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Pteropus livingstonii.

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***Pteropus livingstonii* Gray, 1866**

Comoro Flying Fox

Pteropus livingstonii Gray, 1866:66. Type locality "Island of Johanna, Comoro Group."

Pteropus edwardsi Peters, 1867:325. Not *Pteropus edwardsi* É. Geoffroy St.-Hilaire, 1810:92.

Pteropus livingstonei Andersen, 1912:247. Unjustified emendation of *Pteropus livingstonii* Gray, 1866:66.

CONTEXT AND CONTENT. Order Chiroptera, suborder Megachiroptera, family Pteropodidae, subfamily Pteropodinae, genus *Pteropus*. The genus *Pteropus* contains 65 species (Simmons 2005). *Pteropus* may contain 17 groups with *P. livingstonii* in the *melanopogon* group (Andersen 1912). Alternatively, *P. livingstonii* and *P. melanopogon* are in separate monotypic groups (Simmons 2005). No subspecies are recognized.

DIAGNOSIS. *Pteropus livingstonii* (Fig. 1) was previously allied to *P. melanopogon* (Nowak 1999), but ears of *P. livingstonii* are rounded above, fur is much longer, and furred area of back is of normal width; *P. livingstonii* is smaller in size than *P. melanopogon* (Andersen 1912). Lateral membranes of wings arise more closely together than seen in other members of *melanopogon* group. Skull is similar in shape to that of *P. melanopogon* but is smaller with narrower premaxilla and relatively smaller orbits. Front surface of upper canines has a vertical groove that is shallower (almost obsolete) than that of *P. melanopogon* (Andersen 1912). In the western Indian Ocean region, only *P. niger* and *P. rufus* attain the same dimensions as *P. livingstonii*. *P. niger* differs from *P. livingstonii* in having small, pointed, nonexposed ears and a different color pattern. *P. rufus* has large pointed ears and a brownish yellow to orange-yellow mantle, which strongly contrasts with dark body fur of *P. livingstonii* (Bergmans 1990). Only 2 other fruit- and nectar-eating bats occur on the Comoro Archipelago: *P. s. comorensis* and *Rousettus obliviosus*. On Ajouan and Moheli, *R. obliviosus* is considerably smaller than either *Pteropus* (Carroll and Thorpe 1991; Cheke and Dahl 1981; Young et al. 1993). *P. livingstonii* and *P. seychellensis comorensis* are sympatric where *P. livingstonii* occurs. *P. s. comorensis* has a brownish yellow to orange-yellow mantle and relatively pointed ears that are smaller than those of *P. livingstonii* (Bergmans 1990). Body mass of *P. livingstonii* is 27% larger than that of *P. s. comorensis* (Lindhe Norberg et al. 2000) and *P. livingstonii* has a larger wingspan than *P. s. comorensis* (Andersen 1912; Lindhe Norberg et al. 2000; Trewhella et al. 2001). Compared with *P. s. comorensis*, *P. livingstonii* has a slightly lower wing loading (2%), lower relative wing loading (10%), slightly longer wingspan in relation to body size, higher aspect ratio (20%), smaller wing-tip length and area ratios, and similar wing-tip shape index.

