MAMMALIAN SPECIES No. 642, pp. 1–6, 3 figs.

Pteropus vampyrus.

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Published 12 May 2000 by the American Society of Mammalogists

Pteropus vampyrus Linnaeus, 1758

Large Flying Fox

Vespertilio vampyrus Linnaeus, 1758:31. Type locality restricted to "Java" by Andersen (1912).
Vespertilio celaeno Hermann, 1804:13. Type locality "Batavia, Java."
Vespertilio nudus Hermann, 1804:15. Type locality unknown.
Pteropus edulis Geoffroy St. Hilaire, 1810:90. Type locality "Timor."
Pteropus javanicus Desmarest, 1820:109. Type locality "Java."
Pteropus funereus Temminck, 1837:63. Type locality "Timor, Amboine, Borneo et Sumatra," restricted to Timor by Andersen (1912).
Pteropus pluton Temminck, 1853:56. Type locality restricted to Bali by Kuroda (1933).
Pteropus pteronotus Dobson, 1878:48. Type locality "Java."
Pteropus lanensis Mearns, 1905:432. Type locality "Pantar, near Lake Lanao, Mindanao," Philippine Islands.
Pteropus intermedius Andersen, 1908:368. Type locality "Amherst, near Moulein," Tenasserim, Burma.

CONTEXT AND CONTENT. Order Chiroptera, suborder Megachiroptera, family Pteropodidae, genus *Pteropus,* which includes 58 species (Koopman, 1993). Andersen (1912) divided *Pteropus* into 17 species groups; *P. vampyrus* is in the *vampyrus* group, which also includes *P. giganteus, P. intermedius,* and *P. lylei* (Corbet and Hill, 1992). Seven subspecies are recognized (Koopman, 1994):

P. v. edulis Geoffroy St. Hilaire, 1810, see above (*funereus* Temminck is a synonym).
P. v. intermedius Andersen, 1908, see above.
P. v. lanensis Mearns, 1905, see above.
P. v. malaccensis Andersen, 1908:368. Type locality "Kuala Tembeling, Pahang, Malay Peninsula," West Malaysia.
P. v. natunae Andersen, 1908:369. Type locality "Pulo Panjang, North Natuna Islands," northwest of Borneo.
P. v. pluton Temminck, 1853, see above (*kopangi* Kuroda is a synonym).
P. v. vampyrus Linnaeus, 1758, see above (*celaeno* Hermann, *javanicus* Desmarest, and *pteronotus* Dobson are synonyms).

DIAGNOSIS. *Pteropus vampyrus* can be distinguished from most other flying foxes by color of pelage and by a 180–220 mm length of forearm. Lengths of forearm for similar species include *P. hypomelanus,* 121–150 mm; *P. giganteus,* 137–180 mm; *P. intermedius,* ca. 180 mm; *P. lylei,* 145–160 mm; and *Acerodon jubatus,* 165–220 mm (Andersen, 1912; Corbet and Hill, 1992; Ingle and Heaney, 1992; Payne et al., 1985; Taylor, 1934; Van Peenen et al., 1969). *P. vampyrus* possesses blackish underparts. Color of underparts of *P. vampyrus* is similar to dark color of dorsum, whereas *P. giganteus* and *P. lylei* (but not *P. intermedius*) have pale underparts that contrast with dorsum. Underparts of *P. giganteus* are buffy brown, those of *P. intermedius* are blackish brown, and those of *P. lylei* are blackish brown (Corbet and Hill, 1992). *P. giganteus* and *P. intermedius* possess a yellowish mantle (pelage on shoulder and neck) that usually can be distinguished from the tawny, tawny brown, dark brown, or black mantle of *P. vampyrus* (Payne et al., 1985). However, one color morph of *P. vampyrus* has a light-colored mantle, similar to that of *P. giganteus* and *P. intermedius,* thus limiting usefulness of mantle color for distinguishing among species. A smaller forearm and blackish-brown underparts distinguish *P. intermedius* from *P. vampyrus. A. jubatus* (body mass, 900–1,200 g) is the only pteropodid that may exceed *P. vampyrus* (645–1,092 g) in body mass. Wingspan of *A. jubatus* (ca. 1,550 mm) also exceeds that of *P. vampyrus* (1,320–1,500 mm). *A. jubatus* typically has a yellow-gold patch of fur on the top of its head; if a gold patch is present in *P. vampyrus,* it usually extends posteriorly to a sharp border on dorsum (Ingle and Heaney, 1992). Nearly pointed pinnae of *P. vampyrus* also distinguish it from the bluntly rounded ear tips of *A. jubatus* (Ingle and Heaney, 1992).

