981; black-tailed deer, *Odocoileous hemionus*: MÜLLER-SCHWARZE, 1971; mountain goat, *Oreamnos americanus*: 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, *Cervus elaphus*: MCCULLOUGH, 1969; caribou: LENT, 1965; reindeer: ESPMARK, 1964; white-tailed deer, *Odocoileous virginianus*: MOORE & MARCHINTON, 1974; eland, *Taurotragus oryx*: HILLMAN, 1976; mountain goat: GEIST, 1964; domestic goat, *Capra hircus*: FRASER, 1980; Bactrian camel: WEMMER & MURTAUGH, 1980; dromedary, *Camelus dromedarius*: COBLENTZ, 1976; Asian elephants: JAINUDEEN *et al.*, 1972a; African elephants: POOLE & MOSS, 1981). The urine of rutting males usually has a strong odor (LINCOLN, 1971; COBLENTZ, 1976).

In most ungulate species females breed seasonally, a pattern that is most likely a response to predictable seasonal abundance of resources critical to the energetics of lactation and, thus, calf survivorship. Males respond to this predictable period of female receptivity by showing a heightened interest in females and increased aggression towards other males. Thus in most polygamous ungulates the majority of males compete for access to mates simultaneously. The term rut, which comes from the Latin *rugire*, meaning to roar, is used by biologists to refer to this intense period of concentration on breeding activities by males. It originally referred to the annually recurring state of sexual excitement of male deer and has since been applied to a wide variety of animals, including camels, asses and elephants.

In African elephants the "breeding season" is less pronounced than in most ungulates. Although a peak in breeding activity occurs during and following the rainy season(s) (HANKS, 1969; LAWS & PARKER, 1968; POOLE, 1982), estrous females may be observed throughout the year (POOLE, 1982), causing the sexually active periods of males to be asynchronous (POOLE & MOSS, 1981; POOLE, 1982).

The phenomenon of musth, originally documented in male Asian elephants (DARWIN, 1871; SANDERSON, 1882), refers to a period of heightened sexual and aggressive activity. The term musth comes from the Urdu, *mast* meaning intoxication. Recently, POOLE & MOSS (1981) and HALL-MARTIN & VAN DER WALT (1984) have shown that musth also occurs in African elephants, contrary to conclusions of previous research (SIKES, 1971; HANKS, 1973; BUSS *et al.*, 1976; HANKS, 1979). In both genera musth refers to a set of physical and behavioral characteristics displayed periodically by adult males. The most obvious manifestations are a sharp rise in aggressive behavior, copious secretions from enlarged temporal glands and a continuous discharge of urine (Asian: JAINUDEEN *et al.*, 1972a; GALE, 1974 and African: POOLE & MOSS, 1981; POOLE, 1982; HALL-MARTIN & VAN DER WALT, 1984). The period of musth is associated with high concentrations of testosterone (Asian: JAINUDEEN *et al.*, 1972b; African: POOLE *et al.*, 1984) and frequent association with female groups (Asian: EISENBERG & LOCKHART, 1972; African: POOLE, 1982).

This paper describes the characteristics of musth observed during a long-term study of free-ranging elephants in Amboseli National Park, Kenya, and compares these with musth in the Asian elephant.

Methods

1. Study area.

Observations were made on a population of free-ranging African elephants from January, 1976 to June, 1986 in Amboseli National Park, Kenya. An intensive study of musth was carried out from January, 1980 to July, 1981 and again from December, 1984 through June, 1986. Amboseli National Park covers an area of 390 sq.km and consists of semi-arid wooded, bushed and open grassland interspersed with a series of permanent swamps. The area in the vicinity of the swamps provides a dry season concentration area; during the wet season the migratory herbivores, including elephants, frequently move onto privately owned ranchland surrounding the Park. The Amboseli ecosystem receives an average of 350 mm of rainfall a year falling in late November through December and again from mid-March to early May. Thus, the standing biomass of vegetation is higher from mid-December through June than it is during the latter half of the year (WESTERN & LINDSAY, 1984).

2. Study animals.

The Amboseli elephant population presently numbers 670 individuals, of which 500 are cows and calves and 170 are independent adult bulls. All elephants are known individually. A description of their social organization can be found in Moss & Poole (1983). The basic social structure of this population is similar to that reported in other areas of Africa (Buss, 1961; Laws & Parker, 1968; Douglas-Hamilton, 1972). Elephant society is matriarchal and elephants are born into stable groups of related females. Upon reaching sexual maturity, females remain in their families while males slowly become independent. By an average age of 14 years males have either temporarily joined another family unit or have begun associating with other young males. Although nutritional status may affect the age of sexual maturity among individuals and between populations (Laws *et al.*, 1975), free-living males can be said to be sexually mature by age 17 (Laws, 1969). However, they are not able to compete successfully for access to estrous females until approximately 30 years of age (Poole, 1982). By age 25, males have begun to exhibit alternating periods of sexual activity and inactivity defined in terms of hormonal changes and association patterns (Poole, 1982; Poole *et al.*, 1984).

Since male elephants continue to grow until late in life, age can be estimated from shoulder height (Laws, 1966) or from hind footprint length (Western *et al.*, 1984; Lee & Moss, 1986). For the purposes of this study, adult males have been divided into five age classes based on ages known from birth records, the degree of eruption and wear of teeth collected from dead elephants, visual estimates of relative shoulder height, measurements of footprint length and from photographs of known individuals taken during the early 1960s: Class 1A: 10-14.9 years (n = 23); Class 1B: 15-19.9 (n = 47); Class 2: 20-24.9 (n = 42); Class 3: 25-34.9 (n = 36); Class 4: 35-49.9 (n = 19); Class 5: 50+ (n = 2). The oldest male in the population was estimated to be 51 years.

3. Determining musth in African elephants.

The occurrence of musth in male Asian elephants can be determined by the onset of temporal gland secretion (Jainudeen *et al.*, 1972a). Unlike Asian elephants, two types of secretion may be observed from the temporal glands of African elephants. One type is common to both males and females of all ages and is watery and evaporates quickly; the second, produced only by older males, is sticky and stains for a longer period of time. The latter secretion is characteristic of males in rut. Since these two types are often difficult to distinguish in the field, Poole & Moss (1981) found the presence of urine dribbling, or the evidence of recent urine dribbling, to be the most reliable means of determining musth in African elephants. While urine dribbling was almost invariably associated with secretion from the temporal glands, temporal gland secretion (TGS) did not necessarily predict urine dribbling. In 509 sightings of males over 35 years (each male was observed at least 15 times), Poole (1982) found that 40.3% showed urine dribblng in conjunction with TGS, 51.3% exhibited neither, 7.8% showed only TGS and 0.6% were observed with urine dribbling but without TGS. Poole (1982) referred to males who showed both TGS and urine dribbling as "musth males". While urine dribbling was the most reliable indicator of musth, it should be pointed out that during some activities, such as an extended bout of feeding, urine dribbling by a musth male frequently ceased for a period of time (Poole, in press). In these cases a male was considered in musth if TGS was associated with swollen temporal glands and if urine dribbling had previously been present and subsequently resumed.

4. Field methods.

During the 1980-81 study period 754 half-hour focal samples (Altmann, 1974) were made of the 30 largest adult males; 323 of these samples were of males in musth. To monitor differences in the behavior of males with changing sexual state, an attempt was

made to sample each individual once every two weeks. However, younger males with predictably shorter musth periods (see below) were sampled more frequently during musth than were older males with longer musth periods. During the 1985-86 study period an additional 200 three-hour focal samples were accomplished on males in musth. To monitor the sexual state of the larger adult males I also recorded detailed information on the presence or absence of temporal gland secretion and urine dribbling on every day that any male 25+ years was encountered. Five physical characteristics were recorded on a scale of increasing amount. These are described here in detail as an aid to the recognition of musth in the field:

a. *Temporal gland secretion.*

The presence or absence of temporal gland secretion (TGS) was noted. TGS was classified as being either "fresh" (dark and watery), "congealed" (dark, but more viscous; associated with musth) or "old" (barely visible light brown stain).

The amount of TGS, when present, was classified in four categories depending upon the distance it flowed from the gland orifice (Fig. 1): 1) from the gland orifice to the lower extent of the eye; 2) to the top of the upper jaw; 3) to the corner of the mouth; 4) to the base of the lower jaw. In addition, the width of the secretion was described as being thin, medium or wide.

b. *Temporal gland swelling.*

The degree of temporal gland swelling was classified in four categories (Fig. 2): 0) no swelling; the area surrounding the gland orifice remained sunken. 1) slight swelling in evidence; the gland area was flush with the skull. 2) swelling was obvious; the gland area was swollen beyond the skull. 3) the temporal gland was extremely swollen and rounded; puffiness began immediately behind the eye and extended well beyond the skull.

c. *Urine discharge.*

Urine dribbling was categorized according to the amount being discharged (see Fig. 3):

0) no evidence of urine dribbling; both the penis and the inside of the legs were dry;
1) no discharge of urine, but the insides of the legs and/or the penis were wet from recent dribbling;
2) urine was discharged in a series of discrete drops with a greater than one second pause between drops but at least one drop per minute;
3) urine was discharged in a series of discrete drops with a one second pause between drops;
4) urine was discharged in a series of discrete drops with no pause between drops;
5) dribbling alternated between discrete drops and a thin but continuous stream of urine;
6) urine was discharged as a thin stream with no breaks;
7) the equivalent of several thin streams of urine: either one wide stream or several thin streams;
8) several wide streams of urine;
9) several wide streams of urine in addition to urine being expelled in spurts straight out from the penis orifice;
10) urine was expelled from the orifice of the penis with a force equal to that during normal urination.

The amount of urine discharged by a male changed frequently, often several times per minute, depending upon the male's activity and on the activity of those around him or within his hearing. Body size and the relative dominance of other males appeared to influence the amount of urine discharged over a longer period (POOLE, in press).

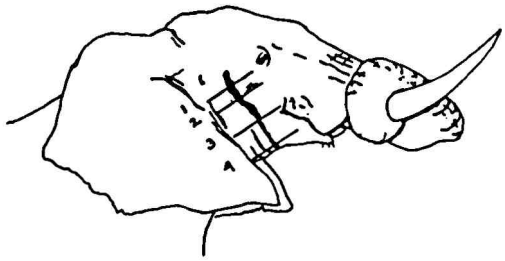

Fig. 1. Illustration of the amount of secretion from the temporal glands. See text for explanation.

