RESEARCH

Changes in elephant demography, reproduction and group structure in Tsavo East National Park (1966–1994)

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Abstract

A study of 557 individually recognized African elephants *(Loxodonta africana)* in Tsavo East National Park, Kenya, aimed to determine demography, reproductive status and group dynamics and to relate them to poaching, the environment and past research findings. More than half of the population number sampled in 1994 was > 20 years old. The age classes ≤ 20 years were skewed in favour of males while females dominated the > 21-year age classes with few males > 35 years old. No known female younger than 15 years was accompanied by a newborn, and the average intercalf interval was 5 years. Males in musth were observed year-round. Mean group size was large, with aggregations of over 50 individuals sighted during the dry season when resources were limited. Almost half of the female groups surveyed were missing an older matriarch or contained calves and juveniles that were not the offspring of the females present. The skewed sex structure, increase in group size and fragmented family groups were attributed to the disruptions that poaching had caused. The recovery of the elephant social structure and calf survival will depend on there being no poaching in the future.

Résumé

Une étude de 557 éléphants d'Afrique (*Loxodonta africana*) connus individuellement a été menée au Parc National de Tsavo Est, au Kenya, afin de déterminer leur démographie, le statut de leur reproduction et la dynamique des groupes et de les relier au braconnage, à l'environnement et aux recherches antérieures. Plus de la moitié de la population étudiée en 1994 avait moins de vingt ans. Les classes d'âge < ou = à 20 ans comprenaient plus de mâles alors que les femelles dominaient les classes d'âge > à 20 ans, où peu de mâles avaient plus de 35 ans. On n'a vu aucune femelle connue de moins de 15 ans suitée d'un nouveau-né, et l'intervalle entre deux mises-bas était de 5 ans. On a pu observer des mâles en rut tout au long de l'année. La taille moyenne des groupes était importante, avec des rassemblements de plus de 50 individus observés en saison sèche, lorsque les ressources étaient limitées. Près de la moitié des groupes de femelles étudiés ne possédaient pas de matriarche plus âgée, ou comprenaient des petits et des juvéniles qui n'étaient pas la progéniture des femelles présentes. On a attribué les déséquilibres de sex-ratio, l'augmentation de la taille des groupes et la fragmentation des groupes familiaux aux perturbations occasionnées par le braconnage. Le rétablissement de la structure sociale des éléphants et la survie des petits dépendront de l'existence ou non de braconnage dans le futur.

Introduction

The Tsavo elephant population within the vast Tsavo ecosystem (40,000 km^2) has suffered from environmental pressures of a severe drought in the 1970s and subsequent intense pressures of poaching during the 1980s.

The 1970–71 drought led to the deaths of over 5000 elephants, primarily reproductive females and young individuals (Corfield 1973). During this time poachers took advantage of these deaths to collect the tusks. As the number of deaths from the drought decreased, poachers began shooting the remaining elephants. Between 1976 and 1989 the Tsavo elephant population was reduced by almost 80%, from approximately 28,000 in 1969 to about 5000 in 1988 (Douglas-Hamilton *et al.* unpubl.). In 1994, an aerial count estimated the population at about 7000 individuals. Whether this reflected an actual increase or increased accuracy in survey techniques is difficult to ascertain.

The first study in Tsavo of elephant population dynamics was in 1966; it was of culled animals, before the drought and before large-scale poaching (Laws 1966, 1969). In 1972 and 1974, following the drought and again before intense poaching, data were collected on age structure and group dynamics (Leuthold 1976a, b). During the poaching era of the 1980s, aerial surveys were conducted to determine age structure (Ottichilo 1986). In 1989 a four-day road survey was conducted to determine the effects poaching had had on the elephant population (Poole unpubl., Poole and Thomsen 1989). Although the research techniques between these elephant studies varied (table 1), they offer an overview of the changes in the Tsavo elephant dynamics so that visual comparisons can be made. The Amboseli data from south-western Kenya represent an undisturbed population for comparative purposes (Lee and Moss 1986, Moss 1988, Poole unpubl., Poole and Thomsen 1989).

