POPULATION DYNAMICS OF THE AFRICAN ELEPHANT IN THE MKOMAZI GAME RESERVE TANZANIA, EAST AFRICA

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ABSTRACT

POPULATION DYNAMICS OF THE AFRICAN ELEPHANT
IN THE MKOMAZI GAME RESERVE
TANZANIA, EAST AFRICA

by Lawrence D. Harris

Observations on the temporal and structural dynamics of the African elephant (Loxodonta africana) population in the 1265 square mile thorn bush reserve are presented. Sixteen monthly aerial surveys and 377 counts along ground transects measured density changes; five sizes were used in analyzing age structure.

Two migratory populations, totaling about 2000 elephants, increased the rainy season densities to two to three times the dry season level. The eastern migratory population which inhabits the Mkomazi Reserve during the rainy season, moves northward across the Kenya border during the long dry season. The mean herd size of this population is over three times that of the western population and the animals seemed considerably more truculent. The western migratory population totaled about 500 and moved from the Mkomazi northward during the dry season into Tsavo National Park, Kenya.

Based on the size classification of 2001 elephants and a revised body growth curve, it was calculated that the population age structure comprised 8.6% young of the year; 9.1% aged 1-4 years; 10.2% 5-8 years old; 11.1% aged 9-15; and 60.6% which were 16 years and older. From these data it was estimated that infant mortality must approximate 30 per cent during the first year. After that, the rate evidently decreases until, according to age-at-death figures for 440 specimens reported from East African game sanctuaries, it reaches about one per cent per annum for the years 16 to about 45. Beyond age 45, mortality accelerates rapidly until by age 60 the rate is again nearly 30 per cent per year.

The calculated crude birth rate is 11.2 per cent per year. If, as believed, the female age of puberty is about nine years and the gestation period is 22 months, then the mean calving interval for the Mkomazi population is about four years. The greater herd size and the more truculent nature of the eastern population correlated with and is believed to be due to the less stable habitat and the greater interaction with humans and livestock there. Recommendations for the management of Mkomazi elephants are given.

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INTRODUCTION

Because of its size, longevity and numerous other biological traits, the African elephant (*Loxodonta africana*) is as intriguing for scientists as it is for laymen. It is a unique animal for scientific research.

Studies of elephants are important for various reasons. Their ability to alter their environment makes them one of the most important biological components of the eco-system wherever they exist in moderate to high numbers (Daling, 1960). Felling trees for browse, digging water holes in otherwise dry areas, and opening up dense thickets are but a few ways elephants affect the living conditions of other animals. Elephants are also a main attraction for the expanding East African safari industry and their conservation is of economic as well as esthetic value. Further, since elephants are the sole living representatives of a much larger group of extinct proboscideans, knowledge of the behavior and adaptations which have permitted their survival is of considerable scientific interest.

But serious local overpopulations of elephants resulting from severed migratory routes and restricted free ranges because of human settlement have created considerable problems in recent years (Priestley, 1962; Pienaar *et al.*, 1966). Habitat degredation from compressed populations is especially acute in several East African game sanctuaries (Petrides and Swank, 1958; Buechner and Dawkins, 1961; Glover, 1963; Lamprey *et al.*, 1967). Unfortunately, control operations are often hampered by political as well as economic considerations. Additional knowledge of elephant population dynamics and requirements is necessary before sound management and conservation policies can be initiated on the areas where these animals still exist.

Although Aristotle provided an anatomical description of the elephant as early as 300 B.C., his information was most probably second-hand and of questionable scientific value (Benedict, 1936). Most literature on the subject since that time suffers from similar defects. In 1936, Benedict published results of an exhaustive physiological study on captive Asian elephants (*Elephas maximus*). Although he assumes, "that what is reported . . . for the Indian elephant applies likewise to the African elephant," certainly wild animals of two different species do not have precisely the same physiological, morphological, reproductive or behavioral attributes.

Only during the last 20 years have field studies contributed significantly to our knowledge of wild African elephants. Throughout the nineteen fifties and early sixties, American Fulbright scientists conducted studies on elephant food habits, behavior and general ecology (c.f. Buss, 1961; Buss and Brooks, 1961; Buechner *et al*., 1963; Quick, 1965). Descriptions of population structure and dynamics were also published (Quick, 1963; Petrides and Swank, 1966), but these were hindered by the lack of suitable age determination techniques.

Intending to describe the dental characteristics and to develop an age determination technique, Morrison-Scott (1939, 1947) published some of the earliest observations on elephant dentition. But he was unable to establish a reliable formula even for identifying the several molars which succeed each other in this family (Sikes, 1966). Johnson and Buss (1965) attempted a direct correlation of age with molar development and wear. Their paper has since been revised (Krumrey and Buss, 1968). Sikes (1966, 1967) and Laws (1966) have presented similar correlations between molar development and age, and with their lucid photographs, charts, and descriptions it is possible now to approximate the age of collected specimens.

The purpose of this paper is to record and analyze the temporal and structural dynamics of a population of living, African elephants in light of recent age determination and reproductive studies. The herds investigated were located in the Mkomazi Game Reserve, Tanzania, East Africa, and the study was conducted there from late 1964 through mid 1967.

THE STUDY AREA

The Mkomazi Game Reserve is situated in northern Tanzania adjoining the Kenya border. It extends from within about 30 miles of the Indian Ocean to nearly 60 miles from Mount. Kilimanjaro (Fig. 1). Its total area of 1,265 square miles is mostly contained between 3°, 30' and 4°, 30' south longitude and 37°, 45' and 38°, 45' east latitude. The area is approximately 80 miles long and averages about 20 miles in width.

Foothills of the North Pare Mountains and the semi-arid Umba Steppe are the main physiographic features of the reserve. The slightly southeastward-sloping plain increases in elevation from 75 feet above sea level in the east to 2,500 feet in the northwest. With peaks reaching 5,000 feet, the mountain foothills and other hill masses comprise 10 per cent of the total area.

Because of topographic variation, the climate of different areas within the reserve is diverse. In accord with Chapman's Rule (Allee _et al_., 1949), the mean ambient temperature of the lower, eastern end is about 10°F greater than the higher western end. Recordings made during the study at a meteorological station at 3000 feet elevation in

