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Pipistrellus nanus.

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Pipistrellus nanus (Peters, 1852)

African Banana Bat

Vespertilio pipistrellus var. *africanus* Rüppell, 1842:156. Type locality "Shoa province, Ethiopia."
Vespertilio nanus Peters, 1852:63, pl. 16, Fig. 2. Type locality "Inhambane [Mozambique], 24° Lat."
Vesperugo pusillulus Peters, 1870:124. Type locality "Loango, Angola."
Vesperugo stampflii Jentink, 1888:54. Type locality "Farmington River, Liberia."
Vesperugo pusillus Noack, 1889:216, pl. V, Fig. 2. Type locality "Boma, near mouth of the Congo River, Zaire," = Democratic Republic of the Congo.
Vesperugo pagenstecheri Noack, 1889:220, pl. V, Fig. 3. Type locality "Netonna, Congo, West Africa."
Pipistrellus minusculus Miller, 1900:647, Fig. 43. Type locality "Mount Coffee, Liberia."
Pipistrellus culex Thomas, 1911:458. Type locality "Kabwir, Northern Nigeria."
Pipistrellus nanus australis Roberts, 1913:67. Type locality "Port St. Johns, South Africa," not *Pipistrellus hesperus australis* Miller, 1897.
Pipistrellus abaensis J. A. Allen, 1917:442. Type locality "Aba, Oriental Province, Zaire," = Democratic Republic of the Congo.
Pipistrellus fouriei Thomas, 1926:288–289. Type locality "Ukualukasi, N.W. Ovamboland" = Namibia.
Pipistrellus nanus: Allen, 1939a:95. First use of current name combination.
Pipistrellus africanus meesteri Kock, 2001:129–130. Replacement name for *Pipistrellus nanus australis* Roberts, 1913:67.
Neoromicia nanus: Kearney et al., 2002:68. Name combination.

CONTEXT AND CONTENT. Order Chiroptera, suborder Yangochiroptera (Van Den Bussche and Hoofer 2004), family Vespertilionidae, subfamily Vespertilioninae, genus *Pipistrellus*, subgenus *Pipistrellus*. Species name *nanus* Peters, 1852 is antedated by *P. africanus* Rüppell, 1842 (Koopman 1975). Although seniority of *africanus* was identified by Koopman (1975), this senior binomen is seldom used (Dumont et al. 1999). As most literature uses the binomen *P. nanus*, Happold (2003) made a formal application (Case 3240, International Commission on Zoological Nomenclature) to conserve use of *nanus* and suppress use of *africanus*. A declaration of nonsupport for this suppression was made by Kock (2004). Seven subspecies of *Pipistrellus nanus* are recognized (Bronner et al. 2003; Koopman 1994; *P. nanus* = *P. africanus*):

P. n. africanus (Rüppell, 1842:156), see above (*abaensis* Allen, 1917 is synonym).
P. n. culex Thomas, 1911:458, see above.
P. n. fouriei Thomas, 1926:288–289, see above.
P. n. helios Heller, 1912:3. Type locality "Merelle Water, 30 miles south of Mount Marsabit, Kenya."
P. n. meesteri Kock, 2001:129–130, see above (*australis* Roberts, 1913 is synonym).
P. n. nanus (Peters, 1852:63, pl. 16, Fig. 2), see above (*pusillulus* Peters 1870, *pusillus* Noack 1889, *pagenstecheri* Noack 1889 are synonyms).
P. n. stampflii (Jentink, 1888:54), see above (*minusculus* Miller, 1900 is synonym).

DIAGNOSIS. *Pipistrellus nanus* (Fig. 1) has bicolored hair throughout pelage, not just ventrally, as in *P. nanulus* (Rosevear 1965). Shapes of tragus and antitragus distinguish *P. nanus* from *P. nanulus*, which has a sub "sickle-shaped" tragus with rounded outer margin and a semicircular antitragus (Rosevear 1965).

Although anterior upper premolar is very small, it occurs in all *P. nanus* and is absent in most, but not all, *Eptesicus* (Koopman 1975; Rosevear 1965). Lamboidal crests of skull are present, but not prominent, in *P. nanus* (Fig. 2) and do not form "backwardly produced helmet" present in other *Pipistrellus* (Rosevear 1965: 267).

GENERAL CHARACTERS. *Pipistrellus nanus* is one of the smallest mammals (Rosevear 1965). Ears are roughly triangular with outer edges slightly convex and tips pointed (Smithers 1983). Antitragal lobe at base of concave margin is a "pronounced subrectangular flap, largely free of the main margin of the ear" (Rosevear 1965:265). Tragus is "hatchet-shaped" with straight inner margin and outer margin consisting of 2 "almost straight edges meeting at an obtuse angle" with "little or no trace of any lobule at the base of the outer margin" (Rosevear 1965:265). Dorsal fur is dark at base with tips yellowish golden-brown or deep reddish-brown. Ventral fur is dark at base, but tips are much lighter, sometimes grayish or whitish-brown. Adult specimens from Congo are dark brown dorsally with faint reddish cast, and dull and pale buffy brown ventrally (Allen 1917). Color of adults varies with geographic location; specimens from east coast of Africa were paler on underside than West African specimens (Allen and Coolidge 1930), and specimens from Malawi were much darker than those from southern Tanzania and Kenya (Lawrence and Loveridge 1953). Variation in color also occurs between individual adults and is not influenced by gender (Lang and Chapin 1917a). Immature specimens are much darker than adults and, in some cases, nearly black (Allen 1917). Wings and interfemoral membranes are brown (Smithers 1983). Some specimens show traces of a white border on hind margin of wing (Aellen 1952; Allen and Coolidge 1930).

