

Loxodonta africana. By Larry Laursen and Marc Bekoff

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Loxodonta africana (Blumenbach, 1797)

African elephant

Elephas africana Blumenbach, 1797:125. From a tooth in Göttingen University. Type locality undesignated, subsequently restricted to the Orange River, South Africa, by Pohle, 1926 (see Allen, 1939, for comment).

Elephas capensis F. Cuvier, 1798:149. Type locality Orange River region, South Africa.

Elephas (Loxodonta) oxyotis Matschie, 1900:196. Type locality Upper Atbara River, Anglo-Egyptian Sudan.

E[lephas] cyclotis Matschie, 1900:194. Type locality Yaunde, southern Cameroons.

CONTEXT AND CONTENT. Order Proboscidea, Family Elephantidae. The genus *Loxodonta* Cuvier, 1827, contains two extinct species and one living species: *L. africana*. The popular view is that there are two divisions to the species but considerable overlap is evident (see Remarks). For a summary see Ansell (1971); for a comparison of synonymies see Lydekker (1907), Frade (1955), and Deraniyagala (1955).

africana division ("savannah" or "bush" elephant)

L. a. africana Blumenbach, 1797, see above (synonyms are *angolensis* Frade, *capensis* Cuvier, *mocambicus* Frade, *selousi* Lydekker, *toxotis* Lydekker, *zukowskyi* Strand, *typicus* Blumenbach).

L. a. knochenhaueri Matschie, 1900. Type locality Barikiwa, southern Tanganyika territory (synonyms are *cavendishi* Lydekker and *peeli* Lydekker).

L. a. orleansi Lydekker, 1907. Type locality northern Somaliland (was synonymized with *oxyotis* by Frade, 1955, and Deraniyagala, 1955).

L. a. oxyotis Matschie, 1900, see above (*rothschildi* Lydekker is a synonym); Deraniyagala (1955) placed *cavendishi* with *oxyotis* rather than *knochenhaueri* as was done by Frade (1955).

cyclotis division ("forest" elephant)

L. a. cyclotis Matschie, 1900, see above *albertensis* Lydekker, *cottoni* Lydekker, *fransseni* Schoutenden, and *pumilio* Noack are synonyms).

L. a. pharaohensis Deraniyagala, 1948. Extinct. Type locality is Ptolemais Thermon on Red Sea coast of Ethiopia (*berbericus* Seurat and *hannibaldi* Deraniyagala are synonyms).

DIAGNOSIS. A number of characteristics distinguish the African elephant (*Loxodonta africana*) from the Asiatic elephant (*Elephas maximus*). *Loxodonta* is higher at the shoulder and generally weighs more, although there is some overlap. The African elephant has large ears, its highest body point is the shoulder, there are two fingerlike processes at the tip of the trunk, both sexes carry tusks and are swaybacked. In contrast the Asiatic elephant has small ears, its highest body point is the head which is twin-domed and dished in the forehead, there is only one fingerlike process at the trunk tip, only males generally carry tusks and the back is level or convex. In addition, the African elephant has larger molars and fewer laminae per molar than the Asiatic elephant and the occlusal surfaces are further apart and not parallel as they are in *Elephas maximus*.

GENERAL CHARACTERS. This is the largest living land animal. Size differs slightly according to sex, habitat, and subspecies. Adult females weigh from 2160 to 3232 kg and range from 2.20 to 2.60 m in shoulder height. Adult bulls weigh from 4700 to 6048 kg and measure from 3.20 to 4.01 m in height. Bulls are distinguished from cows by the curved profile of the head, wider forehead (see figures 1 and 2), thicker tusks in proportion to length, distinct saddle-back, and heavier build. There is no scrotum, testes are internal. Cows have an angular profile to the forehead, a narrower forehead (see figure 3), a pair of mammary

glands in the axillae of the forelegs, and a back that is somewhat straighter. General skin color is gray. *L. a. africana* differs from *L. a. cyclotis* (see Remarks) in larger body size, sparser hair covering, triangular-shaped ears rather than smaller round ears, gray skin rather than brown as in the "forest" elephant, and horizontal, thick, curved tusks as opposed to the straight, narrow, downward-pointing tusks of *L. a. cyclotis* (Frade, 1931, and Morrison-Scott, 1948.)

DISTRIBUTION. Formerly, within the last three centuries, inhabited all of sub-Saharan Africa except for the desert and desert-steppe areas. At present (figure 4) can be found north as far as 12° N, in the Sudan and westward. Elephants occur in isolated areas around Lake Chad, in Mali, and in Mauritania. They range south to South Africa where they are found in the Addo Elephant, Knysna, and Kruger National parks. They no longer occur in most of southern South West Africa (Namibia), Botswana, or (in the north) in Ethiopia or northern Somalia. They are abundant in Kenya, Rhodesia, Tanzania, Zambia, Uganda, and Zaire but are mainly restricted to protected sanctuaries. They occupy many types of African habitat and are found at altitudinal levels from sea level to 3660 m and exceptionally in snow to 4570 m (Stewart and Stewart, 1963).

FOSSIL RECORD. A fossil molar of *Loxodonta africana* containing eight visible laminae (dimensions unreported) was found in a middle Quaternary bed at Ounianga Kebir I, in Chad (20°33' E, 19°03' N) approximately 180 km northeast of Largeau, Chad (Coppens, 1967). Two fossil species of *Loxodonta* have been recognized (Maglio, 1973).

FORM. The skin is creased, folded, and covered with projections called papillae. It grades from the thick corneal or "studded" skin (up to 30 mm thick) of the forehead, dorsum, flanks, legs, rump, and tail; through the warty or bumpy skin of the cheeks, trunk, inside legs, neck, shoulders, and jaw; to the smooth skin of the ears, eyelids, lips and openings of the genitalia, anus, and trunk (Eales, 1925). Keratinisation of the skin resembles the cornification process of mammalian nails and claws and reptilian skin (Spearman, 1970). Horstman (1966) described histological details of the skin.

