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Hipposideros caffer (Chiroptera: Hipposideridae)

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Abstract: *Hipposideros caffer* (Sundevall, 1846) is a hipposiderid bat commonly called Sundevall's leaf-nosed or roundleaf bat. *H. caffer* is a medium-sized insectivorous bat with a horseshoe-shaped nose leaf and 2 color phases in adulthood. It is 1 of 67 species in the genus *Hipposideros* and is found in the southwestern Arabian Peninsula, in most of Africa south of the Sahara (excluding the central forested region), and in Morocco, Zanzibar, and Pemba. *H. caffer* is a savanna-dwelling species and inhabits a variety of roost types including caves, hollow trees, and abandoned buildings. It often roosts in groups of thousands of individuals, is very common, and is not of special conservation concern. DOI: 10.1644/845.1.

Key words: Africa, bat, echolocation, insectivore, Sundevall's leaf-nosed bat, Sundevall's roundleaf bat

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Hipposideros caffer (Sundevall, 1846)
Sundevall's Leaf-nosed Bat

Rhinolophus caffer Sundevall, 1846:118. Type locality "Circa Port-Natal [= Durban]," South Africa.
Phyllorrhina gracilis Peters, 1852:36. Type locality "Africa orientalis … 17° Lat." Tete, Zambezi River, Mozambique.
Phyllorrhina bicornis von Heuglin, 1861:4, 7. Type locality "Kérén, Eritrea."
Phyllorhina angolensis Seabra, 1898:256. Type locality "Rio Coroca," Angola.
Hipposiderus tephrus Cabrera, 1906:358. Type locality "Mogador [= Medina of Essaouira]," Morocco.
Hipposiderus caffer: Andersen, 1906:269. Name combination.
Hipposideros nanus J. A. Allen, 1917:434. Type locality "Faradje, Uele district, Belgian Congo [= Democratic Republic of the Congo]."
Hipposideros caffer: de Beaux, 1924:155. First use of current name combination.
Hipposideros caffer aurantiaca de Beaux, 1924:155. Type locality "Belet Mamu, Basso Giuba [Lower Juba River]," Somalia.
Hipposideros braima Monard, 1938:73. Type locality "Bagingara," Guinea-Bissau.

CONTEXT AND CONTENT. Order Chiroptera, suborder Yinpterochiroptera (Teeling et al. 2002), family Hipposideridae (Simmons 2005). Although subspecies limits are not clearly defined, 4 subspecies are currently recognized (Simmons 2005):

H. c. caffer (Sundevall, 1846:118). See above; *aurantiaca* de Beaux, *bicornis* Heuglin, and *gracilis* Peters are synonyms.
H. c. angolensis (Seabra, 1898:256). See above.
H. c. nanus J. A. Allen, 1917:434. See above.
H. c. tephrus (Cabrera, 1906:358). See above; *braima* Monard is a synonym.

Fig. 1.—Adult *Hipposideros caffer* in the orange (bright) color phase in the northern part of Kruger National Park, South Africa. Used with permission of the photographer, M. B. Fenton.

NOMENCLATURAL NOTES. Conflicting views of the status of *H. caffer* versus *H. ruber* are common, and some have considered the 2 taxa to comprise the "*caffer–ruber*" group (e.g., see Lawrence 1964). *H. caffer* and *H. ruber* are not currently considered to be conspecifics (Simmons 2005). Tate (1941) considered *H. caffer* as part of the *H. galeritus* group, and multiple subspecies or "races" that are not currently recognized as such have been grouped under *H. caffer* by Tate and others. This species is considered part of the *bicolor* group (e.g., Horáček et al. 2000). Simmons (2005) noted that *H. caffer* may include multiple species. *H. caffer* is sometimes called the common African leaf-nosed bat (Happold 1987).

The genus name *Hipposideros* is Greek for horse (hippos) and iron (sideros), which refers to the horseshoe shape of the nose leaf (Rosevear 1965). The species name *caffer* is from *kafir*, which is "a formerly commonly used but inaccurate term for a South African tribe" (Rosevear 1965:221).