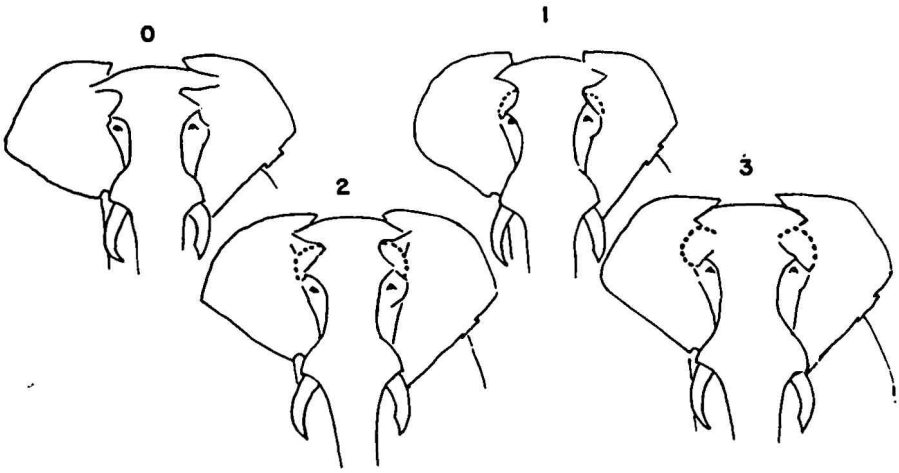

Fig. 2. Illustration of the degree of temporal swelling during musth. See text for explanation.

d. *Penis discoloration.*

When a male had been discharging urine heavily (greater than rate 4) for an extended period of time, the distal part of the sheath/proximal portion of the penis developed a greenish coloration. This was termed green penis or "G.P." (Poole & Moss, 1981) and was recorded as absent, slight or strong coloration.

e. *Odor.*

The urine discharge from a male in musth was associated with a particular odor which could be detected by human observers both on the male, especially when associated with G.P., and in the urine trail left by a musth male. This odor was described as absent, slight or strong.

5. Recording protocol.

To record the very low frequency vocalizations made by males in musth I used a Nagra tape recorder IVSJ with QSJC and two Seinheiser MK110 microphones. Manufacturer's

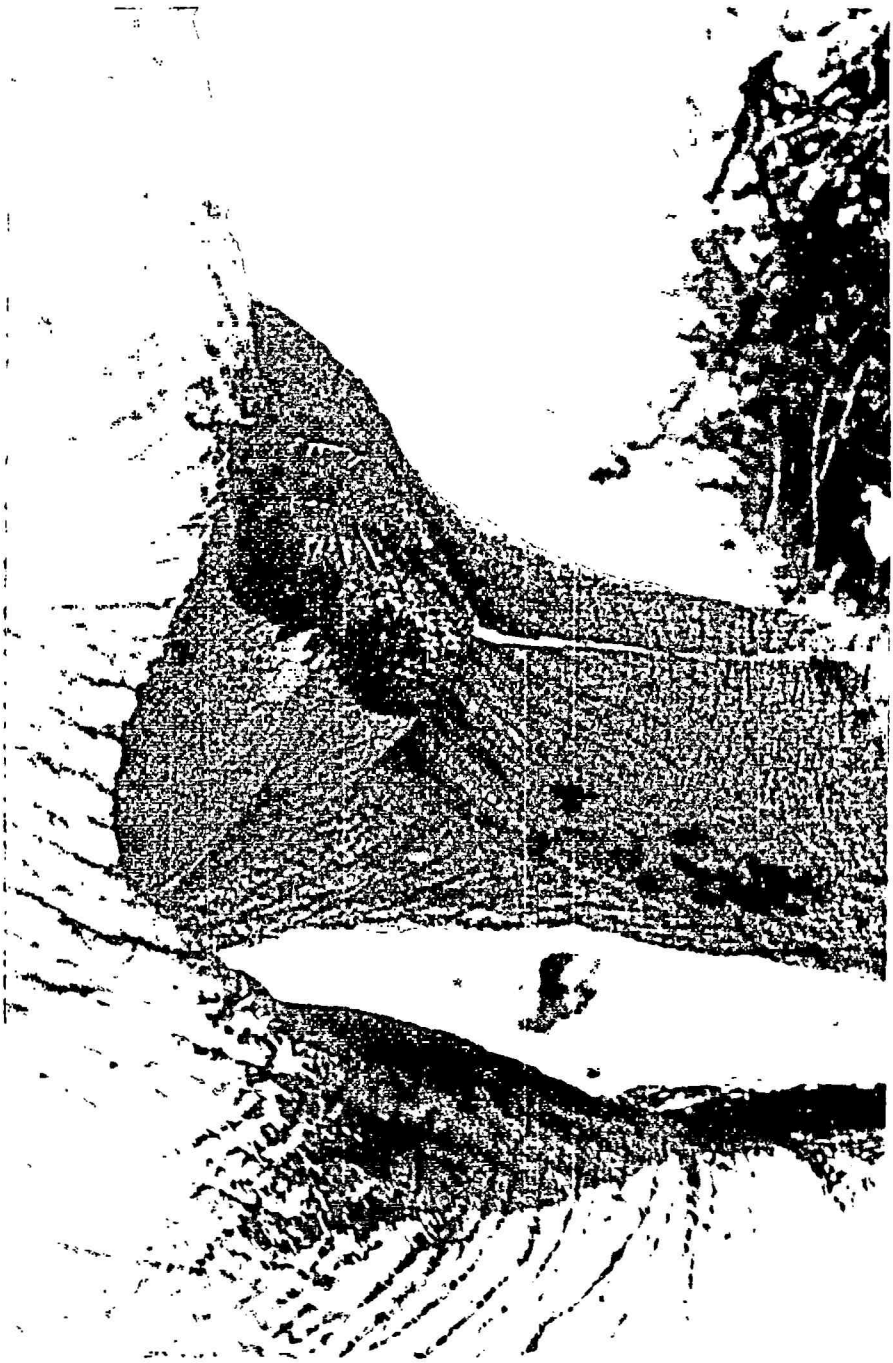

Fig. 1. Illustration of urine dribbling at rate 6.

curves were used to determine the frequency and amplitude performance of all the components, and field calibrations were made by means of a Bruel and Kjaer model 4230 acoustic calibrator. Recordings were made at 38.1 cm/sec. Using the same Nagra recorder spectograms were made of vocalizations using a Kay 7029A Sonagraph 5-16000 Hz Spectrum Analyzer.

6. Definitions.

Musth male – any male exhibiting an association between temporal gland secretion and urine dribbling or the evidence of recent urine discharge.

Sexually inactive – any male over 25 years in association with males in an all-male group and not in musth. Hormonal analysis (Poole *et al.*, 1984) showed that males in all-male groups have significantly lower levels of urinary testosterone concentrations than do males in association with females.

Sexually active – any male over 25 years old in association with females, or any male in musth regardless of association. Hormonal analysis (Poole *et al.*, 1984) showed that males in association with females have high concentrations of urinary testosterone and males in musth have significantly higher concentrations. Lone non-musth males were considered active or inactive depending upon the pattern of their recent associations.

Threat – Elephant threats included ear-folding, ear-waving, shaking the head or holding it up high, tossing the trunk, walking towards another elephant with the head high and ears folded or waving, chasing or tusking. The receiving individual would either look away or walk away, depending upon the intensity of the threat, with head and ears low. Threats by musth males were infrequently accompanied by a "musth rumble" (see below) while attacked males would often give a "bellow" if tusked or a "groan" when chased.

Listening posture – an elephant seldom stands completely still except when listening or resting. When resting an elephant relaxes its head and ears, allowing its head to hang below its shoulders and its ears to flop forward. A listening elephant, on the other hand, stands with its head raised, its ears lifted and slightly extended and may turn its head slowly to the left and right as if trying to locate a sound. During tests on elephant hearing ability, Heffner *et al.* (1982) found that elephants only stood in this posture when attempting to localize a sound, but did not extend their ears during the tests on absolute sensitivity or frequency discrimination.

Musth duration – the duration of a male's musth period was considered the number of days between the first and last sightings of the elephant on which signs of musth could be detected.

Results

1. Musth and association with females.

The occurrence of musth and male association was examined using data collected in 1980-81 on eight of the largest Class 4 and 5 focal males (males 13, 126, 22, 28, 41, 73, 117 and 99). Males in musth were significantly more likely to be found in association with females than in association with other males (Wilcoxon matched-pairs signed-ranks $T = 0$, $n = 8$, $p = 0.01$; Fig. 4). The same males, when in a non-musth state, were significantly more likely to be observed in the company of other males than with females ($T = 0$, $n = 8$, $p = 0.01$; Fig. 4). Each male was observed at least 24 times.

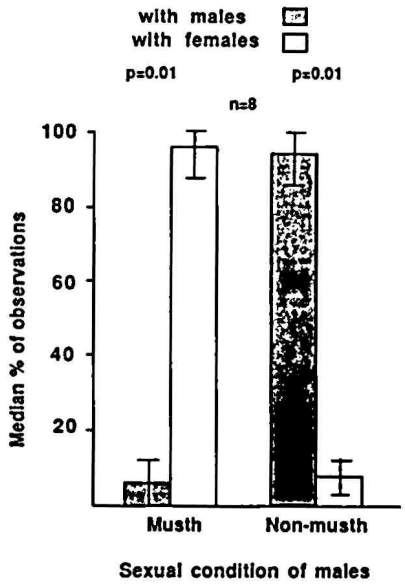

Fig. 4. Percent of observations of males (n = 8) in association with other males or with females when in musth or out of musth. Medians and interquartile ranges are shown.

2. Frequency of aggression: musth and non-musth.

The frequency of aggression (including only those behaviors defined as threats) was calculated from the 1980-81 focal samples of musth and non-musth males. The data have been divided according to whether threats were directed at elephant or non-elephant objects (*i.e.* the observer's vehicle and other species), and according to whether they occurred between males in association with females, in all-male groups or alone.

The rate of aggressive interactions towards other elephants increased significantly from non-musth to musth state both when in association with females (Wilcoxon matched-pairs signed-ranks $T = 19$, $n = 15$, $p < 0.02$; Fig. 5) and when in association with other males $T = 13$, $n = 16$, $p < 0.01$; Fig. 5). The rate of aggression towards non-elephant objects also increased from non-musth to musth state when in association with females (matched-pairs signed-ranks $T = 0$, $n = 7$, $p < 0.02$; Fig. 6) and when in association with other males ($T = 0$, $n = 11$, $p < 0.01$; Fig. 6). In addition, lone males threatened non-elephant objects more often when in musth than when not in musth ($T = 6.5$; $n = 17$, $p < 0.01$; Fig. 6).