Hairs are found all over the body and vary in color, length, thickness, and density. Laterally flattened blackish-gray hair reaching 0.76 m in length and 3 to 5 mm in thickness (Sikes, 1971) grow along the dorsal and ventral edges of the tail dock. Eyebrows and eyelashes are composed of long fine hair. Calves have a covering of reddish-brown to black "downy" hair that later is replaced by short, soft bristles. Long soft hair surrounds the ear orifices and lower lip. Short tactile hair covers the trunk.

A pair of axillary mammae, the size and weight of those of an average human female, are located between the forelegs. The milk is less concentrated than that of the smaller mammals and

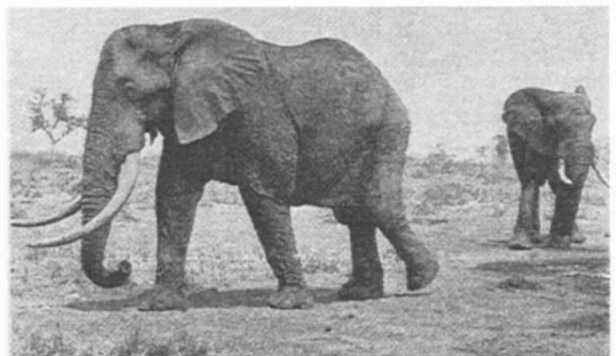


FIGURE 1. Male African elephant, *Loxodonta africana*. Male characteristics evident in the photograph include sway-back, thick long tusks, wide forehead, and curved forehead profile (photograph courtesy of the South African National Parks Board).



FIGURE 2. Family group of African elephants, *Loxodonta africana*. All those with heads visible are females. General female characteristics shown are the angular forehead profile (nuchal eminence), less swaybackedness than in males and thinner smaller tusks. Also note the position of the temporal gland as shown by the stain of the temporal fluid (photograph courtesy of the Zambian Government).

has low protein and fat concentrations. Basic anatomy and physiology have been described by Eales (1925, 1926, 1929), Hill (1955), and Sikes (1971). Limb structure is pillarlike, with limited flexibility at the joints. Because of the structure of the fibrous cushionlike sole of the feet, stance and gait are pseudoplantigrade rather than semiplantigrade as they might appear without the cushion. Medullary bone cavities and marrow are generally lacking. Skulls are massive pneumatised structures with many air sinuses (figure 5). The cerebral cavity of about 6500 cm² lies posteroventrally in the skull. Individual variations in vertebral formula occur. The thorax shape resembles that of the horse.

The dental formula is $i\ 1/0, c\ 0/0, p\ 3/3, m\ 3/3$. Deciduous premaxillary incisors or "tushes" (5 to 12 cm) are present at birth and are replaced after a year by a pair of continually growing tusks. Record tusk length is 11.5 feet (3.45 m) and record single weight is 259 lbs. (117 kg) (Best, 1969). Present-day average is approximately 35 lbs. (16 kg) according to Brooks and Buss (1962b). The tusks are entirely of ivory or dentine after a conical cap of smooth enamel is worn away. Tusk pulp consists of mesenchymal connective tissue containing lymph and blood sinuses. Elephant ivory is identified by a system of criss-crossing lines, visible in transverse section, that divide it into a diamond-shaped pattern. The six grinding teeth are referred to as molars I to VI (Morrison-Scott, 1948). They grow and move forward, replacing each other in the jaw throughout life. Each molar has a composite, ovoid, multiple root structure and a flattened crown that wears down to produce a ridge-patterned grinding surface. Sizes and weights of each molar are given in Table 1. Further details on dentition were given by Sikes (1971). Elephants with supernumerary or malformed tusks are occasionally found.

Muscles of the neck and body differ little in general arrangement from that of the horse. Detailed treatment was given by Eales (1925, 1926, and 1929). Head muscles were described by Sikes (1971). The main trunk muscle, *Levator proboscidis*, arises from the frontals above the junction with the nasals and runs longitudinally down the dorsal side of the trunk to the fingerlike processes at the tip (see General Characters). The *depressores proboscidis*, the ventral trunk muscles, arise from the premaxillae and are directed longitudinally and laterally in the outer lamina and reversed in direction in the deep lamina.

The heart (27.5 kg), as in the Indian elephant and unlike that of other mammals, is apically bifurcated and possesses paired anterior vena cava (Sikes, 1971). Red blood corpuscles are large (9.5 to 9.6 μm in diameter), but the almost total absence of bone marrow makes their origin uncertain.

The brain, which is near full adult weight and size at birth, weighs 4.2 to 5.4 kg in males and 3.6 to 4.3 kg in females (Sikes, 1971). Its weight, relative to that of the body, does not compete with man or anthropoid apes (Frade, 1955). The central and pe-

ripheral nervous systems and the endocrine system are situated and function in the normal mammalian pattern. Histological examinations of the thyroid (Boyd, 1963), pituitary gland (Johnson, 1964) and adrenal gland (O'Donoghue *et al.*, 1967) and biochemical analyses of the adrenal lipids (Moore and Sikes, 1967) show that they resemble those of man.

The nasal passages start at the nares of the trunk tip, pass the olfactory mucous membrane clothing the vertically oriented ethmo-turbinals of the trunk and lead to the larynx. Vocal cords (50 to 70 mm long) are strong and situated in a pharyngeal groove. Lungs are large, the right is usually larger than the left. Rectal temperatures average 97.6°F (36.4°C) and intramuscular temperatures 97.5°F (36.3°C) (Buss and Wallner, 1965).

