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Glauconycteris variegata (Chiroptera: Vespertilionidae)

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Abstract: *Glauconycteris variegata* (Tomes, 1861), commonly known as the variegated butterfly bat, is 1 of 12 species in the genus *Glauconycteris*. It is a pale-yellow or light-gray bat with pale, translucent wing and tail membranes that are reticulated with a prominent lattice of darkly pigmented venation. It is widespread across savannah, woodland, and bushveldt habitats in sub-Saharan Africa. It roosts most often in trees, eats insects—especially moths—on the wing, and echolocates with high-intensity, frequency-modulated calls typically sweeping from 70 to 30 kHz. *G. variegata* is considered a species of "Least Concern," albeit population trends are unknown. DOI: 10.1644/870.1.

Key words: Africa, bushveldt, *Chalinolobus*, *Glauconycteris machadoi*, leaf-winged bat, savannah, variegated butterfly bat, woodland

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Glauconycteris Dobson, 1875

Kerivoula Gray, 1842:258. Type species *Kerivoula poensis* Gray, 1842:258, by subsequent designation (Dobson, 1875:387).

Vesperus (*Hesperoptenus*) *krausii* Peters, 1868:638. Type species *Glauconycteris poensis* Peters, 1868:638, by subsequent designation (Thomas, 1913:145).

Chalinolobus (*Glauconycteris*) Dobson, 1875:383. Described as subgenus of *Chalinolobus*.

Glauconycteris de Winton, 1901:46. Type species *Kerivoula poensis* Gray, 1842:258.

CONTEXT AND CONTENT. Order Chiroptera, family Vespertilionidae, subfamily Vespertilioninae, tribe Vespertilionini (Simmons 2005). The genus includes 12 extant species (Simmons 2005). The following key to those species is based on information from Allen (1917), Dobson (1875), Eger (2001), Eger and Schlitter (2001), Gray (1842), Happold (1987), Hayman (1939, 1963), Hayman and Hill (1971), Hayman and Jones (1950), Heller et al. (1994), Juste and Ibáñez (1994), Peterson (1982), Peterson and Smith (1973), Rosevear (1965), Thomas (1901, 1913), and Tomes (1861).

1 Fur of face with white markings 2
No markings present on fur of face 3
2 Dorsal and ventral fur black with white facial markings and shoulder spots or dorsolateral flank stripes or both; length of forearm > 45 mm ..... *G. superba*
Dorsal and ventral fur uniform brown with single white band along sides of face and on throat; dorsolateral flank stripe absent; length of forearm < 45 mm ..... *G. kenyacola*
3 Dorsal or ventral fur extending onto parts of uropatagia or propatagia 4
No fur present on patagia 7
4 Wing and tail membranes pale or brown and with conspicuous blackish-brown pigmentation of reticulated venation 5
Wing and tail membranes pale or dark brown and with faint or no pigmentation of reticulated venation 6
5 Dorsal pelage bicolored and brown; wing and tail membranes dark and opaque ..... *G. machadoi*

Fig. 1.—An adult female *Glauconycteris variegata* from Mana Pools National Park, Zimbabawe. Photograph used with permission of photographer M. B. Fenton.

Dorsal pelage tricolored and pale; wing and tail membranes pale and translucent ..... *G. variegata*

6 Inner margin of tragus strongly curved; white shoulder spot and dorsolateral flank stripe present ..... *G. poensis*

Inner margin of tragus straight; white shoulder spot and dorsolateral flank stripe not present ..... *G. argentata*

7 Dorsal and ventral fur overall pale clay or white; patagia pale white and translucent ..... *G. gleni*

Dorsal and ventral fur brown or blackish brown; patagia brown, dark brown, or blackish brown and not translucent 8

8 Inner margin of tragus concave ..... *G. egeria*

Inner margin of tragus straight 9

9 Dorsal hair tricolored and contrasting with blackish brown base, pinkish buff medial band, and umber or sepia terminal band ..... *G. curryae*

Dorsal hair bicolored and less contrasting with blackish brown base and brown, sepia, or dark brown terminal band 10