Some males and females possess tail glands; these oval structures are 1.2–3.8 mm long and are located on both sides of tail on anterior quarter of interfemoral membrane (O'Shea 1980). A group of African banana bats in Kibwezi, Kenya, had these glands (O'Shea 1980), while in the Ivory Coast, some individuals had them and others did not (Happold and Happold 1996). Although *P. nanus* is considered a single species (Koopman 1993), 2 species might be differentiated by presence or absence of these glands (Happold and Happold 1996).

Measurements (range, in mm, both sexes, $n \geq 7$) for *P. nanus*

FIG. 1. Photograph of an adult *Pipistrellus nanus* from Sengwa Wildlife Research Station 18°10′S, 28°13′E, Zimbabwe, January 1982. Used with permission of the photographer M. B. Fenton.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult female *Pipistrellus nanus* (Royal Ontario Museum 71310, 8.5 km from Gargen on Galole Road, Kenya). Condylocanine length is 10.08 mm. Used with permission of the photographers M. B. Fenton and E. Bernard.

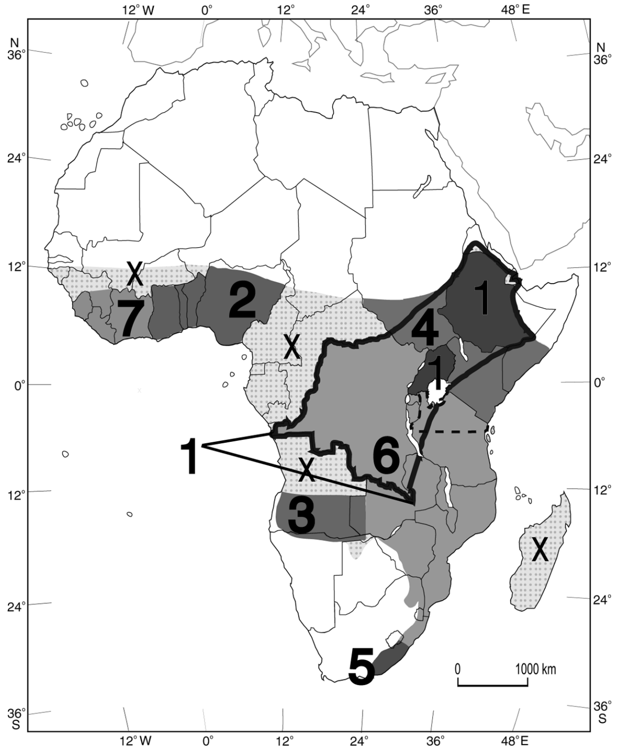

FIG. 3. Geographic distribution of *Pipistrellus nanus*. Subspecies are 1, *P. n. africanus* (Ethiopia to Democratic Republic of the Congo, mostly in highlands) as delineated by shading and dark outline; 2, *P. n. culex* (Nigeria and Ghana); 3, *P. n. fouriei* (southern Angola, western Zambia, northern Namibia); 4, *P. n. helios* (southern Sudan and southern Somalia to northern Tanzania); 5, *P. n. meesteri* (Eastern Cape, South Africa); 6, *P. n. nanus* (Democratic Republic of the Congo and Tanzania to Kwazulu-Natal, South Africa); 7, *P. n. stampflii* (Ivory Coast to Sierra Leone). Dashed line delineates overlap of 4 and 6. *P. nanus* is present in textured areas without numbers (x), including Pemba, Zanzibar, and Madagascar, but subspecies are not defined in these areas. Map used with permission of J. D. Skinner, and adapted from its original form (Skinner and Smithers 1990).