GENERAL CHARACTERS. *Pteropus vampyrus* is one of the largest species of bat in the world and is noted for its dog- or foxlike face, a characteristic common to all flying foxes (Fig. 1; Medway, 1969; Rabor, 1977). *P. vampyrus* has no tail. Ears are long and pointed (Taylor, 1934). Hairs are short and stiff on upper back and longer and woolly on lower back, mantle, underparts, and sides. Hairs comprising the mantle are longer than those on other parts of the body (Lekagul and McNeely, 1977). Hairs on the venter have a crinkly and coarse appearance and extend halfway down the forearm (Rabor, 1977). Color and texture of pelage vary according to age and sex (Goodwin, 1979). Pelage of males seems to be slightly stiffer and thicker than pelage of females (Taylor, 1934). Males also may have glandular neck-tufts of stiffer fur, in which bases of hairs are darker than tips (Andersen, 1912). Immature specimens often are uniformly dull gray-brown (Payne et al., 1985). Young *P. vampyrus* are born with a dark-colored mantle that in males may become lighter in color upon maturity (Taylor, 1934).

FIG. 1. Photograph of female *Pteropus vampyrus* from Indonesia, housed in captivity at The Lubee Foundation, Inc., Gainesville, Florida. Photograph by T. H. Kunz.

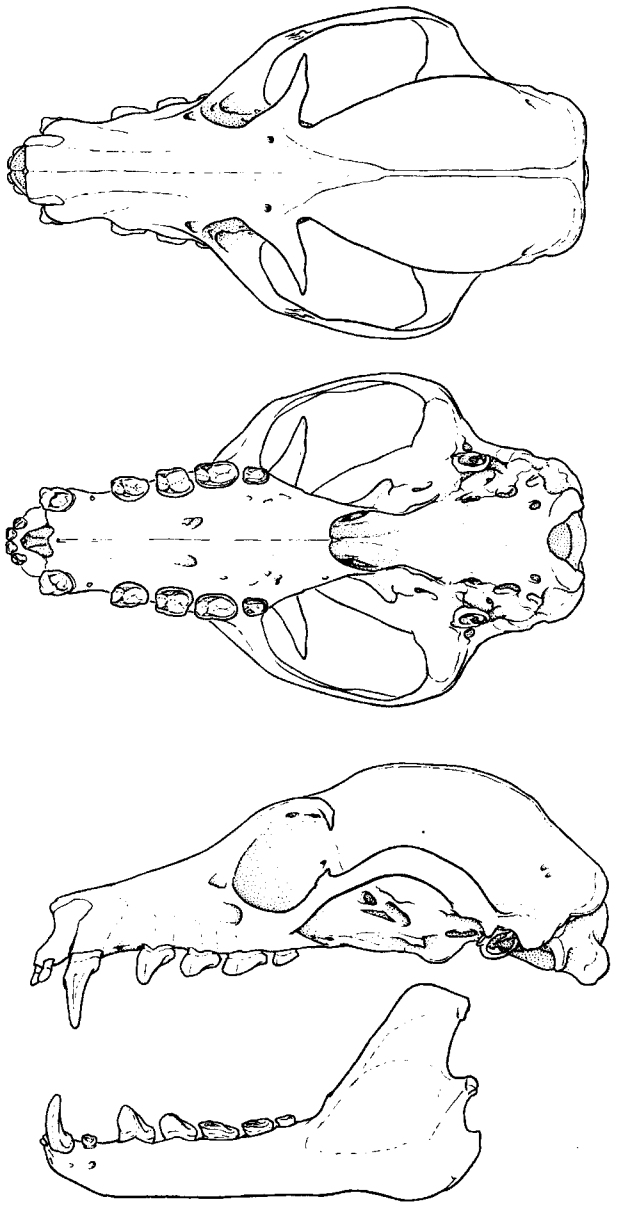

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of a male *Pteropus vampyrus* from the Philippines (University of Michigan Museum of Zoology [UMMZ] 158849). Greatest length of skull is 72.5 mm. From Ingle and Heaney (1992). Reprinted with permission of the Field Museum.