GENERAL CHARACTERS. *Pteropus livingstonii* has large, protruding ears that are rounded half-circles above (Andersen 1912; Bergmans 1990; Cheke and Dahl 1981). Inner margins of ears are convex, outer margins are straight or flatly convex, and length from notch to tip is 30.3 mm (Bergmans 1990). Hair on ventral side of adults is directed backward, spreading onto mantle, with length (in mm) of fur: dorsum, 21; mantle, 25–27; ventrum, 25 (Andersen 1912). Color of pelage is blackish over most of body with a dark russet hue, sprinkled with golden or tawny hairs on rump, sides of belly, and flanks (Andersen 1912; Bergmans 1990). Tawny hairs also may occur on dorsum in a band ≤6 cm wide and 1–1.5 cm long anteroposteriorly with tufts of tawny-colored fur on each shoulder (Bergmans 1990). Deep reddish brown (or tawny)–colored hairs form a ring around genitals and continue laterally as a short stripe (Cheke and Dahl 1981). Tawny color is confined to tips of hairs with shading through ochraceous-buff subapically to silvery-grayish white in basal area (Andersen 1912; Bergmans 1990). Tawny-colored markings vary, with markings completely absent and uniform black throughout or with markings present or absent in different sections of body (Carroll and Thorpe 1991; Cheke and Dahl 1981). Upper inner side of tibia and adjoining tail membrane are covered with dense fur (Bergmans 1990). Wings are dark, shiny, and devoid of hair. Forearms, tibia above, hind legs, ears, and nose also are devoid of hair (Andersen 1912; Bergmans 1990; Trewhella et al. 2001).

Mean (±*SD*) body mass (in g) and length of forearm (in mm) for 21 males and 2 females, respectively, are: 576.3 ± 48.0 and 170.8 ± 4.0; 601.5 and 168.3 (Clark et al. 1997). External measurements (mean ± *SD*; in mm) for 15 males and 2 females, combined, are: length of thumb, 43.9 ± 1.5; 2nd digit, length of metacarpal, 92.4 ± 3.4; length of 2nd digit, 1st phalanx, 27.3 ± 2.1; length of 2nd digit, 2nd phalanx, 16.0 ± 1.0; length of 3rd digit, metacarpal, 121.9 ± 3.9; length of 3rd digit, 1st phalanx, 91.9 ± 3.3; length of 3rd digit, 2nd phalanx, 115.9 ± 4.8; length of 4th digit, metacarpal, 119.6 ± 3.7; length of 4th digit, 1st phalanx,

FIG. 1. Photograph of an adult female *Pteropus livingstonii* from the Jersey Zoo, Trinity Parish, Jersey, Channel Islands of the United Kingdom. Used with permission of the photographer, J. Morgan, Durrell Wildlife Conservation Trust.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult female *Pteropus livingstonii* (Natural History Museum, London, United Kingdom 88.5.9.1 [purchased from Frank, dealer; ca. 1888]) from Johanna Island (=Anjouan). Greatest length of skull is 69.1 mm (Bergmans 1990).

74.6 ± 3.0; length of 4th digit, 2nd phalanx, 64.9 ± 3.1; length of 5th digit, metacarpal, 127.2 ± 3.7; length of 5th digit, 1st phalanx, 57.8 ± 2.4; length of 5th digit, 2nd phalanx, 52.5 ± 2.4; length of tibia, 81.9 ± 2.3 (Clark et al. 1997). Upper and lower postorbital processes of skull are sometimes fused and completely encircle orbits (Fig. 2; Andersen 1912). Cranial measurements (ranges, in mm; *n* in parentheses—Bergmans 1990) are: greatest length of skull, 69.1–72.4 (3); condylobasal length, 70.4–71.1 (2); zygomatic width, 37.7–39.3 (3); width of cranium, 23.0–24.2 (4); palatal length, 39.1–41.3 (6); length of rostrum, 28.8–30.3 (6); interorbital width, 12.0–12.5 (7); postorbital width, 8.9–10.0 (6); length of mandible, 56.4–58.8 (7); height of mandible, 27.5–29.9 (7); length of upper toothrow, C–M2, 27.3–30.0 (6); length of lower toothrow, c–m3, 31.0–33.4 (7); width across canines (externally), 13.9–14.9 (6); width across upper molars (externally), M1–M1, 20.4–21.2 (6); width across upper molars (externally), M2–M2, 17.8–18.4 (4). Additional cranial measurements (ranges, in mm; *n* = 3—Andersen 1912) are: width of braincase at zygomata, 25.0; postorbital constriction, 8.9–10.7; interorbital constriction, 12.0–12.8; combined width of upper incisors, 7.0; lachrymal width, 17.2–18.2; orbital diameter, 13.0–13.5; width of mesopterygoid fossa, 9.0–9.7; length from front orbit to tip of nasals, 25.8–26.5; height of coronoid process, 28.2–31.5. Length and width of dentition, respectively (ranges, in mm; *n* = 3—Andersen 1912) are: P3, 5.3–5.7, 3.7–3.8; P4, 5.7–5.8, 3.8–3.9; M1, 6.0–6.3, 3.6–3.7; M2,