in West Africa are: length of forearm, 25–32.5; length of tail, 24–41; length of tibia, 10–13.5; length of 3rd metacarpal, 25.5–31.5; length of 5th metacarpal, 25–29.5; greatest length of skull, 11–12.5; mastoid breadth, 6.5–7.0; length from canine to 3rd molar, 3.6–4.3; width between 1st molars, 4.2–5 (Rosevear 1965). Measurements (range, in mm or g, sex and sample size not stated) for *P. nanus* in East Africa are: length of head and body, 36–40; length of tail, 24–41; length of forearm, 25–32.5; mass, 2–4 (Kingdon 1974). Females are slightly larger (LaVal and LaVal 1977). Measurements (mean, range in parentheses, in mm or g) for 10 males and 10 females, respectively, from Zimbabwe are total length, 77 (72–82), 80 (74–84); length of tail, 36 (34–38), 36 (36–38); length of ear, 11 (10–11), 11 (11–12); length of hind foot, 6 (5–7), 6 (5–7); length of forearm, 32 (30–32), 32 (31–32); mass, 4.0 (3.0–4.0), 4.0 (3.0–4.0—Smithers and Wilson 1979). Length of forearm length increases from west to east from Sierra Leone to southeast Cameroon (Rosevear 1965), and larger individuals occur in the Imatong mountain region than in the rest of Sudan (Koopman 1975). *P. nanus* has been recorded with a mean forearm size <29 cm (male) and <31 cm (female) in the following areas: southern Sudan outside of the Imatong mountain region (Koopman 1975), Niger (National Park W—Poché 1975), Kenya (Kibwezi—O'Shea 1980), Liberia (Miller 1900), Guinea (Lopes and Crawford-Cabral 1990), Nigeria (female data only—Bergmans 1977; Thomas 1911), and Senegal (female data only—Verschuren 1982). *P. nanus* has been recorded with a mean forearm size ≥ 29 cm (male) and ≥ 31 cm (female) in the following areas: northeastern Democratic Republic of the Congo (Allen 1917), Equatorial Guinea (Jones 1971), Sudan in the Imatong mountain region (excluding Lokwi—Koopman 1975), Zimbabwe (Smithers and Wilson 1979), and Mozambique (Lopes and Crawford-Cabral 1990). Extensive measurements are available for 1 female and 1 male from the Kikwit area, Bandungu Province, southwestern Democratic Republic of the Congo (05°13′S–18°49′E—Van Cakenberghe et al. 1999).

DISTRIBUTION. African banana bats occur throughout Africa south of the Sahara Desert, except in arid zones of Namib and Kalahari deserts (Fig. 3; Skinner and Smithers 1990). Records are from Angola, Democratic Republic of the Congo, Ivory Coast, Kenya, Malawi, northeast Mozambique, Somalia, Sierra Leone, southern Sudan, Tanzania (including Pemba and Zanzibar), Uganda, Zambia (Koopman 1994; Smithers 1983), Cameroon (Aellen 1952), Equatorial Guinea (Jones 1971), Ethiopia and Mali (Hayman and Hill 1971), Gabon (Brosset 1966), Ghana (Jeffrey 1975), Guinea (Lopes and Crawford-Cabral 1990), Liberia (Allen and Coolidge 1930), Madagascar (Dorst 1947), southern Niger (Poché 1975), Nigeria (Bergmans 1977; Thomas 1911; Vielliard 1974), and Senegal (Verschuren 1982). *P. nanus* is restricted to northern parts of southwest Africa, including northern Namibia and northern Botswana (throughout the Okavango Delta and south to Lake Ngami). *P. nanus* is widespread in Mana Pools National Park and Sengwa Wildlife Area, Zimbabwe (Rautenbach and Fenton 1992), but is not found in parts of the dry west and south of the Zambezi River in Mozambique. *P. nanus* has been recorded in the northern and eastern parts of South Africa (Rautenbach and Fenton 1992; Smithers 1983). No fossils are known.

FORM AND FUNCTION. Thumb pad attaches to flexor side of 1st metacarpal with small attachments to 2nd metacarpal and phalanx I.1 (Thewissen and Etnier 1995). Surface of pad is highly ridged with ridge surfaces appearing smooth when magnified. Bulk of pad is dermal tissue with large sebaceous glands that are associated with hairs and that open onto edge of pad. Proximal side of pad and side that faces radius have higher concentrations of sebaceous glands. Stratum corneum layer of epidermis is thin and thickness of stratum malpighii varies but is usually thicker than stratum corneum. Elastic fibers are embedded in collagenous septa in deeper parts of pad. A strong connective tissue band with an embedded piece of cartilage connects epidermis of pad on radial side to adductor brevis muscle, which also inserts on metacarpophalangeal joint (Thewissen and Etnier 1995). Because adductor brevis inserts in center of pad, it can raise the center for suction. Pads of *P. nanus* may be used to generate friction (LaVal and LaVal 1977) or may function as suction pads (Allen 1939b; Smithers 1983). Insertion of adductor brevis muscle allows suction-cup formation, but rim cannot easily be sealed due to surface relief. Some deeper folds in center of pad may be sufficiently smooth to seal, providing some mechanical adhesion, but overall surface relief of pad suggests *P. nanus* uses friction rather than wet or dry adhesion (Thewissen and Etnier 1995). Some *P. nanus* specimens have subcutaneous fat in thumb pads (Schliemann and Schlosser 1978; Thewissen and Etnier 1995). Thumb pad is anatomically distinct from that of *Glischropus* and *Tylonycteris* and evolved independently (Thewissen and Etnier 1995).