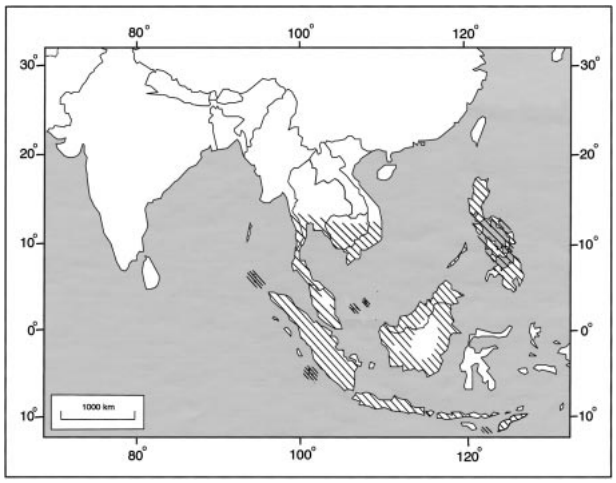

FIG. 3. Geographic distribution of *Pteropus vampyrus* (modified from Corbet and Hill, 1992). Current subspecific distributions are not well defined.

Color of pelage on head ranges from mahogany-red and orange-ochreous to blackish. Underparts vary from blackish to brown, with a sprinkling of other colors, ranging from chocolate to gray or silver (Andersen, 1912; Corbet and Hill, 1992; Goodwin, 1979). Andersen (1912) described the color of 12 then-recognized subspecies, but variation in mantle color among these forms raises questions about his classification scheme (Goodwin, 1979). Two color morphs of *P. vampyrus* have been described for the Philippines (Heideman and Heaney, 1992); one has a light-colored mantle, ranging from pale dirty-buff to orange yellow, with a dark-golden brown or dark russet chest. Head, chest, and mantle of the other morph are black or dark brown. Dorsal pelage of both morphs is dark, ranging from pure black to black mixed with gray or brown (Andersen, 1912; Corbet and Hill, 1992; Davis, 1962; Goodwin, 1979; Ingle and Heaney, 1992; Kuroda, 1933).

Skull of *P. vampyrus* is large and robust (Fig. 2). Ranges of external and cranial measurements for 50 specimens, representing all subspecies are (in mm): length of forearm, 179–220; total length, 270–340; length of hind foot, 50–68; length of ear from notch, 35–45; length of calcar, 26–32; length of lower leg, 86–107; wingspan, 1,302–1,500; length of pollex, 73–93; digit I: length of metacarpal, 17–22; length of phalanx I, 37–50; digit II: length of metacarpal, 91–112; length of phalanx I, 20–29; length of phalanx II–III, 18–24; digit III: length of metacarpal, 123–145; length of phalanx I, 88–110; length of phalanx II, 122–151; digit IV: length of metacarpal, 116–144; length of phalanx I, 72–96; length of phalanx II, 74–92; digit V: length of metacarpal, 120–148; length of phalanx I, 54–74; length of phalanx II, 55–74; greatest length of skull, 72–91; condylobasal length, 69–79; zygomatic width, 39–50; width of braincase at zygomata, 27–30; zygomatic breadth, 40–45; length of palate, 35–46; width of mastoid, 22–24; length of maxillary toothrow, 28–32; length of molariform toothrow, 18–21; length of postorbital constriction, 8–12; interorbital constriction, 9–12; width across m1 (externally), 19–25; width across canines (externally), 13–19; combined width of upper incisors, 6–9; lachrymal width, 15–20; orbital diameter, 15–18; width of mesopterygoid fossa, 8–10; length of front of orbit to tip of nasals, 24–33; length of mandible, 56–74; height of coronoid process, 26–34; length of c–m2, 28–36; and length of c–m3, 32–40 (Andersen, 1912; Corbet and Hill, 1992; Davis, 1962; Goodwin, 1979; Heideman and Heaney, 1992; Ingle and Heaney, 1992; Mudar and Allen, 1986; Rabor, 1977; Taylor, 1934; Van Peenen et al., 1969). In the Philippines, adult males are larger than females in most cranial measurements (Rickart et al., 1993).