The stomach (36 to 45 kg) is approximately 1.2 m long and 0.4 m wide (Hill, 1955). The spleen averages 9.5 kg (Sikes, 1971). Intestinal tracts have a combined length of 18 m. The liver varies in weight from 36 to 45 kg in cows and 59 to 68 kg in bulls (Sikes, 1971). There is no gall bladder. The pancreas is 0.5 m long and weighs between 1.5 and 2.0 kg (Sikes, 1971).

The male reproductive system differs from that of other mammals by having no distinct epididymis. Testes, 3 kg each (Johnson and Buss, 1967), are retained intra-abdominally throughout life. The penis (ca 49 kg) is well developed and muscular (Short *et al.*, 1967). Morphologically, spermatozoa resemble those of a horse (Johnson and Buss, 1967). Testicular testosterone levels vary seasonally from 490 μg per 100 g to 3 μg per 100 g (Buss and Johnson, 1967). The female reproductive system has been described by Perry (1964), Buss and Smith (1966), and Short (1966). The peniform clitoris is conspicuous (0.5 m long) and together with the anterior location of the vulva parallels the reproductive anatomy of the female spotted hyena (*Crocuta crocuta* Erxleben). Foetal membranes and placenta were described by Amoroso and Perry (1964). Biochemical and histological studies of the corpora lutea were conducted by Short (1966) and Short and Buss (1965).

The temporal gland (see Behavior) resembles salivary tissue, grows during life, and may reach 1.5 kg in weight (Johnson and Buss, 1967).

Ears have a fanlike arrangement of subcutaneous blood vessels on the medial side (see Function).

FUNCTION. Hair around the ears as well as the long eyelashes afford protection from foreign objects during movement and feeding. Hair on the trunk is associated with nerve endings providing discriminatory tactile sensations (Eales, 1926). Because of limited joint mobility and structure of the limbs, movements are slow and deliberate. Walking pace of 6 km per hr may be hurried to a shuffling gait, but not a true run, of 24 km per hr. The head cannot turn sideways to any great extent. The pneumatised bone

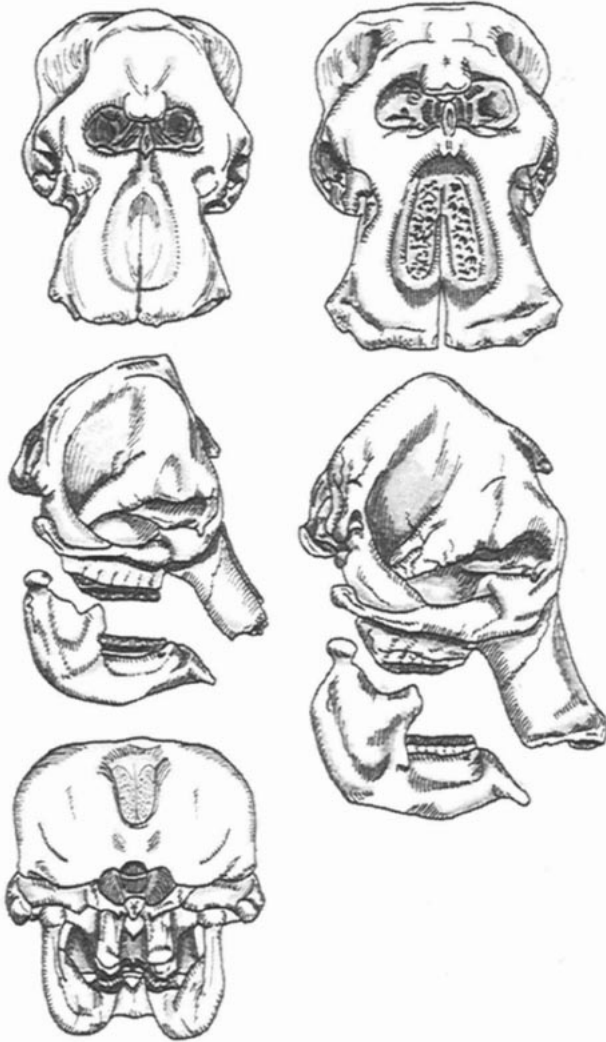


FIGURE 3. Skulls of African elephant (*Loxodonta africana*). Female skull minus tusks (at left, viewed from front, side and back). Male skull minus tusks (at right). The forehead of the bull viewed laterally has convex frontals and parietals and curves smoothly to the anterior nares. In contrast the cow's forehead is flat and dished and there is a nuchal eminence at the summit. This is an important characteristic for sexing elephants in the wild. See also figures 2 and 5.

and multiple sinuses of the skull assist in making it lighter and easier to hold up. Because auditory acuity is so great it has also been suggested that the sinuses somehow improve hearing (Sikes, 1971).

Both the trunk and mouth are used in breathing. Respiration is produced entirely by movements of the chest musculature and therefore any prolonged pressure against the brisket can result in suffocation (Pienaar *et al.*, 1966b). African elephants have been known to survive temperatures from 120°F (49°C) to -20°F (-29°C) (Sikes, 1971), however they suffer heavily from sunstroke and dehydration if exposed (Sikes, 1969). Blood vessels in the ears have been shown to function in temperature regulation (Buss and Estes, 1971).

TABLE 1. Measurements of complete lower right molars of East African elephants as collected by Sikes (1971).