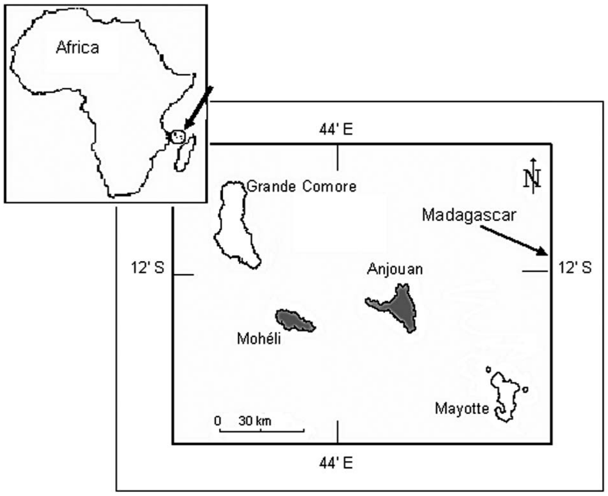

FIG. 3. Geographic distribution of *Pteropus livingstonii*. Map adapted from Trewhella and Reason (1992).

3.0–3.2, 2.2–2.5; p1, 2.7–2.9, 2.0–2.5; p3, 5.6–5.8, 3.1–3.2; p4, 5.9–6.2, 3.2–3.3; m1, 5.3–5.9, 3.2–3.6; m2, 4.2–4.8, 3.0–3.1; m3, 2.7–2.8, 1.9–2.0. It is not clear if sexual dimorphism occurs in *P. livingstonii* because sufficient numbers of adult females have been difficult to collect in the wild (Clark et al. 1997; Trewhella et al. 1995a; Young et al. 1993). Existing measurements of male and female *P. livingstonii* do not show significant differences by sex.

DISTRIBUTION. *Pteropus livingstonii* is endemic to 2 of the 4 Comoro Islands northwest of Madagascar: Anjouan (formerly Johanna) and Moheli (Fig. 3; Trewhella et al. 2001). No fossils are known.

FORM AND FUNCTION. Dental formula of *P. livingstonii* is i 2/2, c 1/1, p 3/3, m 2/3, total 34 (Dobson 1878). *P. livingstonii* flies with a slow, flapping flight and uses soaring flight, often in circles to gain height quickly after taking off (Cheke and Dahl 1981; Lindhe Norberg et al. 2000; Trewhella et al. 2001; Young et al. 1993). When leaving roosts, *P. livingstonii* performs either short circling flights (usually on exiting the roost when sun is out and usually before noon) or longer, commuting flights (when *P livingstonei* ascends quickly and sometimes circles first to gain height—Trewhella et al. 2001). Wing and flight characteristics for adult male *P. livingstonii* (*n* = 4) are: wing area (mean ± *SD*) 0.245 ± 0.011 m^2; aspect ratio, 6.52; wing loading, 25.8 N/m^2; relative wing loading, 3.04; wing-tip length ratio, 1.24 ± 0.137; wing-tip area ratio, 0.51 ± 0.031; wing-tip shape index, 0.71; minimum sinking speed, 0.62 m/s; minimum sinking at forward speed, 8.2 m/s; lift coefficient, 0.62; glide ratio at minimum sinking speed, 13.2; best glide speed, 9.3 m/s; best glide speed at $(L/D)_{max}$, 14.3; turning radius at 35° bank, 11.9 m; and turning radius at sinking speed, 0.83 m/s (Lindhe Norberg et al. 2000). *P. livingstonii* has a large body mass for a soaring species but because it is diurnal it can use thermals to compensate; also its long wingspan and large wing area lower its wing and relative wing loadings (Lindhe Norberg et al. 2000).