Pteropus vampyrus is among the largest members of the Pteropodidae. Body masses for mature specimens from Malaya, Borneo, and Thailand ranged from 645 to 1,092 g (Lekagul and McNeely, 1977; Medway, 1969; Payne et al., 1985; Utzurrum, 1995; Widmaier and Kunz, 1993). In the Philippines, body mass ranging from 725 to 810 g has been reported for ≥10 individuals (Ingle and Heaney, 1992). Davis (1962) recorded a 725-g pregnant female captured in North Borneo.

DISTRIBUTION. Geographic range of *P. vampyrus* (Fig. 3) almost exactly corresponds to Wallace's Indo-Malayan subregion (Andersen, 1912). This bat occurs from southern Burma and Thailand eastward to the Philippines and southward to Sumatra, Java, Borneo, and Timor (Andersen, 1912; Corbet and Hill, 1992; Medway, 1969). In Peninsular Malaysia and in Borneo, this bat is most common in coastal regions, but it also occurs inland at altitudes up to 1,370 m (Medway, 1969). Insular distribution may coincide with the fruiting season of trees (Payne et al., 1985). *P. vampyrus* has no fossil record.

FORM AND FUNCTION. Dental formula of *P. vampyrus* is i 2/2, c 1/1, p 3/3, m 2/3, total 34 (Lekagul and McNeely, 1977). Upper incisors are separated from one another and I1 is slightly larger than I2. Lower incisors are smaller than upper ones, and i2 is almost twice as large as i1. C1 has a distinct heel (talonid), but no secondary cusp. Upper canines are long and pointed, with a deep longitudinal groove on anterior surface and a smaller groove

on inner surface; lower canines are smaller and have no grooves. P1 is small and peglike and usually is present only in immature specimens (leaving a distinct diastema next to the upper canine in adults). Molars and premolars are unspecialized; M1, M2, and M4 are broad and short, and their anterolingual cusps are tiny or absent; P3 is larger than M3; whereas M2 is the smallest molar and has no prominent cusps (Andersen, 1912; Lekagul and McNeely, 1977; Rabor, 1977; Taylor, 1934).

Skull has a nearly complete orbit and a wide, strong zygomatic arch (Lekagul and McNeely, 1977). Postorbital process almost reaches middle part of the zygomatic arch and a slight projection from the zygomatic arch rises to approach the postorbital process (Rabor, 1977). Variation in palatal ridge depends on occasional formation of weaker, divided ridges between ninth and 10th 'normal' ridges (Andersen, 1912). For specimens with a mean body mass of 680 g, length of greater curvature of the stomach averaged 64 mm, and mean intestinal length was 1,280 mm (Richardson et al., 1987).

Pteropus vampyrus has short, slightly rounded wing tips, which produce a slow, maneuverable flight. Wing membranes are naked except near the body where they are distinctly furred. Wings are strengthened by longitudinal ribs of thickened skin (Lekagul and McNeely, 1977). A fringe of hair is present on the trailing edge of the wing membrane, extending from the foot to the terminal phalanx of the fifth finger. A heavy growth of fur on antebrachial membrane and on sides of forearm extends about four-fifths along its length. Wing membranes are attached along the back ca. 28–30 mm apart (Taylor, 1934). Wing-loading is 57.8 Mg/S (Nm^{-2}) and aspect ratio (A) is 8.4. Tip to length ratio is 1.30, tip to area ratio is 0.72, and tip to shape index is 1.24 (Norberg and Rayner, 1987).

Veins in wings of *P. vampyrus* have the same general form as in other mammals, but exhibit specializations in the innervation of vascular smooth muscle and endothelium. Special modifications in the epithelium include many unipolar branched processes in the albuminal side of the cells. These 10-μm-long processes terminate in collagenous and elastic tissue, giving the endothelium an arcadelike appearance, and may play a role in contraction as in the actin–myosin system of muscle cells. Tunica media of these vessels is made of spindlelike muscle cells that contain significantly more mitochondria than the same cells in veins that are not autonomously contractile (Schipp, 1978).