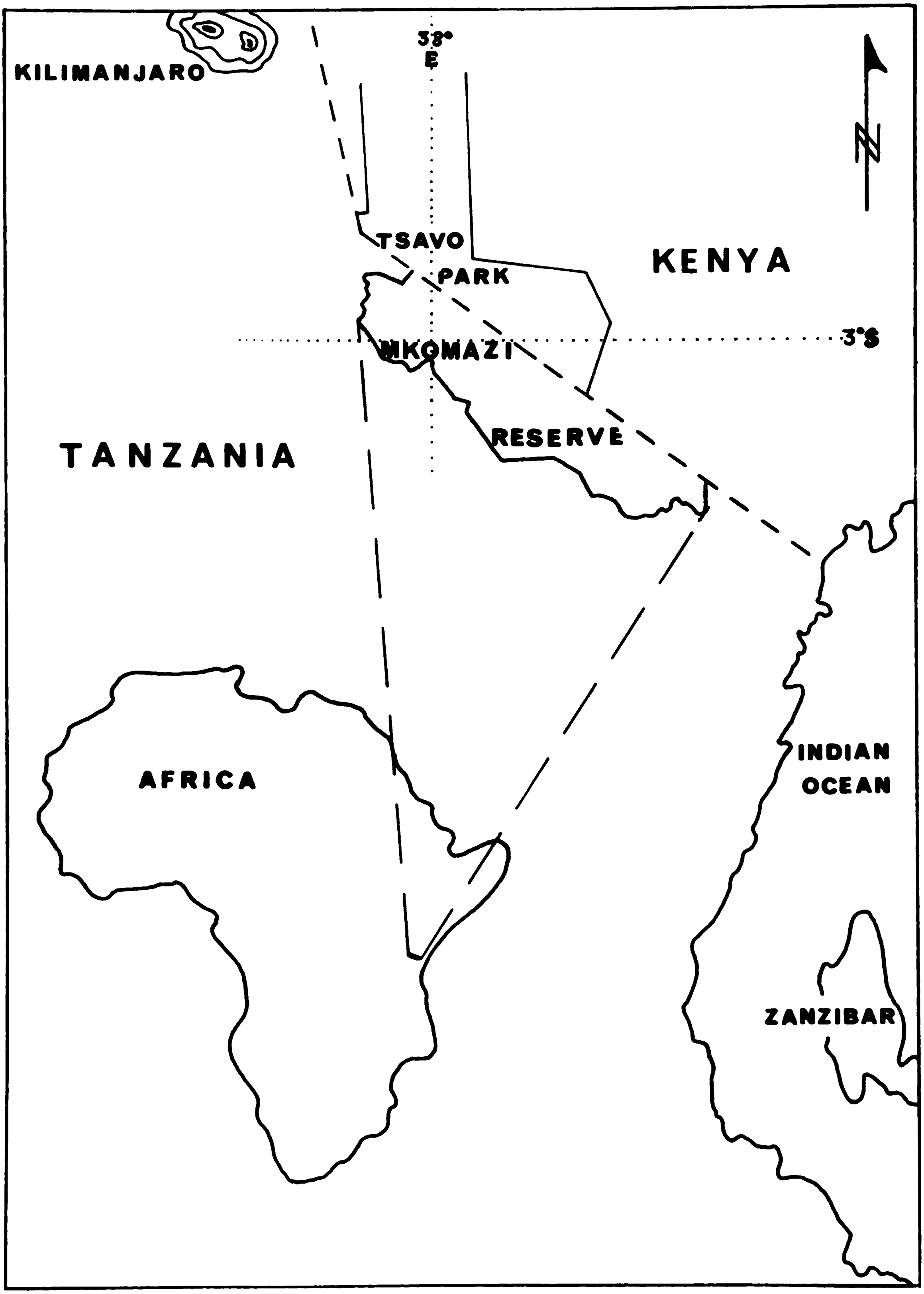


Fig. 1. The Mkomazi Game Reserve of northern Tanzania lies along the Kenya-Tanzania border between Mt. Kilimanjaro and the Indian Ocean.

the western section indicated maximum and minimum temperatures of 100°F and 49°F, respectively with a mean annual temperature of 74°F.

Rainfall varies along an east-west gradient, the eastern section receiving less than 15 inches annually and the western end approximately 22 inches. But extreme annual variation occurs and the hill masses receive higher rainfall than the surrounding plains. Most of the annual rain falls during a "long" rainy season from late February through April, but significant amounts also fall during the "short" rains of November and December. The period from June through September is usually one of severe dessication. Since temperature variation is slight compared to the dramatic precipitation patterns, rainfall is the dominant climatic factor. Permanent water sources are limited to a river forming the southeastern border and an artificial lake in the extreme northwestern corner of the reserve.

The most extensive vegetation type of the reserve is bushland dominated by shrubs and dwarf trees less than 20 feet in height. *Commiphora* and *Acacia* trees together with *Cassia*, *Cordia*, and *Grewia* bushes with crown coverage of 20 to 50 per cent dominate. Sparse clump grasses, predominantly of the genera *Chloris*, *Digitaria*, *Cenchris*, *Sporobolus*, and *Aristida* comprise the low ground cover.

In the western area of the reserve where rainfall averages 20 inches or more per year, the vegetation is mostly bushed and wooded grassland. The grasses, consisting of *Themeda triandra*, *Heteropogon contortus* and *Digitaria spp.*, are taller and denser than in the east, and the woody plants are more generally clear-boled. Several species of *Acacia* as well as *Commiphora schimperii*, *Platycephalum voense*, *Boscia salicifolia* and *Melia volkensii* are common.

Interspersed through both vegetation types and appearing as long narrow corridors, are grassed, heavy clay drainageways. Dry montane forests occur on most of the mountain tops above 3,500 feet elevation. The overstory trees of these forests (40 feet and taller) provide nearly complete cover, but scattered open glades and less densely crowned areas allow rank grasses and other understory plants to persist.

Seventy-seven wild animal species, including 20 ungulates and six large carnivores, are recorded for the reserve (Harris, 1967). But although the species diversity is quite high, overall densities are low and little species interaction with elephants was observed. Approximately 3000 cattle are allowed in the eastern half of the reserve and they undoubtedly compete with elephants for grazing.

STUDY TECHNIQUES

Ground Count Transects: In late 1964, I began residing in the Mkomazi Reserve where I initiated extensive studies and developmental projects. Since no roads were present and only about 25 miles of track existed, logistics were a problem. As a consequence, game-count transects had to be localized in the western section of the reserve (Fig. 2). Four of these transect routes were located in the mountainous areas and animals were counted while walking along cleared and demarcated paths similar to the walking cruises of Hahn (1949) and the transects of Lamprey (1963). The walking varied from 11.5 to 16.5 miles in length. Six other transects traversed the open bush and counts were conducted while driving at a slow speed in a 4-wheel drive vehicle. The length of the latter varies from 9.5 to 42 miles.

An attempt was made to conduct each of the transect counts at least once per month during the 2 1/2 year period of the study. Certain transects were counted more frequently, however, as time permitted. Other counts were sometimes missed because of non-functional transport or long periods of saturated and impassible soils.

Fig. 2. Locations of the 10 ground-count transects in relation to the major hill masses of the Mkomazi Reserve. The locations of seven storage-type rain gauges are marked with x's.

Fig. 3. Permanent transect routes used for monthly aerial game surveys.

The counting technique was simple and straightforward. More than one observer was always present, and when driving through the bush an African game scout stood in the back of the open vehicle to help sight animals. After a sighting was made with the unaided eye, 7 x 42 binoculars were used to count and to classify the animals into one of five size categories. Recordings were tabulated on standard game-count forms and a system of numbers with parentheses and superscripts was devised to denote the composition of each herd. All animal species were counted, classified, and recorded upon sight, but only data for elephant recordings are considered in this paper.

Size Classification: The criteria used to categorize individuals into size classes were based on the growth stage in relation to a fully grown animal. This is a logical reference point since adults are nearly always present (Buss, 1961; Buss and Smith, 1966; Petrides and Swank, 1966). Fully grown individuals and those animals which were tall enough to extend above an imaginary line drawn between the base of the tail and the eye of a fully grown individual were ranked as adults (class V). Individuals standing below the line between the eye and the base of the tail of an adult, but yet of nearly adult stature were ranked as subadults (class IV) (see Fig. 4). Animals classed as immatures (class III) stand below the

