

*Eidolon helvum*. By Sheri L. DeFrees and Don E. Wilson

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***Eidolon Rafinesque, 1815***

*Eidolon* Rafinesque, 1815:54. Type species *Vespertilio vampyrus helvus* Kerr, by subsequent designation (Andersen, 1908).

*Pterocyon* Peters, 1861:423. Type species *Pterocyon paleaceus* Peters.

*Leiponyx* Jentink, 1881:60. Type species *Leiponyx büttikoferi* Jentink.

**CONTEXT AND CONTENT.** Order Chiroptera, Suborder Megachiroptera, Family Pteropodidae, Genus *Eidolon*, which includes only the species *E. helvum*.

***Eidolon helvum* (Kerr, 1792)**

Straw-colored Fruit Bat

*Vespertilio vampyrum helvus* Kerr, 1792:91. Type locality not specified; subsequently fixed as Senegal (Andersen, 1907).

*Pteropus stramineus* E'. Geoffroy St.-Hilaire, 1803:48. Type locality not specified; subsequently fixed as Senaar by Koopman (1975).

*Pterocyon paleaceus* Peters, 1861:423. Type locality "Africa"; restricted to Senaar by Matschie (1899).

*Pteropus mollipilosus* H. Allen, 1861:159. Type locality "Gaboon."

*Pteropus palmarum* Heuglin, 1865:34. Type locality "Middle and Upper White Nile and between Senaar and Fazogli along the Blue Nile"; subsequently fixed as Senaar by Koopman (1975).

*Pteropus dupreanus* Schlegel and Pollen, 1867:419. Type locality "Madagascar."

*Xantharpyia leucomelas* Fitzinger, 1866:544. Type locality "Upper Nile lands"; subsequently fixed as Senaar by Koopman (1975).

*Leiponyx büttikoferi* Jentink, 1881:60. Type locality "Liberia, St. Paul's River (Millsburg)."

*Pterocyon sabaesus* Andersen, 1907:505. Type locality "Lahej, Aden" [Saudi Arabia].

*Eidolon helvum*: Andersen, 1912:2. First use of current name combination.

**CONTEXT AND CONTENT.** Context same as for genus. Three subspecies are recognized (Hayman and Hill, 1971):

*E. h. helvum* Kerr, 1792:91, see above (*stramineus* E'. Geoffroy St.-Hilaire, *paleaceus* Peters, *mollipilosus* H. Allen, *palmarum* Heuglin, *leucomelas* Fitzinger, and *büttikoferi* Jentink are synonyms).

*E. h. dupreanus* Schlegel and Pollen, 1866:419, see above.

*E. h. sabaesum* Andersen, 1907:505, see above.

**DIAGNOSIS.** Dobson (1878) united *Eidolon* with *Rousettus* in the genus *Cynonycteris*, but Andersen (1912) demonstrated their distinct generic status. *Eidolon* has a larger p1 and a relatively longer rostrum, character states that might be considered more primitive than those of *Rousettus*, the genus with which it is most closely related (Andersen, 1912). However, the development of a short, bony auditory meatus, distinctly separated premaxillaries (in contact or often fused in *Rousettus*), a lengthened M1, a reduced M2, clearly visible sexual differentiations in color (absent in *Rousettus*), and generally larger dimensions suggest that *Eidolon* is more specialized. *Eidolon* has a greater wing span than *Rousettus*, its wings are more tapered and pointed, and its flight is more linear (Kingdon, 1974). The second digit is clawed as in *Rousettus* and *Pteropus*. Wing membranes extend from the sides of the dorsum and the back of the first toe in *Eidolon* and *Pteropus*. *Eidolon* has a tail less than half the length of the hind foot with 2.0 to 2.5 vertebrae protruding (similar to *Rousettus*, slightly longer than *Myonycteris*); *Pteropus* has no tail. In *Eidolon*, as in *Pteropus*, the basicranial axis is deflected; however, the occiput is neither elongated

nor tubular. The palate broadens posteriorly, is widest between M2 to M2, then narrows at the posterior border to a width approximately equal to that between the lingual edges of P4 to P4. This dimension is much narrower in *Pteropus*. The length of the rostrum is much greater than the lacrimal width of the skull in *Eidolon* as compared to *Pteropus*. In *Myonycteris*, the front of the orbit is located vertically above the anterior portion of M1, whereas in *Eidolon* it is located above the middle to posterior portion of M1 (Fig. 1).