Ratio of medullar to cortical thickness of kidney is 1.7 (Geluso, 1980; Sperber, 1942). In captivity, food (bananas impregnated with 1-mm-diameter plastic beads and covered with 2-μm dust) was completely eliminated from the gut in 5.5 h (Richardson et al., 1987). As measured in captive animals, circulating adrenal steroid levels (mean ± *SE*) of cortisol (598 ± 67 ng/ml) and corticosterone (102 ± 38 ng/ml) are among the highest reported for mammals (Widmaier and Kunz, 1993). Plasma levels of glucose (88 ± 9 mg/dl) in unstressed *P. vampyrus,* as reported by Widmaier and Kunz (1993), were within the normal mammalian range (80–100 mg/dl), although values reported by Heard and Whittier (1997) were markedly higher (143 ± 30 to 170 ± 6 mg/dl; ± *SD*) and may reflect differences in times of capture. Hematocrit averaged 49.7 ± 1% (Heard and Whittier, 1997; Widmaier and Kunz, 1993). Total cholesterol reported for nonpregnant females was 35 ± 8 mg/dl (Widmaier et al., 1996), a value within the range reported for nonpregnant females by Heard and Whittier (1997). Total cholesterol reported for males and pregnant females averaged 7 ± 9 and 15 ± 5 mg/dl, respectively (Heard and Whittier, 1997). Compared with other mammals, low cholesterol and urea levels of *P. vampyrus* may be related to their diet of fruit and nectar (Heard and Whittier, 1997). Lymphocytes were the primary white blood cells in *P. vampyrus* (Heard and Whittier, 1997).

As in other members of the genus, *P. vampyrus* lacks a bony patella, and instead has a fibrocartilage and hyaline cartilage within the quadriceps tendon (Smith et al., 1995). The quadriceps tendon forms from dense regular connective tissue deep within the belly of the quadriceps muscle. A pad of hyaline cartilage similar to articular cartilage is found on the deep surface of the tendon. This cartilage adjoins a layer of "herringbone" fibrocartilage, in which large bundles of collagen fibers are located at acute angles to each other. Distally, the fibrocartilaginous layer of connective tissue eventually blends with the normal, dense connective tissue, which forms the bulk of the tendon (Smith et al., 1995).

Baculum of *P. vampyrus,* as in other members of the genus, is saddle-shaped when viewed laterally, but it lacks an apical prominence (Krutzsch, 1962; Lanza, 1963). Horns (proximal prongs) on the baculum in *P. vampyrus* are separate instead of fused as in many other pteropodids; size of medial opening may decrease with age (Lanza, 1963). Baculum ranges from 4.5 to 8.2 mm long and from 5.5 to 10.0 mm wide (Krutzsch, 1962; Lanza, 1963). Ratio of length to width ranges from 0.80 to 0.90, indicating that the baculum is wider than long as in *P. giganteus* and *P. geddiei.* Longitudinal and transverse spinosa areas of baculum have 22 and 11 spines, respectively. Dorsal length and maximum width of caput penis (head of penis) range from 9.7 to 10.6 and 7.7 to 10.1 mm, respectively. Characteristics of caput penis and baculum may differ between two groups within the genus *Pteropus.* The group that includes *P. vampyrus* has a caput penis with a lateroventral groove at least as long as one-half the length of the spinous area and no transverse, subapical groove (Lanza, 1963).

ONTOGENY AND REPRODUCTION. Populations of female *P. vampyrus* give birth synchronously during a single annual peak (Lekagul and McNeely, 1977), although the peak varies geographically and seasonally. In Peninsular Malaysia, pregnancies peak from November to January (Medway, 1969), but can occur in other months (Heideman and Heaney, 1992). In Thailand, where pregnancies are reported to occur during this same period, young are born in March or early April (Heideman and Heaney, 1992; Lekagul and McNeely, 1977). In the Philippines, females reportedly give birth during April and May (Heideman, 1995; Rabor, 1977). Typically, *P. vampyrus* gives birth to a single young (Lekagul and McNeely, 1977). Young bats usually are carried by their mothers for the first few days, but later are left in the roosts while their mothers forage. Young suckle from their mothers for 2–3 months (Lekagul and McNeely, 1977). Two adult males, collected from a mixed-sex colony in Timor, had testes measuring 25 by 20 mm and 22 by 15 mm (Goodwin, 1979).