Dental formula is i 2/3, c 1/1, p 2/2, m 3/3, total 34 (Rosevear 1965). Upper incisors are nearly equal in length with inner ones bifid (Dobson 1878) but not deeply cleft (Koopman 1975). Degree of bifidy is highly variable (Rosevear 1965). Outer upper incisors are unicuspidate and relatively long, ca. half the length of inner upper incisor (Koopman 1975). Lower incisors are trifid and not crowded (Dobson 1878). Anterior upper premolar is small and usually just visible from outside of toothrow in gap between canine and 2nd premolar (Rosevear 1965). Lower jaw is comparatively weak with no ascending ramus; a short broadened surface with a low coronoid is present for attachment of jaw muscles, and lower part of mandibular symphysis is often strong, allowing for an extraordinarily wide gape (ca. 120°—Lang and Chapin 1917a). Sagittal crest is absent. Lamboidal crests are not pronounced (Rosevear 1965), and a concavity occurs where forehead meets rostrum (Koopman 1975).

Wing loading (±*SD*, *n* = 5) is 8.4 ± 2.0 Nm^{-2}, mean aspect ratio ranges from 6.7 to 7.3 (Aldridge and Rautenbach 1987; O'Shea and Vaughan 1980), and wingtip shape index is 1.4 ± 0.5 (±*SD*, *n* = 5—Aldridge and Rautenbach 1987). Maneuverability during flight was quantified for 6 (sex not specified) *P. nanus* using strings suspended in a flight tunnel, and average minimum negotiable interstring distance was 0.20 ± 0.07 m (±*SD*—Aldridge and Rautenbach 1987).

Baculum of *Pipistrellus nanus* is ca. 1.7 cm long. The expanded base is divided into paired lobes and is sharply flexed to shaft with distal part expanded and downwardly directed. Baculum has a bulbous undivided tip in same plane as base (Hill and Harrison 1987; Kearney et al. 2002).

Individuals roosting in leaves and in thatched roofs use daily torpor (Happold and Happold 1990a, 1996; O'Shea 1980). Although sustained torpor in cool weather is not possible given ephemeral nature of furled leaves (Happold and Happold, 1996), limited use of daily torpor occurs in a leaf-roosting population in Malawi (Happold and Happold, 1990a, 1996). Some African banana bats taken from furled leaves were torpid at end of December (mid–wet season) and all bats were torpid in June (cool dry season). Torpor was not observed in Kwazulu-Natal, South Africa (LaVal and LaVal 1977).

ONTOGENY AND REPRODUCTION. Male reproductive tract consists of paired testes and associated epididymides, which move from a position in lower abdomen during spermatogenesis. Cauda epididymides extend several millimeters beyond distal end of testis when full of spermatozoa and are sheathed in a black, pigmented membrane, the tunica vaginalis. Accessory glands include paired seminal vesicles and a compound prostate. Ampullary and urethral glands are absent. During early spermatogenesis, epithelium of seminiferous tubules is 2 cells thick, but progressively thickens to 4 cells by end of wet season. Development of spherical spermatids is followed by production of spermatozoa before start of mating season (Bernard et al. 1997). In a Malawian population of *P. nanus*, early spermatogenesis began in February and, by June, late spermatogenesis was underway in almost all seminiferous tubules, and prostate and seminal vesicles were starting to secrete fluids into lumina (*n* = 18—Bernard et al. 1997). In June, thickness of seminiferous epithelium decreased, indicating no new division of spermatogonia. By late September, spermatogenesis was complete, but spermatozoa remained in cauda epididymides and secretory material remained in lumina of accessory glands (*n* = 24—Bernard et al. 1997). Reproductive males show distension of sacculum with elongation occurring during testicular hypertrophy and subsequent filling of epididymis, therefore making male reproductive state visible upon examination (O'Shea 1980).

Prior to estrus, endometrium is thin (mean thickness ± *SD*, in μm; 97.5 ± 8.1, *n* = 2), with few short, straight uterine glands and ovaries house primary and secondary follicles of mean diameter (±*SD*, in μm) 127.4 ± 13.2, but no Graafian follicles (Bernard et al. 1997). By onset of mating, endometrium is unchanged, but secondary follicles have increased in size. As copulation occurs, large numbers of spermatozoa collect in upper end of uterine horns and uterotubal junctions (Bernard et al. 1997). Female *P. nanus* store sperm (Bernard et al. 1997). Vaginal plugs have not been observed (Bernard et al. 1997). In a Malawian population, all females captured in July had mated and had small Graafian follicles present for the 1st time (Bernard et al. 1997). By late July, endometrium was thicker (187.7 ± 29.1 *SD*, μm, *n* = 8), uterine wall was more vascularized, uterine glands were longer and more coiled, and average diameter of Graafian follicles was 275.4 ± 38.4 *SD* μm (*n* = 8—Bernard et al. 1997).

P. nanus gives birth once per year at beginning of wet season (November) and lactates for 8 weeks in South Africa (Kwazulu-Natal, 28°55′S and 30°24′S—LaVal and LaVal 1977), Malawi (Zomba, 15°23′S; 35°19′E—Happold and Happold 1990a; Namadzi, 15°31′S; 35°11′E—Happold and Happold 1996; other locations in Malawi—Happold et al. 1987; Lawrence and Loveridge 1953), and Kenya (near Kibwezi, 2°18′S and 38°7′E—O'Shea 1980). In Kenya and Malawi, birth is to twins (Happold and Happold 1990b; Kershaw 1922). Reproduction is aseasonal and twins are either rare or unknown in Democratic Republic of the Congo (Shaba province, 11°39′S; 27°28′E—Anciaux de Faveaux 1983; 5°N–5°S—Lang and Chapin 1917a; Parc National de la Garamba, 3°40′N–4°40′N—Verschuren 1957; Virunga [Albert] National Park, 1–2°N—Verschuren 1966), in Rwanda (1–3°S—Anciaux de Faveaux 1983), and in Gabon (ca. 1°N—Brosset 1966). Polyoestry is not evident (Happold and Happold 1990b).

