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**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 comments).

*Elephas capensis* F. Cuvier, 1798:49. Type locality Orange River region, South Africa.

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

*Elephas* (Loxodonta) 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 synonyms 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, mobuncensis Frade, selous Lydekker, toxotes Lydekker, zooksyki Strand, typicus Blumenbach).

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

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

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

**cyclotis division** (“forest” elephant)

*L. a. cyclotis* Matschie, 1900, see above albertensis Lydekker, cottoni Lydekker, fransensi Schoutendyn, and pumilie Noack are synonyms.

*L. a. pharaohensis* Deraniyagala, 1948. Extinct. Type locality is Ftolemais Thermon on Red Sea coast of Ethiopia (berbericus Seurat and kannubidi 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, and it has 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 occipital 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 3222 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, Kransna, and Kruger National Parks. They no longer occur in most of southern 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 Oumanga Kebir I. in Chad (20°33' E, 19°03' N) approximately 180 km northeast of Langerae, 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 corny 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 leg, neck, shoulders, and jaw; to the smooth skin of the ears, eyelids, lips and openings of the genitalia, anus, and trunk (Eales, 1928). Keratinization 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 mm in length and 3 to 5 mm in thickness (Sikes, 1971) grows 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 mammarys, 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

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**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).
has low protein and fat concentrations. Basic anatomy and physiology have been described by Eales (1925, 1926, 1929), Hill (1932), and Sikes (1971). Limb structure is pillar-like, with limited flexibility at the joints. Because of the structure of the fibrous cushion-like sole of the feet, stance and gait are semiplantigrade rather than semiplantigrade as they might appear without the cushion. Medullary bone cavities and marrow are generally lacking. Skulls are massive pneumatized structures with many air sinuses (figure 5). The cerebral cavity of about 6500 cm³ lies posterovertrally in the skull. Individual variations in vertebral formula occur. The thorax shape resembles that of the horse.

The dental formula is 1/1, 0/0, p 3/3, m 3/3. Deciduous premolar 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 (Frida, 1955). The central and peripheral 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'Donaghey et al., 1967) and biochemical analyses of the adrenal lips (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 Waller, 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 pneumatized bone
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 (Plenaar et al., 1966). 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).

<table>
<thead>
<tr>
<th>Molar no.</th>
<th>Maximum grinding length (mm)</th>
<th>Maximum grinding width (mm)</th>
<th>Maximum weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>24</td>
<td>11</td>
<td>9.6</td>
</tr>
<tr>
<td>II</td>
<td>55</td>
<td>25</td>
<td>75.3</td>
</tr>
<tr>
<td>III</td>
<td>95</td>
<td>43</td>
<td>180–190</td>
</tr>
<tr>
<td>IV</td>
<td>135</td>
<td>55</td>
<td>950</td>
</tr>
<tr>
<td>V</td>
<td>175</td>
<td>75</td>
<td>2440</td>
</tr>
<tr>
<td>VI</td>
<td>210</td>
<td>75</td>
<td>3740</td>
</tr>
</tbody>
</table>

**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 3.

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

<table>
<thead>
<tr>
<th>Researcher(s)</th>
<th>Area of study</th>
<th>Subject matter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brooks and Buss</td>
<td>Uganda</td>
<td>Distribution and ranges</td>
</tr>
<tr>
<td>Buechner et al. (1963)</td>
<td>Kabalega National Park, Uganda</td>
<td>Seasonal distribution</td>
</tr>
<tr>
<td>Buss and Brooks (1961)</td>
<td>Uganda</td>
<td>Population dynamics</td>
</tr>
<tr>
<td>Buss and Savidge (1966)</td>
<td>Uganda</td>
<td>Seasonal distribution</td>
</tr>
<tr>
<td>Croze (1974a)</td>
<td>Serengeti National Park, Tanzania</td>
<td>Bull movement and population dynamics</td>
</tr>
<tr>
<td>Croze (1974b)</td>
<td>Serengeti National Park, Tanzania</td>
<td>Vegetation destruction</td>
</tr>
<tr>
<td>Douglas-Hamilton (1970)</td>
<td>Lake Manyara National Park, Tanzania</td>
<td>Vegetation destruction and population dynamics</td>
</tr>
<tr>
<td>Field (1972)</td>
<td>Ruwenzi National Park, Uganda</td>
<td>Habitat destruction</td>
</tr>
<tr>
<td>Hauk and McIntosh (1973)</td>
<td>Zambia</td>
<td>Population dynamics</td>
</tr>
<tr>
<td>Lampey et al. (1967)</td>
<td>Serengeti National Park, Tanzania</td>
<td>Habitat destruction</td>
</tr>
<tr>
<td>Laws and Parker (1968)</td>
<td>Kabalega National Park, Uganda</td>
<td>Population dynamics and distribution</td>
</tr>
<tr>
<td>Laws et al. (1965)</td>
<td>Bunyoro county, Uganda</td>
<td>Detailed ecology</td>
</tr>
<tr>
<td>Pienaar (1963)</td>
<td>Kruger National Park, South Africa</td>
<td>Detailed ecological status of Africa</td>
</tr>
<tr>
<td>Smith and Buss (1975)</td>
<td>Uganda, Zambia</td>
<td>Reproductive ecology</td>
</tr>
<tr>
<td>Van Wyk and Fairall (1969)</td>
<td>Kruger National Park, South Africa</td>
<td>Habitat utilization</td>
</tr>
<tr>
<td>Wing and Buss (1970)</td>
<td>Forest areas, Uganda</td>
<td>Detailed ecology</td>
</tr>
</tbody>
</table>