Molar no.	Maximum grinding length (mm)	Maximum grinding width (mm)	Maximum weight (g)
I	24	11	9.6
II	55	25	73.3
III	95	43	180-190
IV	135	55	950
V	175	75	2440
VI	210	75	3740

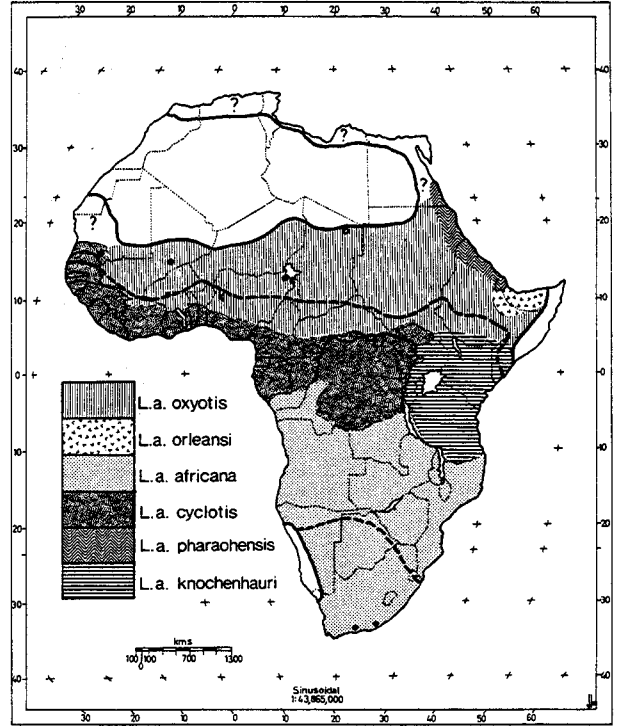


FIGURE 4. Map of Africa showing the distribution of *Loxodonta africana* and its subspecies. Solid lines show former range, dashed lines the present range, solid circles some present by isolated populations outside the general range, and open circle a Pleistocene fossil site.

Jaw motion is antero-posterior. Although defecation takes place hourly, Bax and Sheldrick (1963) found that the stomach of a tame elephant was emptied every 12 hours.

The penis is large and highly muscular. Although copulation takes place "a posteriori," the vulva of the female is situated anterior to the hind legs (Short *et al.*, 1967).

Tusks are utilized during fighting, digging, eating, and marking (see Behavior). The trunk is a multipurpose instrument used in communication, feeding, drinking (holding up to 5 liters), dig-

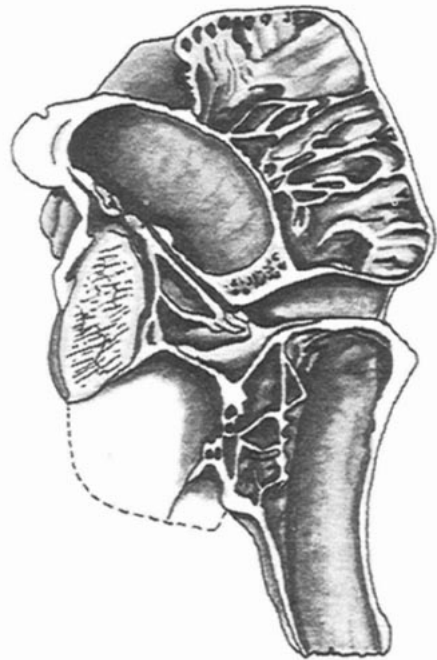


FIGURE 5. Longitudinal cross section of the skull of an African elephant (*Loxodonta africana*) showing position of sinuses and cerebral cavity.

TABLE 2. Some studies of the African elephant (*Loxodonta africana*) dealing with various ecological parameters in differing habitats.

Researcher(s)	Area of study	Subject matter
Brooks and Buss (1962a)	Uganda	Distribution and ranges
Buechner <i>et al.</i> (1963)	Kabalega National Park, Uganda	Seasonal distribution
Buss and Brooks (1961)	Uganda	Population dynamics
Buss and Savidge (1966)	Uganda	Seasonal distribution
Croze (1974a)	Serengeti National Park, Tanzania	Bull movement and population dynamics
Croze (1974b)	Serengeti National Park, Tanzania	Vegetation destruction
Douglas-Hamilton (1973)	Lake Manyara National Park, Tanzania	Vegetation destruction and population dynamics
Field (1972)	Ruwenzori National Park, Uganda	Habitat destruction
Hauk and McIntosh (1973)	Zambia	Population dynamics
Lamprey <i>et al.</i> (1967)	Serengeti National Park, Tanzania	Habitat destruction
Laws (1969)	Mkomazi and Tsavo National Parks	Reproductive cycles
Laws and Parker (1968)	Kabalega National Park, Uganda	Population dynamics and distribution
Laws <i>et al.</i> (1970)	Bunyoro county, Uganda	Detailed ecology
Pienaar (1963)	Kruger National Park, South Africa	Distribution and ecological status
Smith and Buss (1973)	Uganda, Zambia	Reproductive ecology
van Wyk and Fairall (1969)	Kruger National Park, South Africa	Habitat utilization
Wing and Buss (1970)	Forest areas, Uganda	Detailed ecology

ging, and as a general "hand." Its high degree of mobility and well-developed olfactory membranes help detect scent location, quality, and concentration. The tongue tip is tactile in sensory function and is probably used to identify food types. Eyesight is good in dull light but considerably reduced in bright light, then reaching a maximum range of 50 yds (46 m) (Sikes, 1971). Vocal cords allow a wide variety of communicatory sounds (see Behavior).

REPRODUCTION AND ONTOGENY. Courtship and copulation will be described under Behavior. Copulation takes place "a posteriori" with the bulbous penis base locking into the vaginal sphincter (Short, 1966). Testosterone concentration cycles have been shown to exist in bulls, those with the highest concentrations being sexually active around female clans (Buss and Johnson, 1967). Copulation and conception dates gathered throughout Africa show that elephants breed throughout the year with no distinct overall seasonal acceleration (Perry, 1953; Buss and Brooks, 1961; Buechner *et al.*, 1963; Buss and Smith, 1966; Hanks, 1969) although for the most part calves seem to be born in seasons that are best for calf survival (Laws and Parker, 1968; Laws 1969; Smith and Buss, 1973). Implantation of the fertilized egg is of the central type and usually occurs in the part of the uterus where the horns are fused.