**GENERAL CHARACTERS.** Short pelage covers the head, dorsum, and venter of the straw-colored fruit bat. On the neck the fur is thick, and nearly absent on the face in front of and below the eyes (Fig. 2). The ears are hairless posteriorly with fur at their base (Andersen, 1912). Pelage extends over the upper arm and slightly onto the forearm and upper surface of legs and interfemoral membrane, but not onto the wing membrane (Nowak and Paradiso, 1983;

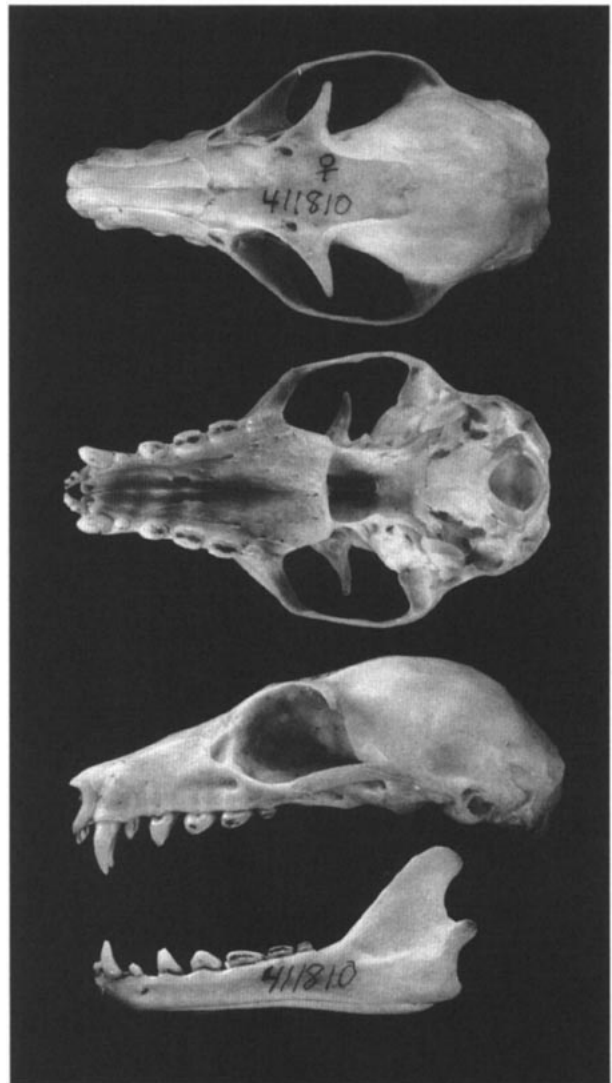


FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of female *Eidolon helvum*, U.S. National Museum of Natural History 411810, from Ghana. Greatest length of skull is 53.6 mm.



FIG. 2. *Eidolon helvum* photographed in Kenya by Merlin Tuttle.

Smithers, 1983). Despite its name, the color of *E. helvum* is not a consistent shade of golden-yellow. Color varies between areas of the body of the same individual as well as between individuals. However, the general appearance ranges from a pale yellow-gray to a dark sepia-gray. Adults usually have a bright orange to deep tawny-colored collar, which is brighter and more pronounced in males (Rosevear, 1965). The young are similar in color to adult males, although generally darker and lacking a collar (Andersen, 1912). Individual hairs are buff at the base and tipped with brown. Hairs on the venter are yellowish-buff laterally and brown in color midventrally. Males appear darker due to the longer brown tips of the hair on the head, lower part of the back, and dorsal side of the tibiae. The hair of the collar is longer than the remainder of the short, fine, close-lying fur.

Wings of this species are long, pointed and somewhat narrow, and are a dark blackish-brown. At rest, the ends of the wings are folded back with the tips folded in; the second phalanges of the third and fourth digits lie flat against the lower surface of the wing (Allen et al., 1917). Wings extend from the sides of the dorsum close to the spine, and from the back of the first toe. The metacarpal and first phalanx of the first digit lie within the membrane (Andersen, 1912). Wing areas average 739.4 cm<sup>2</sup> in males and 545.3 cm<sup>2</sup> in females (Jones, 1972).