10 White shoulder spot conspicuous; 2 white dorsolateral flank stripes present ..... *G. alboguttata*

White shoulder spot conspicuous or faint; dorsolateral flank stripes absent 11

11 Ears grayish brown with long and narrow tragus .... *G. beatrix*

Ears yellowish brown with short and broad tragus ..... *G. humeralis*

NOMENCLATURAL NOTES. Dobson (1875) established *Glauconycteris* as a subgenus of the Australian genus *Chalinolobus* (Peters, 1866), a taxonomic rank also recognized by Honacki et al. (1982), Koopman (1971, 1984, 1993, 1994), Lunde et al. (2001), Meester et al. (1986), Rautenbach et al. (1993), Ryan (1966), and Simpson (1945). Conversely, Eger and Schlitter (2001), Ellerman et al. (1953), Hayman and Hill (1971), Hill and Harrison (1987), Koopman (1989), Miller (1907), Peterson and Smith (1973), Rosevear (1965), Simmons (2005), Tate (1942), and Volleth and Heller (1994) consider *Glauconycteris* a distinct genus.

Glauconycteris variegata (Tomes, 1861)
Variegated Butterfly Bat

Scotophilus variegatus Tomes, 1861:36. Type locality "Otjoro, Damaraland [Otjihoro, Ovamboland], Namibia."

Chalinolobus variegatus Dobson, 1875:388. Based on *Scotophilus variegatus* Tomes.

Glauconycteris papilio Thomas, 1905:77. Type locality "Entebbi [Entebbe], Uganda."

Glauconycteris phalaena Thomas, 1915:560. Type locality "White Nile, near Fashoda [Kodok], Sudan."

Glauconycteris congicus Monard, 1935:54. Type locality "Mupanda, Angola."

Glauconycteris variegata: Allen, 1939:88. First use of current name combination.

CONTEXT AND CONTENT. Content as for genus. Two subspecies are currently recognized (Simmons 2005):

G. v. phalaena (Thomas, 1915:560). See above.
G. v. variegata (Tomes, 1861:36). See above.

NOMENCLATURAL NOTES. Previous to clarification of the species by Simmons (2005), 3 subspecies of *G. variegata* were recognized. Rosevear (1965) recognized *G. variegata phalaena* Allen, 1939, and *G. v. variegata* Allen, 1939, but suggested that *G. v. papilio* Thomas, 1915, is synonymous with *G. v. variegata*, whereas Koopman (1965, 1993, 1994) recognized *G. v. papilio* and *G. v. phalaena*. Hayman and Hill (1971) considered *G. v. phalaena* a northern race of *G. v. variegata*.

Glauconycteris machadoi was previously regarded as a melanistic mutant population of *G. v. variegata* by Koopman (1971), who 1st gave *G. v. machadoi* subspecific rank, because it resembles *G. variegata* in every aspect of its morphology (e.g., physical dimension) other than color of fur (Hayman 1963; Koopman 1971). However, Largen et al. (1974) suggested that variation in color of fur is not a reliable characteristic to determine subspecific ranks of *G. variegata*. *G. machadoi*, known only from the holotype captured in Lac Calundo, East Angola, is considered a distinct species by Corbet and Hill (1986), Crawford-Cabral (1989), Hayman (1963), Hayman and Hill (1971), Peterson (1982), Peterson and Smith (1973), and Simmons (2005) but not by Koopman (1971, 1993, 1994), Honacki et al. (1982), Meester et al. (1986), and Rosevear (1965).

The butterfly bat was named for its resemblance to a large butterfly or moth while in flight, though the name may also refer to its attractive appearance (Rosevear 1965; Smithers and Wilson 1979). The generic name (Greek *glaucos* meaning bluish gray and *nycteris* meaning a night hunter) alludes to the grayish color of the type specimen, *Glauconycteris poensis* Gray (Rosevear 1965). The specific name *variegata* refers to the variegated reticulations on membrane of wings and tail (Rosevear 1965). *G. variegata* is also called the leaf-winged bat because wing patterns resemble venation of a leaf (Lang and Chapin 1917; Rosevear 1965). The subspecific name *phalaena* is Greek for moth (Jaeger 1978).