DIAGNOSIS

A suite of characteristics, particularly those pertaining to the nose leaf, aids in distinguishing *Hipposideros caffer* from other members of the genus. *H. caffer* has no clublike process on the central nose leaf and has 2 secondary leaflets on either side (Rosevear 1965). The internarial septum is low and small, the nostrils are visible, and the frontal sac opens through a horizontal slit (Happold 1987; Rosevear 1965). *H. caffer* is similar to *H. beatus* (benito leaf-nosed bat) but the former has a greater forearm length (usually >44 mm—Happold 1987). *H. caffer* can be difficult to distinguish from *H. ruber* (Noack's leaf-nosed bat), and some have considered the 2 conspecific in parts of Africa (e.g., Angola—Koopman 1975); however, *H. caffer* currently is considered a distinct species (Simmons 2005). *H. caffer* and *H. ruber* may be distinguished by forearm length, with *H. caffer* having forearm lengths < 48 mm and *H. ruber* having forearm lengths > 48 mm (Hayman and Hill 1971), but this may not always hold true (Heller 1992). In these situations, skull measurements or other methods (e.g., analysis of echolocation calls) have been used to distinguish the 2 taxa (Heller 1992). Relative to *H. ruber*, *H. caffer* has small medial nasal swelling compartments and large posterolateral nasal swelling compartments (Lawrence 1964). Compared to *H. ruber*, echolocation calls of *H. caffer* are more intense (louder—Fenton and Fullard 1979) and higher in frequency, particularly when the 2 species are sympatric (Heller 1992).

Compared with *H. ruber*, *H. caffer* has wider lateral nasal inflations of the skull (Hayman and Hill 1971) and condylocanine lengths < 15.5 mm (Koopman 1975). In addition, the median posterior narial compartment of the skull is narrower in *H. caffer* (Fenton 1986; Hayman and Hill 1971). Both species are dichromatic. In the dull color phase, the fur of *H. caffer* is more grayish, whereas that of *H. ruber* is more brownish (Hayman and Hill 1971). In the bright color phase, *H. caffer* is generally orange (Fig. 1), and *H. ruber* is more rufous in color (Hayman and Hill 1971). *H. caffer* is generally found in savanna areas, whereas *H. ruber* is typically considered a forest species (Kingdon 1974).

GENERAL CHARACTERS

Hipposideros caffer is about 80–90 mm long (total length) and has a forearm length of about 43–50 mm, with a wingspan of about 200 mm and a body mass of about 8–10 g. *H. caffer* is not considered sexually dimorphic. Individuals are smaller in Yemen, eastern Africa, northern Africa, on the west coast (south to Sierra Leone), and on the Gold Coast, than those found in western Kenya, Uganda, and Tanzania through the Congo, which are smaller than those found in Angola and southwestern Africa (Hill 1963). This species has relatively long, woolly hair, and fur may be a variety of colors. The ventral fur is paler, and the wings are dark brown (Happold 1987). Albino individuals have been reported from Dar-es-Salaam (Kingdon 1974).

Adults of *H. caffer* are dichromatic, displaying gray, reddish gold-orange, and intermediate color phases (Bell 1987; Kingdon 1974; Menzies 1973). Molting and the breeding cycle have been reported as synchronous, with pregnant and nursing females having brighter fur (Brosset 1968). However, some authors have found no correlation between color and age or sex of bats (Jones 1971). The following pelage colors and conditions were reported for bats captured from March to December from a cave in northern Nigeria (Menzies 1973): March—0 gray, 22 gold, 0 molting; May—3 gray, 39 gold, 1 molting; July—1 gray, 23 gold, 5 molting; November—0 gray, 57 gold, 0 molting; December—0 gray, 50 gold, 0 molting. As examination of the data indicates, gray bats were reported only from May through July. The molting season appeared to be May through July for females, and molting began with the shoulders. In May, some lactating females had bare or gray shoulders with gold bodies (Menzies 1973). The youngest bats were gray but changed to gold by November. In another collection of *H. caffer* from a well in Dada, Nigeria, gray and gold bats of all ages were found (Menzies 1973). Adult females in Zimbabwe ranged from chocolate brown to rufous orange to bright burnt orange, whereas young were a dull gray-brown, and adult males possessed bright-red or chocolate-brown fur (Bell 1987).