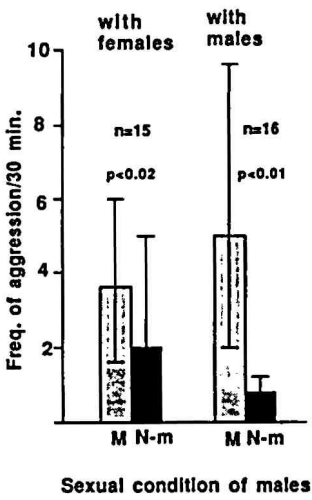

Fig. 5. The frequency of aggressive interactions per 30 minutes directed at other males by musth and non-musth males when in association with female groups and when in all-male groups. Medians and interquartile ranges are shown.

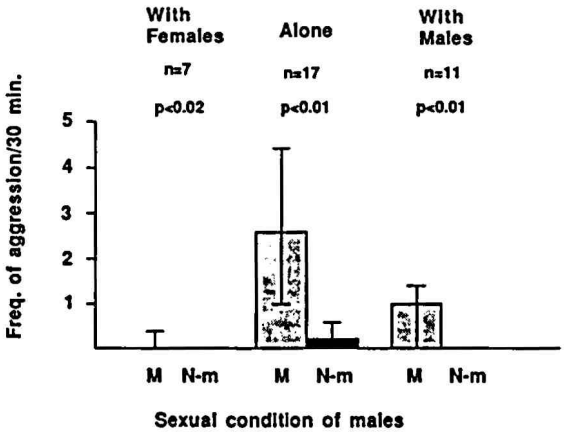

Fig. 6. The frequency of aggressive interactions per 30 minutes directed at non-elephant objects by musth and non-musth males when in groups with females, alone, or in groups with other males. Medians and interquartile ranges are shown.

3. Behavioral characteristics of musth.

There were several behaviors, postures and vocalizations that were performed either primarily or exclusively by males in musth. With the exception of the more detailed analyses of the musth vocalization, results presented in this section are based on males (n = 17) during musth and

TABLE 1. Percent of samples on musth and non-musth males in which particular behaviors were observed

	EW li		EW hi		MR		TrH		MT		UPS	
Males	M	Nm	M	Nm	M	Nm	M	Nm	M	Nm	M	Nm
10	40	0	20	0	83	0	5	0	4	0	5	0
13	41	0	35	0	50	0	0	0	2	0	6	0
22	36	0	9	0	92	0	0	0	10	0	0	0
28	25	0	10	0	3	0	0	0	18	0	5	0
41	30	0	10	0	67	0	30	0	0	0	10	0
44	20	0	0	0	20	0	20	0	20	0	0	0
51	0	0	0	0	57	0	0	0	0	0	18	0
73	57	0	43	0	7	0	0	0	7	0	0	0
78	15	0	8	0	8	0	54	0	0	0	15	0
80	20	0	20	0	100	0	60	0	9	0	20	0
99	67	11	44	22	92	0	11	22	15	0	0	0
107	22	0	11	0	11	0	22	0	22	0	56	0
114	30	0	0	0	10	0	0	0	23	0	10	0
117	69	0	0	0	23	0	0	0	31	0	8	0
119	33	11	0	0	100	0	11	0	17	0	0	0
126	7	0	0	0	0	0	0	0	12	0	7	0
154	27	0	9	0	9	0	27	0	0	0	10	0

EW li = ear wave low intensity; EW hi = ear wave high intensity; MR = musth rumble; TrH = trunk to head; MT = marking trees with TGS; UPS = urination with penis sheated; M = in musth; Nm = not in musth. Each male contributed at least eight samples in each state.

non-musth in 1980 and 1981. Each male was sampled at least eight times in each state. A particular behavior was scored on a one-zero basis within a focal sample. For each behavior I have compared the proportion of samples in which each behavior occurred during musth and non-musth state for each male separately (see Table 1).

a. *Ear wave.*

Ear flapping in elephants functions in both thermoregulation (McKAY, 1973) and communication (DOUGLAS-HAMILTON, 1972). Elephants have many ear signals: rapid ear flaps with head extended (female-female threat), earfold (general threat), ear-fold with head and ears lifted high (greeting within a bond-group), ear flap-slide (a signal of intention to move or change activity); ear flapping accompanies many vocalizations. In contrast to other ear signals, the ear wave is accomplished by moving only one ear at a time. The inner and upper portion of the ear is thrust vigorously forward allowing the lower and outer portion of the ear to

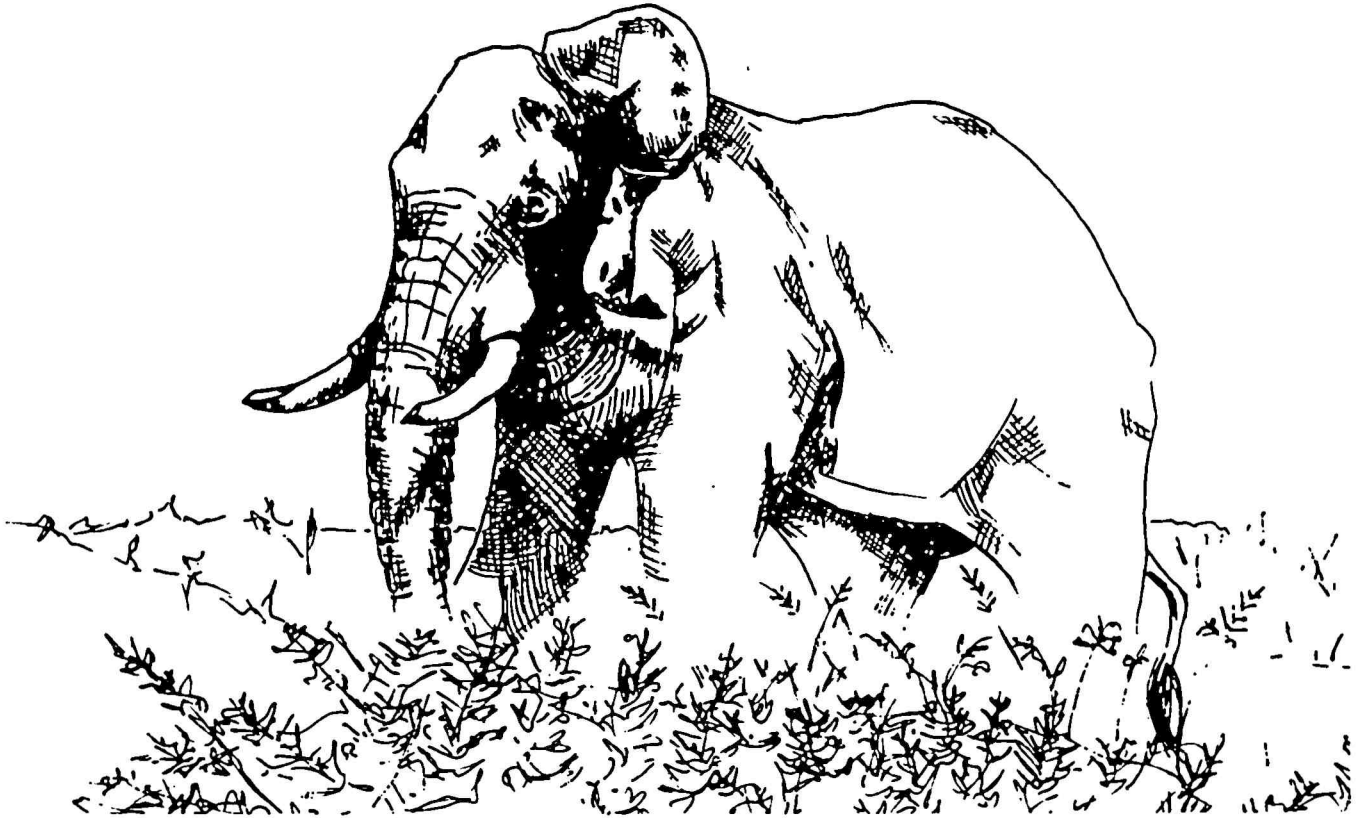

Fig. 7. The ear wave. This behavior was performed only by males in musth and may function to waft the scent of the temporal gland secretion towards other elephants.

follow behind. This motion creates a wave diagonally across the ear (Fig. 7) and may be done once (low intensity) or more than once (high intensity). Ear waving was most often used during agonistic interactions between males or when musth rumbling (see below).

Males ear-waved during a higher proportion of samples on musth males than during samples on non-musth males (low intensity EW: Wilcoxon matched-pairs signed-ranks $T = 0$, $n = 16$, $p < 0.01$; high intensity EW: $T = 0$, $n = 11$, $p < 0.01$; Table 1) and with the exception of two samples, both on male 99, males were observed to ear-wave only when in musth.

b. *Trunk to head.*

This behavior was performed by lifting the head high and, with the mouth open, reaching up with the trunk to rub the temporal gland area (Fig. 8). The trunk to head was observed only in musth males with the exception of two samples on a non-musth male ($T = 2.5$, $n = 9$, $p < 0.02$; Table 1). Both of these samples were on male 99 who had left his bull area (see Moss & Poole, 1983) and joined females for several days. He behaved aggressively towards other males, but did not show the overt signs of musth until several months later.

c. *Marking.*

Males rubbed the temporal gland area against trees both in and out of musth, but this behavior occurred more frequently during musth ($T = 0$, $n = 13$, $p < 0.01$; Table 1). On one particular occasion a male in musth rubbed his temporal gland on several trees and then returned later to smell where he had marked.

d. *Urination with penis retained in sheath.*

Male elephants normally urinate with a partial erection, standing with their legs apart and directing the stream out between their hind legs. During musth, males who had been dribbling at a low rate (less than rate 4) for more than an hour, urinated with the penis still sheated, allowing urine to spray on to the insides of their hind legs. Males were only observed to urinate in this fashion when they were in musth ($T = 0$, $n = 12$, $p < 0.01$; Table 1). Males in musth who had been dribbling urine at rate 4 or greater were not observed to urinate.