Gestation lasts approximately 22 months (649 to 661 days, Lang, 1967). Little is known of the early stages of embryo development but detailed studies of the foetal membranes and placenta have been made by Amoroso and Perry (1964).

Parturition takes place away from the clan; the mother and frequently another female go off alone and prepare a soft spot in the ground by loosening the dirt with their forefeet. The mother stands during birth and drops the calf head-first, rupturing the umbilical cord in the process. At birth a male may weigh up to 120 kg and a female between 90 and 100 kg (Sikes, 1971). Both sexes

measure approximately 1.2 m from occiput to tail. Twinning has been reported at a general rate of 1 to 2% (Seth-Smith and Parker, 1967; Laws and Parker, 1968; Laws, 1969). At birth the bluish-gray skin of the infant is loose, wrinkled, and hairy and the large ears are pressed close to the head. There is no ability in controlling the trunk. Within 15 to 29 minutes the neonate can stand and will follow the mother back to the family unit where it is thoroughly inspected by the other members. From that point on it will follow its mother closely. Suckling, which lasts on the average from two to three years (range one to nine, Laws, 1969), occurs at frequent intervals during which only small quantities of milk are taken. Cow-calf and calf-herd relationships are described under Behavior.

Growth continues throughout life over a potential life-span, dependent on ecological parameters, of 55 to 60 years. Puberty, also dependent on ecological factors, is reached by both bulls and cows between eight and 13 years (Buss, 1961; Pienaar *et al.*, 1966a; Johnson and Buss, 1967; Laws, 1969; Smith and Buss, 1973). Pubertal bulls leave the family units. The female can be a monovular or polyovular polyestrous animal (Hanks and Short, 1972) with estrus cycles lasting for two to three weeks over a two-month period. Estrus itself lasts from 24 to 48 hours (Short, 1966). Corpora lutea are added to the ovaries each time and accumulate until fertilization intervenes. There are no visible external signs of estrus. Cows may average four calves during their lifetime (range one to nine, Laws 1967), the number dependent on environmental influences.

As the adults become older, movement is more deliberate, the skin takes on a baggy and more wrinkled appearance, shoulder blades and protrusions of the skull become more prominent and the sixth molar is worn down so that only water vegetation can be chewed. Eventual death results from human predation, disease, starvation, and natural accidents such as falls or drowning.

ECOLOGY. Man is the only predator that has a limiting effect on elephant populations. Other predators include lions (*Felis leo*), wild dogs (*Lycan pictus*), hyenas, and crocodiles (*Crocodilus niloticus*), which usually prey on isolated calves of less than two years. In general, there is a peaceful coexistence with all animals that share the habitat. Smaller animals that sometimes surprise elephants are not always tolerated. Some fatal encounters with the black rhinoceros (*Diceros bicornis*) have been reported (Nicholson, 1955). Lions and cheetah (*Acinonyx jubatus*) have been chased away from kills over which the elephant has later been reported to stand guard (Grzimek, 1970). They share their distribution and ecological niche with the Cape buffalo (*Synceus caffer*) to which some aggression is sometimes shown. Warthogs (*Phacochoerus aethiopicus*) have been seen grubbing for roots under elephants. Birds, the most common of which is the white egret (*Bubulcus ibis*), are seen on the ground near elephants or on their backs and they presumably feed on skin parasites.

According to Khalil (1922), Westhuyzen (1938), and Sikes (1971), who summarized reports of parasites in elephants, the following have been recorded: two species of flukes (*Trematoda*), 32 species of roundworms (*Nematoda*), 21 species of ticks, one species of lice, three species of botfly and warble, one species of protozoan parasite (*Babesia*) and at least four species of blood-sucking flies (*Anthomyidae*). Botflies and warbles always can be found infesting intestines, subsurface skin layers, and wounds. The tsetse fly (genus *Glossina*) carriers of the protozoan parasites (*Trypanosoma*), which cause sleeping sickness in man, infests elephants to a great degree. There is no evidence however to suggest that the elephant serves as host to any species pathogenic to man.

Various abnormalities of the skin, external organs, skeleton, musculature, and tusks have been summarized by Sikes (1971). Diseases of captive animals include anemia, pneumonia, and tuberculosis. Cardiovascular diseases are habitat related (Sikes, 1969) and include aneurysms, varicose veins, medial sclerosis, and atheroma, all resembling the same diseases in man. Bile stones (Sikes, 1971), virally induced herpes nodules in the lungs (McCully *et al.*, 1971), stomach ulcers (Basson *et al.*, 1971), and fibrosarcoma (Brown *et al.*, 1973) all have been reported. Sunstroke and heat stress affect many elephants. Elephants are also subject to foot and mouth disease (Hedger *et al.*, 1972), rabies, and anthrax (one case of anthrax reportedly transmitted to man (Seideman and Wheeler, 1947)).

Elephants are extremely adaptable to a variety of African environments from semidesert to gallery forest and therefore population dynamics, home ranges, migration, feeding structure, and the influence on the habitat are highly varied. Individual studies in different areas showing this variation are summarized in Table 2. Mean calving intervals from different groups vary from 3.8 to 8.9 yrs. Calf mortality, during the first three years seems continentally uniform at 33 to 38% dropping to 3% per year for the period of three to 45 yrs and rising again to about 10% after that (Buss and Brooks, 1961; Pienaar *et al.*, 1966a; Laws and Parker,

1968; and Laws, 1969). In forest or woodland habitats there are no serious competitors. When restricted to grassland or degenerative savannah woodland, competitors include the black rhinoceros, hippopotamus (*Hippopotamus amphibius*), Cape buffalo, and lesser grazers and browsers.