ONTOGENY AND REPRODUCTION. *P. livingstonii* produces 1 offspring a year in autumn, most often during the 1st half of September (Trewhella et al. 1995b). Environmental cues may affect timing of fertility in females, with environmental fluctuations resulting in different timing of births (Trewhella et al. 1995b). In the wild, infants are observed in July, August, and mid-January (Trewhella et al. 1995b).

In captivity, 2 infant *P. livingstonii* were completely weaned at 8 months; 2 others foraged independently at 2.5 and 5 months of age (Courts 1998). Casual fighting and mounting among captive infants are important to social development (Courts 1998). Early on, infants play with their mothers, but as they grow, infants play with peers, adult females, and subordinate males. In captivity, at 6 months of age, male aggression rises during territory establishment (Courts 1998).

ECOLOGY. *Pteropus livingstonii* depends on primary, native, montane forests (Carroll and Thorpe 1991; Cheke and Dahl 1981; Granek 2002; Reason and Trewhella 1994; Trewhella et al. 1995a, 1998). Thirteen sites on Anjouan (maximum elevation 1,595 m) were found between 500 and 960 m, with no roosts <300 m (Granek 2002; Trewhella et al. 1998). Roosts of *P. livingstonii* typically occur near ridge tops on Anjouan (Trewhella et al. 2001). Roosts on Moheli (maximum elevation 790 m) are few compared with Anjouan; only 1 roost was found during the dry season in 1995 (Trewhella et al. 1998) and 2 during the rainy season (Granek 2002). Intra-island movement among roosts is likely, but interisland movement is unknown. Anjouan and Moheli are 50 km apart at their nearest point and the 2 closest roosts on each island are ca. 90 km apart.

Since 2002, 20 roosts of *P. livingstonii* have been found on Anjouan and Moheli (Trewhella et al. 2005). Roost composition and size change substantially between dry season (May–September) and rainy season (October–April—Granek 2002; Reason and Trewhella 1994). Number of *P. livingstonii* at roosts ranges from a few to >100 individuals (Granek 2002; Reason and Trewhella 1994; Trewhella et al. 1998).

Deforestation has significantly reduced roosting habitat for *P. livingstonii*. The natural forest on Anjouan has declined from 120 km^2 in 1925 to 80.8 km^2 in 1972 to 21.6 km^2 in 1987; this represents a 73% loss from 1972 to 1987 (Trewhella et al. 1998). The natural forest on Moheli declined from 33.3 km^2 in 1969 to 15.5 km^2 in 1987, or a 53% loss (Trewhella et al. 1998). Some roosts of *P. livingstonii* occur in forest underplanted with crops (Granek 2002; Trewhella et al. 1995a). Natural forest and forests with underplanted crops, which could contain roosts, totaled 82.8 km^2 on Anjouan and 34.6 km^2 on Moheli in 1987 (Trewhella et al. 1998). Only a few roosts occur in locations of mixed forests and fields, and remnant populations occur at 2 closely situated roost sites, where up to 90% of the forest is depleted (Granek 2002). *P. livingstonii* was only seen at higher-elevation roosts on Anjouan before the major habitat loss in the 20th century (Humblot in Milne-Edwards and Oustalet 1888).

In endemic forest, trees used as roosts, including *Brachylaena ramiflora*, *Ficus*, *Gambeya*, and *Nuxia pseudondentata*, dominate (Granek 2002). Other tree species sometimes used as roosts are *Albizia lebbeck*, *Khaya comorensis*, *Ocotea comoriensis*, and *Terminalia catappa* (Granek 2002). The predominant native, upper-canopy trees at roost sites are *K. comorensis* and *N. pseudondentata*, which reach 30 m in height; midcanopy forest genera include *Anthocleista*, *Ficus*, and *Tambourissa* (Granek 2002). Roosts of *P. livingstonii* also occur on Anjouan and Moheli at midelevation dense, evergreen rain forest (canopy height >15 m) and contain *Anthocleista*, *Ficus*, and *Tambourissa*. Two exotic trees, *A. lebbeck* and *Ceiba*, also are present (Granek 2002). Roost trees of *P. livingstonii* average 103 cm diameter at breast height and 24 m in height (Granek 2002).