Fig. 8. The trunk to head. This behavior is performed by males in musth. By rubbing the temporal glands during this motion males may collect some secretion on the hairs and in the grooves of their trunk. As the male walks along some of this secretion may contact vegetation leaving a scent trail for other elephants.

e. *Musth walk.*

Males in musth had a characteristic posture which was particularly noticible when they were moving. Normally, males carried their heads level with or below their shoulder blades and extended slightly forward, with their ears relaxed and back. During musth, males carried their heads high, well above their shoulders and held at such an angle that the chin looked tucked in. The ears, held tensely, were spread and carried high. Musth males walked with a controlled swinging motion to the head and tusks. This posture (Fig. 9) allowed me to recognize males in musth from a distance of 500 meters.

f. *Head oscillation.*

During this behavior elephants swung their heads with vigor in a figure of eight motion often lifting a foreleg off the ground to retain balance. This movement was sometimes combined with the trunk to head. The sample size was too small to test statistically, but *ad lib.* data suggest that it occurs primarily in younger males during the first few weeks of musth.

g. *Tusking.*

Males got down on their knees during this behavior and tusked the ground, lifting up clods of dirt, mud or grass. Tusking vegetation, throwing logs, bushes and other objects at vehicles or other elephants was also observed. While this behavior was seen occasionally in all age/sex classes of elephants, it always occurred during fights between musth males.

h. *Musth rumble.*

Musth rumbles are very low pulsating sounds of up to 108 decibels (recorded at 15 meters from the source and extrapolated to 1 meter) with fundamental frequencies as low as 14 Hz (Fig. 10). They are performed in conjunction with an ear-wave or an ear-fold with a loud ear-flap marking the end of the vocalization. Musth rumbles recorded from Male 119 at >10 meters from the source had a mean sound pressure level of 105 dB $\pm$ 2 dB (extrapolated to 1 meter; $n = 13$). This sound was never made by non-musth males ($T = 0$, $n = 16$, $p < 0.01$; Table 1).

Data collected during 1985 and 1986 showed that males musth rumbled when alone, and apparently searching for female groups, significantly more frequently than when they had joined females (Wilcoxon matched-pairs signed-ranks $T = 0$, $n = 6$, $p < 0.05$; Fig. 11). In addition, males rumbled even less often when they were in association

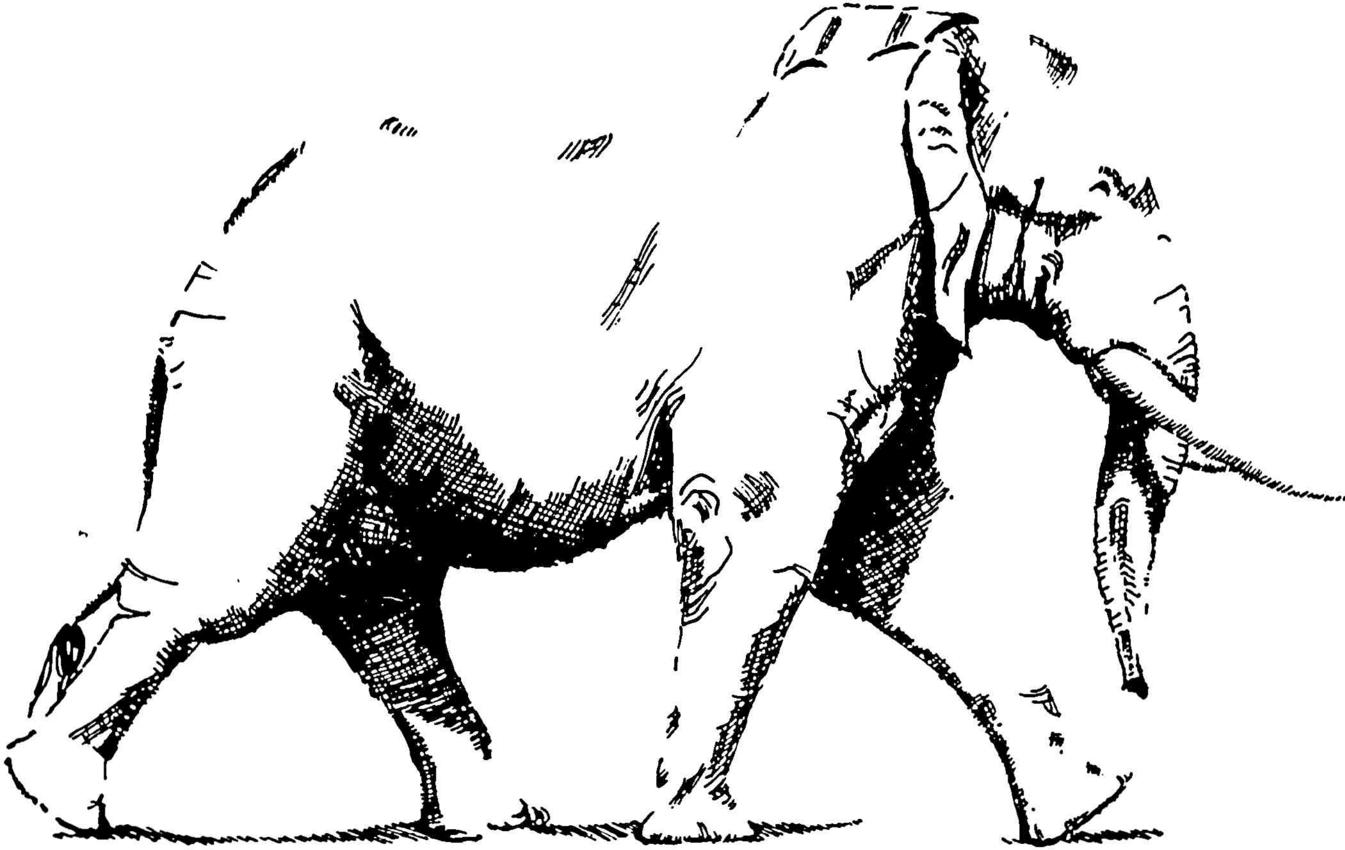

Fig. 9. The musth walk. Males in musth have a characteristic posture, particularly when moving. The head is carried well above, rather than below, the shoulder blades and held at such an angle that the chin looks tucked in. The ears are tense and carried high and spread.

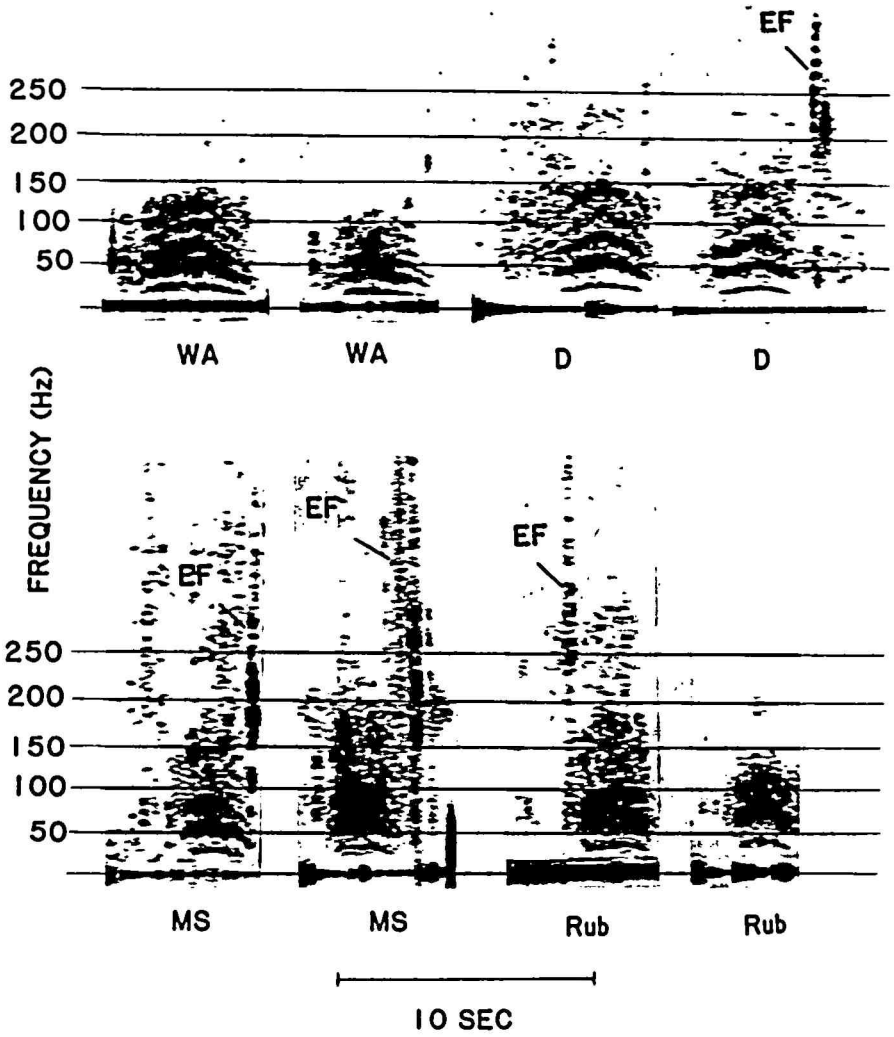

Fig. 10. Sonograms showing examples of musth rumbles given by a single individual during a 45 minute period under a variety of contexts: when suddenly changing activity and walking away (WA); when drinking (D); when mud splashing (MS); when marking a tree with temporal gland secretion (Rub). The X-axis shows time; the Y-axis shows frequency in intervals of 50 Hz. EF = ear flap. The higher frequency sound in the drinking and mudsplashing examples is water being splashed around by the elephant. In the rubbing examples some of the noise is the rasping sound of the elephant's body being rubbed against the tree.

with, or guarding, an estrous female ($T = 0$, $n = 6$, $p < 0.05$; Fig. 11). Females often responded to musth rumbles with a specific loud (up to 111 dB) low frequency vocalization.

Large males aged 40 years or older vocalized significantly more frequently than did smaller males of less than 40 years (Mann-Whitney $U = 9$, $n_1 = 8$, $n_2 = 8$, $p = 0.007$; Older males: median = 3.6 per hour, interquartile range 2.0-6.6; Younger males: median = 1.1 per hour, interquartile range 0.2-2.2).

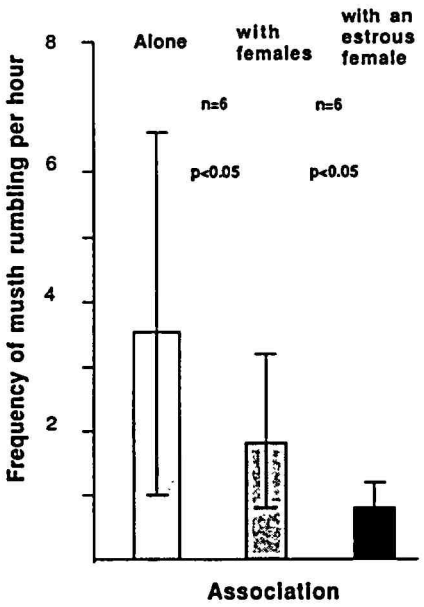

Fig. 11. A comparison of the frequency of musth rumbling per hour by lone musth males, those in association with female groups and those in association with an estrous female. Median rates and interquartile ranges are shown.