In captivity (The Lubee Foundation, Inc., Gainesville, Florida) the peak birth period is in May and June (J. Seyjagat, in litt.). At birth, body mass and length of forearm in *P. vampyrus* average 133 g and 79.5 mm, respectively. These values represent 11.7% and 35.4% of maternal body mass and length of forearm, respectively (Kunz and Hood, in press). Logistic growth constant (K) and asymptotic body mass for captive *P. vampyrus* are 0.025 and 755.5 g, respectively. Logistic growth constant (K) and asymptotic size (A) for length of forearm are 0.027 (K, 1/time) and 190.4 mm, respectively (Kunz and Hood, in press).

Dry matter content of milk in *P. vampyrus* is comparable to other members of the Megachiroptera, averaging 16.2% and 17.4% in early and late lactation, respectively (Kunz and Hood, in press). Average percentages of fat, protein, and carbohydrate in milk are 6.3%, 3.1%, and 5.8% early in lactation and 7.9%, 2.6%, and 5.5% in late lactation, respectively. Energy content of milk from early to late lactation averages 0.8 and 1.1 kJ/g (wet mass), respectively. Mineral content of milk (ml/g) from *P. vampyrus* is as follows: Na^+, 0.85; K^+, 0.73; Ca^{2+}, 1.05; Mg^{2+}, 0.11; and P, 1.01 (Kunz and Hood, in press).

ECOLOGY. *Pteropus vampyrus* occurs in many habitats, including primary forests, mangrove forests, coconut (*Cocus nucifera*) groves, and mixed fruit orchards (Heideman and Heaney, 1992; Rickart et al., 1993). Trees in mangrove forests and coconut groves are common day roosts (Davis, 1962; Goodwin, 1979; Payne et al., 1985). In Malaysia, this bat is found most often in lowland habitats below 365 m (Lim, 1966). In Borneo, *P. vampyrus* is common in lowland coastal areas, but may invade nearby islands during the fruiting season (Payne et al., 1985). On the island of Pulau Rambut (ca. 10 km off the coast of Jakarta), *P. vampryus* sometimes roosts in kedoya trees (*Amoora aphanamixis*) but more commonly roosts in kepuh trees (*Sterculia foetida*—Wiriosoepartha et al., 1986). On Sumatra, this bat roosts in cultivated kapok trees (*Ceiba pentandra*—Heideman and Heaney, 1992). On the Krakatau Islands, near West Java, *P. vampyrus* roosts in *Terminalia* trees. Roosts of *P. vampyrus* are in tops of trees on leafless branches (Goodwin, 1979; Kitchner et al., 1990; Payne et al., 1985) and are more often in level lowland forests than in hilly, forested regions (Heideman and Heaney, 1992). At the Bogor Botanical Gardens, West Java, this bat roosted in dead and living trees of several species (Kitchner et al., 1990).

Roosting groups of *P. vampyrus* range from a few individuals to thousands. A colony of ca. 2,000 individuals inhabited a dense

mangrove forest in Timor (Goodwin, 1979). The small number of individuals in mangrove roosts in Malaysia, compared with the number in lowland roost sites, suggests that mangrove forests are used only as temporary resting places (Lim, 1966). However, a colony of ≥15,000 *P. vampyrus* was observed in mangroves along Klumpang Bay in southwestern Borneo (Lyon, 1911). On the island of Palau Rambut, a colony of *P. vampyrus* was estimated to include 9,000–21,000 individuals (Wiriosoepartha et al., 1986). Individuals and groups roosted as high as 30.5–45.7 m in trees (Lim, 1966).

Pteropus vampyrus roosted in large colonies in the canopy of emergent trees on the island of Mindanao (Philippines), often sharing roosts with *A. jubatus* (Heideman and Heaney, 1992). Mixed groups of these two species may range from 500 to ca. 150,000 individuals (Heideman and Heaney, 1992; Mudar and Allen, 1986; Taylor, 1934). An important distinction between roosting habits of *A. jubatus* and *P. vampyrus* in the Philippines is that the latter species also roosts in orchards and coconut groves (Heideman and Heaney, 1992). On the island of Timor, *P. vampyrus* formed loose feeding associations with *P. griseus, A. jubatus,* and *Dobsonia peroni* (Goodwin, 1979).