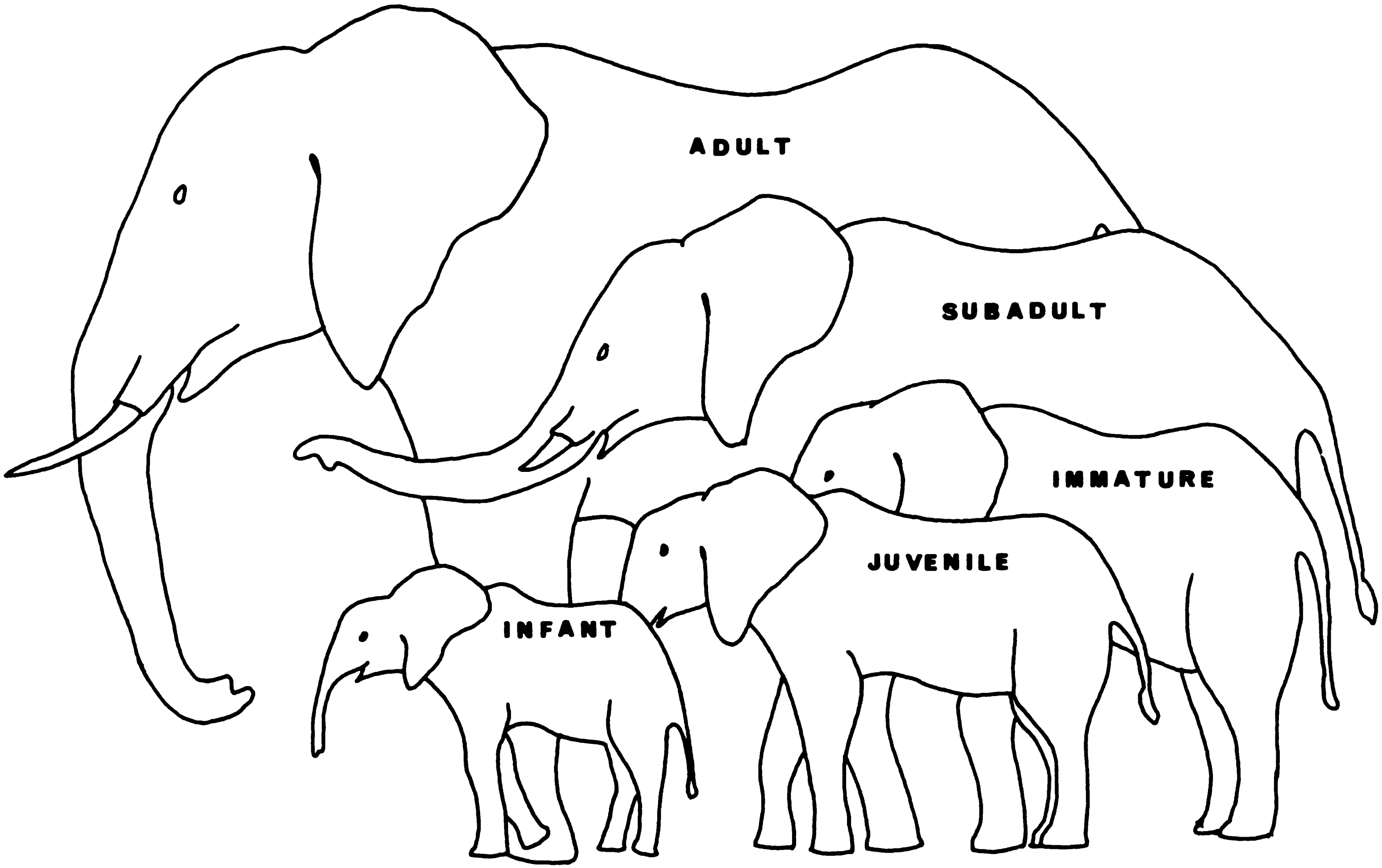


Fig. 4. Five ele[illegible] size classes [illegible] to describe elephant herd composition in the L[illegible]zi Reserve. Modified [illegible], 19[illegible].

same imaginary line drawn on class IV animals and juveniles (class II) stand below the same line drawn on class III animals. A second, equally useful, measure was that animals of each of these size classes stood below the notch formed by the lower junction of the ear pinna and the head skin of animals in the next higher size class. Since it is generally accepted (Buss and Brooks, 1961; Buechner et al., 1961; Laws, 1966) that calves of the year are able to pass between the forelegs of their mothers, this was the criterion used for size class I.

Size classes are subjective, to be sure, and dependent on the relative sizes of individuals in the herd. But the judgment of the observer is greatly enhanced by field experience, and unless some unknown systematic bias exists, small errors in classification should tend to balance out in a large sample size. The data presented in this paper regarding herd structure are based only on observations made after 18 months of field experience and the random classification of several thousand elephants.

Aerial Surveys: A dual-seated Piper Supercub airplane was made available in January, 1966 and supplementary monthly aerial surveys of the game reserve were initiated at that time. A system of 18 permanent transects crossing the reserve transversely and spaced approximately 5 miles apart was established (Fig. 3, page 11). The starting, turning and terminal points of the transects were located at specific topographic features such as waterholes, drainage ditches, rock outcrops, or artificial markers along the reserve boundary. Similar features, as well as peculiar trees, vegetation-association boundaries and compass bearings also were used as route markers.

Since the total linear distance of the transects was about 350 miles and required a flying time of more than 4 1/2 hours, the combined transects were divided into three nearly equal segments. The three segments of approximately 115 miles each were flown on consecutive days at monthly intervals. The counts were normally started about 1 1/2 hours after sunrise. Flying speed was held constant at 75 miles per hour at a standard altitude of 300 feet.

All animals seen along the transect routes were tallied on standardized sheets and their approximate locations were marked on maps. Occasionally a portable tape recorder was used to facilitate data recording. Upon sighting a large herd, perhaps of several hundred elephants, the pilot circled in a counter-clockwise direction and climbed to an altitude of 500 feet or more while the observer counted and rechecked the number of animals below. After counting such a herd the original position along the transect was determined and the normal procedure was resumed.

FIELD OBSERVATIONS

Temporal Population Dynamics: Game counts along the 10 ground transects were conducted 377 times during the study. The monthly averages of transect counts are graphed in Figure 5 along with the results of aerial surveys over the same area and mean monthly rainfall figures for seven storage gauges. From the graph, it appears that there may be seasonal patterns in the fluctuations of numbers of elephants, but the variation is great.

There is no significant correlation at the 5 per cent level between the numbers of elephants recorded from the ground and aerial surveys ($r = .312$, d.f. = 14). Further, when the data are lumped in this manner, no significant correlation exists between the monthly rainfall averages for the seven stations and the results of either ground ($r = .322$, d.f. = 13) or aerial counts ($r = .458$, d.f. = 13).

But the overall correlation of elephant numbers with climatic and habitat variations is evident when seasonal averages of the elephants seen from the air are compared with seasonal rainfall and habitat conditions (Table 1). During the months of heavy rainfall

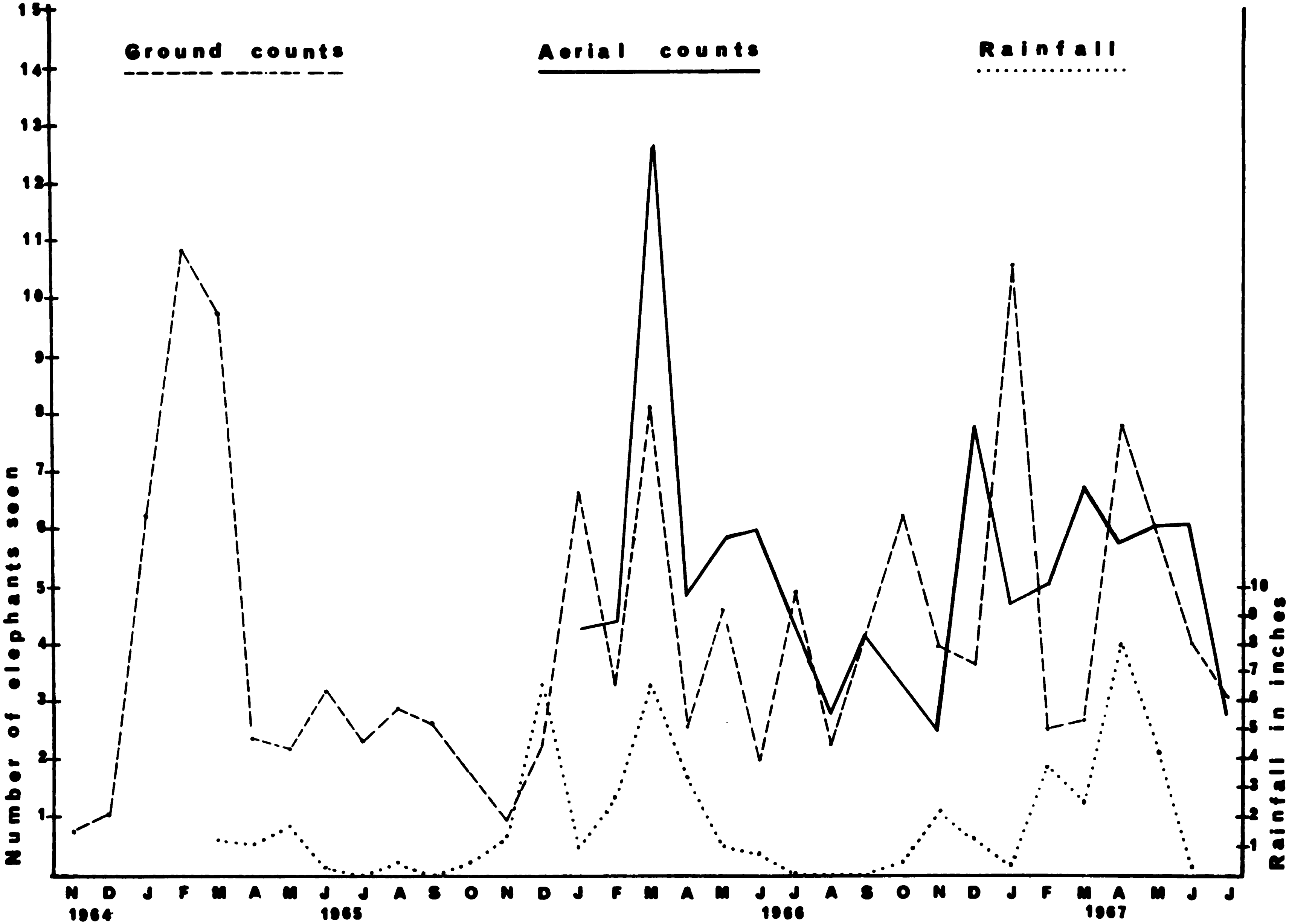


Fig. 5. The relation between the monthly average number of elephants seen along the ground-count transects, the number recorded from the air, and the average amounts of rainfall recorded from seven gauges. The scale of numbers is read in tens when referring to the ground counts and hundreds when referring to the aerial counts.