Abiotic factors are strongly associated with roosts of *P. livingstonii* (Granek 2002). On Anjouan, most remaining montane forest occurs on steep slopes, and thus roosts of *P. livingstonii* have slopes >30° (Carroll and Thorpe 1991; Cheke and Dahl 1981; Clark et al. 1997; Granek 2002; Reason and Trewhella 1994; Trewhella et al. 1995a, 1998, 2001; Young et al. 1993). Moheli has not experienced the same degree of deforestation as Anjouan; roost sites have slopes <30° (Granek 2002; Trewhella et al. 1998). Roosts are usually located on southeast-facing slopes, which provide shade from midday sun in the Southern Hemisphere (Granek 2002; Trewhella et al. 2001). Most roosts are located in close proximity to water and where slopes on 3 sides moderate climate or provide some regulation of atmospheric conditions (Granek 2002).

Pteropus livingstonii prefers different foods based on seasonal availability (Granek 2002; Trewhella et al. 1998, 2001). *P. livingstonii* consumes fruits, leaves, nectar, and pollen in montane forests (Reason and Trewhella 1994; Trewhella et al. 2001). The food items include Asteraceae (*Brachylaena raiiflora*), Bombacaceae (exotic *Ceiba pentandra*), Cunoniaceae (*Weinmania comorensis*), Monimiaceae (*Tambourissa comoriensis*), Moraceae (*Ficus lutea* and *F. pirifolia*), and Sapotaceae (*Gambeya*—Trewhella et al. 2001). *P. livingstonii* preferentially selects *F. lutea* during the dry season and *F. antandronarum* during the rainy season (Sewall 2002). *P. livingstonii* also selects *A. grandiflora* during the rainy season, but despite high availability of its fruit during the dry season, it is not selected over *F. lutea* (Sewall 2002). The only other fruit consumed by *P. livingstonii* is *Callophyllum inophyllum* (Clusiaceae). Flowers from an unknown Malphigiaceae and *Gyrostipula* or *Neonauclea* (Rubiaciae) also are consumed (Sewall 2002). Kapok (*C. pentandra*) flowers and associated nectar are highly favored by *P. livingstonii*, but its fruit is much less preferred (Reason and Trewhella 1994; Trewhella et al. 1995a, 2001; Young et al. 1993).

Comoro flying foxes maintained at the Jersey Zoo in Trinity Parish of Jersey, in the Channel Islands of the United Kingdom, frequently hunt insects around artificial light sources (Courts 1997a). Insects eaten by captive *P. livingstonii* include angle shade moths (*Phologophora meticulosa*), green lacewings (*Chrysopa septempunctata*), and silvery moths (*Autographa gamma*—Courts 1997a). When the zoo released moths in enclosures, hunting response was immediate (Courts 1997a). Eleven captive *P. livingstonii* at the Jersey Zoo consumed in descending order, willow (*Salix*), bamboo (*Arundinaria* and *Phyllostachys*), ash (*Fraxinus excelsior*), and bramble (*Rubus fruticosus*—Masefield 1999).

The 3 fruit- and nectar-eating bats on the Comoro Archipelago partition some aspects of their resource use, based on size and physiology. *P. s. comorensis* is common on all the Comoro Islands, and *R. obliviosus* is endemic to Grande Comore, Anjouan, and Moheli (Carroll and Thorpe 1991; Cheke and Dahl 1981; Trewhella et al. 1998, 2001; Young et al. 1993). Flight dynamics differ between congeners; *P. livingstonii* commonly soars and *P. s. comorensis* rarely soars (Lindhe Norberg et al. 2000; Trewhella et al. 2001). Wingbeat frequency during normal flapping flight is slower for *P. livingstonii* (3.2 Hz) than *P. s. comorensis* (2.2 Hz—Lindhe Norberg et al. 2000).