Table data:

- The table lists various studies conducted by different researchers on the African elephant, focusing on ecological parameter differences in various habitats.
- Researchers include Brooks and Buss, Buechner et al., Buss and Brooks, Buss and Savidge, Croze, and others.
- The studies cover areas such as Kabalega National Park, Lake Manyara, Ruwenzi National Park, and various regions in Africa.
- The ecological parameters include distribution, seasonal changes, population dynamics, and reproductive cycles.

ECOLOGY. Man is the only predator that has a limiting effect on elephant populations. Other predators include lions (Felis leo), wild dogs (Lycaon pictus), hyenas, and crocodiles (Crocodylus niloticus), which usually prey on isolated calves of less than two years of age. In general, there is a peaceful coexistence with all animals that share the habitat. Smaller animals that are not considered a threat to elephants are not always tolerated. Some fatal encounters with the black rhinoceros (Diceros bicornis) have been reported (Nicholson, 1985). Lions and cheetahs (Acinonyx jubatus) have been chased away from kills over which the elephant has later been reported to stand guard (Grimek, 1970). They share their distribution and ecological niche with the Cape buffalo (Syncerus 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 genera of the family Pinnotheridae, both of which are parasitic on various birds, Rebec et al. (1969) and include aneurysms, varicoses, veins, medial sclerosis, and antheroma, all resembling the same diseases in man. Bile stones (Sikes, 1971), vitally infected herpes nodules in the lungs (McCully et al., 1971), stomach ulcers (Basson et al., 1971), and fibrosarcoma (Brown et al., 1973) have all been reported. Sunstroke and heat stress affect many elephants. Elephants are also subject to foot and mouth disease (Hedges et al., 1972), rabies, and anthrax (one case of anthrax reported to man [Seidman and Wheeler, 1947]).

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 diseases and are usually present in elephants that are not adapted to the African savannah ecosystem. The presence of these diseases varies depending on the area and may not be reflected in Table 2. Mean calving intervals from different groups vary from 3.8 to 8.9 years. Calving mortality, during the first three years seems to be the most critical period, ranging from 33.3 to 28% with a mean calving interval of two years. After the first three years, the calving interval drops to about 43% and increases to about 10% after that (Buss and Brooks, 1961; Pienaar et al., 1966a: Laws and Parker, 1967).
1968; and Laws, 1969). In forest or woodland habitats there are no serious competitors. When restricted to grassland or degraded 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 of areas of dietary habitat have reduced overall viability. At present there are approximately 60 national parks and game reserves as well as numerous controlled areas throughout Africa where elephants are governed. 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 less 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 (Thespesia 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 semi-protective 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 exploration 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 Province except for two isolated populations in Knyasa and Addo (now national parks). By 1885, the Trekboers had wiped out the herds south of the Zambezi. Early African kings 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 headbands, wallets, boots and other leather products, tail hairs are woven into bracelets and feet are converted into bars tools and lamp bases. Ivory was formerly used for billiard balls, dice, and piano keys and still is used for pens. 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. The price of ivory has risen from $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 Proteus II along the Red Sea and later at Adulis in Ethiopia and continued until 217 B.C. 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 B.C. 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 Bodo (3°40' N, 29°10' E) on a small scale. Training of 12 to 15 year olds takes 10 to 12 months (Huffman, 1931).

Hand-rearing of young orphan elephants is difficult. Some have successfully been introduced into herds (Woodford and Trevor, 1970).