Seasonal migrations of several hundred miles formerly took place from gallery forest to open savannah or from high to low altitudes. At present the elephant is confined to protected areas where movement is restricted. Immigration into protected areas has caused high density and overtaxation of many habitats. In general, prolonged restrictions interfering with the tendency to migrate and prolonged isolation and restriction of dietary habits appear to reduce overall viability. At present there are approximately 60 national parks and game reserves as well as numerous controlled areas throughout Africa where elephants are governmentally protected. Here military and police patrols guard the animals. Ecological study centers, financed largely from abroad exist in each and monitor all parameters. Elephant control policies have become controversial and complex. Large scale cropping schemes have been advocated in many areas because of habitat destruction.

Approximately 50 gallons (225 l) of water are taken in daily. Salt licks are utilized where available. The diet includes bark, fruit, grass, herbs, and tree foliage of a number of species, and may differ from one area to another. Listings of food utilized are referred to in Table 3. Some toxic plants (*Thevetia peruviana* and *Tribulus terrestris*) have been eaten without effect (Dougall *et al.*, 1964), others (*Euphorbia tirucalli*) have caused death (Perkins, 1947). Coprophagia has been reported in a semicaptive individual (Dougall and Sheldrick, 1964).

Elephants have probably always been utilized by man when available. Pit-falls, falling weighted spears, hamstringing, poison arrows, wheel traps, trunk-snares, and fire have been and still are used by the indigenous peoples. Early exploitation from outside Africa came from the Romans in the north and the ivory traders in the West and East. By 1830, the Boers had exterminated all the elephants in the Cape Province except for two isolated populations in Knysna and Addo (now national parks). By 1885, the Trekboers had wiped out the herds south of the Zambezi. Early Arabs, Swahilis, and Europeans began the extermination in East and Central Africa. A treaty was signed in 1901 by some African colonies stopping the extermination of wildlife. Laws were passed but did not stop the slaughter, and up until 1950 approximately 17,400 elephants were shot annually in East and Central Africa (Hill, 1955). Elephants are still subject to cropping, culling, scientific sampling, sport hunting, and poaching.

Elephant ear leather is made into handbags, wallets, boots and other leather products, tail hairs are woven into bracelets and feet are converted into bar stools and lamp bases. Ivory was formerly used for billiard balls, dice, and piano keys and still is used for carvings. Ivory dust was reputed to have medicinal properties as a vermicide and emetic. Ivory poaching is on the increase with at least 1000 elephants reported killed per month in Kenya alone in 1973 (Spinage, 1973). The price of ivory has risen from \$2.80 to \$45 per lb. in a few years. The history of ivory exploitation is well described by Spinage (1973). Ivory is sold both legally and illegally through Mombasa, Zanzibar, Dar-es-Salaam, London, Bombay, and Hong Kong.

Domestication of the African elephant for military purposes began with Ptolemy II along the Red Sea and later at Adulis in Ethiopia and continued until 217 BC when a superior force of more easily tamed Indian elephants was captured at the Battle of Raphia. Hannibal used African elephants from the Atlas mountains against the Romans until he was defeated in 202 BC near Carthage. In 1900, King Leopold II of Belgium established a training station for elephants in the Congo (now Republic of Zaire), which still operates at Gangala na Bodio (3°40' N, 29°10' E) on a small scale for local work. Training of 12 to 15 year olds takes 10 to 12 months (Huffman, 1931).

Handrearing of young orphan elephants is difficult. Some have successfully been reintroduced into herds (Woodford and Trevor, 1970).

Elephants have been captured in ethological and ecological studies for marking and relocating by means of drugged darts fired from a crossbow or rifle. The most successful drug has been M-99 (6,14-endoetheno-7 α (2-hydroxyl-2-pentyl)-tetrahydronororipivane) a morphine-based drug with an analgesic activity 6000 times that of morphine. The drug used to reverse the effects of M-99 is the related derivative M-285 (N-cyclopropyl-methyl-6,4-endoetheno-7(2-hydroxyl-2-propyl)-tetrahydronororipivane). Dosages and mixtures of M-99 and M-285 as well as other drugs used have been discussed by Harthoorn (1963) and Pienaar *et al.* (1966b). Overdoses of M-99 have been used in culling operations.

Marking practices include painting numbers on the hide and attaching streamers to the ears. Censusing, recording, and monitoring of most African elephant populations have been car-

TABLE 3. Sources listing plant species utilized as food by African elephants (*Loxodonta africana*) in different areas and habitats.

Area	Author	Subject Matter
Captivity	Reuther (1969)	Foods utilized
Kibale Forest, Uganda	Wing and Buss (1970)	Species listing and free size preference
Kruger National Park, South Africa	Pienaar <i>et al.</i> (1966a)	Preferences
Mara-Masai National Park, Kenya	Lamprey (1963)	Species listing, preferences
Ruwenzori National Park, Uganda	Field and Laws (1970)	Preferences
Ruwenzori National Park, Uganda	Field (1972)	Species listing, chemical composition and seasonal diet
Serengeti National Park, Tanzania	Lamprey <i>et al.</i> (1967)	Species listing and destruction
Serengeti National Park, Tanzania	Croze (1974a)	Preferences and destruction
Tsavo National Park, Kenya	Bax and Sheldrick (1963)	Species listing, chemical composition and preferences
Tsavo National Park, Kenya	Dougall and Sheldrick (1964)	Species listing, chemical composition and preferences
Tsavo National Park, Kenya	Dougall <i>et al.</i> (1964)	Species listing, chemical composition
Uganda Forest Areas	Buss (1961)	Species listing, consumption and preferences
Uganda Forest Areas	Laws <i>et al.</i> (1970)	Species listing, chemical composition and seasonal diet

ried out on the ground or in the air with relatively good success. The use of a helicopter has been advocated in such instances because it allows for recounts, excellent photographs, and analysis of herd structures (Pienaar *et al.*, 1966a).