Spatial separation between *P. livingstonii*, *P. s. comorensis*, and *R. obliviosus* occurs during flying and in their positioning in trees from which they feed. *P. livingstonii* uses the upper canopy when roosting and foraging (Trewhella et al. 1995a, 2001; Young et al. 1993). *R. obliviosus* can fly and feed within and below the canopy whereas the larger *Pteropus* species fly above the canopy; however, *R. obliviosus* also flies at upper-canopy level (Reason et al. 1994; Young et al. 1993). When all 3 bats are present in kapok trees, *P. livingstonii* forages in the upper canopy, *P. s. comorensis* in the middle canopy, and *R. obliviosus* in the lower canopy (Reason et al. 1994). *P. livingstonii* and *P. s. comorensis* sometimes roost together, albeit infrequently. *P. s. comorensis* roosts from sea level to 750 m, commonly in and around cultivated fields or more degraded habitat, whereas *P. livingstonii* predominantly roosts in less-degraded habitat or montane forests between 500 and 960 m on Anjouan (Trewhella et al. 1995a, 1998, 2001; Young et al. 1993).

Niche separation occurs temporally between *Pteropus* species in the Comoro Archipelago. *P. livingstonii* is a cathemeral fruit bat, active during the day and night, often flying by 1200 h and again several hours before dusk when these bats fly to their feeding sites (Cheke and Dahl 1981; Trewhella et al. 2001; Young et al. 1993). On Anjouan and Moheli where these congeners are sympatric, *P. s. comorensis* rarely flies during the day and arrives at feeding sites at dusk (Cheke and Dahl 1981; Trewhella et al. 2001); *P. s. comorensis* commonly flies during the day on islands where *P. livingstonii* does not occur (Trewhella et al. 2001). Timing of parturition differs between *Pteropus* when sympatric; *P. livingstonii* gives birth up to 2 months earlier than *P. s. comorensis* (Trewhella et al. 1995b, 1998, 2001).

Overlap of diet commonly occurs between *Pteropus* species in the Comoro Archipelago. *P. livingstonii* typically depends on food items in montane forests, and *P. s. comorensis* consumes the same food items as *P. livingstonii* but has a more varied diet, commonly consuming cultivated fruits and other food items found at lower elevations (Reason and Trewhella 1994; Trewhella et al. 2001). Both *Pteropus* species strongly select *F. lutea* during the dry season, but *P. s. comorensis* also selects *F. antandronarum* during both rainy and dry season (Sewall 2002). The 2 *Pteropus* species vary in their consumption of exotic species (Sewall 2002). *P. livingstonii* is known to only consume (predominantly flowers) from 1 exotic, *C. pentandra*, whereas *P. s. comorensis* consumes items from 5 exotic tree species and consumes a greater variety of native species (Sewall 2002). Where overlap occurs, and where food items are worth defending (such as the flowers of kapok), *P. livingstonii* defends a feeding area (Trewhella et al. 2001). Because *P. livingstonii* often arrives at foraging sites before *P. s. comorensis*, *P. livingstonii* claims and defends the area where these bats are hanging and feeding, after dusk, from any intruders (*P. s. comorensis* and conspecifics who arrive later). *P. livingstonii* successfully defends and takes over feeding areas from *P. s. comorensis*, except male *P. s. comorensis* can usurp feeding areas from female *P. livingstonii*.

Unconventional mist-net rigging is required to capture *P. livingstonii* in the upper canopy and above the canopy (Carroll and Thorpe 1991; Clark et al. 1997; Trewhella et al. 1995a; Young et al. 1993). Rigging generally consists of a static top-line to keep poles from bending and nets from sagging, with >1 net (1 below the other, giving vertical depth) attached to vertical ropes with pulleys. Poles are positioned in trees or tied to other trees to ensure nets sit at the desired canopy level (Clark et al. 1997; Trewhella et al. 1995a; Young et al. 1993).