DIAGNOSIS

Glauconycteris variegata lacks markings on the fur of the face, dorsum, and venter (Fig. 1), which distinguishes it from *G. alboguttata* (striped butterfly bat), *G. beatrix* (Beatrix butterfly bat), *G. humeralis* (spotted butterfly bat), *G. kenyacola* (Kenyacola butterfly bat), and *G. superba* (pied

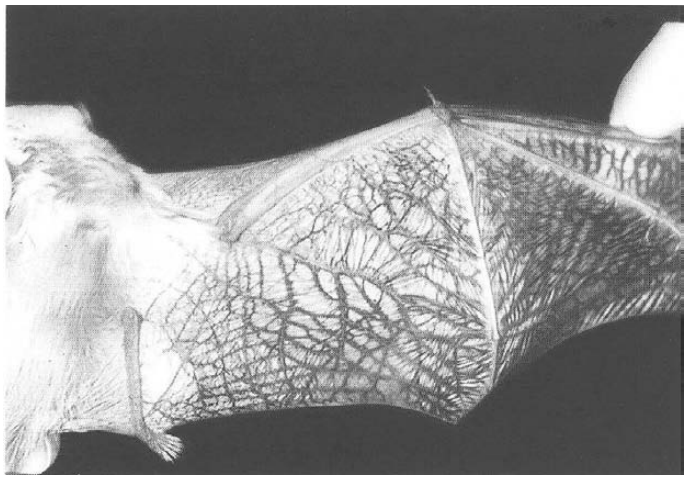

Fig. 2.—Wing membrane detail of an adult female *Glauconycteris variegata* from Mana Pools National Park, Zimbabawe. Photograph used with permission of photographer M. B. Fenton.

butterfly bat—Allen 1917; Hayman 1939; Peterson 1982; Rosevear 1965) and it is also distinguished by its prominent lattice of pigmented venation on membranes of wings and tail (Fig. 2). The pale dorsal fur of *G. variegata* is similar to that of *G. argentata* (common butterfly bat), but the wing and tail venation of *G. argentata* are generally faint or absent (Dobson 1875; Thomas 1913). *G. variegata* is easily distinguished from *G. curryae* (Curry's butterfly bat) and *G. egeria* (Bibundi butterfly bat), both of which have blackish brown, dark brown, or brown fur and dark, opaque patagia (Eger and Schlitter 2001; Thomas 1913). Compared to the tricolored dorsal pelage, heavily pigmented and intricate cross-venation, and >18.0-mm tibia of *G. variegata*, *G. gleni* (Glen's butterfly bat) has distinctly quadricolored dorsal pelage, lighter and less intricate membrane venation, and ≤17.0-mm tibia (Peterson and Smith 1973), whereas *G. machadoi* (Machado's butterfly bat) has bicolored dorsal pelage and dark, opaque patagia with blackish brown reticulations (Hayman 1963). *G. variegata* lacks the postcalcaneal lobe present in *G. poensis* (Abo butterfly bat—Dobson 1875). The lower jaw of *G. variegata* has a less-prominent posterior angle than do other species of *Glauconycteris* (Tomes 1861).

GENERAL CHARACTERS

The fur of *Glauconycteris variegata* is long, fine, woolly, and silky at its tips (Hill and Carter 1941; Tomes 1861). Although the color of individuals varies widely within and between populations, *G. variegata* is generally yellowish (cream, pale buff, or fawn) or light gray (Hill and Carter 1941; Rosevear 1965). The dorsal fur is banded and generally darkish brown at its base, creamy white in the middle, and light gray, cream, yellow-orange, rufous, or light brown at its tips (Hayman and Hill 1971; Lang and Chapin 1917; McLellan 1986; Rosevear 1965; Tomes 1861). The ventral fur is unicolored white, creamy, grayish white, or bicolored with an ashy tinge at the base (Allen 1917; Hill and Carter 1941; Rosevear 1965; Tomes 1861). Thick short fur covers the sides of the face and the bridge of the nose (Tomes 1861). The ears and muzzle are pale brown (Tomes 1861). The membranes of the wings and tail are covered on the dorsal and ventral surfaces with long, scattered hairs; the tail is pointed and completely enclosed to the base of the hallux within the uropatagium (Hill and Carter 1941; Tomes 1861). The calcaneum is long, but a cartilaginous postcalcaneal lobe is lacking (Dobson 1875; Tomes 1861).