Elephants have been caught 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-endotheno-7o(2-hydroxy-2-pentyl)-tetrahydro
doripavana) a morphine-based drug with an anesthetic activity 60 times that of morphine. The drug is effective for about 5 hours. The related derivative M-285 (N-cyclopentyl-methyl-6, 4-endotheno-7o(2-hydroxy-2-propyl)-tetrahydronoripavana). Dosages and mixtures of M-99 and M-285 as well as other drugs usable for locational purposes are described by Hartmann (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 carr

| 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      |
| Kilhe Forest,       | Wing and    | Species listing     |
| Uganda              | Buss (1970) | free size preference|
| Kruger National     | Pienaar et al. (1966a) | Preferences |
| Park, South Africa  |              |                     |
| Mara-Masai National | Lamprey (1963) | Species listing,    |
| Park, Kenya         |              | preferences         |
| Ruwenzori National  | Field and   | Preferences         |
| Park, Uganda        | Laws (1970) |                     |
| Ruwenzori National  | Field (1972) | Species listing,    |
| Park, Uganda        |              | chemical composition |
|                     |              | and seasonal diet   |
| Serengeti National  | Lamprey and  | Species listing,    |
| Park, Tanzania      | Buss and    | chemical composition|
|                     | Sheldrick    | and preferences     |
| Serengeti National  | Dougall and |
| Park, Tanzania      | Sheldrick    | Specie listing,     |
|                     | (1964)      | chemical composition|
|                      |              | and preferences     |
| Tsavo National Park,| Bax and     | Species listing,    |
| Kenya               | Sheldrick    | chemical composition|
|                     | (1963)      | and preferences     |
| Tsavo National Park,| Dougall and  | Species listing,    |
| Kenya               | Sheldrick    | chemical composition|
|                     | (1964)      | and preferences     |
| Tsavo National Park,| Dougall et   | Species listing,    |
| Kenya               | al. (1964)  | chemical composition|
|                    |              | and preferences     |
| Uganda Forest Areas | Buss (1961) | Species listing,    |
|                     |              | consumption and     |
|                     |              | preferences         |
| Uganda Forest Areas | Laws et al.  | Species listing,    |
|                     | (1970)      | 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 structure (Pienaar et al. 1966).

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 "rogue"st, are often seen, whereas senile females remain in the clans until they die. A less stable group is the "congrega-

"tion," 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, cooperation 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, 1974c). Fighting between bulls takes two forms. "Mock" battles, usually found in minor leadership dominance disputes or between
Learning probably occurs through trial-and-error, observation, and insight. Because of tight social organization and the long life of an elephant, information and certain learned behaviors are probably passed on by observation and positive reinforcement to others in a group, thus becoming distributed within the population. Information is passed on through generations. Elephants are highly intelligent and have been observed both using (Kühne, 1963; Nicholson, 1955; Grzimek, 1970) and manufacturing (Gordon, 1966) tools.

Drinking may take place at any time of day and thrice daily is influenced by availability. Water is sucked into the trunk and squirited in a jet stream into the mouth. Year old infants drink directly from the water hole. They may be fed by having their mouths filled. The 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 bales of chaffed 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, 1976; Henschaw 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 and selected items are chosen and eaten. Only upper shoots of grass are eaten (Buss, 1961; Bax and Sheldon, 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. Tail hairs are plucked by pushing with a raised trunk against the stem so that the crown or the roots may be reached. Taste seems to be selective (Crozé, 1974) and once topped a tree may remain on the same tree from five to ten days. In defecation, branches remain. Individual food sources such as trees are often shared and no dominant feeding pattern arises (Crozé, 1974).

In their natural habitat elephants appear to sleep or doze off at night, and then spend a deep immobile night sleep for about three hours. Morning hours for a daily total of about four hours (Kühne, 1963; Wyatt and Eltingham, 1974). Grooming takes two forms in that elephants may bathe 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 rolled again off and the animal will feed. During the rainy season 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., 1966). Attempts to lift dead or fallen elephants using the tusks have also been reported (Nicholson, 1955; Buss, 1961; Douglas-Hamilton and Douglas-Hamilton, 1975) along with observations of elephants "burying" both dead elephants and humans with branches and bushes (Nicholson, 1970). A clan of elephants is the largest domesticated animal and 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 elephants and smaller animals (Leuthold and Sale, 1973; Douglas-Hamilton and Douglas-Hamilton, 1975), observation of captive animals and the subsequent documentation of reproductive and dominance behavioral repertoires (Kühne, 1961, 1963), and field studies using observations and individual member identification through ear patterns and task individualities to understand social interactions (Crozé, 1974a; Douglas-Hamilton and Douglas-Hamilton, 1975).

Genetics. Cultured somatic cells of both the African (Loxodonta africana) and Asian (Elephas maximus) species 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 (Thiuring, 1970).

Remarks. Probably too many subspecies are recognized. Some were described as a function of the breeding and the number and origin of the breed. 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 African elephants. Douglas-Hamilton and Douglas-Hamilton (1975) summarized for popular consumption the results of their detailed behavioral studies at Lake Manyara National Park, Tanzania, and information on African 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. Laurisen (1975) summarized work on African elephant ethology and its ecological parameters throughout Africa and provided an account of the history of elephant studies prior to 1973. The authors would like to thank Dr. Irven O. Buss and Dr. John Hanks for their valuable comments on a rough draft of this paper.

LITERATURE CITED


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