Asynchronous parturition occurs in Democratic Republic of the Congo, Gabon, Rwanda, and Tanzania (Anciaux de Faveaux 1973; Baagøe 1978; Brosset 1966; Lang and Chapin 1917a; Verschuren 1957, 1966); whether sperm storage occurs under these conditions is unknown (Bernard et al. 1997). When 84 bats in the Usambara Mountains of northern Tanzania were examined between July 25 and August 7, no juveniles or scrotal males were found, and only 1 of 49 females was pregnant (twin fetuses—Baagøe 1978). In Garamba National Park, Democratic Republic of the Congo, females captured in April and May were neither pregnant nor lactating, and juveniles (<1 month old) were captured in late July (*n* = 2—Verschuren 1957). In Parc National du Niokolo-Koba, Senegal (ca. 11°N–12°30′N) females captured in May (*n* = 9—Verschuren 1982) were nonreproductive. In National Park W in southern Niger, 2 females captured in late February and early March were nonreproductive and 8 males all had scrotal testes averaging 3 by 2 mm (Poché 1975). In Rio Muni, Equatorial Guinea (ca. 1–2°N), a lactating female was found in August and a scrotal male (testes 5 by 3 mm) in November (Jones 1971).

In Malawi, the year can be divided into 3 seasons: hot dry season (HDS) extending from end of August to mid-November; hot wet season (HWS) from mid-November to end of April; cool dry season (CDS) from May to August (Bernard et al. 1997; Happold and Happold 1990a, 1996). Males become nonreproductive in the HDS and females are pregnant. Fertilization success is close to 100% (Bernard et al. 1997). Parturition occurs at the beginning of the HWS, a period characterized by high night-time temperatures and insect abundance. Spermatogenesis begins during the 2nd half of the HWS and testes reach maximum size by end of April (including those males born the previous November). Juveniles reach adult size by end of the HWS. Start of the CDS coincides with release of spermatozoa into cauda epididymides, and mating proceeds from mid-June to early July, when harem-like groupings are observed. In July and August, spermatogenesis and sperm storage occurs, and further matings may occur. In late August, ovulation and implantation occur and gestation lasts ca. 10 weeks (Happold and Happold 1996). Some African banana bats at higher altitudes ovulate later (Bernard et al. 1997). In Kenya, the chronology is similar, with testes evident at the end of March and mating starting mid-May (O'Shea 1980). Testes are present from April until September and gestation begins at the end of August with parturition in late November. Data from Kwazulu-Natal, South Africa, are similar, with testes evident from beginning of March to end of August (LaVal and LaVal 1977). Pregnancy spans September–November, parturition occurs in late November–early December (slightly later than in Kenya and Malawi), and lactation occurs until early January. Females with juveniles occur at all times of the year in East Africa (5°N–12°S), suggesting aseasonal breeding (Kingdon 1974).

Twinning occurs when 1 fetus develops in each uterine horn (Happold and Happold 1990a). Occurrence of twinning varies with geographic locality, ranging from 50% in South Africa (LaVal and LaVal 1977) to 100% in equatorial and subequatorial regions (Happold and Happold 1990a; O'Shea 1980). Lactating females with 1 or 2 young were obtained in March in Ghana (6°10′N—Jeffrey 1975). In August and September in Zimbabwe (16–20°S), most pregnant females had twins (mean = 1.9 fetuses; *n* = 26—Smithers and Wilson 1979). Females with 2 young have been reported in Malawi (ca. 17°S, 35°E; *n* = 3—Kershaw 1922) and Liberia (ca. 4–8°N; *n* = 7—Kuhn 1962).