TABLE 1. Seasonal variation in the amounts of rainfall, the habitat condition, and the average number of elephants recorded by aerial survey in the Mkomazi Reserve during 1966-67

Season	Light rains 1966	Heavy rains 1966	Dry season 1966	Light rains 1966-67	Heavy rains 1967
Average rainfall	1.8 inches per month	3.6 inches per month	0.6 inches per month	1.8 inches per month	3.7 inches per month
Habitat condition	Moderate food and water	Abundant food and water	Limited food and water	Moderate food and water	Abundant food and water
Average number of elephants recorded	1052	1723	605	1065	1464

(March-May) the average number of elephants counted in the reserve was about 1450. During the long dry season (July-October) the average number recorded was about 600, and during the light rainy season or transitional months the average number seen was midway between the two, at about 1000.

The seasonal differences in elephant density obviously imply migration. Mountains and dense human settlement prevent outward movement from the reserve along the western and southern boundaries. Sparse settlement also exists east and southeast of the reserve, yet elephants do inhabit much of this area. The times when elephants occupy this bush, however, are largely in synchrony with the times of high density within the reserve. Therefore, an eastward movement out of the reserve does not seem to be an important part of the migration pattern. The main migration is at the beginning of each dry season, when most of the elephants migrate northward from the reserve into Kenya. It is after the next season's rains have stimulated forage growth and filled many of the temporary waterholes in the Mkomazi that they again return southward into the reserve. The usual migration pattern for Africa's game sanctuaries is one of egress during the rainy seasons and ingress during the dry seasons when permanent water sources are unavailable outside. The Mkomazi migration pattern is unusual in this respect.

Distinct from this north-south migration is an east-west movement within the reserve. In January-February 1965, January 1966, again in March 1966 and April 1967, elephants concentrated around the northern-most hill mass in the central section of the reserve. These concentrations numbered about 1200-1600 and were made up of animals from both the eastern and western sections of the reserve. After a week or two, the concentrations dispersed and the distribution throughout the reserve returned to normal. East-west movement is an uncommon phenomenon for animals of the Mkomazi (Harris, 1967), and elephants from the eastern end were never observed moving westward past the central hill mass, nor were elephants from the western half ever seen moving into the eastern section.

The exact reasons for the concentrations are unknown. Possibly they play a role in the breeding behavior of the different populations (Quick, 1965; G. A. Petrides, personal communication), but no breeding activity was observed among the herds during these short periods. Another alternative is that the herds converge on a source of highly palatable forage at a particular growth stage. This is not convincing since the local vegetation (Grewia spp., Cordia spp.) is not apparently different from surrounding areas. Until further investigated, the reasons for the concentrations remain unknown.

The mean herd size for all elephants recorded in the western half of the reserve was 8.7. The mean for all herds recorded east of the central hill mass was 25.3. The elephants of the eastern section are considerably more truculent, and fewer calves were observed among them. Collectively, these observations suggest that the elephants of the eastern and western sections of the reserve represent two distinct populations. Aerial observations and monthly distribution maps support this belief.

The eastern population migrates northward across the international boundary between the Mkomazi Reserve and the area east of Tsavo National Park in Kenya. The number migrating into the reserve from the north is estimated at 1500, but many more may migrate southward from Kenya into the bush country east of the reserve. Approximately 3000 cattle also graze the eastern half of the reserve, and along with the low rainfall, low forage production, and higher frequency of fire this certainly reduces the dry-season carrying capacity of the area for elephants. Because of these factors the seasonal density fluctuations of elephants are great in this section of the reserve.

The western population is smaller and moves a much shorter distance than the eastern population. While migrating, and for some time during the dry season, the herds form an aggregate of some 400-500 elephants and their movements are easily recorded from a light airplane. The number that migrate between the reserve and Kenya probably does not exceed 500 and their north-south movement is only some 50 miles (R. M. Watson, personal communication). During the rainy season this group moves into the north-western corner of the reserve and then gradually disperses throughout the western section. Because of the higher rainfall, the greater forage production (Harris, 1968), the permanent water of Dindira Dam, and possibly the absence of cattle, the dry season carrying capacity is higher in the west. For these reasons, the density changes are not nearly so great as those of the eastern section.

Size Class Recordings: Because of inherent errors in estimating the relative sizes of elephants from 300 feet above, no aerial observations are included in the recordings for herd structure analysis. To further eliminate inaccuracies, I present only the recordings made from July 31, 1966 to July 31, 1967. Of more than 5000 elephants recorded from the ground during this period, over 3000 are excluded because of incomplete tallies of all members of the herd.

For 2001 positively-classified elephants, the numbers in each size class were: calves of the year, 172 (8.6%); juveniles, 190 (9.1%); immatures, 205 (10.2%); subadults, 222 (11.1%) and adults, 1212 (60.6%).

DISCUSSION

The Growth Curve: To convert size-class data to more usable age-structure information, relative ages were assigned to each of the size classes, using a growth curve.

Johnson and Buss (1965) developed a hypothetical growth curve based on the measurements of one captive animal and measurements of specimens collected in Uganda. Petrides and Swank (1966) constructed a similar curve based on the weights of two captive elephants and the measurements of Buss' specimens. Laws (1966) referred to growth data for other captive elephants as well as to those for two semi-wild elephants in East Africa. Using all available data, I present another growth curve which is different from those so far published (Fig. 6).

Gross weight is a poor measure of body growth because of varying amounts of food and water in the gut (Sikes, 1966). Since elephants drink up to 80 liters of water at one time, and probably as much as 200 liters per day (Sikes, 1966; Benedict, 1936), a variation of 100 kg. or 5 per cent of a 2000 kg. animal's weight may occur. Further, variation due to the amount of food in the gut may equal or even exceed this amount since elephants

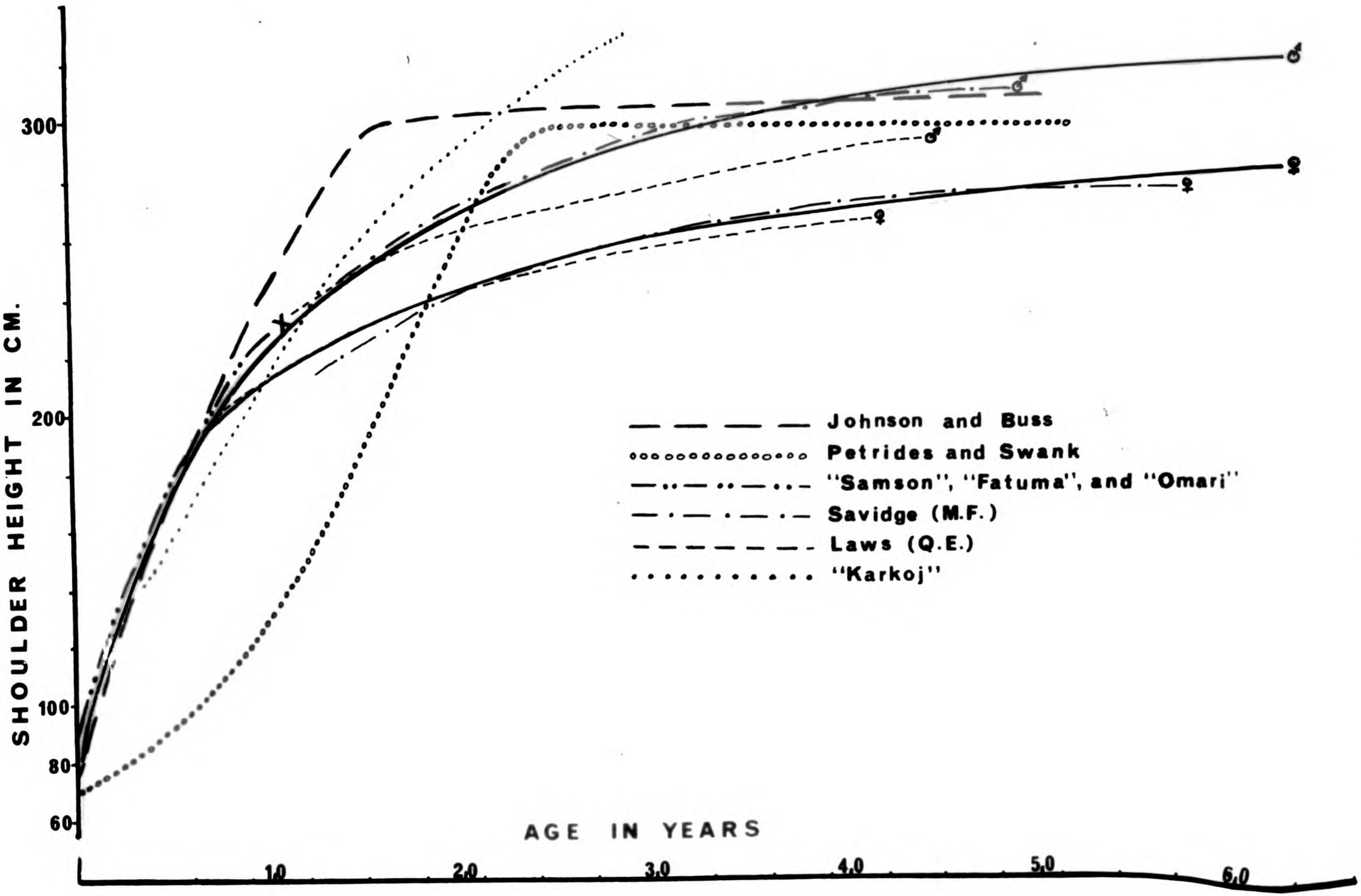


Fig. 6. A revised growth curve for the individual sexes of the African elephant based on the caliper measurement of shoulder height with age.

normally consume up to 225 kg. of forage per day (Buss, 1961; Pienaar, *et al.*, 1966).