Musth rumbles were given under a variety of diverse but specific contexts: during agonistic encounters and escalated contests with other males of a similar rank; when approaching the observer's vehicle; when hearing another low frequency sound such as a plane passing overhead or the approach of a vehicle; during marking behavior such as rubbing the temporal gland on a tree, using a mud wallow or when urinating; prior to or after standing in a listening posture and presumably hearing very low frequency or distant calls or answers that the observer was unaware of;

when approaching, entering or leaving a body of water; when drinking; immediately prior to driving and copulating an estrous female (Table 2). Preliminary spectral analysis suggests that the "musth rumble" may be a class of calls composed of several different rumbles that are context specific. Fig. 10 gives examples of musth rumbles associated with specific contexts (walking away, drinking, mudsplashing and marking a tree with temporal gland secretion) given by a single male during a 45 minute period (note the differences in fundamental frequency, duration and degree of modulation).

TABLE 2. The frequency of musth rumbling in different contexts is presented. The results are based on 414 hours of focal sampling on 16 different males

DUE	D	MS	WSw	Rub	Car	Pln	TC	TM	IF	MRL	LMR	WA	SmGr	SmAr	Unk
28	90	174	55	68	280	21	72	31	39	21	41	66	12	10	208

Each male contributed at least 12 hours and no greater than 39 hours (median = 25.5). A total of 1,216 vocalizations were heard and were associated with the following contexts: DUE = defecation, urination or erection; D = drinking; MS = mudsplashing; WSw = approaching water or the swamp; Rub = rubbing the temporal gland on trees; Car = hearing the sound of an approaching vehicle's engine; Pln = hearing the sound of a plane passing overhead; TC = threatening the observer's car; TM = threatening another male; IF = interacting with females; MRL = Musth rumble followed by listening behavior; LMR = listening followed by a musth rumble; WA = activity change marked by walking away; SmGr = smelling the ground with the trunk; SmAr = smelling the air with the trunk raised high; Unk = context unknow.

4. Age distribution, duration and timing of musth periods among males of the Amboseli population.

a. *Age distribution of musth.*

As of June, 1986 all Class 5 (n = 2), 18 class 4 (n = 19) and 18 Class 3 (n = 36) males have been observed in musth on at least one occasion. The remaining 113 adult males (those over 10 years) have yet to be observed in musth (Fig. 12). Based on males whose first year of musth onset was known to within one year, the mean age of first observed musth was 29 years (+/-3; range = 24-37; n = 30). No males under 24 years have been observed in musth.

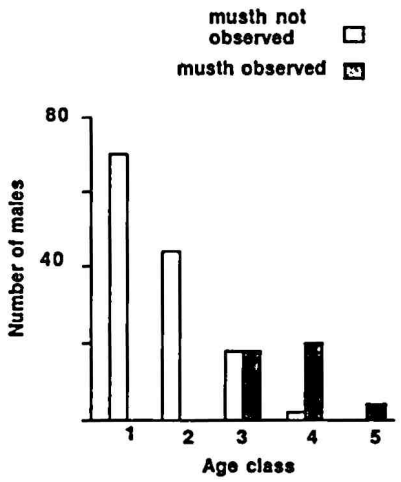

Fig. 12. Age distribution of musth in the Amboseli population.

b. *Duration of musth periods.*

The duration of musth periods was highly variable between individuals; males remained in musth from one day up to 127 days (Fig. 13). However, the length of musth periods for individual males was, in general, similar from one year to the next (see in Fig. 13 those males for whom the 1980-81 dates of musth onset and termination were known to within one week: males 99, 80, 57, 119; see also Fig. 16). The duration of musth periods was positively correlated with male age (and therefore body size; Spearman rank correlation $r_s = 0.83$; $t = 6.8$, $n = 23$, $p < 0.001$; Fig. 14).

c. *Timing of musth periods.*

Males were observed in musth throughout the year (Fig. 13) with the highest occurrences in the first seven months of the year, during and following the two rainy periods. Peak numbers of musth males coincided with the months when the frequency of estrous females was also the highest (Fig. 15). In addition, poor/good rainfall years with low/high numbers of receptive females resulted in correspondingly low/high numbers of males observed in musth. Since the period of estrus lasts only a few days (Moss, 1983) and musth periods may last several months, the number of males in musth should not be viewed as a direct response to the number of receptive females observed in a particular month. However, under certain circumstances the presence of an estrous female may stimulate the onset of musth in a particular male.

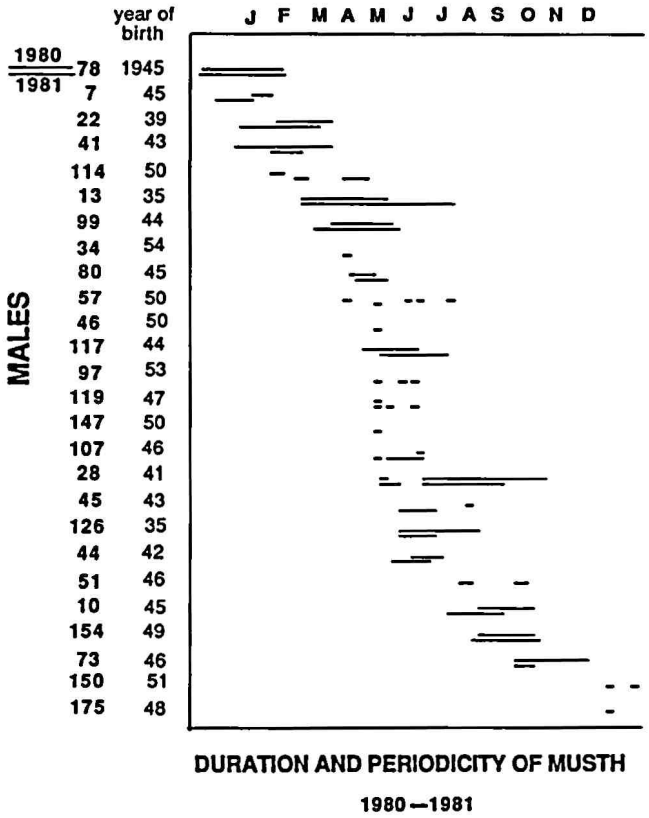

Fig. 13. Musth duration and timing for all males observed in musth during the 1980-81 study period (n = 26). The dates of musth onset and termination are given as the first and last date that an individual was seen in musth. For each male the upper line represents his 1980 musth period while the lower line represents 1981. The year of birth is ± three years.

The onset of an individual's musth periods was usually closely synchronized from one year to the next (Fig. 16 illustrates the musth periods of males for whom there were at least six years of data). Exceptions included males who were either increasing in rank and were therefore moving gradually into a reproductively better time of the year (*i.e.* M10), or males who, over the years, were declining in rank and whose musth periods were becoming shorter and more sporadic (*i.e.* M41).

d. *Patterns of musth onset and termination.*

In the Amboseli population three age related patterns of musth onset and

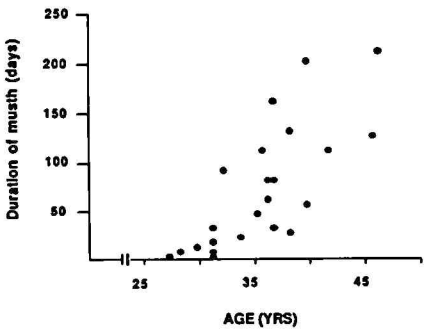

Fig. 14. The relationship between age and the duration of musth. Musth duration was taken as the combined length of the males' 1980 and 1981 periods.

termination could be distinguished. The oldest males came into musth before they were seen associating with female groups. They remained in musth for the full time that they were seen in the vicinity of females and only dropped out of musth when they had returned to their bull area. The younger Class 4 males joined female groups and actively tested and competed for access to estrous females, but did not show the physical and behavioral signs of musth until they had been in association with females for several weeks. Males from this age group usually dropped out of musth well before they left female groups and returned to their bull areas. Males from Class 3 tended to come into musth after having associated with females for up to a month. They rarely stayed in musth for more than a few days at a time and would come into musth several times during one sexually active period. The days between bouts of musth were termed "inter-musth" periods.

Discussion

1. Why musth was overlooked in African elephants.

Given its highly visible symptoms, it seems surprising that musth in African elephants should have gone undetected for so many years. There are several possible explanations.

In most of the early studies elephants were not individually recognized, so that individual behavior patterns went largely unnoticed. Those studies in which animals were recognized individually either concentrated on females (DOUGLAS-HAMILTON, 1972) or on males in bull areas