This study presents new baseline data for 1989 to 1994, following the drought and the end of intense poaching and after a prolonged absence of research on the Tsavo elephant population of both individuals and groups. These population categories will be used for future studies in Tsavo to monitor trends and to provide comparisons for other elephant populations.

Study area

The study area (4200 km^2) was in the semi-arid Tsavo East National Park, Kenya, south of the Galana River. Rainfall is variable and inconsistent with an annual average of 270–740 mm between March–April and November–December. The vegetation has changed considerably over the past 30 years. During the 1960s and 1970s, the woodlands were dominated by *Commiphora* spp. and *Acacia* spp. but were altered to open grassland by the influence of fire and large numbers of elephants immigrating into the protected park (Glover 1963, Leuthold 1977). Since that time, the elephant population has decreased substantially and the woody vegetation is beginning to recover (Wijngaarden 1985, Leuthold 1996).

Study animals

A photographic identification file was started in 1989 using standard field techniques, noting ear patterns, tusk shape and physical features or anomalies (Douglas-Hamilton unpubl., Moss 1988). The individually recognized elephants (n = 557; 313 females, 244 males) represented 20.6% of the elephants that could potentially be studied in Tsavo East National Park.

The tusk records from Tsavo East Park headquarters and the Community Wildlife Service between January 1993 and March 1995 were reviewed to record mortality and, where possible, cause of death. Standard techniques regarding the shape and size of tusks were employed to estimate sex and age distribution (Laws 1966, Elder 1970, Corfield 1973, Pilgram and Western 1986).

Field methods

Scan and focal sampling (Altmann 1974) were used at each sighting of one or a group of elephants and during waterhole surveys. The following data were collected: date, time, location, individual identification, group structure and size, age and sex structure of the group, activity, and the percentage of greenness of the vegetation. Identification photographs were also taken. Observations were made from a vehicle on park

Table 1. Summary of the data on Tsavo elephant population dynamics from 1966 to the current study completed in 1994

	Predrought and prepoaching 1966	Postdrought and poaching 1974	Poaching 1989	Postpoaching 1994	Natural population Amboseli 1989
Demography					
% >15 years old	49.5	57.5	43.5	56.4	49.7
% females	53.2		81.7	66.9	59.7
% males	46.8		18.3	33.1	40.3
% tuskless				5.5	3.0
Reproduction					
age at first conception	11.7 years (± 0.9)			11–15 years (33%)	11–15 years (50%)
% females > 11 years old	83.8		95.0	78.8	77.9
% males > 25 years old	15.2		5.0	21.2	22.1
mean calving interval (yr)	6.8			5.0 (± 1.8)	4.6
Group dynamics					
mean group size	8.2	6.79 (± 5.3)	9 median	22.9 (± 15.1)	19 median
mean bull group size	2.43			2.5 (± 0.9)	3 median
range in bull group size	2–14			2–22	2–11
Family structure					
average family size	6.0			7.8 (± 0.4)	12
% of fragmented families			31.2	45.3	6.4
ratio female (> 20 yr) to calves (0–5 yr)	1:1.3		1:1.1	1:0.7	1:1.1
Total population estimate in national park (year)	15 038 (1965)	22 174 (1973)	4327 (1988)	5119 (1991)	708 (1989)
method (*n*)	culled (296)	aerial (368)	road survey (503)	known individuals, road surveys (557)	known individuals (708)

Data for the Amboseli elephants represent a relatively undisturbed and natural elephant population. Predrought, prepoaching 1966 (Laws 1966, 1969), postdrought 1974 (Leuthold 1976a, b), poaching 1989 (Poole 1989), postpoaching 1994 (McKnight 1996) and the natural population—Amboseli (Lee and Moss 1986, Moss 1988, Poole 1989, Poole and Thomsen 1989), Tsavo National Park elephant population estimates (Douglas-Hamilton et al. 1994).

roads. All roads in the study area were covered by vehicle once a month. However, areas where elephants were known to concentrate were visited frequently to monitor known individuals and to add to the photographic identification file.