Height at the shoulder is believed to be the most useful.measure of body growth and reflection of relative age. Data on the shoulder height at different ages is available for only 10 known-age African elephants. Of these "Omari," in the Basel Zoological Gardens; "Khartoum," a deceased Bronx Zoo animal; "Karkoj," of the Giza Zoological Gardens, and "Dicksie," in the London Zoological Gardens are all captive animals. "Sampson" and "Fatuma" are young male and female orphans tamed by the warden of Tsavo National Park, but left to forage freely in the bush (Sheldrick, 1966). Other observations by Bellinge and Woodley (1964), Taylor (1965), Sikes (1966) and Bere (1966) provide measurements for animals from birth to about a year old. Records by Bourliere and Verschuren (1960 in Laws, 1966) are not considered here since they apply to the smaller Congo elephant (*L. a. cyclotis*).

From these sources, a shoulder height of 80 cm. is average for a calf at birth. Measurements of the semi-wild "Sampson" and "Fatuma," "Omari," and "Karkoj" are almost identical at several different ages (Laws, 1966; Johnson and Buss, 1965; Flower, 1947) and the growth curve to age 11 (Fig. 6) is based largely on these four animals. Benedict (1936) described "Khartoum" as a huge animal, but he was smaller in his early years than these four animals.

Laws' records for Queen Elizabeth National Park, Uganda, (Q.E. in Fig. 6) fit the initial curve-segment well, but level off at a lower asymptotic height. Laws attributes this to hybridization with the smaller forest elephants. Measurements of "Dicksie," "Khartoum" and data from the Savidge collection (in Laws, 1966) indicate that the curve should be somewhat higher. All this information has been considered in constructing the revised curve of Figure 6.

Using his growth curve, the measured shoulder heights of 41 female specimens, and photographs of different-sized elephants, Laws (1966) established the height relationships for seven different aged elephants. After referring to my revised growth curve and comparing my size classes with Laws' field criteria, age designations were assigned to each category: calves, below one year old; juveniles, 1-4 years old; immatures, 5-8; subadults, 9-15; and adults, 16 years and older.

Longevity and Population Structure: Although the oldest known-age African elephant ("Karkoj") only attained 40 years of age (Flower, 1947), other information is available for estimating the maximum ages of elephants. Flower (1947) mentions Asian elephants living up to 67 years old and then supports this with Mc Naughton's records of over 1700 working Burmese elephants. These records, kept over a 50-year period, indicate that 1.4 per cent of the herd was over

65 years old. Other information by Benedict (1936) and Perry (1953) suggests that African elephants probably attain the same maximum age. Simpson and Kinloch (1953), Bigalke (1957), Petrides and Swank (1966) and Laws (1966) have accepted a maximum potential longevity of about 70 years for wild African elephants. Petrides and Swank hypothesize that only one animal in a thousand reaches this maximum. Mc Naughton's data and those of others support this hypothesis.

Considerable information on wild elephant population structure is available in the literature. Although field observations have been made in the Congo (Kinshasa), Uganda, Kenya, Tanzania and South Africa, all are concerned with populations centered in and around national parks or game reserves. The bulk of these observations was obtained by censuses of different size classes in living populations. In describing the various populations, researchers have invariably used three, four, or five size classes. Even though the classes are quite general, in terms of respective ages, the data are remarkably similar and large samples have minimized the effect of observational errors.

Bourliere and Verschuren (1960, in Petrides and Swank, 1966) used only three size classes. Judging from Petrides and Swank (1966) they found the Kivu National Park (Congo, Kinshasa) elephant population to contain 13.8% calves less than 18 months old, 24.1% immatures and subadults to about 14 years of age, and 62.1% adults, 15 years and older. Hill *et al*. (1953) also referred to Congo elephants and reported that 50% were immatures and 50% adults (Petrides and Swank, 1966).

The elephants of western Uganda (including Queen Elizabeth and Murchison Falls National Parks) have probably been studied more than any others. Petrides and Swank (1966) reported on sightings of some 1000 elephants observed in Queen Elizabeth Park during 1956-57. Their observations indicated that there were 14.6% infants under the age of 2 years, 24.3% immatures, 14.4% subadults and 46.7% adults. Studying in the same region two years later, Buss and Brooks (1961) recorded more than 3000 elephants. Their size class proportions are: young of the year, 7.7%; immatures, 16.7%; subadults, 15.6% and adults, 58.8%. Bere (1966), in a very general breakdown for the same area, which may be based at least in part on the observations of other workers, gives 8% calves of the year, 16% immatures, 16% subadults and 60% adults.

Although working in a national park over 2000 miles away, Pienaar *et al*. (1966) concluded that the relative proportions of the Kruger National Park (South Africa) population were not significantly different from those recorded for Uganda. They found that 7.4% of the total observed were below 1 year old, 28.1% were not yet sexually mature (below 12 years) and 64.5% were of breeding age. After combining two of my age categories, the observed population structure for the Mkomazi elephants (Table 2) was quite similar to those reported for these other areas.

Measurements of collected specimens reported in the literature provide still further information regarding the age distribution of adult-size animals. By comparing shoulder height measurements with the growth curve and the recorded dental characteristics with the age determination guides of Laws (1966) and Sikes (1966, 1967), it is possible to estimate the age at death of 184 adult animals collected by various workers (Perry, 1953; Sikes, 1966; Johnson and Buss, 1965; Laws, 1966). Even though errors of a year or two may have occurred in assigning ages to these specimens, this is believed to be of little consequence where categories of 5 year magnitudes are used. The data from the collected specimens indicate that for animals over 16 years of age the survival rate to age 45 is about 99 per cent per annum. The mortality rate then increases rapidly in each succeeding year until only two out of 200 adults (one per cent) reach 65 years.

Laws (1966) recovered a total of 325 jaw bones from elephant carcasses found in the two Uganda national parks. Presumably, these are not representative of the population because the younger age classes are under-represented in the sample (i.e. only 21.2% of the total were under 16 years of age). This is probably because of

TABLE 2. A comparison of elephant (Loxodonta africana) population structures reported in the literature with the observed structure of the Mkomazi population

Observers and location	Age in years: 0	1	2	3	4	5	6	7	8	9	10	15	16	70
Bourliere and Verschuren Kivu Park, Kinshasa 1960 in Petrides and Swank 1966		13.8%				24.1%							62.1%	
Buss and Brooks (1961) western Uganda		7.7%					16.7%					15.6%	58.8%	
Petrides and Swank (1966) Queen Elizabeth Park, Uganda		14.6%				23.4%					14.4%		46.7%	
Pienaar et al. (1966) Kruger Park, South Africa		7.4%					28.1%						64.5%	
Bere (1966) western Uganda	8%				16%						16%			60%
This study Mkomazi Reserve, Tanzania		8.6%		9.1%				10.2%			11.1%			60.6%

the greater perishability of the smaller jaws, much as for Murie's mountain sheep (Laws, 1966; Deevey, 1947).