The large flying fox feeds on flowers, nectar, and fruit, but more frequently on flowers and nectar when all are available (Davis, 1962; Goodwin, 1979; Gould, 1977; Harrisson and Harrisson, 1966; Lekagul and McNeely, 1977; Medway, 1969; Payne et al., 1985; Utzurrum, 1984). *P. vampyrus* feeds on pollen, nectar, and flowers of coconut (*C. nucifera*) and durian trees (*Durio zibethinus*); fruits of rambutan (*Nephelium lappaceum*), fig (*Ficus*), and langsat (*Lansium domesticum*) trees; and other wild and cultivated fruits such as mangoes (*Mangifer indica*) and bananas (*Muca*—Davis, 1962; Goodwin, 1979; Gould, 1977; Harrisson and Harrisson, 1966; Heideman and Heaney, 1992; Lim, 1966; Rickart et al., 1993; Utzurrum, 1984). An 800-g *P. vampyrus* can carry a food load up to 200 g (Marshall, 1985). When this bat feeds on fruit, it typically slices open the rind and extracts the pulp (Davis, 1962).

When feeding on flowers of durian trees, *P. vampyrus* licks nectar with its long tongue but apparently does not damage the flowers. Each bat visits several different flowers at least twice each night and defends the tree from conspecifics (Gould, 1977). The stomach of one individual contained 8 ml of clear liquid (presumably nectar), a small amount of pollen, and 1 ml of flower parts. Assuming average nectar content of a durian flower is 0.36 ml (Gould, 1977), this individual visited ≥22 flowers. During nightly feeding, *P. vampyrus* may move to adjacent trees, gliding among the lower branches (Gould, 1978).

Because humans eat large flying foxes, *P. vampyrus* was originally assigned to *Pteropus edulis* (Geoffroy St. Hilaire, 1810; Hill and Smith, 1984). Illegal poachers and international trade continue to find a market for *P. vampyrus* as a prized food item. Several shipments of bats, originating in the Philippines and confiscated in Guam, contained the carcasses of 20 *P. vampyrus* (Wiles, 1992).

In some areas *P. vampyrus* is considered a nuisance to farmers, in whose orchards individuals sometimes feed (Lim, 1966; Medway, 1969). Tactics such as flapping and whirling devices and lights have been used to discourage this and other species from feeding on fruit crops (Medway, 1969). In the Philippines, mixed colonies of *P. vampyrus* and *A. jubatus* have declined severely since the 1920s, largely due to intensive hunting pressure (Heideman and Heaney, 1992). *P. vampyrus* is a frequent target of hunters because it is noisy and conspicuous. Roosting sites of *P. v. malaccensis* in mangroves and lowland forests in Malaysia also are threatened by deforestation (G. W. H. Davison, in litt.).

The filarial parasite *Litmosa maki* (Filarioidea: Onchocercidae) is known from the abdominal cavity of *P. vampyrus* (Ramachandran et al., 1966; Tibayrenc et al., 1979). Ectoparasites from the families Laelapidae, Nycteribiidae, and Spinturnicidae also have been reported from Malaysian specimens (Beck, 1971). Members of the family Nycteribiidae occur more frequently, but in relatively low numbers. Rectal bacterial flora reported from *P. vampyrus* include gram-positive rods (*Bacillus, Corynebacterium*), gram-positive cocci (*Enterococcus, Staphylococcus aureus, Streptococcus*—hemolytic and group D), gram-negative rods (*Escherichia coli, Morganella morgannii*), and yeast (Heard et al., 1997).

Maximum life span of *P. vampyrus* in captivity is at least 15 years (Lekagul and McNeely, 1977). Selected aspects of captive husbandry of *P. vampyrus* were discussed in Marshall and Lim (1968).

BEHAVIOR. Colony members of *P. vampyrus* leave roost sites near sunset in a silent and loose stream (never a dense flock) that may continue past nightfall (Lekagul and McNeely, 1977; Medway, 1969). *P. vampyrus* may fly nightly up to 50 km to reach its feeding grounds (Lawrence, 1939; Marshall, 1985; Medway, 1969), often following a set route each night. Interisland movements may occur at high altitude (Rabor, 1977). Individuals may shift feeding sites in response to changes in food availability.