Determining age

Photographic shoulder height measurements and comparison of relative body size and shape between individuals were used to estimate ages (Douglas-Hamilton unpubl., Lee and Moss 1995, McKnight unpubl.). In addition, footprint-length measurements (Western *et al.* 1983) were taken with a minimum of three clear footprints for each individual. Finally, shoulder height and footprint length measurements were correlated in a linear regression to establish age classes. Age classes were divided into 5-year intervals: newborns (1–3 weeks; McKnight 1992), 0–5, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35, 36–40, 41–45 and > 45 years.

Reproductive status

FEMALE SEXUAL MATURITY

After approximately nine months of pregnancy, female elephants start to develop mammary glands (Moss 1988). Recognized young females were monitored for changes in the development of their mammary glands to determine age of first conception. Three classifications were used to describe the stages of mammary gland development:

- *No swelling*—torso flat, no loose skin (that is, no development past or present), not pregnant or lactating
- *Swollen or full*—distended glands, suggesting pregnancy or lactation
- *Shrunken*—area around mammary glands consisting of loose folds of skin with no swelling (Poole unpubl.)

INTERVAL

The time between the birth date of one calf and the birth of the next for recognized mothers was monitored. Estimation of the ages for successive calves born to the same female was determined by newborn date of birth, date the tusks became visible (2 1/2 years; Laws 1966) and the calf's height relative to that of siblings.

Group dynamics

GROUP COMPOSITION

During road surveys members of a group that were feeding, resting or moving as a coordinated unit were recorded into one of the following group structures.

- *Female group*—one or more adult or subadult females and calves, with no males > 20 years old
- *Mixed group*—a female group with one or more males > 20 years old
- *Bull group*—two or more males within 60 m of each other in the absence of females
- *Lone bull*—a single male elephant, no other elephants in sight

FAMILY STRUCTURE

To decrease the possible biases of known family units, a dry-season waterhole survey was conducted. As a female group of elephants moved from the bush into a clearing towards a waterhole, the sex and estimated age of each individual were recorded. Recognized family units were noted and ear sketches of unknown individuals were made to avoid double counting. Young males older than 10 were not counted, as they tended to move from group to group at the waterhole (group structure modified from Poole unpubl.). Families were categorized as follows.

- *Intact family a) Old:* At least one female in the group was > 30 years old with calves, juveniles and subadult females, all of an age to belong appropriately to the females present; *b) Young:* A group with one or more females that were all ≤ 30 years old, with offspring of the appropriate age to indicate relatedness.
- *Fragmented family:* The calves and juveniles within a female group the same age or too close in age to be the offspring of the females present; for example, young individuals < 2 years apart were considered not to be siblings. Three classes were used. *a) Old:* One or more females > 30 years; *b) Young:* One or more females ≤ 30 years old; *c)* All individuals in the female group ≤ 20 years old.

Results

Shoulder height and footprint-length measurements

Shoulder height (*SH*) and footprint length measurements in centimetres were collected for 43 individuals, ranging in age from newborns ($n = 4$) to calves whose tusks were visible (2 1/2 years old; $n = 5$) and a further 34 individuals of progressively larger body size. A highly significant correlation was found between the shoulder height and the footprint-length measurement from each individual. For females ($n = 24$) $SH = (-10.635 + 5.913)$foot, $r^2 = 0.91$, $n = 24$, $p < 0.001$. For males ($n = 19$) $SH = (-4.9124 + 6.150)$foot, $r^2 = 0.88$, $n = 19$, $p < 0.001$. This correlation, divided into 5-year age intervals, was used as a guide to estimate ages for additional individuals sighted (fig. 1).