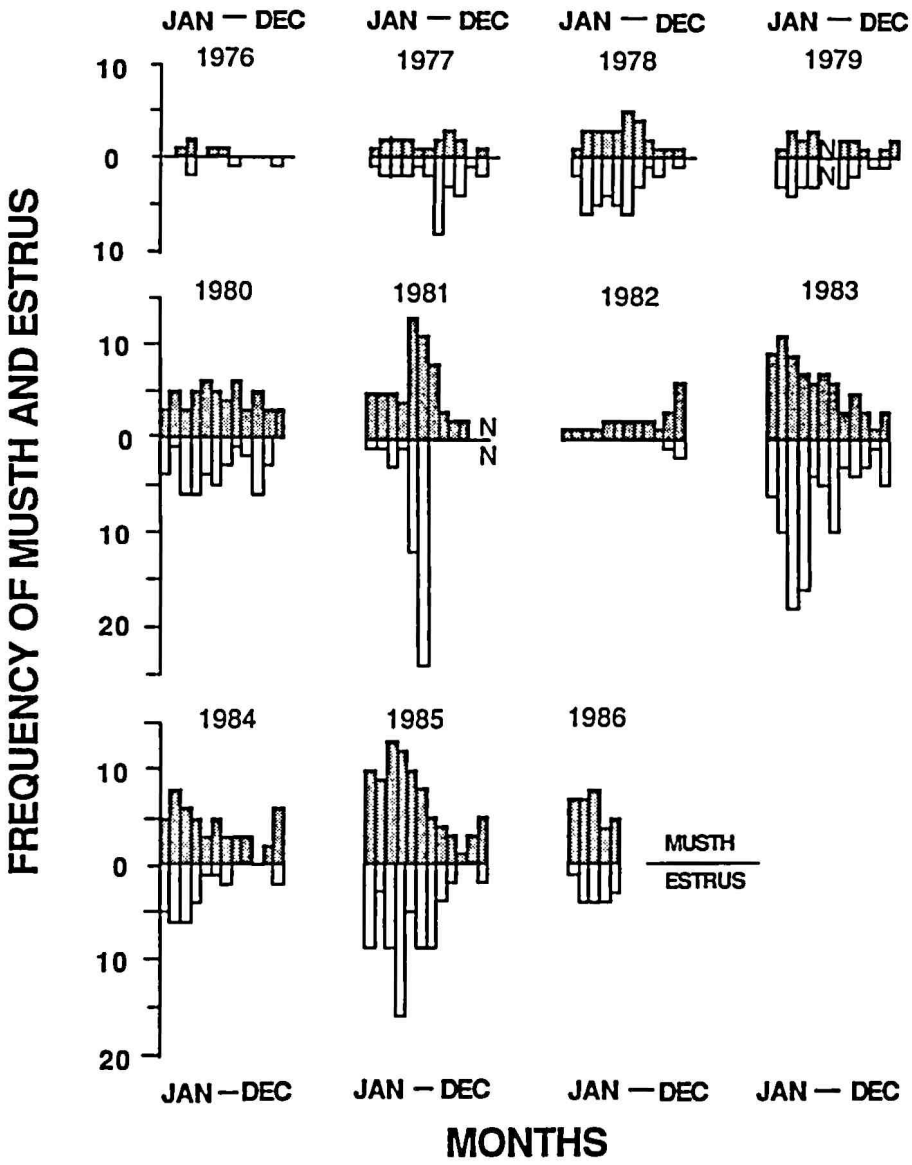

Fig. 15. The numbers of males in musth and females in estrus is illustrated by year and by month from January, 1976 through May 1986. N = no records available. These are observed frequencies and, therefore, the numbers depend on the amount of time that an observer was in the field. The years 1978, 1979, late 1981 and early 1982 had fewer observer days than did other years. 1976, 1977, 1980, 1982, 1984 and 1986 were low (less than 300 mm) rainfall years (a rainfall year is considered the combined rains from November/December of the previous year with the March/April/May rains of that year).

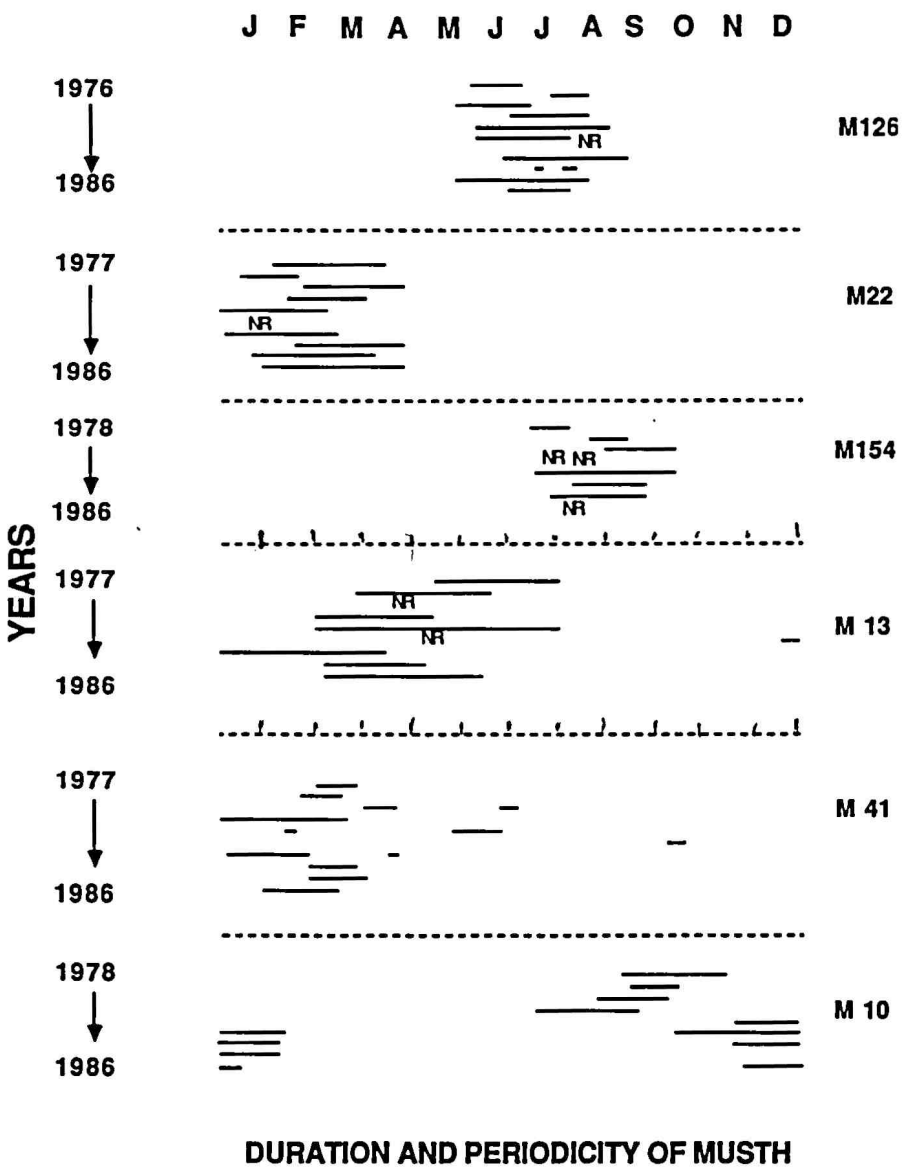

Fig. 16. Musth timing and duration for males (n = 6) for whom there are records for at least six years. Dates of musth onset and termination are given as the first and last days that musth could be detected. NR = no records available.

(CROZE, 1974). In either case, musth males may have seldom been observed or noticed.

A second reason that musth was overlooked probably concerns confusion over secretion from the temporal glands. In Asian elephants the most important indicator of musth is the onset of temporal gland secretion which, with rare exceptions, occurs only in males in this condition (EISENBERG *et al.*, 1971; JAINUDEEN *et al.*, 1972a). In African elephants, however, temporal gland secretions of short term duration occur frequently in both sexes. In fact, females have been shown to secrete from the temporal glands more often than males (DOUGLAS-HAMILTON, 1972; POOLE, 1982). Previous authors could find no relationship between such secretions and sexual activity (PERRY, 1953; SHORT *et al.*, 1967; SIKES, 1971; HANKS, 1973 and 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 estrous females (SHORT, 1966).

The discussion of musth in African elephants has been further confused by the incorrect use of the term, which in this species has often been 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 secretion. In African elephants, secretion from the temporal glands may either be associated with musth (POOLE & MOSS, 1981) or with social excitement and interactions, separation and reunion with family members, and stress (pers. obs.; see also SIKES, 1971; BUSS *et al.*, 1976; WHEELER *et al.*, 1982; HALL-MARTIN & VAN DER WALT, 1984). My own observations and those of EISENBERG (pers. comm.) suggest a qualitative difference between the two secretions. The secretion associated with musth is more viscous and dries more slowly than that secreted by non-musth elephants.

2. Musth in Asian and African elephants: a comparison.

a. *Physical and behavioral characteristics.*

The physical and behavioral characteristics of musth in Asian and African elephants are strikingly similar. In both species early musth is marked by the onset of temporal gland swelling and secrtion and increas-

ing aggression (African: this paper; Asian: FERNANDO *et al.*, 1963; EISENBERG *et al.*, 1971; JAINUDEEN *et al.*, 1972a; GALE, 1974). As musth progresses secretion from the temporal glands flow in a wide stream and is associated with a strong smelling discharge of urine (African: this paper; Asian: JAINUDEEN *et al.*, 1972a; VON ELKE SCHEURMANN & JAINUDEEN, 1972; GALE, 1974). When TGS and the discharge of urine are both in evidence the elephant is said to be in "full musth" and becomes extremely aggressive (POOLE, 1982, this paper; Asian: JAINUDEEN *et al.*, 1972b). This stage may last from a few days up to several months (African: this paper; Asian: FERNANDO *et al.*, 1963; JAINUDEEN *et al.*, 1972a). Musth is associated with, and perhaps caused by, a sharp rise in testosterone levels (African: POOLE *et al.*, 1984; HALL-MARTIN & VAN DER WELT, 1984; see also HOWARD *et al.*, 1984; Asian: JAINUDEEN *et al.*, 1972b; RASMUSSEN *et al.*, 1984).

Asian and African musth elephants share several behavior patterns in common. During musth males rub their temporal gland area with their trunks (African: this paper; Asian: JAINUDEEN, 1972a; VON ELKE SCHEURMANN & JAINUDEEN, 1972). Free-living elephants mark vegetation with temporal gland secretion more often when in musth than when out of musth (African: this paper; Asian: EISENBERG *et al.*, 1971; KURT, 1974). In zoo elephants, RASMUSSEN *et al.* (1984) found that Asian males in musth showed considerable interest in temporal gland secretion rubbed on the enclosure wall by another musth male. Head oscillation, using the trunk to rub the forehead and temporal glands and tusking the ground were all behaviors associated with musth (African: this paper; Asian: JAINUDEEN, 1972a; VON ELKE SCHEURMANN & JAINUDEEN, 1972; GALE, 1974). Although males usually attain a partial erection at micturition, during musth this pattern is altered and the penis remains sheathed (African: this paper; Asian: JAINUDEEN *et al.*, 1972a).