The upper surface of the tongue contains a pattern of different kinds of papillae. The central papillae, which can be seen with the unaided eye, are rasplike and directed posteriorly. The thumb is long and terminates in a sickle-shaped claw. The toes also have sickle-shaped claws (Rosevear, 1965).

Sexual dimorphism in size of *E. helvum* is not great (Andersen, 1912). Jones (1972) found measurements of forearms of males to average 13% greater than those of females. *E. helvum* is the second largest of the West African fruit bats, exceeded in size only by the hammer-headed fruit bat, *Hypsignathus monstrosus* (Okon, 1975; Rosevear, 1965). Ranges of external and cranial measurements (in mm) are: total length, 150.0 to 195.0; length of forearm, 117.0 to 132.0; wingspan, 750.0 to 950.0; length of thumb, 42.0 to 50.5; digit II—length of metacarpal, 51.2 to 62.0; length of phalanx I, 15.3 to 18.5; length of phalanges II and III, 10.5 to 16.8; digit III—length of metacarpal, 76.5 to 88.8; length of phalanx I, 50.2 to 56.2; length of phalanx II, 74.5 to 91.5; digit IV—length of metacarpal, 74.0 to 86.0; length of phalanx I, 39.8 to 46.8; length of phalanx II, 47.2 to 55.0; digit V—length of metacarpal, 70.5 to 84.5; length of phalanx I, 30.0 to 39.7; length of phalanx II, 32.3 to 40.0; length of ear from notch, 27.2 to 28.0; greatest width of ear, flattened, 18.5 to 20.0; front of eye to tip of muzzle, 23.2 to 25.0; length of tail, 10.0 to 15.5; length of tibia, 47.0 to 52.0; length of hindfoot, 31.5 to 38.5; skull—total length to front of premaxillaries, 54.5 to 62.2; width of brain case at zygomata, 20.8 to 23.5; zygomatic width, 32.0 to 36.0; width between M2s, externally, 16.0 to 18.0; width across canines, 9.8 to 11.0; posterior palate to incisive foramina, 26.0 to 30.0; front of orbit to tip of nasals, 19.0 to 22.8; length of mandible, 43.0 to 49.5; length of maxillary tooththrow, 21.0 to 23.8; length of mandibular tooththrow, 23.0 to 26.2 (Andersen, 1912; Fayenuwo and Halstead, 1974; Kingdon, 1974; Rosevear, 1965).

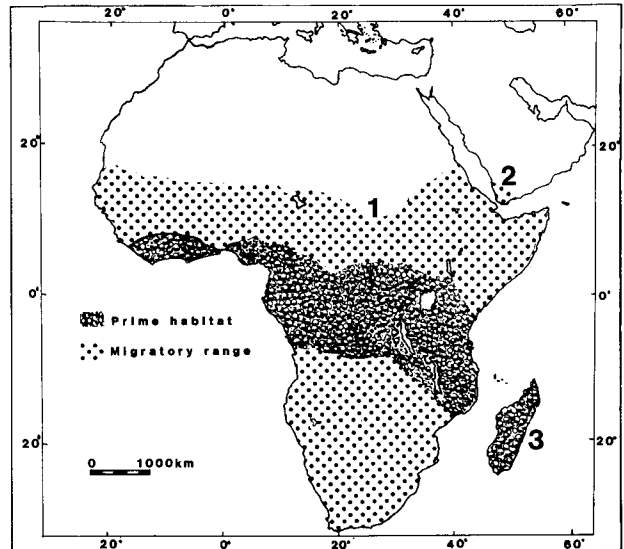


FIG. 3. Distribution of *Eidolon helvum*. Central area is occupied year-round, and migratory routes extend range north and south. The continental subspecies (1) is *E. helvum helvum*. The Arabian peninsula form (2) is *E. h. sabaeum*, and the Malagasy subspecies (3) is *E. h. dupreanum*.

The dental formula of *E. helvum* is  $i\ 2/2, c\ 1/1, p\ 3/3, m\ 2/3$ , total 34 (Rosevear, 1965). Teeth are without special modifications and no secondary cusps appear in canines or cheekteeth. Molars contain a longitudinal median groove separating a higher outer and lower inner ridge. The upper incisors are small, rounded, and subequal in size. Lower incisors are similar to uppers and usually in contact with each other and with canines. All post-canine teeth are slightly separated. Ten palatal ridges are present; four anterior, three middle, and three posterior (Andersen, 1912).