Glauconycteris variegata has a high, broad braincase, a short, obtuse rostrum, and a domed cranium with no sagittal crest (Dobson 1875; Miller 1907; Rosevear 1965; Tate 1942; Tomes 1861). The supraoccipital crest is poorly developed, and the frontal region of the skull not hollowed (Rosevear 1965; Smithers 1983). Basisphenoid pits are shallow and indistinct (Miller 1907). Additional descriptions of the skull can be found in Hill and Carter (1941), Rosevear (1965), and Tomes (1861).

The nostrils are subcylindrical and open laterally (Rosevear 1965). Well-developed glandular protuberances separate the nostrils by a deep groove (Dobson 1875; Hill and Carter 1941), giving a tumid appearance to the muzzle (Thomas 1901). The upper lips are simple and somewhat overhanging (Tomes 1861), whereas the underlip is thick and padded (Rosevear 1965). *G. variegata* has a distinctly short, blunt lobule at the internal base of the ear conch that connects, by a ridge, to a fleshy lobe at the base of the lower lip (Dobson 1875; Miller 1907; Rosevear 1965; Tomes 1861). The ears are small, short, broadly rounded, and irregularly ovoid or conch-shaped, with the outer margin distinctly convex and extending forward toward mouth (Dobson 1875; Hill and Carter 1941; Kingdon 1974; Tomes 1861). The tragus is short and broadly sickle or semilunate (Hill and Carter 1941; Rosevear 1965 with illustration; Tomes 1861). The baculum is very small and triangular (illustration in Hill and Harrison 1987).

Female *G. variegata* are slightly larger than males in body dimensions but not in body mass (Peterson and Smith 1973). Mean body measurements (mm or g; *n* in parentheses) for female and male *G. variegata*, respectively, from Peterson and Smith (1973) are: total length, 105.0 (8), 101.6 (19); length of tail, 48.5 (8), 45.7 (18); length of hind foot, 9.2 (9), 8.6 (18); length of ear from notch, 12.8 (8), 12.4 (16); length of tibia, 19.5 (9), 19.3 (19); length of forearm, 42.9 (12), 41.7 (18); wingspan, 323.5 (2), 311.2 (6); body mass, 10.3 (4), 11.5 (10). Lengths of metacarpals and phalanges are given in Peterson and Smith (1973).

Mean cranial measurements (mm; *n* in parentheses) for female and male *G. variegata* (Fig. 3), respectively, from Peterson and Smith (1973) are: greatest length of skull, 14.1