Free-ranging male elephants spend more time with females during their musth periods than during non-musth (African: this paper; Asian: KURT, 1974). As the period of musth begins males leave their "bull areas" (African: MOSS & POOLE, 1983) and move into habitats used predominantly by females (African: POOLE, 1982; Asian: EISENBERG & LOCKHART, 1972; KURT, 1974) where they move from group to group in search of estrous females (African: POOLE, 1982; see also BARNES, 1982). Although males can and do mate successfully whether in or out of musth, the high dominance status associated with the musth period may enhance reproductive success among free-ranging populations (African: POOLE, 1982 and in press; Asian: EISENBERG *et al.*, 1971).

b. *Age distribution of musth.*

Among free-living African elephants no male under 24 years was observed in musth, while among domesticated Asian elephants males as young as eleven years have been observed in musth (EISENBERG *et al.*, 1971; JAINUDEEN *et al.*, 1972a). Since, in captivity, several male African elephants in their teens have been observed exhibiting the signs of musth (EISENBERG, pers. comm.), this observation may be attributed to differences in nutritional status. In both species there was a gradual increase in the proportion of males observed in musth with age (African: this paper; Asian: JAINUDEEN *et al.*, 1972a).

c. *Seasonality of musth.*

In both African and Asian elephants musth was observed throughout the year with peak occurrences during and following the rainy seasons when vegetation was abundant (African: this paper; Asian: EISENBERG *et al.*, 1971; JAINUDEEN *et al.*, 1972a; but see KURT, 1974) and coincided with the months of highest conception frequency (African: this paper; Asian: GALE, 1974).

d. *Duration of musth periods.*

The duration of musth between individuals of both species was highly variable ranging from one day up to several months (African: this paper; Asian: JAINUDEEN *et al.*, 1972a; GALE, 1974). However, the duration of musth periods for individual males was relatively consistent from year to year (African: this paper; Asian: JAINUDEEN *et al.*, 1972a). The length of musth periods was age related; in younger males musth lasted from one day to several weeks, while among older individuals musth periods were several months in duration (African: this paper; Asian: JAINUDEEN *et al.*, 1972a).

e. *The recurrence of musth periods.*

An annual periodicity was observed in the timing of musth among individuals of both species although members of populations were not in synchrony (African: this paper; EISENBERG *et al.*, 1971; JAINUDEEN *et al.*, 1972a). Irregularities in this pattern were observed among the younger males (African: this paper; Asian: JAINUDEEN *et al.*, 1972a) and those in poor condition (African: POOLE, unpublished data; Asian: JAINUDEEN, 1972a; GALE, 1974).

Some controversy has surrounded the suggestion that male African elephants exhibit musth. As recently as 1984 elephant biologists claimed that musth was a phenomenon "unique to Asian bull elephants" (RASMUSSEN *et al.*, 1984). As the present paper illustrates, musth does occur in African elephants and appears to be similar to the phenomenon in Asian elephants in physical and behavioral characteristics as well as temporal patterning. The only significant difference between the two species appears to be that Asian elephants experience first musth at an earlier age than do African elephants.

However, many of the data reported on the age distribution of musth in Asian elephants were collected from captive animals. Among free-ranging African elephants, POOLE (1982; in press) found that high ranking males were able to "force" lower ranking males out of musth through repeated threats. In addition, the temporal occurrence of inter-musth bouts in low ranking males and their coincidence with periods of association with high ranking musth males suggests that higher ranking males were able to suppress musth in lower ranking males (POOLE, 1982; in press). It seems reasonable, therefore, to suggest that the age difference observed in the first onset of musth could reflect both differences in nutrition and the intensity of dominance relationships between free-ranging and domesticated elephants, rather than a genus difference. There are few adult male African elephants in captivity, but reports suggest males in their teens showing signs of musth (EISENBERG, pers. comm.).

Finally, I have been unable to find any report of musth rumbles in Asian elephants. I suspect, however, that a vocalization associated with musth exists.

3. Musth, male-male competition and female choice.

In Amboseli, males in musth were more successful at guarding estrous females and obtaining matings than were non-musth males (POOLE, 1982). The increased reproductive success of musth males was primarily due to their enhanced ability to compete with rival males although benefits due to female preference were also apparent (POOLE, 1982; Moss, 1983).

Males in musth had higher levels of urinary testosterone concentrations and exhibited higher rates of aggression than did either sexually active or sexually inactive non-musth males (POOLE, 1982; POOLE *et al.*, 1984; this paper). During musth, males increased in dominance and ranked above larger non-musth males (POOLE, 1982 and in press). Males

retreated from a musth male at a greater distance than they did from the same threat given by an equally sized non-musth male (POOLE, in press). For these reasons males in musth were more successful at gaining access to estrous females than were non-musth males. Females in estrus purposely outrun younger non-musth males (Moss, 1983) and were only observed to solicit guarding from, and maintain proximity to, males in musth (POOLE, 1982). Thus, although non-musth males can and do mate, their success during the peak of estrus is severely restricted by the presence of a musth male and by female preferences for musth males.

4. Possible functions of some musth signals.

Must can be viewed as a rutting period. Like other rutting mammals, male elephants advertise their state and their location by marking and by vocalizing. Unlike most other rutting species, however, the musth periods of males are asynchronous. Musth males rank above non-musth males and the unusual temporal patterning of musth means that a male's rank and fighting ability relative to another may change rapidly (POOLE, in press). Since escalation is dangerous, selection should favor males whose signalling honestly reflects their changing fighting ability as well as males who are able to assess these signals accurately (see CLUTTON-BROCK & ALBON, 1979). Thus, we should expect to find signals associated with musth which not only announce identity (and therefore body size) but also reflect changing body condition and possibly testosterone levels.

The urine trails left by males in musth are carefully inspected by females and by other musth and non-musth males (POOLE, unpublished data). Females presented with soil soaked with urine from a musth male will often stop, test the soil and sometimes vocalize loudly. Preliminary data suggest that the response of musth males to urine from another musth male depends on whether the urine is from a higher or lower ranking elephant.

Males in musth mark trees and other vegetation with secretion from the temporal glands. BUSS *et al.* (1976) found that the temporal gland secretion collected from elephants showed individual differences in cholestorol levels and suggested that the secretion may function in individual recognition. RASMUSSEN *et al.* (1984) found that secretion from the temporal glands of Asian musth males contained extremely high levels of testosterone.

The ear wave, observed during aggressive interactions and when a male was musth rumbling, may function to waft the scent of the temporal gland secretion towards rival males. It is also possible that males use ear waving to modulate the sound of their musth rumbles. During the trunk to head movement, males pass the trunk over the temporal glands and by doing so may collect some secretion on the hairs and grooves of the trunk. As the elephant walks along some of this secretion may then contact vegetation leaving a scent trail for other elephants.

In addition to these olfactory signals, males may be announcing their sexual state, body size (MORTON, 1977), identity, location and possibly their activity by vocalizing. That males in musth vocalized most often when they were alone suggests that these sounds were used in communication over long distances. The loud, very low frequency sounds made by elephants are ideal for long distance propagation (PAYNE *et al.*, 1986; POOLE *et al.*, in prep.). Musth rumbles had fundamental frequencies as low as 14 Hz with sound pressure levels of up to 108 dB, suggesting that males may have been communicating with other elephants over several kilometers.

Musth males in association with females vocalized significantly less frequently than when they were alone, while males who were guarding, or in association with, an estrous female vocalized even less often. Since females often responded to mush rumbles with loud low frequency calls and males were frequently seen listening after rumbling, males may musth rumble to locate females (POOLE *et al.*, in prep.).

Data showing that younger, smaller musth males vocalized significantly less often than older, larger males suggest that smaller elephants may have, on occasion, been trying to avoid detection. However, since young males were not always silent, there must, presumably, have been some benefits afforded to them by calling (see DAVIES & HALLIDAY, 1978). By rumbling a young male may still deter males lower ranking than himself (all non-musth males and musth males who are either smaller or who are in poorer condition) and advertizes his condition to potentially receptive females.

Summary

1. The physical and behavioral characteristics and the temporal patterning of musth were studied over a ten-year period in a free-ranging population of African elephants.
2. Males spent more time in association with females during musth than during non-musth periods.
3. Males were more aggressive during their musth periods than during non-musth.
4. The occurrence and duration of musth were age-related: no male under 24 years

was seen in musth; bouts of must among younger individuals were short and sporadic, while older males experienced longer more predictable periods of musth on an annual basis.

5. Although males in musth were observed year-round, the frequency of musth males was highest during and following the two rainy seasons and, in general, good rainfall years had higher frequencies of males in musth than did poor rainfall years.

6. The number of males in musth per month correlated closely with the number of females observed in estrus. However, since the period of estrus lasts only four to six days (Moss, 1983), while musth may last several months, the onset of musth was not necessarily triggered by the onset of estrus in a particular female.

7. The musth periods of different males were asynchronous and each male came into musth at a specific time of year. This period was relatively consistent from one year to the next, particularly among the older males.

8. Males in musth advertised their heightened sexual and aggressive state through visual and olfactory signals and by vocalizing. It is suggested that these signals function to announce identity, condition and location to both rival males and to potentially receptive females.

9. The physical and behavioral characteristics and temporal patterning of musth in African and Asian elephants are compared and found to be remarkably similar.

10. The physical and behavioral manifestations of musth in elephants are similar to those described for other male mammals during rut. Since estrus in female elephants is less clumped relative to most ungulates, male elephants have a different temporal pattern of rutting. Although the musth periods of male elephants are asynchronous the phenomenon can functionally be considered a rutting period.

References

ALTMANN, J. (1974). Observational study of behavior: sampling methods. — Behaviour 49, p. 227-267.

BARNES, R. F. W. (1982). Mate-searching behaviour of elephant bulls in a semi-arid environment. — Anim. Behav. 30, p. 1217-1223.

BUSS, I. O. (1961). Some observations of food habits and behavior of the African elephant. — J. Wildl. Mgmt 25, p. 131-148.

——, RASMUSSEN, L. E. & SMUTS, G. L. (1976). The role of stress and individual recognition in the function of the African elephant's temporal gland. — Mammalia 40, p. 437-451.

CLUTTON-BROCK, T. H. & ALBON, S. D. (1979). The roaring of red deer and the evolution of honest advertizement. — Behaviour 69, p. 145-170.

COBLENTZ, B. (1976). Functions of scent urination in ungulates with special reference to feral goats. — Am. Nat. 110, p. 549-557.

CROZE, H. (1974). The Seronera bull problem. 1. The elephants. — E. Afr. Wildl. J. 12, p. 29-47.

DARWIN, C. (1871). The descent of man and selection in relation to sex. — 2nd Edition. A. L. Burt Company, New York.

DAVIES, N. B. & HALLIDAY, T. R. (1978). Deep croaks and fighting assessment in toads, *Bufo bufo*. — Nature 391, p. 56-58.

DOUGLAS-HAMILTON, I. (1972). On the ecology and behavior of the African elephant. — D. Phil. Thesis, University of Oxford.

ELKE SCHEURMANN, G. VON & JAINUDEEN, M. R. (1972). "Musth" beim Asiatischen Elefanten, *Elephas maximus*. — Zool. Garten N.F., Leipzig 42, p. 131-142.