Kingdon (1974) gave the range in body mass of *E. helvum* as 250 to 311 g. According to Fayenuwo and Halstead (1974), the mean body mass of males during the breeding season increased from 230 to 330 g and the corresponding mean body mass of females from 240 to 350 g. In females the increase was due to the developing embryo.

**DISTRIBUTION.** Andersen (1907) reported the African distribution of *E. helvum* to be from Somaliland (Somalia, Djibouti, southeastern Ethiopia), Sennaar (Sudan), and Senegambia (Senegal and Mali) in the north, to Nyasaland (Malawi), Namaqualand (Southwest Africa, South Africa), and Mashonaland (Zimbabwe) in the south. The straw-colored fruit bat is a migrant from its prime habitat, the tropical forests of the central part of the African continent, which supply the bats with a variety of fruits throughout most of the year, to areas both north and south of this optimal territory (Fig. 3). The availability of food determines the occurrence of this species elsewhere. *E. helvum* has been recorded in forested habitats from Guinea to Nigeria and Cameroon, Gabon, and Zaire to the Rift Valley and parts of the Sudan, Uganda, Kenya, Tanzania, and northern Angola. Areas where *E. helvum* may be considered a year-round resident include parts of northeastern Zambia, Malawi, and possibly northeastern Mozambique and northeastern Natal (Smithers, 1983). Hayman and Hill (1971) reported an even wider distribution from Senegal to Sudan, Ethiopia, Tanzania (including Zanzibar, Pemba, and Mafia Islands), Zimbabwe, and South Africa. In the west, the range covers the islands of Fernando Poo, Sao Tome, Principe, and Annobon. Outside of the African continent, these bats are known from the southwestern Arabian Peninsula and Madagascar (Fig. 3). Records are infrequent from Namibia, in Zimbabwe as far west as the Matopo Hills, and in Mozambique south of the Zambezi River in the central and southern parts of the country. In the southwest province of Transvaal these bats are considered "wanderers." In addition, *E. helvum* has been taken in the Orange Free State and in the eastern Cape Province as far west as the Bredasdorp district (Smithers, 1983). Rosevear (1965) reported that this species had been taken out at sea 250 km from the nearest land. It has been recorded on several islands off the Cameroon (Ambas and Bimbina) and Sierra

Leone coasts, and on islands in the Congo River and in Lake Kivu (Zaire).

There is no fossil record for this species.

**FORM AND FUNCTION.** The skin underlying the brighter-colored collar behind the head is composed of an epidermal layer two to three cells thick in addition to a dermal layer containing numerous sebaceous glands. These glands are better developed in males than in females and are not evident in juveniles (Mainoya and Howell, 1979; Mutere, 1967). In males, glandular layers compose up to 75% of the total skin thickness; in females up to 42% (Mainoya and Howell, 1979). These glands secrete a musky-smelling fluid, the production of which has been observed to increase when individuals are disturbed (Allen et al., 1917; Kingdon, 1974). The nipples are axillary (Rosevear, 1965).

*Eidolon helvum* has been used in studies of the development of the web muscles of the wing and the origins of satellite cells. According to Church (1969:436), "The web arises as a bud on the lateral body wall and is invaded early by axons. The web muscles appear . . . in a pattern and distribution presaging the adult arrangement." Before birth, cells remain divided into two types—muscle fibers and surrounding satellite cells. The latter supply myoblasts in developing and regenerating muscle and are located between the basement and plasma membranes of muscle fibers (Muir et al., 1965). Ladhani and Thies (1968) studied single fibers of motor nerves from web muscles. The mean length of 57 isolated intact fibers was 14.1 mm. The end plate loci lie within the middle half of each fiber, generally near the center.

Measurements show the heart of males is significantly larger and more heavily developed than that of females in all respects except for the thickness of the right ventricular wall. The anterior vena cava is immense compared to the posterior vena cava, reflecting the circulatory system requirements for flight. The free margin of the sinus septum forms an exceptionally thick, muscular ridge between the left anterior and posterior vena cava (Rowlatt, 1967).