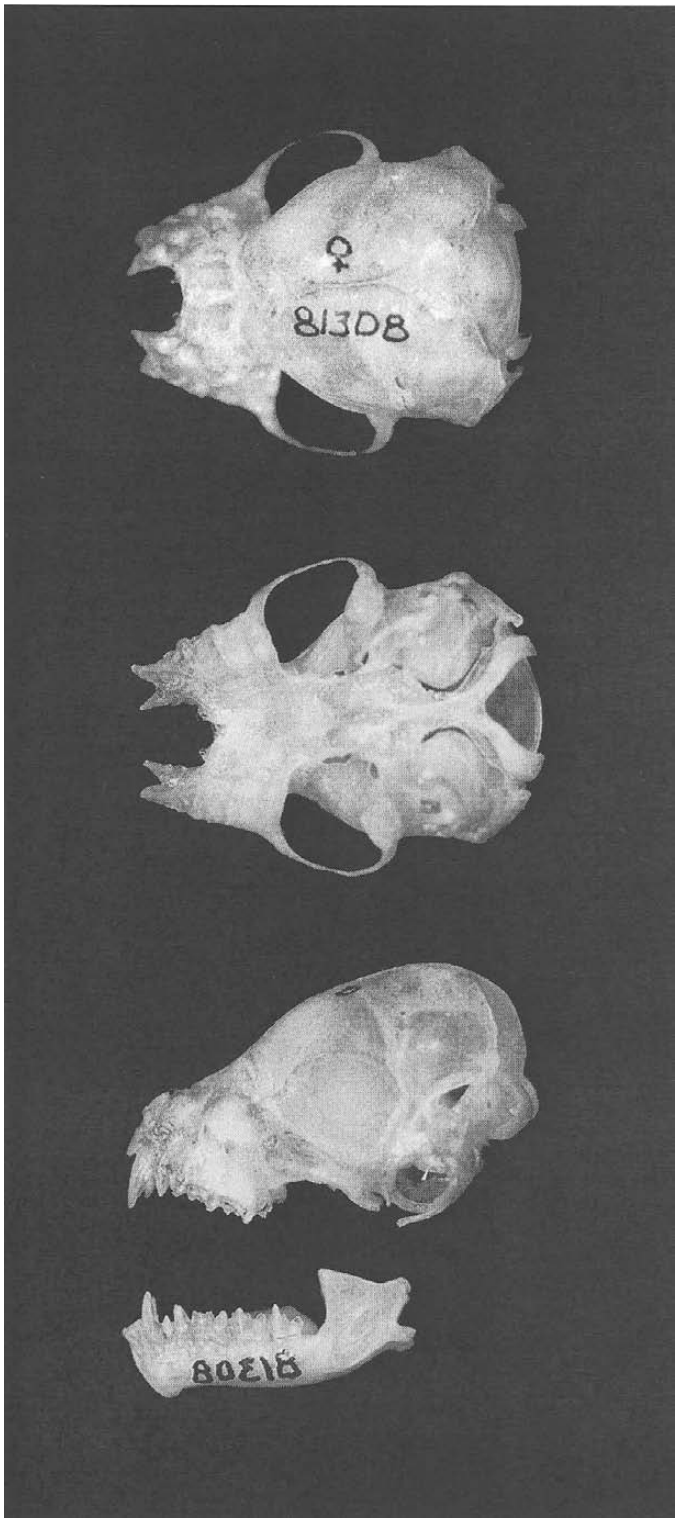

Fig. 3.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult female *Glauconycteris variegata* (ROM [Royal Ontario Museum mammal collection] 81308) from Kakamega Forest, West Kenya. Occipitonasal length is 13.68 mm. Photograph used with permission of photographer M. B. Fenton.

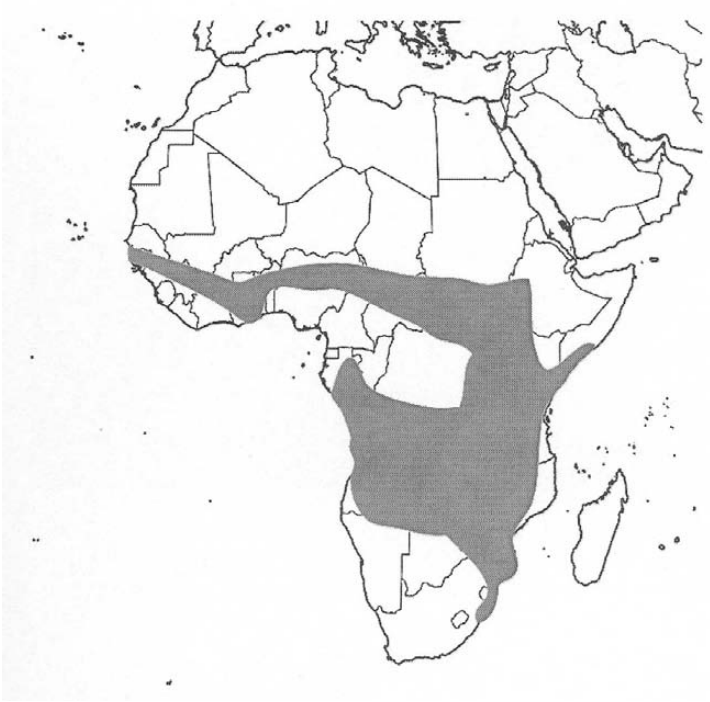

Fig. 4.—Geographic distribution of *Glauconycteris variegata* throughout Africa. Map modified from International Union for Conservation of Nature and Natural Resources (2010).