ECOLOGY. African banana bats are widely distributed in rainforests, open country, and plantations, but avoid open places of villages. *P. nanus* often roosts in cracks and holes in buildings (Rosevear 1965; Shortridge 1934), culverts, rafters, nearly full-grown bunches of green bananas, and dead leaves of musaceous plants (Kingdon 1974; Lang and Chapin 1917a; Rosevear 1965), palms (O'Shea 1980; Rosevear 1965), and palm-leaf thatched roofs (Allen and Coolidge 1930; Lang and Chapin 1917b; LaVal and LaVal 1977; O'Shea 1980; Rosevear 1965). Individuals also roosted in deserted nests of Weaver birds (*Ploceus*—Happold and Happold 1990a). *P. nanus* most commonly roosts in the long narrow tube formed by the unfolded terminal leaf of banana or plantain plants (*Musa*) and in curled leaves of *Strelitzia caudata* or *S. nicolaii* trees (Baagøe 1978; Kingdon 1974; LaVal and LaVal 1977; Rosevear 1965; Smithers 1983; Verschuren 1957), *Ensete* (Verschuren 1957); or wild loquat, *Uapaca kirkiana* (Happold et al. 1987). In furled banana leaves, African banana bats are located 1–4 m above ground (Happold and Happold 1990a), and plants taller than 1.5 m are preferred (Baagøe 1978). Opening diameter of the cylindrical tube formed by the unfurled banana leaf ranges from 3 to >24 cm (Baagøe 1978; Happold and Happold 1990a). African banana bats are not found in leaves with opening sizes <16 cm^2, and openings of 101–950 cm^2 are preferred (Baagøe 1978). Individuals roost from 10–750 mm from top of leaf at points in tube averaging 38 mm in diameter (LaVal and LaVal 1977). Suitable banana leaves are not limiting because most plants have new leaves year round and bats occupy <32% of suitable leaves (Happold and Happold 1990a, 1996; LaVal and LaVal 1977). *P. nanus* prefers *Musa* to *Ensete* and *Strelitzia* (LaVal and LaVal 1977; Verschuren 1957), perhaps because *Musa* produce more leaves in closer proximity (LaVal and LaVal 1977). Furled leaves typically last 1–3 days (Happold and Happold 1990a). *P. nanus* has atypically been found in a cave (Aellen and Brosset 1968).

Thumb pads and somewhat flattened skull allow *P. nanus* to roost in many small refuges in addition to furled leaves (LaVal and LaVal 1977). Opinions differ concerning whether *P. nanus* uses its pads when moving in a furled leaf (Rosevear 1965; Smithers 1983) or if it merely uses its claws (Brosset 1966) to wedge itself into the tube-like leaf.

Diet varies between individuals and season; small moths are eaten during cool, dry seasons, but seldom during wet seasons (Happold and Happold 1996). One individual in the dry season in Zimbabwe (18°10′S; 28°13′E) had eaten 50% Coleoptera and 50% Lepidoptera; in the same area in the wet season, fecal analysis (*n* = 10, 50 pellets) revealed 52% Coleoptera, 40% Lepidoptera, and 8% Diptera (Fenton et al. 1977; Fenton and Thomas 1980). Ability to crawl may allow *P. nanus* to gather at least part of its insect diet from within leaves and around fruit at its roosting location (Lang and Chapin 1917b). Orthopterans, mainly katydids, occur in furled banana leaves, along with frogs and large hunting spiders; none of these shared a leaf with an African banana bat (LaVal and LaVal 1977).

In some areas, *P. nanus* roosts in the same bunch of bananas as *Myotis boccagei* (Lang and Chapin 1917a). Interspecific competition for roosts is unlikely due to abundance of suitable banana leaves (Happold and Happold 1990a). In Masalani, Kenya (2°18′S; 38°7′E), *Neoromicia somalicus* and *P. nanus* co-exist (O'Shea and Vaughan 1980) and have similar horizontal gapes (measured as width between outsides of last upper molars; ratio of *N. somalicus* to *P. nanus* is 1.07), indicating slight to no resource partitioning on basis of prey size. *P. nanus* has a higher frequency range of echolocation (sweep of 70–35 kHz for *N. somalicus*—O'Shea and Vaughan 1980) and *N. somalicus* forages in more open areas (O'Shea and Vaughan 1980).

Sex ratios vary with geographical location. In Kwazulu-Natal, South Africa, a 1:1 adult sex ratio (92 females : 94 males) was reported (LaVal and LaVal 1977). In Zomba, Malawi, adult females (*n* = 141) outnumbered adult males (*n* = 84) for at least 7 months of the year, but equal sex ratios were observed for juveniles (*n* = 58—Happold and Happold 1990a, 1996). In Namadzi, Malawi, adult sex ratio varied with season and females (*n* = 28) outnumbered males (*n* = 12) during HDS (late August census), while males (*n* = 24) outnumbered females (*n* = 17) in mid-June (1st half of the cool dry season), although evidence suggests that adult sex ratios differ annually (Happold and Happold 1996). In Burundi (males : females, 19:1—Niort 1970), Democratic Republic of the Congo (277:85—Verschuren 1966), and Kenya (80:39—O'Shea 1980), adult males outnumbered adult females. Differential mortality may contribute to skewed sex ratios (Happold and Happold 1990a; O'Shea 1980). Predation at roosts during times of torpidity may result in higher female mortality due to harem-like roosting arrangement (Happold and Happold 1990a). Predation by African false vampire bats (*Cardioderma cor*) has been observed and arboreal snakes (especially *Psammophis*) may prey on *P. nanus* (O'Shea 1980).

BEHAVIOR. Flight of *P. nanus* is unsteady, nearly fluttering, with a zigzag motion, but no abrupt turns (Lang and Chapin 1917a). *P. nanus* is an aerial insectivore (O'Shea and Vaughan 1980) that flies close to the ground (2.1–5.1 m aboveground; mean = 3.6—Kingdon 1974) and feeds on insects within 1 m of vegetation (O'Shea and Vaughan 1980). *P. nanus* flies continuously and, although it uses a range of habitats, spends much of its foraging time just above the canopy (Aldridge and Rautenbach 1987). Foraging under the canopy occurs (Fenton et al. 1977). *P. nanus* pursues small insects around lighted lamps (Lang and Chapin 1917a).