BEHAVIOR. *Pteropus livingstonii* roosts with wings folded around body (Carroll and Thorpe 1991; Cheke and Dahl 1981). Flying and foraging reach a peak from 2200 to 0200 h (lull around midnight), with a steady decline in activity until 0400 h (Trewhella et al. 1995a, 2001). Comoro flying foxes may bask and stretch their wings in sunlight, but activity is reduced with cloud cover. During high temperatures, *P. livingstonii* thermoregulates by urinating on its wing membranes and fanning itself (Trewhella et al. 2001).

When feeding on *C. pentandra* flowers, *P. livingstonii* arrives at feeding sites individually and hangs without feeding until dusk (Trewhella et al. 2001). Comoro black flying foxes defend their feeding territories from *P. s. comorensis* and conspecifics by chattering vocalizations, approaching, chasing, and clapping wings toward intruders. If such interactions become aggressive, then thumb claws are used and biting occurs (Trewhella et al. 2001).

Movement, feeding, elimination, and stationary postures of captive *P. livingstonii* are similar to those of other *Pteropus* (Courts 1996). Threat or intimidation postures by captive *P. livingstonii* include wing shaking, marching with wings alternately moving back and forth, chattering vocalization, and 1–6 wing claps (Courts 1996). More direct aggression includes approaching intruder, chasing, using long thumb claws against intruder, biting, wrestling, and territory takeover with retreat of loser. Alarm or apprehension consists of subtle body jerks with wings open, folded on either side of body, or wrapped ventrally; side-to-side swaying with wings in any position; and simultaneous wing-spreading by a group of Comoro flying foxes while in the roosting position (Courts 1996). The entire process of eating, from securing the food to spitting out the ejecta pellet, takes 3–8 min (Courts 1996).

Hierarchy-associated behaviors of captive *P. livingstonii* include body or genital sniffing and male scent-marking by rubbing sides of head and back of neck on a substrate (Courts 1996). Mature females, mothers and daughters, subordinates, and members of male–female pairs exhibit play behaviors, including prolonged gentle wrestling, holding, mouthing, biting, and genital sniffing and grooming, all without vocalizations (Courts 1996). Prolonged play of *P. livingstonii* may result in pseudocopulation (males without erect penis—Courts 1996). Albeit rare, captive *P. livingstonii* share food, which involves 1 bat vigorously licking the mouth of a chewing bat. The chewer may hold the licking bat by the head, the licking bat may hold the chewer, or they may hold each other (Courts 1996). Such behavior by *P. livingstonii* occurs between males and females, mothers and offspring, and subordinate males.

Captive *P. livingstonii* displays several vocalizations. A low, audible chatter is emitted when a male approaches a female to smell her or to ward off others. Different vocalizations occur during aggression or territorial defense. One vocalization sounds like several, discrete, 2-toned calls in succession and is made mostly by males; females make the sound in a quieter tone. Another is a cackle sound used during aggressive fighting by females to deter advancing males. Captive *P. livingstonii* make 2 sounds in response to alarm or fear, which consist of squeaking sounds made by subordinates and deep, repetitive, monotone clucking sounds (Courts 1996).

Mating system of captive *P. livingstonii* consists of dominant males maintaining a harem of adult females and their female offspring (Courts 1997b). Relationships of captive males are complex, composed of a shifting linear dominance hierarchy (Courts 1997b). Captive *P. livingstonii* females act aggressively toward pre- and postcopulatory licking of their genitals by courting males (Courts 1996). In captivity, copulation by *P. livingstonii* occurs while the male holds the female dorsally, restrains her forelimbs with his, and holds the scruff of her neck in his mouth (Courts 1996). Females emit low-pitched grunting and rasping sounds followed by high-pitched screeches during copulation and loud, distinct chattering upon separation from the male; males make a constant, rasping, squelching noise throughout copulation (Courts 1996). A copulatory episode usually consists of a single intromission with thrusting, possible ejaculation, and copulatory lock. Length of intromission is 2–6 min in captive *P. livingstonei* (Courts 1996). *P. livingstonii* does not perform sequential copulations and usually postcopulatory allogrooming of genital areas takes place (Courts 1996).