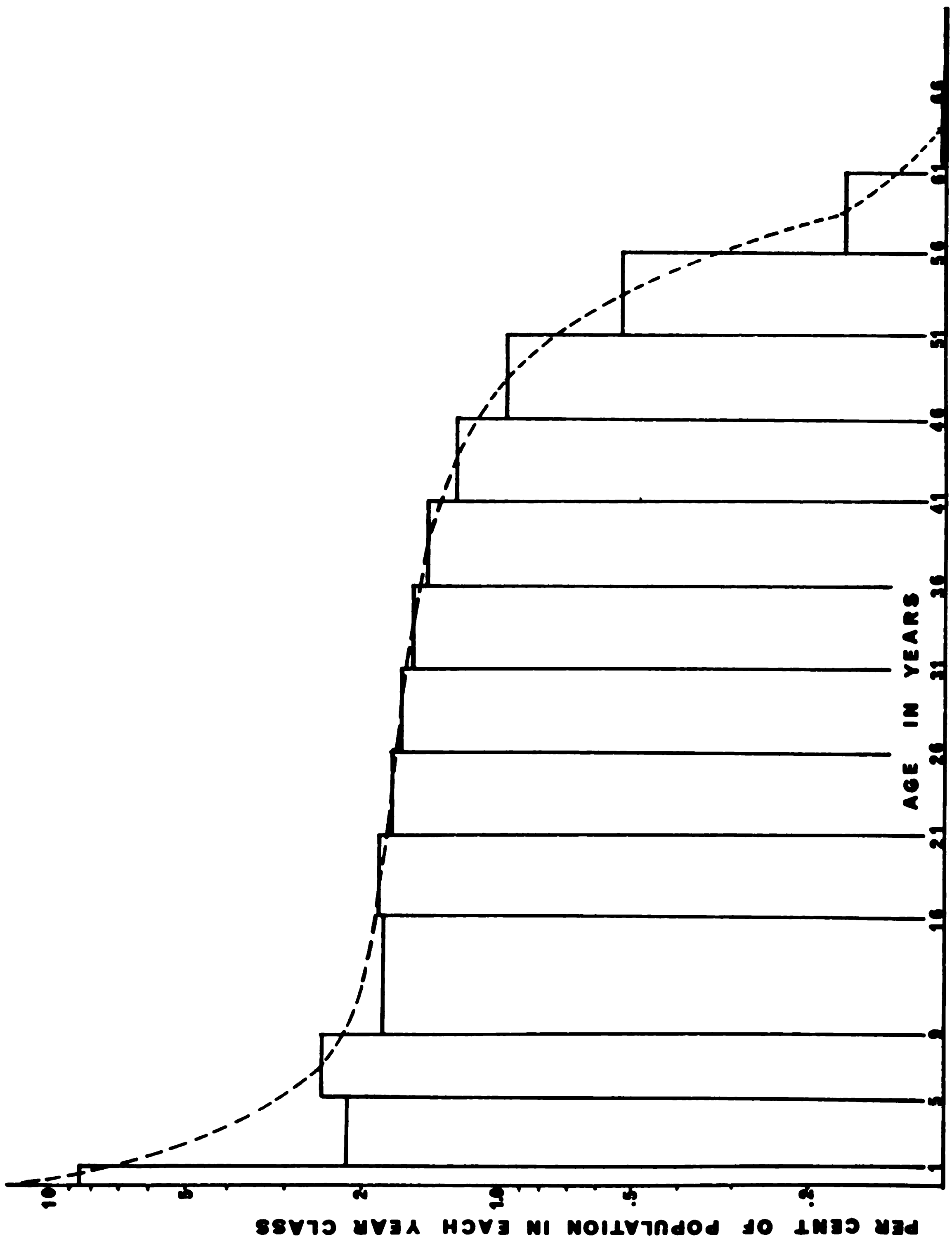
But there is no reason to believe that the adult specimens are not representative of the entire populations and the 256 adult specimens provide a general distribution of ages at death. The frequency distribution of these jaws supports the idea that the mortality rate is low and nearly constant from the beginning of adulthood to about age 50. It then accelerates rapidly. Only one jawbone represented an animal over 60 years old.

Based on the observed population structure of animals 0-15 years of age (those born after the formation of the game reserve), the information derived from the 184 specimens reported in the literature, and the 256 jaw bones recovered by Laws, it is possible to describe a general mortality pattern for wild African elephants. The mortality curve must be of the "U" or "fishhook" form characteristic of most mammals (Caughley, 1966). The juvenile phase is characterized by initial rates of approximately 30 per cent per annum. The rate gradually decreases until age 16, or approximately adulthood, when only about 1 per cent die annually. This rate persists for about 30 years to age 45 and then accelerates to 30 per cent per year again by age 60.

The area in which my observations were recorded has been a game reserve for only 17 years, and the elephants are known to have been heavily hunted before that time. Such additional factors as artificial water supplies and surrounding settlement may well affect elephant population structure in any area. Still further evidence (Glover, 1963; Buechner et al., 1963; Pienaar et al., 1966) suggests that most game-sanctuary populations are increasing. In view of these factors, the age distribution is not considered stable and construction of a life table is not warranted (Caughley, 1966). A histogram of the observed population structure to age 16 has been prepared (Fig. 7), but the observed structure can only be regarded as an instantaneous description of the population during the period of study.

Reproduction: The calf-of-the-year age class comprised 8.6 per cent of the total Mkomazi elephant population. But the observed values represent the mean of those entering and those leaving the year class, and the number of individuals born must be greater than the number observed. By assuming a constant rate of death from age zero to age one and projecting the survival curve upward to its intersection with the ordinate axis of Figure 7, the percentage of newborn young is seen to be 10.1 per cent. The ratio of infants (10.1%) to all other animals in the population (89.9%) yields a crude birth rate of 11.2 per cent (Quick, 1963).

Fig. 7. Histogram illustrating the observed percentage of the total Mkomazi elephant population in each year class to age 16, and the calculated percentage in each year class from year 17 onward. The negative exponential has been plotted to estimate the recruitment at age zero.


PER CENT OF POPULATION IN EACH YEAR CLASS
AGE IN YEARS

By reviewing the literature it is possible to estimate other parameters such as the female age at puberty and the mean calving interval.

Perry (1953) and Buss and Smith (1966) have dealt intensively with reproduction in female elephants and other workers have dealt with the development and structure of the reproductive organs themselves (Perry, 1964; Amoroso and Perry, 1964; Johnson and Buss, 1967; 1967a). Other, more general papers also include observations on elephant reproduction (Simpson and Kinloch, 1954; Buss and Brooks, 1961; Buss and Savidge, 1966; Spinage, 1963; Petrides and Swank, 1966; Laws, 1966; and Pienaar et al., 1966).

Elephant cows are promiscuous and multiple matings during one estrus period have been observed on several occasions (Short, 1966; Buss and Smith, 1966). Several matings of a captive Asian elephant were also recorded in a period of eight months (Buss and Smith, 1966). Because of these multiple matings and other factors, the gestation period has not been accurately measured for the African elephant. Asian elephants are known to have an approximate 22-month gestation period and most workers accept this for the African species as well. Blond (1961) mentions a 20-month gestation period, but gives no evidence to support his statement. Ovarian and uterine studies as well as field observations reveal no seasonal peak in breeding activity, and it is thought that recruitment is year-round (Ansell, 1960; Buss and Smith, 1966; Perry, 1953).

Working with collected specimens, Perry (1953) found that wild female African elephants may reach puberty at nine years, and concluded that most begin to breed between the ninth and tenth year. Since few, if any, known-age wild elephants have been closely observed, researchers have relied upon observations of captives. The youngest Asian elephant female known to mate was in the Portland (Oregon) Zoo. She first mated at four years and then at irregular intervals until she eventually conceived between her sixth and seventh year (Buss and Smith, 1966). But other observations indicate that some females do not reach puberty until eleven years of age, and Buss and Smith (1966) concluded that nine years is probably a mean initial breeding age for female Uganda elephants. Laws' data (1966) from collected specimens support a much later age at puberty, 14-15 years. But nearly 15 years elapsed between the collection of the different Uganda samples, and changes in population structure may account for this and other discrepancies (see beyond).

The maximum age at which elephants breed has been determined with more certainty. One very old, lactating female in Perry's collection has now been aged (Laws, 1966) at some 60 years. This indicates that breeding may occur throughout life in some individuals.

Since the normal lactation period continues from the time of parturition until the subsequent pregnancy, the distribution of pregnant to nonpregnant (lactational anestrus) females can be regarded as a binomial (Perry, 1953). In his sample of 65 adult females, Perry (1953) found that 31 were pregnant and 34 were not pregnant. With 22 months as the average gestation period, his best estimate of the lactational anestrus period was 23.4 months (sic) and the 95% confidence limits were 21.0 and 25.8 months. If his sample was representative of the population, the mean calving interval at that time was slightly under four years (i.e. 22 + 23.4 = 45.4 months).