Foraging individuals have been followed using fluorescent powders and ultraviolet light (Fenton et al. 1977). Flanged metal bat bands have also been used to study behavior and such bands caused minimal injuries (Happold and Happold 1998). *P. nanus* is active on bright moonlit nights and is the 1st species seen in flight each evening. Emergence time after nautical sunset is 43.1 ± 4.5 *SD* min (*n* = 118—O'Shea 1980). Individuals have a relatively small activity range; recaptures occurred within 10–100 m of leaf where they were banded (Happold and Happold 1996; LaVal and LaVal 1977). In a Zimbabwe colony, 3 short periods of foraging activity occurred each night, with the 1st around 1900 h at emergence, the 2nd later in the night, and the 3rd just prior to dawn (Fenton et al. 1977). Although movement is localized throughout much of the year in Kenya, a seasonal phase of dispersal was observed as proportion of daily sightings of unbanded individuals increased and recapture rates of banded individuals decreased at the beginning of the long dry season (O'Shea 1980).

Pipistrellus nanus roosts singly and in pairs, small groups, and colonies of up to 150 individuals (LaVal and LaVal 1977). Group size and composition vary seasonally (Happold and Happold 1990a; LaVal and LaVal 1977; O'Shea 1980). During parturition and lactation, adult males and adult females rarely roost together (Happold and Happold 1996). Seasonal changes in social organization of Malawian bats are divided into 3 periods: lactation, postlactation, and harem formation (Happold and Happold 1990a). During lactation, adult males roost singly and lactating females roost with their young or with 1 or 2 other lactating females and their young. During postlactation, adult males continue to roost individually while postlactating females ($n = 16$) roost singly (19%) or with groups of subadults or other postlactating females (81%). During harem formation, testes of all males are scrotal and all males and 95% of females ($n = 38$) roosted in groups of 2–9 bats. Most groups during harem formation were composed of 1 adult male with 1 or more females; a few all-female groups were found, as were groups containing females with 2 males (Happold and Happold 1990a). Composition of roosting groups is highly labile (Happold and Happold 1996; LaVal and LaVal 1977; O'Shea 1980). Small groups of 2–3 individuals of unknown sex forage together in small areas (O'Shea 1980).

Males roost with multiple females and females roost with multiple males in a highly labile fashion during mating season, with no apparent male–female bonds (Happold and Happold 1990a, 1996; O'Shea 1980). Although the term harem has been used, groups of females are highly labile in composition and therefore do not match the strict definition of harem (Happold and Happold 1996). The mating system in a Kenyan population roosting in permanent thatch-roof structures was resource defense, in which males defended roosts and foraging territories (O'Shea 1980). In both leaf- and thatch-roosting populations, females showed no roost or mate fidelity, whereas males were faithful to particular roosts (thatch) or patches of trees (Happold and Happold 1996; O'Shea 1980). Males roosting in permanent structures displayed the highest degree of roost fidelity (O'Shea 1980). Such fidelity is not possible in banana leaves given their ephemeral nature, although *P. nanus* exhibits fidelity to plantations and clumps of banana plants (roost range—Happold and Happold 1996); males in a Malawian plantation showed greater fidelity to certain clumps of trees than did females.

In leaf-roosting *P. nanus* in Malawi, despite the availability of suitable roost leaves, sex ratio data from roosts ($n = 125$ bats) suggested males exclude other males from roosts, although mechanism of exclusion was unknown (Happold and Happold 1996). Males ($n = 50$) showed fidelity to distinct clumps of banana plants with little overlap between roost ranges (13–28% of occupied clumps were used by >1 male—Happold and Happold 1996). Males in a thatch-roost population patrolled in front of their roosts at all times of the night throughout the year and aggressive interactions between patrolling males increased in frequency at night's end ($n = 116$ chases—O'Shea 1980). Males also defended ellipsoidal foraging territories with a length of 24–25 m ($n = 2$—O'Shea 1980). Certain males attracted more females than others (Happold and Happold 1996; O'Shea 1980). In Malawi, mean number of females found with each male caught 5 or more times with females was 11.3 ($n = 19$ males—Happold and Happold 1996), and mate selection by females was not linked to roost-range quality; males ($n = 18$) that roosted in the more reliable clumps did not necessarily attract more females (Happold and Happold 1996). In Kenya, males ($n = 11$) making more audible vocalizations roosted with the largest number of females (O'Shea 1980).

Search-phase echolocation calls are steep frequency-modulated calls with the following characteristics: mean duration, 4–5 ms; mean dominant frequency (kHz), ca. 70; mean minimum and maximum frequencies, ca. range 62–67 and 86–90, respectively ($n = 5$—Kruger National Park, South Africa—Aldridge and Rautenbach 1987; $n = 3$—Sengwa, Zimbabwe, Fenton and Bell 1981; $n = 4$—Jozini Dam, Kwazulu-Natal, South Africa—Taylor 1999). Call frequencies up to 115 kHz have been detected (Kibwezi, Kenya—O'Shea 1980). Intraspecific variation in search phase calls exists. Search-phase calls of 2 individuals were steep-shallow frequency-modulated calls with the following characteristics: mean duration, 7.5 ms; mean dominant frequency, 43; mean minimum and maximum frequencies, 42 and 82 (Taylor 1999).