EISENBERG, J. F. & LOCKHART, M. (1972). An ecological reconnaisance of Wildpattu National Park. — Smithsonian Cont. Zool. 101, p. 1-117.

——, McKay, G. M. & Jainudeen, M. R. (1971). Reproductive behavior of the Asiatic elephant (*Elephas maximus* L.). — Behaviour 38, p. 193-225.

Espmark, Y. (1964). Rutting behavior in reindeer (*Rangifer tarandus* L.). — Anim. Behav. 12, p. 159-163.

Evans, G. H. (1901). A treatise on elephants. — Government Printing, Burma.

Fernando, S. D. A., Jayasinghe, J. B. & Panabokke, R. G. (1963). A study of the temporal gland in an Asiatic elephant (*Elephas maximus*). — Ceylon Vet. J. 11, p. 108-111.

Fraser, A. F. (1980). Farm animal behavior. — 2nd edition. Bailliere Tindall, London.

Gale, U. T. (1974). Burmese timber elephant. — Trade Corporation Merchant Sheet, Rangoon, Burma.

Geist, V. (1964). On the rutting behavior of the mountain goat. — J. Mammal. 45, p. 551-568.

—— (1971). Mountain sheep: A study in behavior and evolution. — University of Chicago Press, Chicago.

Hall-Martin, A. J. & Walt, L. A. van der (1984). Plasma testosterone levels in relation to musth in the male African elephant. — Koedoe 27, p. 147-149.

Hanks, J. (1969). Seasonal breeding of the African elephant in Zambia. — E. Afr. Wildl. J. 7, 167.

—— (1973). Reproduction in the male African elephant in the Luangwa valley, Zambia. — J. S. Afr. Wildl. Mgmt Ass. 3, p. 31-39.

—— (1979). A struggle for survival. — Country Life Books, London.

Heffner, R., Heffner, H. & Stichman, N. (1982). Role of the elephant pinna in sound location. — Anim. Behav. 30, p. 628-630.

Hillman, J. C. (1976). The ecology and behaviour of free-ranging eland (*Taurotragus oryx* Pallus) in Kenya. — Ph.D. thesis, University of Nairobi.

Howard, JoGayle, Bush, M., Vos, V. de & Wildt, D. E. (1984). Electroejaculation, semen characteristics and serum testosterone concentrations of free-ranging African elephants, *Loxodonta africana*. — J. Reprod. Fert. 72, p. 187-195.

Jainudeen, M. R., Katongole, C. B. & Short, R. V. (1972b). Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant, *Elephas maximus*. — J. Reprod. Fert. 29, p. 99-103.

——, McKay, G. M. & Eisenberg, J. F. (1972a). Observations on musth in the domesticated Asiatic elephant. — Mammalia 36, p. 247-261.

Kurt, F. (1974). Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. — In: The behaviour of ungulates and its relation to management (Geist, V. & Walther, F., eds). IUCN New Series No. 24, p. 618-634.

Laws, R. M. (1966). Age criteria for the African elephant, *Loxodonta a. africana*. — E. Afr. Wildl. J. 4, p. 1-37.

—— (1969). Aspects of reproduction in the African elephant, *Loxodonta africana*. — J. Reprod. Fert. Suppl. 6, p. 193-217.

—— & Parker, I. S. C. (1968). Recent studies on elephant populations in East Africa. — Symp. Zool. Soc. London 21, p. 319-359.

——, —— & Johnston, R. C. B. (1975). Elephants and their habitats: The ecology of elephants in North Bunyoro, Uganda. — Oxford: Clarendon Press.

Lee, P. C. & Moss, C. J. (1986). Early maternal investment in male and female African elephant calves. — Behav. Ecol. Sociobiol. 18, p.353-361.

Lent, P. C. (1965). Rutting behavior of a barren-ground caribou population. — Anim. Behav. 13, p. 259-264.

Lincoln, G. A. (1971). The seasonal reproductive changes in red deer stags (*Cervus elaphus*). — J. Zool. 163, p. 105-123.

——, Guinness, F. E. & Short, R. V. (1972). The way in which testosterone controls

the social and sexual behavior of the red deer stag (*Cervus elaphus*). — Horm. Behav. 3, p. 375-396.

McCULLOUGH, D. R. (1969). The Tule elk: Its history, behavior and ecology. — University of California Publ. in Zoology, Number 88, Berkeley.

McKAY, G. M. (1973). The ecology and behavior of the Asiatic elephant in southeastern Ceylon. — Smithsonian Contri. Zool. 125, p. 1-113.

MOORE, G. W. & MARCHINTON, R. L. (1974). Marking behavior and its social function in white-tailed deer. — In: The behaviour of ungulates and its relation to management (GEIST, V. & WALTHER, F, eds). IUCN New Series No. 24, p. 447-456.

MORTON, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. — Amer. Natur. 111, p. 855-869.

Moss, C. J. (1983). Oestrous behaviour and female choice in the African elephant. — Behaviour 86, p. 167-196.

—— & POOLE, J. H. (1983). Relationships and social structure in African elephants. — In: Primate social relationships: An integrated approach (HINDE, R. A., ed.). Blackwell Scientific Publications, Oxford. p. 315-325.

MÜLLER-SCHWARZE, D. (1971). Pheromones in black-tailed deer (*Odocoileus hemionus columbianus*). — Anim. Behav. 19, p. 141-152.

OSMAN-HILL, W. C. (1953). The reproduction of the African elephant. — In: The elephant in East Central Africa - A monograph (WARD, R., ed.), pp. 61-67. Rowland Ward Ltd. London.

PAYNE, K., LANGBAUER, W. & THOMAS, E. (1986). Infrasonic calls of the Asian elephant (*Elephas maximus*). — Behav. Ecol. Sociobiol. 18, p. 297-301.

PERRY, J. S. (1953). The reproduction of the African elephant, *Loxodonta africana*. — Phil. Trans. Roy. Soc. B 237, p. 93-147.

POOLE, J. H. (1982). Musth and male-male competition in the African elephant. — Ph.D. Thesis, University of Cambridge.

—— & Moss, C. J. (1981). Musth in the African elephant, *Loxodonta africana*. — Nature 292, p. 830-831.

——, KASMAN, L. H., RAMSAY, E. C. & LASLEY, B. L. (1984). Musth and urinary testosterone concentrations in the African elephant (*Loxodonta africana*). — J. Reprod. Fert. 70, p. 255-260.

—— (in press). Honest advertisement of intent: the aggressive state of musth in African elephants. — Anim. Behav.

RASMUSSEN, L. E., BUSS, I. O., HESS, D. L. & SCHMIDT, M. J. (1984). Testosterone and dihydrotestosterone concentrations in elephant serum and temporal gland secretions. — Bio. Reprod. 30, p. 352-362.

SANDERSON, G. P. (1882). Thirteen years among the wild beasts of India. — W. H. Allan, London.

SHORT, R. V. (1966). Oestrous behaviour, ovulation and the formation of the corpus luteum in the African elephant (*Loxodonta africana*). — E. Afr. Wildl. J. 4, p. 56-68.

——, MANN, T. & HAY, M. F. (1967). Male reproductive organs of the African elephant, *Loxodonta africana*. — J. Reprod. Fert. 13, p. 517-536.

SIKES, S. K. (1971). The natural history of the African Elephant. — Weidenfeld and Nicholson, London.

WEMMER, C. & MURTAUGH, J. (1980). Olfactory aspects of rutting behavior in the Bactrian camel (*Camelus bactrianus ferus*). — In: Chemical signals (MÜLLER-SCHWARZE, D. & SILVERSTEIN, R. M., eds). p. 107-124. Plenum Press, New York and London.

WESTERN, D. & LINDSAY, W. K. (1984). Seasonal herd dynamics of a savanna elephant population. — Afr. J. Ecol. 22, p. 229-244.

——, Moss, C. & GEORGIADIS, N. (1983). Age estimation and population age structure of elephants from footprint dimensions. — J. Wildl. Mgmt 47, p. 1192-1197.

WHEELER, J. W., RASMUSSEN, L. E., AYORINDE, F., BUSS, I. O. & SMUTS, G. L. (1982). Constituents of temporal gland secretion of the African elephant, *Loxodonta africana*. — J. Chem. Ecol. 8, p. 821-835.

Resumen

1. Las características físicas y conductuales así como los patrones temporales de frenesí fueron estudiados por un período de diez años en una población libre de elefantes africanos.

2. Los machos permanecieron más tiempo asociados con hembras durante periodas de frenesí que durante períodos de no frenesí.

3. Los machos fueron más agresivos durante sus períodos de frenesí que en cualquier otro período.

4. La presencia y duración de la etapa de frenesí estuvieron asociados con la edad: mingún macho menor de 24 años fue visto en frenesí; ataques de frenesí fueron cortos y esporádicos en individuos jóvenes, mientras que los machos más viejos tuvieron períodos más largos y predecibles de frenesí en patrones anuales.

5. Aunque se observaron machos en frenesí durante todos los años, la frecuencia de machos en frenesí alcanzó su máximo en las 2 estaciones de lluvia y, en general, los años más lluviosos estuvieron asociados con altas frecuencias de machos en frenesí.

6. El número de machos en frenesí por mes fue altamente correlacionado con el número de hembras observadas en etapa estral. Sin embargo, dado que el período de estrus dura solo de 4 a 6 días (Moss, 1983), mientras que el frenesí puede durar varios meses, la aparición de frenesí no fue disparado necesariamente por la presencia de estro en una hembra particular.

7. Los períodos de frenesí de distintos machos fueron no sincrónicos y cada macho entró en frenesí a un tiempo específico del año. Este período fue relativamente consistente año con año, particularmente entre los machos más viejos.

8. Los machos en frenesí anunciaban su estado sexual y de agresividad al través de señales visuales y olfatorias así como por vocalizaciones. Se sugiere que estas señales anuncian identidad, condición y localización tanto de machos rivales como de hembras potencialmente receptivas.

9. Se compararon las características físicas y conductuales así como los patrones temporales de frenesí entre elefantes africanos y asiáticos y se encontraron muy similares.

10. Las manifestaciones físicas y conductuales de frenesí en elefantes son similares a las descritas en otros machos mamíferos durante períodos de brama. Dado que el estro en elefantes hembra es menos agregado que en la mayoría de los ungulados, los elefantes machos tienen un patrón temporal distinto del celo. Aunque los períodos de frenesí de elefantes macho no son sincrónicos el fenómeno puede ser considerado como un período de celo.