CONSERVATION STATUS. In 1888, *P. livingstonii* was abundant in the montane forests on Anjouan (Milne-Edwards and Oustalet 1888). Only ca. 1,200 *P. livingstonii* were estimated on Anjouan and Moheli in 2005 (Trewhella et al. 2005). Human destruction of primary montane forest is the leading cause of decline of *P. livingstonii*, followed by cyclones (Clark et al. 1997; Mickleburgh et al. 1992; Reason and Trewhella 1994; Trewhella et al. 1998, 2001; Young et al. 1993). From 1990 to 1995, Anjouan experienced an annual rate of deforestation of 5.8%, and loss of primary forest habitat is ongoing (Trewhella et al. 2001). Cyclones cause heavy destruction of the vegetation of the Comoro Islands and pass over the area ca. every 10 years (Mickleburgh et al. 1992; Trewhella et al. 1998). Cyclones destroy roosts and food plants of *P. livingstonii* (Reason and Trewhella 1994).

The World Conservation Union (formerly International Union for Conservation of Nature and Natural Resources [IUCN]) lists *P. livingstonii* as critically endangered because of a reduction in population size caused by loss of habitat (2004 IUCN Red List of Threatened Species, http//www.iucnredlist.org, accessed 19 January 2006). The IUCN 1st listed *P. livingstonii* as endangered in 1988, and the species was changed to critically endangered in 1996. The IUCN formulated an action plan for preservation of *P. livingstonii*, and the IUCN/Species Survival Commission Chiroptera Specialist Group further expanded on this action plan (Mickleburgh et al. 1992). The action plan calls for ongoing monitoring and assessment of known populations while continually searching for new populations. Biannual (1 dry season and 1 rainy season) simultaneous counts are conducted at all known roosts of *P. livingstonii* by members of Action Comores (a nongovernment organization) and locally trained volunteers (Clark et al. 1997; Trewhella et al. 1998). The action plan also requires: research on feeding ecology, population biology, and habitat requirements of *P. livingstonii*; establishment of forest preserves; and educational programs on Anjouan and Moheli to protect extant forests and populations of *P. livingstonii*. Educational materials are distributed that focus on the importance of protecting native forest and fruit bats (Trewhella et al. 2005).

Captive breeding colonies of *P. livingstonii* have been established to safeguard against extinction (Mickleburgh et al. 1992). In 1989, the Comorian government (Federal Islamic Republic of the Comores) and the Durrell Wildlife Conservation Trust signed an agreement to take some *P. livingstonii* into captivity; all bats caught and their progeny remain the property of the Federal Islamic Republic of the Comores (Carroll and Thorpe 1991; Clark et al. 1997; Young et al. 1993). Expeditions (4 total) collected *P. livingstonii* for a captive colony at the Jersey Zoo. In 1995, 17 wild *P. livingstonii* were in captivity at the Jersey Zoo (Clark et al. 1997; Courts 1996). Number of individual *P. livingstonii* in captivity increased to 42 in 2002; these individuals are housed as 3 separate populations at 2 zoos (Jersey Zoo and Bristol Zoo in Clifton, Bristol, United Kingdom—Action Comores, in litt.).

Recently formulated conservation efforts highlight education by prioritizing local community-based conservation programs and include protection and management of critical roosting and foraging habitat and development of school- and community-based environmental education programs (Sewall et al. 2003). These efforts follow the recommendations of the IUCN/Species Survival Commission Chiroptera Specialist Group, which encourages continued population monitoring, captive breeding, research to benefit conservation, and collaboration with partner organizations.

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