Using nine years as the age of puberty, 46 months as the mean calving interval, and the observed population structure of the Mkomazi Reserve, a hypothetical reproductive rate can be calculated. The observed percentages of the adult and subadult size classes (nine years and over) total 71.7 per cent of the population. A 1000-strong cohort of females would therefore contain 71.7 per cent sexually mature animals. If twin calving (Seth-Smith and Parker, 1967) offsets prenatal losses and if there are no barren females in the population, then 717 females would bear 717 young every 46 months or 187 calves per year. This yields a refined birth rate (the ratio of young to mature females) of 26.1 per cent. When the ratio compares the 187 calves to the females of all other age classes plus an equal number of males a crude birth rate of 10.3 per cent is derived. This value compares favorably with the 11.2 per cent birth rate of the Mkomazi population and suggests that the female age of puberty approximates 9 years and the mean calving interval is about 4 years in that population. If the age of puberty was 12 years or greater, as estimated for other populations (Laws, 1966; Pienaar *et al*., 1966), and the calving interval was greater than 4 years, then the reproductive rate could not be as high as 10 per cent.

Effects of Environment and Population Density: Perry (1953) collected most of his specimens from western Uganda during 1946-48. His calculated mean calving interval of slightly less than four years applies to those elephants at that time. In 1958, Buss collected 109 females from the area south of Murchison Falls Park and 11 from near the Ruwenzori Mountains. After analyzing these specimens, Buss and Smith (1966) concluded that the initial breeding age was still about nine years, but the mean calving interval had more than doubled (from 45.4 to 103.8 months). Savidge (in Laws, 1966) collected a further 23 mature females from Murchison Falls in 1963-64, and although the calculated calving interval for this sample was only slightly over 7 years, Laws (1966) estimated that the mean age at puberty was 14-15 years.

From the above information it appears that both the age of initial breeding and the calving interval of the Murchison Falls population has been greatly retarded in the last two decades. The percentage of calves observed in the population has also dropped considerably (Buss and Smith, 1966; Buss and Savidge, 1966; Laws, 1966). It is hypothesized (Buss, 1965; Buss and Smith, 1966; Laws, 1966) that this retardation of breeding activity may be the result of a degraded habitat, increased elephant densities, or both.

Sikes (1968) has recently found that the occurence of medial sclerosis and a form of atheroma (fatty arteries) in elephants was highly related to environmental conditions. Animals inhabiting relatively pristine montane forests were found to be free of both diseases, while animals inhabiting Murchison Falls, Queen Elizabeth and Tsavo National Parks were afflicted with a very high incidence of the diseases. She concludes that, "It seems most likely that it is the direct result of the destruction of shade cover. . . ." Cowan _et al_. (1967) also reported the occurence of arteriosclerosis in hippopotami collected from the Queen Elizabeth National Park.

Since the ground count transects and most ground observations of the Mkomazi study were largely limited to the western half of the reserve, the herd structure analysis applies mostly to the western population.

It was mentioned earlier that the eastern population seemingly has a much lower reproductive rate as well as a more truculent disposition and a greater mean herd size. Whereas the western population inhabits a more productive and less-frequently burned range containing a readily accessible, permanent water source, the eastern population is heavily dependent on seasonal forage and surface water. Further, the western section of the reserve is free of domestic stock, and harassment from humans is negligible. This is not the case in the east where competition with cattle, sheep and goats doubtless occurs and where disturbance by humans is inevitable.

It seems likely that mean herd size, reproductive rate and degree of truculence may relate positively with the seasonal variation in environmental conditions and interspecific interactions. Therefore, it seems that habitat trends may be used to predict future herd characteristics of elephants.

CONCLUSIONS AND RECOMMENDATIONS

1) When seasonal averages of all elephants counted from the air are correlated with seasonal rainfall figures, a clear relationship exists. The numbers were characteristically high during the long rainy seasons, low during the long dry seasons, and about midway between the two during the short rains and transitional months. Yet when the results of the ground counts are presented as monthly averages, and the rainfall records for seven stations are also averaged, there is no significant correlation (at the 5% level) between the ground counts and the aerial counts, nor is there any correlation (at the same level) between rainfall and the results of ground counts or aerial surveys.

2) The elephants of the Mkomazi Reserve consist of two distinct populations with the central, northern hill mass forming the borderland between the two.

3) During the dry season when forage and surface water are limited, the eastern population moves northward across the Kenya border into the area east of Tsavo National Park. When seasonal rains fill the many temporary waterholes and stimulate forage growth, as

many as 1500 elephants return south into Tanzania and the Mkomazi Reserve.

4) The western population is composed of nearly equal numbers of residents and migrants. The migratory population, approximately 500 in number, moves northward into Tsavo National Park during the dry season and probably remains close to Lake Jipe throughout the season. With the onset of the rains, they return southward into the Mkomazi Reserve and gradually disperse throughout the western section.

5) On the basis of this survey, there is an apparent relationship between highly variable habitat conditions, interaction with humans and livestock, and certain elephant population characteristics. The eastern elephant population inhabits a lower rainfall and lower forage production area which is frequently burned. This area also contains humans as well as 3000 cattle and other livestock which the western area does not. The elephants are highly migratory, of a more truculent nature, and have a mean herd size more than three times as great as the western population.

6) Distinct from the north-south migration pattern is an east-west movement which tends to concentrate eastern and western elephants around the central, northern hill mass. The reasons for this concentration are unknown, but the total may reach 1500 (40 per sq. mi.) or more.

After a week or two, dispersal occurs and the distribution throughout the reserve returns to normal.

7) Studies comparing the number of large game animals seen from aerial surveys with known-sized populations or ground counts reveal that the percentage seen from the air is variable, but almost always much below the ground count figures (Goddard, 1967; Erickson and Siniff, 1963; Buechner *et al.*, 1951; Edwards, 1954; Petrides, 1953; Lovaas *et al.*, 1966). Based on the highest number of 2240 elephants counted from the air in March 1966 and the relatively small area actually covered by the survey flights, it is estimated that the total number inhabiting the reserve during peak seasons may exceed 3000. The lowest number ever recorded was 427, but undoubtedly many were missed during that survey also.

8) Based on the size classification of 2001 elephants, the age structure of the western Mkomazi elephant population was 8.6% calves of the year, 9.1% juveniles (1-4 years), 10.2% immatures (5-8), 11.1% subadults (9-15) and 60.6% adults (16 years and over).

9) From this observed population structure, it was calculated that the mortality rate must approximate 30 per cent during the first year. Categorizing 184 adult specimens and a further 256 adult jaw bones

reported in the literature into five-year age groupings, an adult mortality rate of approximately one per cent per annum to age 45 is derived. The rate then accelerates until by age 65 it is again about 30 per cent per year.

10) The observed value of 8.6% calves is assumed to represent the mean of those entering and leaving the 0-1 year age class. Assuming a constant rate of death from age zero to age one, a value of 10.1% is established as the number of young being born into the population. From this, a crude birth rate of 11.2% is derived.

11) Assuming an average gestation period of 22 months, a 50:50 sex ratio and that females reproduce throughout life, estimates of the female age at puberty and the mean calving interval are 9 years and slightly under four years respectively.

12) Recruitment into the western Mkomazi elephant population is high with respect to rates reported in the literature for other populations (see Table 2 and Buss and Savidge, 1966). Based on this high reproductive rate, the observed local changes in vegetation (Harris, in preparation), the population characteristics of the eastern elephants, and the effects of degraded habitats on reproduction and the incidence of degenerative diseases in other parks, it is

recommended that elephant population management be included in the management scheme of the Mkomazi Reserve.

14) The calculated birth rate of 11.2 per cent must not be confused with the rate of population increase, since natural mortality normally reduces the latter to zero in a stable population. But cropping may replace much of the natural mortality rather than adding to it. Further, reduction of the population level may enhance both reproduction and survival. Although the maximum allowable kill is dictated by the birth and survival rates, the relative ages of the animals cropped must be in accordance with the management objectives.

15) If meat production is desired, the optimal harvest can be attined from stable-aged populations by cropping both sexes and all age classes in proportion to their relative abundance.

16) If large male "tuskers" are desirable for viewing by tourists, the kill should be limited to the females and younger age classes.

17) Cropping to reduce an overpopulation and restore habitat conditions should be applied to all age classes. Such management would least disturb the existing population structure. Cropping of randomly

selected "family units" will cause the least disturbance to the populations.

18) Since the number of elephants in the reserve is greatest during the rainy season, the maximum harvest would be attained during that time. Based on a 10 per cent reproductive rate and the estimated 3000 elephants present at that time, the maximum sustained yield harvest is about 300 animals per year. The suggested cropping proportions are: 0 to 1 year old, 10%; 1-4 years, 9%; 5-8, 10%; 9-15, 11% and 16 years and over, 60%. It should be noted that since females breed only once every four years (and therefore only 25 per cent breed in any one year) there must be at least a three-fold surplus of males, and because of promiscuity the surplus is probably much greater. A high percentage of these could safely be added to the total crop.