During flight the anastomoses close, disconnecting the arteries and veins and causing the blood to flow through peripheral capillaries in the limbs, which are bypassed while the bat is at rest. The heart receives a sudden increase in venous blood, a process for which it has been modified. In both males and females, the wall of the conus, or outflow tract of the right ventricle, is considerably thinner than that of the sinus, or inflow tract. Thus, the tremendous increase in venous return caused by flight can be accommodated by the heart (Kingdon, 1974; Rowlatt, 1967).

Blood and bone marrow cells of *E. helvum* were examined for response to Sudan black B and periodic acid-Schiff positive material, peroxidase, naphthol ASD chloroacetate esterase, and beta glucuronidase. Strong peroxidase reactivity was seen only in developing granulocytes and monocytes of bone marrow. Intense peroxidase reactivity was observed in developing and mature erythrocytes in blood and bone marrow (Caxton-Martins, 1977).

Food passage in *E. helvum* is rapid (Rosevear, 1965). Rodhain and Bequaert (1916) reared these bats in captivity on a diet of sweet bananas. This fruit passed through the alimentary canal within a short period of time and was passed out nearly unchanged except for the juices. The esophagus is approximately 100 mm long and is marked by two distinct anatomical features uncommon among mammals; a sphincterlike protrusion at the gastroesophageal junction composed of inner circular muscle and a well-developed gastric mucosa at the base of the esophagus occupying approximately 10 mm of the esophagus above its junction with the stomach. The stomach, fully distended, measures approximately 90 mm and consists of four regions—fundus, corpus, pyloric antrum, and pyloric canal. Each section is clearly marked, the fundic being noticeably wider than the corpus, and the pyloric much narrower (about 4 mm in diameter). A peculiar feature of the stomach is the presence of deep, permanent furrows in the outer surface of the pyloric antrum. The presence of both chief and parietal cells in the pyloric mucosa of the stomach is unusual also, pointing to the possibility that *E. helvum* might have potential as a carnivore or might reflect feeding on some other type of protein-rich food source, such as pollen. No topographical differences exist between the large and small intestines; however, they are distinguishable at the histological level. In the proximal duodenum there is a transitional region said to be rich in pyloric-type glands and in Brunner's glands. Unusual in fruit bats, Brunner's glands might serve to protect the duodenum from ulceration by acid-pepsin. One side of the small intestine is thicker than

the other; the thin half is rudimentary, whereas the thicker is fully developed. The large intestine is measured as the final 30 cm of the entire length of small and large intestine, which together measured about 170 cm. Absorptive cells in the large intestine are abundant, whereas goblet cells are not. The appendix and caecum are lacking as in other bats (Okon, 1977).

The presence of enzyme-producing glands along much of the length of the alimentary canal contributes to the feeding efficiency of these bats. Trypsin, pepsin, and amylase are produced even in the distal esophagus; invertase and maltase are found everywhere except in the esophagus and stomach. These enzymes are used in carbohydrate and protein digestion, which also suggests carnivorous food habits, although they may be used to digest pollen. Peptidase, lipase, lactase, and cellulase were not detected in *E. helvum* (Ogunbiyi and Okon, 1976). Despite considerable difference in pH values required for maximal activity, pepsin and amylase are found in all four regions of the stomach, suggesting a regulatory mechanism for controlling secretion events (Okon and Ogunbiyi, 1979).

Interscapular brown adipose tissue undergoes marked diel changes. More multilocular cells appear in the afternoon; more unilocular cells in the evening, and they increase in number during flight. A high number of multiloculate cells indicates high metabolic activity. Thus, brown adipose tissue contributes to daily energy exchanges in this species (Okon, 1980).

The body temperature of *E. helvum* has been recorded from 30 to 40°C, usually from 32 to 37°C (Jones, 1972). The uterus is bicornuate. Both horns and their corresponding ovaries are functional (Mutere, 1967).

**ONTOGENY AND REPRODUCTION.** Breeding is seasonal, with most copulation occurring from April to June (Mutere, 1968). The egg is fertilized and develops until the blastocyst stage, but does not continue development until implantation in October (Funmilayo, 1979; Mutere, 1965a). Births take place from February to May prior to the onset of the higher of the two rainfall peaks. The minimum gestation period is about nine months, although true gestation lasts only four months. Females produce one infant/pregnancy and birth occurs in maternity colonies that are clusters of females (Funmilayo, 1979; Kingdon, 1974; Mutere, 1965b, 1967, 1980).