Three types of audible communication occur: squabble notes (variable and noisy bursts of sound made when bats are in distress), long calls, and short calls (O'Shea 1980). Long calls and short calls are made exclusively by males. Long calls consist of 6–8 syllables and are described as "dee-dee-dee-dee-dee-dee-dip" (O'Shea 1980:183). These calls are given most frequently by males in flight when they are passing roosts, emerging from roosts, or encountering conspecifics while foraging. Short calls have either 3 or 4 syllables and are described as "dee-dee-dip" or "dee-dee-dee-dip" (O'Shea 1980:183). Short calls are often repeated many times in succession and are given more frequently by males at rest in roosts than by males in flight. Short calls are often exchanged between males for periods up to 20 minutes and these 'vocal duels' sometimes end in an aerial chase. Vocalization is more frequent during mating season (May–August) and in the last few hours before dawn (O'Shea 1980). These audible vocalizations have not been reported in other studies of *P. nanus* (Happold and Happold 1996).

GENETICS. *Pipistrellus nanus* has a diploid number of 36, a fundamental number of 50 (Peterson and Nagorsen 1975), and is related karyotypically to *Neoromicia capensis* (Heller and Volleth 1984). The GTG-banded karyotype includes 8 biarmed and 9 acrocentric autosomes, with a medium-sized metacentric X chromosome and an acrocentric Y chromosome that is smaller than the smallest autosome (Kearney et al. 2002). In addition to metacentric chromosomes 1/2, 3/4, 5/6, and 16/17, 4 chromosomes result from Robertsonian fusions between chromosome arms 7/11, 8/9, 10/12, and 13/14. *P. nanus* shares all but the latter fusion pair with *Neoromicia capensis*, *N. rendalli*, and *N. zuluensis* (Kearney et al. 2002). *P. nanus* from South Africa is monomorphic for the same allele in all but 1 of 13 liver-enzyme loci tested; 2 allelic forms exist for glutamate dehydrogenase (Morales et al. 1991). Based on protein electorphoresis, *P. nanus* shows some genetic similarity with *Neoromica zuluensis* and *Pipistrellus hesperus*, but does not group with *Eptesicus furinalis*, *E. fuscus*, or *E. hottentotus*, which group together (Morales et al. 1991). *P. nanus* groups with *P. pipistrellus*, *P. p. mediteraneus*, *P. mimus*, *P. stenopterus*, *Neoromicia somalicus*, and *N. tenuipinnis* based on mitochondrial (mtDNA) cytochrome *b* (Barratt et al. 1995). Using sequences from 12S rRNA, $\mathrm{tRNA^{Val}}$, and 16S rRNA mtDNA, *P. nanus* groups with *Laephotus namibiensis* and *Neoromicia somalicus*, who group closely together, and with *N. brunneus* and *N. rendalli*, who group closely. *P. nanus* does not group with *Eptesicus*, including *E. furinalis*, *E. fuscus*, and *E. hottentotus*, supporting the protein electrophoretic data, nor with other *Pipistrellus*, including *P. abramus*, *P. coromandra*, *P. javanicus*, *P. nathusii*, *P. pipistrellus*, and *P. tenuis* (Hoofer and Van Den Bussche 2003), supporting its removal from *Pipistrellus* into a new genus.

REMARKS. The common name African banana bat derives from habit of roosting in furled banana leaves. Species name *nanus* Peters, 1852 is Latin for dwarf (Rosevear 1965).

Koopman (1994) recognized 6 subspecies, listing *P. n. nanus* for southern Africa. In redescribing *P. n. australis* Roberts, 1913, a junior homonym of *P. hespersus australis* Miller, 1897 (Koopman 1966), as *P. africanus meesteri*, Kock (2001) revived Peterson's (1987) declaration that the larger sized form from Transkei is a distinct subspecies. Two subspecies, *P. n. meesteri* and *P. n. nanus*, are recognized for the southern African subregion (Bronner et al. 2003).

Originally allocated to subgenus *Pipistrellus* (Koopman 1975), Hill and Harrison (1987) moved *P. nanus* to subgenus *Hypsugo* Kolenati, 1856, based on bacular characteristics. Because Horácek and Hanák (1985–1986) elevated *Hypsugo* to generic rank, the binomen *Hypsugo nanus* has been used (Hoofer and Van Den Bussche 2003). Based on GTG-banded chromosome data, Kearney et al. (2002) transferred *nanus* to *Neoromicia* Roberts, 1926. Based on mtDNA sequence data, Hoofer and Van Den Bussche (2003) found polyphyly within *Neoromicia*, and proposed *Neoromicia nanus* be transferred to an as yet unnamed genus along with *N. brunneus* and *N. rendalli*.

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