Demography

In contrast to previous results on Tsavo elephants and Amboseli data, there were more males than females (ratio of 1.4:1) in each of the four age classes between birth and 20 years old. The reverse was true of the > 20-year age classes, 1 male to 2.4 females. Twenty-four individuals (5.5%) were tuskless, including two

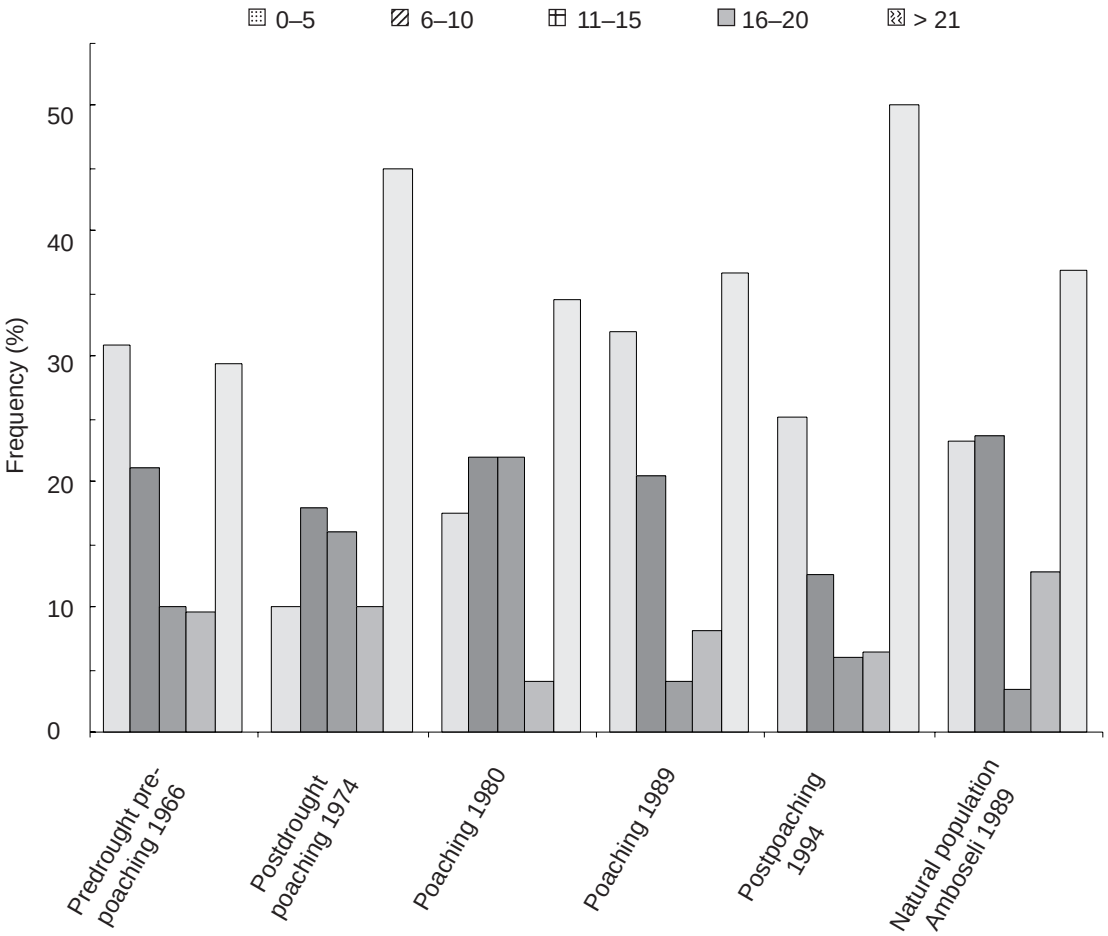

Figure 1. Frequency distribution of the changes in the age structure of Tsavo East National Park counts from 1966 to 1994 and the natural population of Amboseli. Poaching 1980 data from Ottichilo; other references listed under table 1.

males older than 25 years. Nine individuals were missing the tip or a portion of their trunk.

Between January 1993 and December 1994, 43 deaths were recorded. Over half of the individuals were > 20 years old (11 females, 10 males, 6 of unknown sex). Six individuals had been poached, tusks cut away (3 females, 2 males and 1 of unknown sex). Eight males were shot on control and five females > 26 years old were found dead of unknown causes (tusks intact). Six calves (birth to 5 years) of known females were missing and presumed dead. The mortality rate was most likely higher than recorded if any of the 12 adult females that died had an unweaned offspring. The skeletal remains of a very young calf are difficult to detect because they are scattered by scavengers, they decompose quickly, and there are no tusks to measure.