Mean weight of testes increased from 1.0 to 2.5 g (October–November) to 5.2 to 5.5 g (April–June); an increase caused by the increased number of spermatozoa in the epididymides (Mutere, 1967). Jones (1971) listed average dimensions of testes (in mm) as 20 by 18 and 21 by 16 (May and June). Ogilvie and Ogilvie (1964) gave testicular dimensions of one specimen as 15 by 12. Spermatozoa can be found in the female genital tract from April to June. Examination of uteri reveals unimplanted blastocysts from July to September. Reasons for delayed implantation remain obscure (Mutere, 1965a). Pregnancies occur in either the right or left horn of the uterus, never both; a functional corpus luteum corresponds to the side of the horn bearing the embryo (Mutere, 1967).

The fetus has its limbs crossed and tucked near the body with wings on either side of and covering the face. The head is large compared to the rest of the body. Fayenuwo and Halstead (1974) recorded an increase in fetal weight from 1 to 45 g within 16 weeks. The uropatagial muscle becomes well developed before birth. The eyes of newborn *E. helvum* remain closed for several weeks. Hind limbs are well developed for clinging to the mother. Infants, which suckle upside-down with one foot holding on across the mother's stomach, are often attached to a nipple of the mother. Milk teeth are present at birth (Halstead and Middleton, 1975). Continual grooming and attention from the mother are essential for the survival of newborns (Halstead, 1975). Juveniles averaging 120 to 150 g show separation behavior from mothers by mid-June (Funmilayo, 1979). Young males are not sexually mature by the following mating season (Halstead and Middleton, 1975). No spermatogenesis occurs until testes reach a mass of 0.9 g (at a body mass of 240 to 249 g). Females cannot reproduce until they have attained a body mass of 200 g. No records of females in breeding condition exist in southern Africa suggesting the improbability of breeding there due to low population density of these migratory animals (Mutere, 1967). The only known longevity record for *E. helvum* is 21 years, 10 months (Nowak and Paradiso, 1983).

**ECOLOGY.** *Eidolon helvum* feeds entirely on fruiting and flowering trees (Wilson, 1973) and in turn is preyed on by snakes and carnivorous birds and mammals (Funmilayo, 1979). Roost sites

selected during the day are in tall trees, lofts in caves, and rocks. Trees used as day roosts are large with spreading branches, commonly found in dense groves with thick undercover. At night, roosts are chosen according to food availability. Trees are of various heights and sizes, some in groups, others widespread (Okon, 1975). This species roosts in enormous colonies of up to 1,000,000; sleeping groups number about 100 (Kulzer, 1969; Nowak and Paradiso, 1983). Roosting clusters are located 6 to 20 m above ground on sturdy branches (Jones, 1972). During periods of migration, *E. helvum* colonies disperse into small groups and form temporary roosts from which they eventually form "regular" roosts (Mutere, 1980). Baranga and Kiregyera (1982) reported a colony of 70,388 *E. helvum* in Uganda. The average number of bats/tree was 310; the average number of clusters/branch 4; and the average cluster size about 8. Common trees for roosts include *Eucalyptus saligna*, *Cocos nucifera*, *Elaeis guineensis*, and three species of *Ficus* (Jones, 1972). Large roosts cause damage to smaller twigs and branches. *E. helvum* will eat any sweet, juicy fruit, buds and young leaves of certain trees, flowers, nectar, and pollen (Kingdon, 1974). They also chew into soft wood to obtain moisture (Nowak and Paradiso, 1983), causing the destruction of cultivated pine plantations as well as date palms. Despite destructive feeding habits (Funmilayo, 1979), these fruit bats are helpful in pollinating and promoting outcrossing in flowering plants (Harris and Baker, 1959). They are particularly fond of *Ceiba pentandra* and their habit of moving about in large flocks may promote outcrossing in this widespread and common tree species (Baker and Harris, 1959).

Endoparasites of *E. helvum* are unknown. The predominant ectoparasite is a nycteribiid batfly, *Cyclopodia greeffi* (Funmilayo, 1979). This fly has no parasites and has not been found to carry viruses (Aderoumu, 1973). Dusbabek and Bergmans (1980) found 43 specimens of a spinturnicid mite, *Meristaspis kenyaensis*, on 23 *E. helvum*.