Flight of *P. vampyrus* is strong and deliberate and occurs without accompanying vocalizations (Lekagul and McNeely, 1977; Medway, 1969). Upon arriving in feeding areas, large flocks may separate into family or feeding groups numbering from a few to 50 or more individuals. They may circle a fruit tree before landing. Individuals usually land on the tips of tree branches in a head-up position and then fall into the head-down position from which they feed. Feeding aggregations of *P. vampyrus* are very noisy (Gould, 1977, 1978; Harrisson and Harrisson, 1966). One colony in Sarawak, numbering ca. 500 individuals, depleted a 0.64-km^2 area of fruit in 19 days, at which point the bats abandoned the area (Harrisson and Harrisson, 1966; Medway, 1965).

Territorial behavior in *P. vampyrus* seems to be promoted by presence of flowers on trees. This behavior is manifested as bats spread their wings and swing their bodies in a 45° arc while growling at conspecifics (Gould, 1978). This behavior seems to discourage other bats from landing in a defended tree. In Malaysia, two or three bats may occupy one large durian tree when feeding, but only single individuals seem to occupy smaller trees. Two distinct feeding periods occur at 1930–2130 h and 2230–2330 h, between which times bats seem to rest in trees (Gould, 1977).

When *P. vampyrus* returns to its day roost at dawn, it may be met by hostile behavior from conspecifics (Goodwin, 1979; Medway, 1969). Agonistic behaviors such as sparring with wrists and thumbs, biting, and the production of loud vocalizations seem to promote spacing, which maintains individuals just beyond the reach of one another (Goodwin, 1979). The return around dawn is characterized by raucous vocalizations and considerable movement. A bat will use its thumb claws to move to a suitable roosting site after landing, often fighting others as it moves along the branches. *P. vampyrus* commonly roosts with its head downward and its wings wrapped around its body (Medway, 1969; Rabor, 1977); but during warm hours of the day individuals often cool themselves by fanning with partly outstretched wings (Goodwin, 1979). Restlessness of roosting bats continues until midmorning. Some locomotor activity occurs later during the day, often involving short flights around the roost (Lim, 1966; Rabor, 1977). In captivity individuals suspend themselves from their thumbs when they defecate (Medway, 1969).

GENETICS. Diploid and fundamental numbers of chromosomes are 38 and 72, respectively. Autosomal chromosomes consist of eight pairs of metacentrics, nine pairs of submetacentrics, and one subtelocentric pair. The X chromosome is a medium-sized submetacentric, whereas the Y is a dotlike acrocentric. One medium-sized submetacentric pair contains a secondary constriction (Harada and Kobayashi, 1980).

CONSERVATION STATUS. The Convention on International Trade in Endangered Species of Fauna and Flora (CITES) lists *P. vampyrus* in its Appendix II, which designates species that may become threatened with extinction if trade is not regulated (Brautigan, 1992). In Peninsular Malaysia, Sumatra, Thailand, Vietnam, and nearby islands, *P. vampyrus* is threatened by loss and degregation of mangroves for coastal reclamation, aquaculture, commercial logging, and land clearing for rubber plantations (Heideman and Heaney, 1992). Listed as vulnerable in the Phillipines, the status of this species is unknown or not threatened in many other regions. Controls on hunting are considered to be unenforceable. The most effective method for protection may be management of colonies on small islands (Heideman and Heaney, 1992).

REMARKS. Members of the genus *Pteropus* are commonly referred to as flying foxes and fruit bats. Common names of *P. vampyrus* include keluang, paniki, kabog, giant flying fox, island flying fox, Malayan flying fox, Malayan large flying fox, Malaysian flying fox, common flying fox, Sunda Island flying fox, large fruit bat, Malacca fruit bat, and red-necked fruit bat, each reflecting local usage.

The generic name *Pteropus* means 'wing-footed' (Gove, 1983). It originates from the Greek words *pteron* meaning 'wing,' 'feather,'

or 'fin' (Brown, 1954) and *pous* meaning 'foot' (Gove, 1983). The name *vampyrus* is derived from the Slavic word 'wampir,' which means "blood sucking ghost or demon: vampire" (Brown, 1954); this species originally was considered a blood-sucking bat (Andersen, 1912).

We thank L. R. Heaney and P. D. Heideman for suggestions on an earlier version of this manuscript, J. Seygagat for unpublished information, The Lubee Foundation, Inc., for permission to photograph live specimens under its care, and A. A. Stern and C. Cardenuto for their translations of German and Italian articles, respectively. This paper is contribution no. 3 of The Lubee Foundation, Inc.

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