Large cropping schemes and subsequent field autopsies involving thousands of elephants have supplied data on population dynamics and physiology (Laws *et al.*, 1970). To date most research has been ecological in nature. For description of ethological research methods, see Behavior.

BEHAVIOR. The African elephant is a social animal. The basic "family" unit of three to five members is composed of a female and her offspring (Buss, 1961; Laws and Parker, 1968; Sikes, 1971; Douglas-Hamilton and Douglas-Hamilton, 1975). "Clans" numbering from six to 70 individuals are made up of "families" of sisters and daughters and led by the dominant sister, the alpha-female. Adolescent bulls, age 12 to 15 years, are forced from the families and in turn join loosely bound groups made up of sexually immature, mature, and retired bulls (Croze, 1974a). One to three bulls, led by the A-bull may be seen temporarily following clans at a distance, usually for reproductive or sexual purposes only, taking no part in social leadership. Solitary bulls, possibly sexually retired or "rogueish" are often seen, whereas senile females remain in the clans until they die. A less stable group is the "congregation," formed of a number of clans, numbering up to 1240 that usually stay together for only about one week (Wing and Buss, 1970). The extremely high social cohesiveness in clans can be attributed to mutual protection, competition for resources, and social facilitation in learning (Glover, 1963; Pienaar *et al.*, 1966a; Laws and Parker, 1968; Douglas-Hamilton and Douglas-Hamilton, 1975).

The dominance of the alpha-female, usually the largest animal in the clan, is never disputed, and when she dies or is killed her eldest daughter (beta) usually takes over her position even though the alpha-cow's sister (beta-beta) may be present (Sikes, 1971). Bull herd dominance patterns and group composition change frequently. Size, rank, temperament, and role all play a part in determining the dominant bull (Hendrichs, 1971; Croze, 1974a). Fighting between bulls takes two forms. "Mock" battles, usually found in minor leadership dominance disputes or between

young immature bulls, can be likened to wrestling. The object is to raise the head higher than that of the opponent and to push with the base of the trunk down onto the top of his. The end of the fight may be signalled by the loser kneeling down with his ears spread in front of his opponent (Kühme, 1963). "Serious" battles are unritualized and usually occur during disputes over "territorial" (harem) possession and reproduction. Such fights are initiated by a charge and the fatal use of tusks is common. Conflict between attack and escape at this time may be shown by headshaking, the throwing of objects with the trunk and kneeling and digging the ground with the tusks (Kühme, 1963). The end of the dispute is signalled by the retreat or death of the loser. Fighting between cows or between a cow and a bull have not been reported and cows have not been seen to enter a bull herd domain (Croze, 1974a).

Females defend themselves and their families by means of threat postures and if necessary by attack. The threat posture is shown by a raised head and trunk and extended ears in combination with a twitching tail, weaving of the body from side to side, scraping the soil with the forefeet, and a shrill scream from the trunk (Kühme, 1963). When threat fails, a "mock" charge may be made. The head is held high, the ears extended, the trunk in a "teaspout" form sniffing for identification and an advance at a rapid shuffling gait is made for about 27 m (Kühme, 1963; Sikes, 1971). A serious charge, also seen in bulls, is distinguishable from the "mock" by a lowered head, the rolling of the trunk up against the body and the pointing of the tusks at the enemy. Screaming or growling is heard and the trunk may touch the temporal gland (Kühme, 1963; Grzimek, 1970).

An A-bull who has sexual privileges over a clan marks trees and bushes around the group while he is with them, with a secretion from his temporal gland or with his mouth mucosa or by scarring trees with his tusks. Intruders are chased away or challenged although the consort bulls with him and immature bulls are tolerated. He will usurp them if they try to mount a cow before he does (Buss and Smith, 1966; Short, 1966). The estrus state of a cow is sensed by the bull by smelling her urine or vulval area (Kühme, 1961). In courtship the bull approaches the female and caresses her with his trunk at the same time nudging her rump with his tusks as his trunk lays along her back. The cow runs off with the bull in chase. He then stops her retreat and they place their heads together, intertwining their trunks and "caressing" each other. The bull begins nudging again and the cow then presents her hindquarters to him. The copulatory act commences as the bull raises his forelegs onto the cow's back and extends his convexly curved penis to the vulva. The female clitoris simultaneously erects and forces the vulva down and backwards. The bull then rises on his hindlegs and thrusts forward against the cow's hindquarters, his tail stiffly stretched out and his forelegs extended parallel straight along her dorsum. Mounting and copulation may last 120 seconds. Repeated copulations at intervals of 10 to 20 minutes have been witnessed. Intervening periods are spent browsing. Estrus cows may be mounted by more than one bull. Males thwarted in mounting attempts by another bull or the cow herself have been seen to roll themselves along urine soaked ground or hollows (Kühme, 1963; Buss and Smith, 1966).