Reproductive status

FEMALES

None of the females in the 6–10-year age class (n = 29) showed mammary gland development. Two-thirds of the females in the 11–15-year age class (n = 9) showed no swelling and none had offspring with them. Five of the 13 females in the 16–20-year age class showed no mammary gland development. Two of the seven with swollen glands in this age class had a calf of less than 1 year while the other five appeared pregnant. Three of the females that were > 25 years old had shrunken mammary glands. This suggests that 1) the pregnancy was in an early stage when development of the mammary gland was not yet visible, 2) the foetus had been aborted, 3) the calf had died, or 4) there was a long intercalf interval.

POTENTIAL BREEDING SEX RATIO

The age designated for a potential breeding female was calculated from the assessment of mammary gland development. A male ≥ 25 years old was considered socially mature and defined as a potential breeding male (Poole 1987). Based on the mammary gland development data, the ratio of potential breeding adults (females > 15 years old, males > 25 years old) of recognized elephants was 3.6:1.

CALVING INTERVAL

The estimated interval between the birth of one calf and the next for 74 known mothers was 5.0 (± 1.8) years. There were no 10–20-year-old females (n = 21) with more than one offspring with them. Two possible reasons for this are 1) their previous calf was a male that had left the family and become independent or 2) the calf had died.

Group dynamics

FREQUENCY OF AGGREGATION

Groups of 50 or more individuals (third quartile of group distribution) were defined as an aggregation (n = 92). Although there appeared to be wet-season peaks in aggregation size, there was no significant difference between aggregation during wet (n = 42) and dry (n = 50) months (x^2 = 3.14, df = 1, p > 0.10) (fig. 2). Aggregations of 50 or more elephants in months of little or no rainfall were not expected in an environment where resources are limited in the dry season, yet during relatively dry months large groups were sighted. It is likely that there were more aggregations during the rains, but they were difficult to find and see because of the poor visibility resulting from the abundance of vegetation and the fact that many groups moved outside the study area.

GROUP STRUCTURE

Female groups were significantly larger during wet months than during dry months (Kolmogorov-Smirnov x^2 = 6.08, df = 2, p < 0.02). Mixed groups were also significantly larger during wet months than dry months (K-S x^2 = 7.61, df = 2, p < 0.02). Conversely, bull groups were significantly larger during dry months than wet months (K-S x^2 = 17.82, df = 2, p < 0.001). There were significantly more groups of ≥ 5 bulls in dry months than wet months (x^2 = 17.78, df = 1, p < 0.001). Large groups ranging from 10 to 22 bulls were observed more frequently during dry months (n = 21) than during wet months (n = 3); combining all sightings of these groups during dry months, the mean group size was 16.2 bulls (± 3.64). During wet months, three groups with ≥ 10 bulls were