(7), 14.0 (16); condylobasal length, 13.5 (7), 13.4 (16); length of palate, 4.5 (7), 4.3 (18); width across zygoma, 10.3 (6), 10.4 (10); width across mastoid processes, 8.9 (7), 9.0 (17); width of braincase, 8.2 (4), 8.0 (9); height of braincase, 6.0 (7), 6.0 (17); interorbital width, 5.7 (7), 5.8 (18); width across postorbital process, 5.9 (7), 5.9 (18); width of postorbital constriction, 4.6 (7), 4.5 (17); M3 to M3 width, 6.9 (7), 6.9 (18); C to M3 length, 4.9 (7), 4.9 (18); C to C width, 4.9 (7), 4.9 (18); length of mandible, 10.2 (7), 10.2 (18); c to m3 length, 5.4 (7), 5.4 (18); c to c width, 3.4 (6), 3.3 (17).

DISTRIBUTION

Glauconycteris variegata is distributed widely in Africa south of the Sahara (Fig. 4; Smithers and Lobão Tello 1976; Taylor et al. 2004). Its northern distribution limit extends across the continent from the Atlantic coast of southern Senegal eastward to the Indian Ocean in southern Somalia. Its southern limit extends from northeastern South Africa, through the eastern tip and northern extremes of Botswana and Namibia, and north to Gabon (Adam and Hubert 1972; Aellen 1952; Fenton 2001; Funaioli and Simonetta 1966; Happold 1987; Hayman and Hill 1971; Hill and Morris 1971; Koopman 1975, 1989; Koopman et al. 1995; Largen et al. 1974; Skinner and Smithers 1990; Swanepoel et al. 1980; Taylor et al. 2004). There have been no captures from central regions of the Democratic Republic of the Congo,

northern Congo Republic (Congo—Brazzaville), northeastern Gabonese Republic, Equatorial Guinea, southern Cameroon, southern Nigeria, or southern Renin; nor has it been recorded in the Atlantic coastal areas of southwestern Ghana, Cote D'Ivoire, Liberia, or Sierra Leone. *G. variegata* has been found at elevations up to 1,000 m (Hill and Morris 1971). Fossils of *G. variegata* have been recorded in very late Holocene archeological remains at Border Cave in the province of Kwa-Zulu Natal, South Africa (Avery 1991).

FORM AND FUNCTION

The dental formula for *Glauconycteris variegata* is i 2/3, c 1/1, p 1/ 2, m 3/3, total 32 (Smithers 1983). I1 and I2 are unequal in size: I1 is long, acutely pointed, and varies in shape from tricuspid (Tomes 1861) to bicuspid (Rosevear 1965) or unicuspid (Thomas 1905), whereas I2 is almost rudimentary (Tomes 1861). Conversely, i1 is either trifid or inchoately quadrifid with moderately developed cingulum. The incisors are pressed tightly between the canines (Dobson 1875). i2 and i3 are much smaller (Rosevear 1965) and are cone-shaped with broad, evenly developed cingula (Tomes 1861). c1 is acute with cingulum sharply pointed toward the anterior (Tomes 1861). P2 is absent. P1 is large, well developed, and carnassial (Hill and Carter 1941; Roberts 1951; Tomes 1861). Both p1 and p2 are small, conical, and have prominent cingula that form anteroposterior cusps (Roberts 1951; Tomes 1861). Illustrations of upper posterior dentition are in Koopman (1971) and Peterson and Smith (1973).

Glauconycteris variegata has relatively low wing loading (body mass/wing area), a long wingspan, and a high aspect ratio (wing length/wing width—Findley et al. 1972; Obrist et al. 1989). An adult female from Zimbabwe with a 45-mm forearm, 325-mm wingspan, and a body mass of 12.6 g, had a wing area of 15.03 mm^2, an aspect ratio of 7.0, and wing loading of 8.2 N/m^2 (Obrist et al. 1989). The wing tips of *G. variegata* are long and pointed, suggesting efficient low-speed, maneuverable flight (Obrist et al. 1989). *G. variegata* has a minimum power speed of 3.3 m/s, maximum range speed of 4.4 m/s, and mean foraging flight speed of 4 m/s (Obrist et al. 1989).

Echolocation vocalizations are high-intensity, frequency - modulated calls typically sweeping from 70 to 30 kHz, sometimes including a 2nd harmonic, and rarely a 3rd (Fenton and Fullard 1979; Obrist et al. 1989). Obrist et al. (1989) report echolocation frequencies for flying and foraging bats.