Although predation is infrequent and seemingly poses little threat to populations of this bat, several animals eat them: the spotted eagle owl (*Bubo africanus*), crows, steppe buzzards, a kite (*Milvus migrans*; Kingdon, 1974), snakes, palm civets, genets, and hawks (Funmilayo, 1979), pottos (*Perodicticus potto*; Jones, 1972), Ayers' hawk-eagle (*Hieraetus dubius*; Wolf, 1984), and the African hawk-eagle (*Hieraetus spilogaster*; Louette, 1975). One occurrence of an attack on a pied crow by *E. helvum* was recorded by Kingdon (1974).

These bats are eaten in all communities in southwestern Nigeria; hunters often are hired to shoot them for hotels and restaurants. Most people eat whole bats, including the bones (Funmilayo, 1978). Guano of *E. helvum* creates filth and stench problems in some villages and possibly poses a threat to the health of villagers (Funmilayo, 1979). For example, leaves used in cooking often are contaminated by feces (Funmilayo, 1976). However, present control methods are wasteful and need regulation (Funmilayo, 1978).

**BEHAVIOR.** Feeding begins at approximately sunset as bats leave their roosts. Feeding stops just after sunrise. Noise from feeding sites has been reported as annoying to humans (Funmilayo, 1979). The territory explored during feeding reaches approximately 30 km in diameter/10,000 individuals (Huggel-Wolf and Huggel-Wolf, 1965). Feeding behavior is typical for pteropodids; fruit is mashed between teeth by rapid tongue movements and can be stored in cheek pouches (Kulzer, 1969). All but the smallest seeds are spit out as dry pellets, after the juice has been sucked from the fruit (Kingdon, 1974). Food is held mostly in the mouth. Bats occasionally hang by their thumbs and manipulate food with both feet and mouth. They open large fruits at the bottom, and may cling with feet and thumbs to the outside of the fruit or adjacent branches. They leave feeding sites by dropping 0.5 to 2.0 m before taking flight. Defecation occurs as *E. helvum* hangs by its thumbs, swings the posterior part of the body downward, extends the legs, and drops feces (Jones, 1972).

In its natural habitat, this bat remains alert and active during the day with eyes open, ears erect, and in constant motion (Jones, 1972). In captivity, the bat settles down to a deep peaceful sleep all day and is active only at night (Rodhain and Bequaert, 1916). Nocturnal activity consists of "flight to the fruit trees, recognition, flight, feeding, repose, displacement to another perch, repose, flight back to the sleep territory with interruption at specific trees for assembling" (Huggel-Wolf and Huggel-Wolf, 1965:10). Fighting is common in colonies and often consists of wing battering (Smithers,

1983). The constant noise level suggests a considerable degree of vocal communication. Grooming is common throughout the day, especially of the fur and wing membranes (Kulzer, 1969). Visual cues as well as a keen sense of smell are used in returning home and when travelling to feeding sites (Allen et al., 1917; Okon, 1975). Flight is slow, deliberate, and not particularly agile (Jones, 1972). Wing beats are regular and may be interspersed by occasional short glides (Rosevear, 1965). At rest, wing membranes fold against the body as protection from rain and glaring sun (Allen et al., 1917). When tested in ambient temperatures of 10 to 20°C, shivering and abdominal heaving were observed; constant ear and eye movements were greatly reduced. In large colonies, behavioral thermoregulation was correlated with temperature and sun exposure; fanning of wings was observed in warmer temperatures (Jones, 1972).

Nothing has been reported on the genetics of this species.

**REMARKS.** Andersen (1912:12) noted that *Eidolon* "was well-known to the early post-Linnean systematists, who put it down as a variety of *Vespertilio* (or *Pteropus*) *vampyrus*. L. The earliest recognizable figure and description appear to be those given by Pennant, in 1771, under the name 'Lesser Ternate Bat.' . . ." Kerr's description is based on Pennant's figure and description. Rafinesque (1815) raised *Pteropus*, *Eidolon*, and *Pteronotus* to the level of genera (Andersen, 1908). He restricted *Pteropus* to those species without tails and suggested *Eidolon* as a new name for those bats with short tails. The name *Eidolon* is Greek for phantom, presumably referring to the nocturnal appearance of these large bats; *helvus* is Latin and means dun-colored.

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