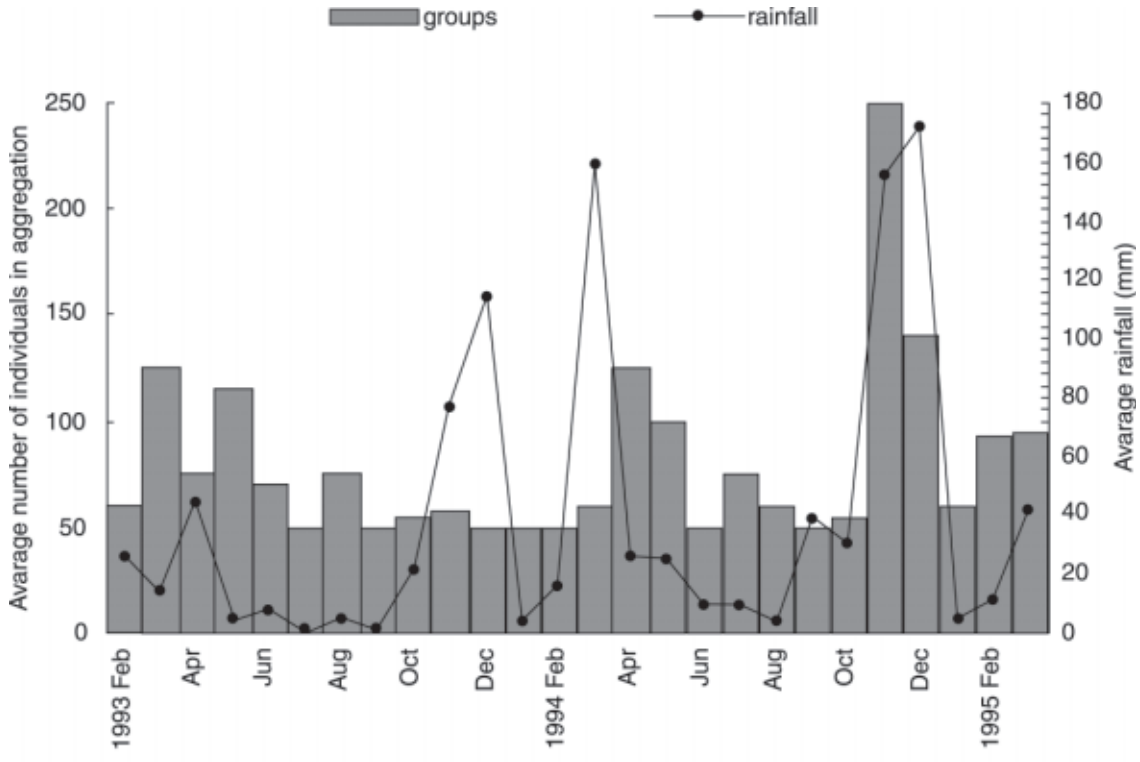

Figure 2. Average number of elephants in an aggregation of 50 or more individuals (n = 92) per month compared to monthly rainfall (average of 20 rainfall gauges) February 1993 to March 1995.

observed: 11,12, 20 bulls (mean group size 14.3 ± 4.93 SD). These large groups of bulls, which were observed feeding and travelling together, were generally all the same height, and thus close in age.

FAMILY STRUCTURE

Of the 106 discrete female groups recorded, the median group size was 6.0 with a range of 2–21 individuals (mean 7.8 ± 0.41). Almost half (45.3%) of the groups consisted of fragmented families, either lacking a female > 30 years old or a group with calves and juveniles that could not be the offspring of the females present. The difference between the 1989 and the 1994 fragmented family structure was not significant (32 groups, $x^2 = 1.98$, $df = 1$, $p > 0.20$, 31.2%, n = 10; Poole unpubl.).

Discussion

The results of this study provide new baseline data on the Tsavo elephant population following poaching and the long-term impact of the 1970s drought. The demographic survey results indicate a low proportion of individuals in the 16–20-year age class; this can be attributed to the effects of the 1970s drought. After the drought in 1974, there were almost three times as many adults as calves. In this study, there were twice as many adults as calves, suggesting calf survival is still below 1966 levels.

The sex ratio per age class was of particular interest. The ratio of more females to males in the older age classes would be expected, as poachers concentrate on bulls (Poole and Thomsen 1989). What is surprising is the ratio of males to females (1.4:1) in

the birth-to-20-year age classes, which is unlike other poached populations and the undisturbed population in Amboseli (see Poole unpubl. data and comparisons with other poached populations). There are two possible reasons for this unusual sex ratio. During the drought 'the mortality of females was consistently higher than for males' (Corfield 1973). This was attributed to strong maternal bonds and long postnatal care, which contributed to the high percentage of deaths among females because they were restricted by the distance they could travel in search of food (Corfield 1973).

The data in this study suggest that, in an effect similar to that of the drought, the social development and greater independence of juveniles and adolescent males may have helped them to survive the loss of older females to poachers. Secondly, mothers in Amboseli invested more in male calves than female calves (Lee and Moss 1986). This in part could explain the higher ratio of males to females in the younger age classes. The data suggest that young females are more vulnerable to the stresses of poaching (loss of matriarch, fragmentation of families) than are the young males and that female survival rates under these conditions were lower.