There are three categories of elephant communication: "distance" signals informing others of food location or distress; "close range" signals involving feeding, reproduction, infant care, defense, aggression, and other emotions; and "time dependent" signals such as olfactory markings. Olfactory communication figures prominently in individual and mother-infant recognition, in the determination of the reproductive state of females, and possibly in demarcation of a bull's "territory." During visual communication, the head, ears, and trunk are used in various combinations (Kühme, 1963). Tree scars also may be visible. Tactile communication, although difficult to interpret, is seen in mother-infant interactions and courtship behavior. Vocal communication can be broken down into two forms: contact maintenance sounds, such as in feeding or drinking, digestion, elimination, and ear-flapping, and vocal sounds that originate from the trunk or larynx. Air blasts and trumpeting from the trunk signal aggression. Sounds from the larynx, which may be described as roaring and screaming, indicate aggression or pain; growling signals disturbance or aggression; rumbling is a sound of unknown function that the entire herd may perform in unison; gurgles or "chortles" are made by infants at play; soft chirps indicate submission or intimidation, and squealing signals fright in infants.

For the first three years of its life an infant is suckled by its mother or foster mother and most interactions are with her. At this stage infants are often seen playing with branches and objects that move. By year three the calf is more independent of its mother and may be helped over or around barriers by other family or clan members, especially juveniles (Sikes, 1971). At this time, the indiscriminant use of the threat display becomes noticeable. By years seven or eight, young animals establish their own behavioral repertoire.

Learning probably occurs through trial-and-error, observation, and insight. Because of tight social organization and the long life of an elephant, information about water and food resources and certain learned behaviors probably are passed on by observation and positive reinforcement to others in a group, thus becoming part of the population information pool, which in turn is passed on through generations. Elephants are highly intelligent and have been observed both using (Kühme, 1963; Nicholson, 1955; Grzimek, 1970) and manufacturing (Gordon, 1966) tools.

Drinking may take place at any time of day and the timing usually is influenced by availability. Water is sucked into the trunk and squirted in a jet stream into the mouth. Year old infants drink directly with their mouths. In dry conditions, shallow water holes may be dug in riverbeds and holes, the diameter of the trunk, are dug down to the water level, where conditions allow. Elephants have been reported to plug these holes with balls of chewed bark (Gordon, 1966). At sodium salt licks the soil may be dug up with the tusks or feet and stirred in with the water or eaten in chunks (Grzimek, 1970; Henshaw and Ayeni, 1971; Weir, 1973).

Feeding is a constant process with a peak in the morning. Elephants are continually on the move while feeding. Food sources are searched over with the trunk tip and selected items are chosen and eaten. Only upper shoots of grass are eaten (Buss, 1961; Bax and Sheldrick, 1963). Bark is chewed for its juice and the fiber is then spit out. Thorns are flattened by passing the branch through a loop in the trunk or between the trunk and a tusk. Tall trees are toppled by pushing with a raised trunk against the stem so that the crown or the roots may be reached. Taste seems to be selective (Croze, 1974b) and once toppled a tree may just be left. At other times it is devoured until only wrist-size branches remain. Individual food sources such as trees are often shared and no dominant feeding pattern arises (Croze, 1974a).

In their natural habitat elephants appear to sleep or doze once at noon, and then go through a deeper sleep during the early morning hours for a daily total of about four hours (Kühme, 1963; Wyatt and Eltingham, 1974). Grooming takes two forms in that elephants may coat themselves liberally with mud by rolling in it or they may splash themselves with water, indulging in playful behavior at the time, and then throw dirt and grass on their head, neck and backs with their trunks. Once dried the earth-pack will be scraped off against trees or anthills. This is often done daily and besides helping to prevent excess body water loss, may also serve to remove ectoparasites.

Elephants have been reported to assist wounded comrades by supporting them between two adults and helping them to move away (Nicholson 1954; Pienaar *et al.*, 1966b). Attempts to lift dead or fallen elephants using the tusks have also been reported (Nicholson, 1954; Buss, 1961; Douglas-Hamilton and Douglas-Hamilton, 1975) along with observations of elephants "burying" both dead elephants and humans with branches and bushes (Nicholson, 1954; Grzimek, 1970). A clan may gather around a dead family member for hours on end (Nicholson, 1954; Buss, 1961; Sikes, 1971). Elephants have been reported scattering and breaking up bones and tusks of elephant skeletons they come across (Grzimek, 1970; Douglas-Hamilton and Douglas-Hamilton, 1975). No explanations have been proposed.

Ethological studies have involved the use of radio transmitters on individuals to study territories and social organization (Leuthold and Sale, 1973; Douglas-Hamilton and Douglas-Hamilton, 1975), observation of captive animals and the subsequent documentation of reproductive and dominance behavioral repertoires (Kühme, 1961, 1963), and field studies using observations and individual member identification through ear patterns and tusk individualities to understand social interactions (Croze, 1974a; Douglas-Hamilton and Douglas-Hamilton, 1975).

GENETICS. Cultured somatic cells of both the African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants have a modal diploid chromosome number of 56 (Hungerford *et al.*, 1966/67). Karyotype differences between the two have not been reported. The X and Y sex chromosomes are clearly identifiable (Thuerig, 1970).

REMARKS. Probably too many subspecies are recognized. Some were described on the basis of only a few partial specimens. The two subspecies generally recognized are *L. a. africana* and *L. a. cyclotis* (Sikes, 1971).

The existence of distinct "pygmy" elephants (Morrison-Scott, 1948; Blancou, 1962) and "water" elephants (Trouessart, 1911) is unproven.

Sikes (1971) provided an excellent description of the physiology and natural history of the African elephant. Douglas-Hamilton and Douglas-Hamilton (1975) summarized for popular consumption the results of their detailed behavioral studies at Lake Manyana. Hill (1955) provided information on the indigenous elephants of East and Central Africa prior to 1953. Laws *et al.* (1970) detailed the results of their extensive ecological survey in

Northern Uganda and proposed some answers to ecological problems. Laursen (1975) summarized work on African elephant ethology and its ecological parameters throughout Africa and provided an extensive bibliography of elephant studies prior to 1975.

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