19) Since vegetation change due to localized overpopulations of elephants in the reserve has already occurred and a reduction of the population may be desired, the threat of over cropping is less important. In any event, the time required for a woodland environment to recover from the effects of an overpopulation is much longer than that required for the elephants to overcome the effects of a slight overcrop.

20) Use of age-specific statistics from collected specimens provides one of the best methods of monitoring population change. Complete field records including body measurements, jaw bones, and the female reproductive tracts of cropped animals should be collected, properly preserved and analyzed. Cropping strategies can then be altered in accordance with the population structure at the time.

LITERATURE CITED

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders, Philadelphia.

Amoroso, E. C. and J. S. Perry. 1964. Fetal membranes and placenta of African elephants. Phil. Trans. Roy. Soc. Lond. 248 (743):1-43.

Ansell, W. F. H. 1960. The breeding of some larger mammals in Northern Rhodesia. Proc. Zool. Soc. Lond. 134:251-274.

Ansell, W. F. H. 1966. Mimeo report on size categories for African ungulates. Chillanga, Zambia.

Bellinge, W. H. S. and F. W. Woodley. 1964. Some notes on the rearing of young African elephants. E. Afr. Wildl. J. 2:71-74.

Benedict, F. G. 1936. The physiology of the elephant. Carnegie Inst., Wash. Publ., 474, 302pp.

Bere, R. 1966. The African elephant. Golden Press, New York.

Bigalke, R. 1957. The ages to which elephants live. Afr. Wildl. 11(2):140-142.

Blond, G. 1962. The elephants. Andre Deutsch Ltd. Lond.

Buechner, H. K., I. O. Buss, and H. F. Bryan. 1951. Censusing elk by airplane in the Blue Mountains of Washington. J. Wildl. Mgmt. 15(1):81-87.

________, I. O. Buss, W. M. Longhurst, and A. C. Brooks. 1963. Numbers and migration of elephants in Murchison Falls National Park, Uganda. J. Wildl. Mgmt. 27(1):36-53.

________, and H. C. Dawkins. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. Ecology 42(4):752-766.

Buss, I. O. 1961. Some observations on food habits and behavior of the African elephant. J. Wildl. Mgmt. 25(2):131-148.

________. 1965. Significance of reproduction to productivity in the African elephant. Int. Biol. Programme Symposium on productivity of large mammal populations, Aberdeen, Scotland.

________, and A. C. Brooks. 1961. Observations on number, mortality, and reproduction in the African elephant. Proc. IUCN, Arusha, Tanganyika. Sp. Ser. no. 1. 117-122.

________, and J. M. Savidge. 1966. Change in population number and reproductive rate of elephants in Uganda. J. Wildl. Mgmt. 30(4):791-809.

________, and N. S. Smith. 1966. Observations on reproduction and breeding behavior of the African elephant. J. Wildl. Mgmt. 30(2):375-388.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47(6):906-918.

Darling, F. F. 1960. Wildlife in an African territory. Oxford U. Press, London. 160pp.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Edwards, R. Y. 1954. Comparison of an aerial and ground census of moose. J. Wildl. Mgmt. 18(3):403-404.

Erickson, A. E. and D. B. Siniff. 1963. A statistical evaluation of factors influencing aerial survey results on brown bears. Trans. N. Am. Wildl. and Nat. Resources Comf. 28:391-409.

Flower, S. S. 1947. Further notes on the duration of life in mammals: V. the alleged and actual ages to which the elephant lives. Proc. Zool. Soc. Lond. 117:680-688.

Glover, J. 1963. The elephant problem at Tsavo. E. Afr. Wildl. J. 1:30-39.

Goddard, J. 1967. The validity of censusing black rhinoceros populations from the air. E. Afr. Wildl. J. 5:18-23.

Hahn, H. C. Jr. 1949. A method of censusing deer and its application in the Edwards Plateau of Texas. Texas Game, Fish and Oyster Comm. Austin. 24pp.

Harris, L. D. 1967. A synopsis of activities and report of biological investigations within The Mkomazi Game Reserve for 1966. Mimeo report. Tanzania Game Div. Arusha. 34pp.

Harris, L. D. 1968. Some preliminary conclusions and recommendations for the Mkomazi Game Reserve based on a three-year ecological study. Type written report to the Tanzania Game Division. 9pp.

Hill, W. C. O., et al. 1953. The elephant in East Central Africa. Rowland Ward Ltd., Lond. 150pp.

Johnson, O. W. and I. O. Buss. 1965. Molariform teeth of male African elephants in relation to age, body dimensions and growth. J. Mammal. 46(3):373-384.

________. 1967. The testis of the African elephant (Loxodonta africana) I. Histological features. J. Reprod. Fert. 13:11-21.

________. 1967. The testis of the African elephant (Loxodonta africana) II. Development, puberty and weight. J. Reprod. Fert. 13:23-30.

Krumrey, W. A. and I. O. Buss. 1968. Age estimation, growth, relationships between body deminsions for the female African elephant. J. Mammal. 49(1): 22-31.

Lamprey, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. E. Afr. Wildl. J. 1:63-92.

________, P. E. Glover, M. I. M. Turner, and R. H. V. Bell. 1967. Invasion of the Serengeti National Park by elephants. E. Afr. Wildl. J. 5:151-166.

Laws, R. M. 1966. Age criteria for the African elephant. E. Afr. Wildl. J. 4:1-37.

Lovaas, A. L., J. L. Egan, and R. R. Knight. 1966. Aerial counting of two Montana elk herds. J. Wildl. Mgmt. 30(2):364-368.

Morrison-Scott, T. C. S. 1939. On the occurence of a presumed first milk molar (mm. 1) in African elephants. Proc. Zool. Soc. Lond. 108(B):711-713.

________. 1947. A revision of our knowledge of African elephants' teeth with notes on the "forest" and "pygmy" elephants. Proc. Zool. Soc. Lond. 117:505-527.

Perry, J. S. 1953. The reproduction of the African elephant-Loxodonta africana. Phil. Trans. of the Roy. Soc. Lond. (Ser. B). 237:93-148.

________. 1964. The structure and development of the reproductive organs of the female African elephant. Phil. Trans. Roy. Soc. Lond. (Ser. B). 248(743): 35-51.

Petrides, G. A. 1953. Aerial deer counts. J. Wildl. Mgmt. 17(1):97-98.

________, and W. G. Swank. 1958. Management of the big game resource in Uganda, East Africa. Trans. N. Am. Wildl. and Nat. Resources comf. 23:461-477.

________. 1966. Estimating the productivity and energy relations of an African elephant population. Proc. Int. Grasslands Comf. 9:831-842.

Pienaar, U. de V., P. van Wyk, and N. Fairall. 1966. An aerial census of elephant and buffalo in the Kruger National Park, and the implications thereof on intended management schemes. Koedoe. 9:40-107.

Priestley, N. de B. 1962. Elephant in North Nigeria. The Nigerian Field. 27(4):170-172.

Quick, H. 1963. Animal population analysis. Chap. 7 in Wildl. Investigational techniques. Henry S. Mosby (ed). The Wildl. Soc. Wash. D.C.

________. 1965. Ecology of the African elephant. Biological Sciences curriculum study pamphlet 21. D. C. Heath & Co. Boston.

Seth-Smith, A. M. D. and I. S. C. Parker. 1967. A record of twin foetuses in the African elephant. E. Afr. Wildl. J. V:167.

Sheldrick, D. 1966. The orphans of Tsavo. Collins and Harvill Press. London. 159pp.

Short, R. V. 1966. Oestrus behaviour, ovulation and the formation of the corpus luteum in the African elephant, *Loxodonta africana*. E. Afr. Wildl. J. 4:56-68.

Sikes, S. K. 1966. The African elephant, *Loxodonta africana*: a field method for the estimation of age. J. Zool. Lond. 150:279-295.

________. 1967. The African elephant, *Loxodonta africana*: a field method for the estimation of age. J. Zool., Lond. 154:235-248.

________. 1968. Habitat stress and arterial disease in elephants. Oryx IX(4):286-292.

Simpson, C. J. H. and B. G. Kinloch. 1954. Elephant numbers and breeding. Annual rept., Game and Fisheries Dept., Uganda. 134-140.

Spinage, C. A. 1963. Elephant numbers. Afr. Wildl. 17(4):325-332.

Taylor, J. L. 1955. The rearing of an African elephant in captivity. Vet. Rec. 67(16):301-302.