A further impact of poaching for ivory can be demonstrated by the percentage of tuskless individuals. The 5.5% identified tuskless elephants appears relatively low in comparison with other poached populations in national parks in East Africa: 7.8% in Meru, Kenya (Demmers and Bird unpubl.), 46.9% in Mikumi, Tanzania, and 38.0% in Queen Elizabeth, Uganda (Poole unpubl.). Nevertheless, the percentage in Tsavo is higher than the 3.0% in the protected population of Amboseli (Poole unpubl.). The six elephants killed by poachers between January 1993 and March 1995 were evidence that poaching was continuing in Tsavo. Furthermore, poachers who set snares for bush meat in and around the park continue to be a hazard for elephants. These snares are most likely the cause of damage to the tip of the trunk, as seen in nine individuals; this could indicate a problem that will need to be monitored.

The results of this study indicate that the majority of females attained first conception when about 15 years old, older than during the 1966 study (Laws 1969) and in a natural population (Amboseli; Poole unpubl.). Furthermore, the mean calving interval of 5.0 years was less than the 6.8-year interval during the 1966 Tsavo study and longer than the average in the Amboseli population of 3.5 years during wet years and 5.6 years in dry years (Lee and Moss 1986).

When adult male elephants live in a population well protected from poaching, the majority of musth bulls are > 30 years old and most of the mating is by bulls > 35 years (Poole 1987). Of the 14 Tsavo bulls observed in musth, 4 were relatively young males in the 21–25-year age class (similar to young Asian elephants; Sukumar 1989). During this study no two males were observed in musth at the same time in the same location, and no fighting between males in or out of musth was observed. The occurrence of young males in musth is most likely because of the low proportion of bulls > 35 years old. Most likely old (40+) and large Tsavo bulls will not have to compete for access to females in oestrus for many years to come. Long-term study on the reproductive behavioural patterns of the bulls in Tsavo will be needed to determine what role musth behaviour will play in a population with few older bulls.

Social organization studies during the prepoaching era in Tsavo (1967 and 1974) showed that the mean group size increased with rainfall and decreased during the dry season (Laws 1969, Leuthold 1976b). Postpoaching group size distribution for females and mixed groups was significantly larger during the wet season than during the dry season. However, the frequency of aggregation sightings year round and the increase in overall mean group make it appear that these large groups are forming as a response to the stress, harassment and lack of matriarchal leadership resulting from poaching in ways similar to other disturbed populations (Eltringham and Malpas 1980, Lewis 1986, Ruggiero 1990, Abe unpubl.).

The grouping patterns of adult males are of special interest, as they were the main targets of poachers. Tsavo males have historically been sighted in large aggregations of 20–35 individuals (Laws 1969). Even after intensive poaching, aggregations of bulls were still observed forming groups of up to 22 individuals in the dry months. The group-size distribution for bulls was significantly larger during dry months than wet months, similar to a study on bull groups in the Serengeti, Tanzania (Croze 1974).

The presence of fragmented female groups (45.3%) and the lack of old and experienced matriarchs in the population can be attributed to

poaching pressure. In the protected Amboseli population, the families were stable, led by a matriarch (median 41 years old) with several related adult females, and on average consisted of 10 members (Moss 1988). Mothers in Amboseli < 25 years old were not as successful at raising their calves as older mothers (Poole unpubl.).

With almost half of the family units fragmented, it is therefore not surprising that aggregations were sighted during the dry season as well as the wet season. These data suggest that young and inexperienced females as well as juveniles of both sexes have joined a group with an older female, possibly to gain from the knowledge that an older female would have about the resources within her environment and for security reasons.

Important conclusions of this study are the unusual ratio of males to females in the younger age classes and the apparently delayed age of first conception, both of which will need to be monitored to determine what effect these factors will have on the future age structure of the population.

The high frequency of fragmented family units is also cause for concern. The loss of the older members of the population to poaching influences all aspects of elephant social organization, with implications for future calf survival, group dynamics and reproductive potential. Even if Tsavo does not experience another severe drought, both biological and social recovery will be a long, slow process and will depend on there being no poaching.

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