ONTOGENY AND REPRODUCTION

Glauconycteris variegata is monestrus (Anciaux de Faveau 1970), albeit seasonal reproductive cycles vary across the species range. In southern Uganda, sexually active males were caught in July and in October (Kingdon 1974), but in Mupanda, Angola, no adults were reproductively active in July (Monard 1935). In Democratic Republic of the Congo, 4 of 10 females were pregnant in March (Lang and Chapin 1917), whereas no adults were reproductively active in April (Schouteden 1947). *G. variegata* inhabiting northern latitudes has a gestation period of 3 months, parturition occurs in April, and young are weaned through May (Anciaux de Faveau 1970). In Zimbabwe, 2 females each carried 1 fetus in August (Smithers and Wilson 1979) and 6 females were found each with newborn in early November (Obrist et al. 1989). Litter size is 1 (Anciaux de Faveau 1970). The breeding season for *G. variegata* varies across latitudes, ranging from an early boreal cycle (parturition about March or April) in the north to a late austral cycle (parturition about November) for southern populations (Anciaux de Faveau 1970; Brosset 1966; Smithers and Wilson 1979; Vershuren 1957). *G. variegata* in northern populations copulates in December and January (Anciaux de Faveau 1970).

ECOLOGY

Glauconycteris variegata typically occurs in savannah, woodland, or open country–bushveldt habitat (Hayman and Hill 1971; Kingdon 1974; Obrist et al. 1989; Smithers 1983). However, Largen et al. (1974) captured a female in a riverine forest near a hot, humid, marshy grassland in Ethiopia and Rautenbach (1982) reports a capture in dense riparian forest in Pafuri, South Africa. Adult *G. variegata* roost in clusters of <10 individuals, often hidden in trees among leaves, palm fronds, or in thatch (Lang and Chapin 1917; Obrist et al. 1989). They have been found in *Litchi* (lychee) trees (Pienaar et al. 1987), 7.5 m above the ground in a *Trichelia emetica* (mahogany) tree (Obrist et al. 1989), and on a low branch of a *Mangifera* (mango) tree (McLellan 1986). Roosting *G. variegata* do not wrap themselves in their wings (Fenton 2001), thus the proposed role of the reticulated membrane patterns as camouflage (Kingdon 1974; Shortridge 1934) is questionable. *G. variegata* remains motionless and is reluctant to fly when disturbed (Kingdon 1974).

Glauconycteris variegata generally does not forage within cluttered habitats (Obrist et al. 1989) but flutters swiftly about 18 m above ground (Lang and Chapin 1917; Shortridge 1934). It forages around lights (Kingdon 1974; Lang and Chapin 1917) and hawks insects close to the ground or over water (Shortridge 1934). In Zimbabwe, *G. variegata* begins foraging just before 1900 h (Obrist et al. 1989), but it has been observed leaving the roost as early as 1700 h, in daylight, in Niangara and Faradje, Democratic Republic of the Congo (Lang and Chapin 1917). It emits audible squeaks (social calls) as it flies (Lang and Chapin 1917). *G. variegata* eats airborne prey, and a high proportion of the diet consists of soft-bodied insects such as moths (Fenton et al. 1977a; Kingdon 1974). Fenton et al. (1977b)

reported no predation on *G. variegata* by bat hawks (*Macheiramphus alcinus*), which instead preyed on larger (>30-g) bat species in Zimbabwe.

GENETICS

In *Glauconycteris variegata*, the diploid number (2n) is 18 and the fundamental number (FN) is 32. Autosomes include 2 pairs of metacentrics, 5 pairs of submetacentrics, and 1 pair of subtelocentrics. The X chromosome is medium sized and subtelocentric and the Y chromosome is small and metacentric (Rautenbach et al. 1993).

CONSERVATION

Glauconycteris variegata requires dispersed areas of savannah, woodland, and bushveldt habitat (Skinner and Chimimba 2005), which are presently being rapidly disturbed by human activity (Nowak 1999). It is considered "Least Concern" because it is widespread across the African continent and because populations are presumed to be stable (International Union for Conservation of Nature and Natural Resources 2010); however, population trends are unknown. *G. variegata* is listed as near threatened in South Africa (Friedmann and Daly 2004).

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