Mean mass reported for 90 individuals from a Zambian cave was 10.2 g (range = 7.7–14.2 g—Whitaker and Black 1976). Adult females from Zimbabwe had a mean mass of 9.5 g (n = 7), compared with 11 g for a male (n = 1) and 7.5 g for young gray bats (n = 7—Bell 1987). Forearm lengths for 30 males and 25 females from Darfur, Kordofan, Equatoria, ranged from 43 to 49 mm (Koopman 1975).

Mean measurements (mm) of 5 females from Cameroon were: total length, 85.4; length of tail, 31.0; length of foot, 8.8; length of ear, 13.0; length of forearm, 47.3 (Jones 1971). One male from the same location had the following measurements (mm): total length, 88.0; length of tail, 32.0; length of foot, 10.0; length of ear, 12.0; length of forearm, 46.7 (Jones 1971).

Measurements for bats from South Africa were as follows ($n = 11$; $\bar{X} \pm SD$): body mass (g), 9.0 ± 0.7; forearm length (mm), 48 ± 1; wingspan (m), 0.28 ± 0.013; wing area (m^2), 0.007 ± 0.0004; aspect ratio, 6.0 ± 0.3; wing loading (N/m^2), 6.6 ± 0.8; tip length ratio, 0.972 ± 0.096; tip area ratio, 0.713 ± 0.075; tip shape ratio, 2.85 ± 0.60 (Bowie et al. 1999). Seven females from Rio Muni measured as follows (means): total length, 88.6 mm; length of tail, 31.4 mm; length of foot, 9.0 mm; length of ear, 11.4 mm; length of forearm, 50.7 mm; mass, 9.2 g (Jones 1971). Two males from this location had mean measurements of: total length, 85.5 mm; length of tail, 32.0 mm; length of foot, 8.0 mm; length of ear, 13.0 mm; length of forearm, 48.0 mm; mass, 8.8 g (Jones 1971). The wing measurements ($\bar{X} \pm SD$) of 5 individuals from South Africa were: forearm (mm), 49 ± 1; wing area (cm^2), 134.2 ± 4.5; wingspan (cm), 28.1 ± 1.1; wing loading (N/m^2), 6.6 ± 1.2; aspect ratio, 5.9 ± 0.4 (Jacobs 2000).

The antitragus is well developed in *H. caffer* (Happold 1987). In the nasal region, *H. caffer* has 2 leaflets that are lateral to the horseshoe (Tate 1941). This species also has a secondary transverse ridge, which rises from behind the base of the primary nose leaf, and has a serrated crest (Tate 1941). The median posterior narial compartment is narrow, and wide lateral inflations are present (Hayman and Hill 1971). The posterolateral corner of the inflated nasal area is rounded in *H. caffer* (Koopman 1975). Frontal sacs that open transversely also are present (Hayman and Hill 1971). *H. caffer* has no pits in the basisphenoid and basioccipital bones (Debaermaeker and Fenton 2003) and is considered to have intermediate skull robustness (Fig. 2; Freeman 1981). The rostrum exhibits an intermediate level of lateral expansion (Tate 1941).

Hipposideros caffer has zygomata with a high jugal process, and elongate anteorbital foramen closed by a narrow bar (Hill 1963). The upper canines are flattened on the anterior face, or possess a shallow groove and moderate anterior cusp, whereas the posterior cusp is somewhat higher (Hill 1963).

Hipposideros caffer from northern Nigeria had the following measurements (range and mean; mm): width across M3–M3, 6.9–7.5 (7.2); length of C–M3, 7.0–7.3 (7.1); greatest length of skull, 16.7–17.3 (16.9); length of forearm, 46.7–49.4 (48.2—Menzies 1973). Mean measurements for 5 females from Cameroon were as follows (mm): greatest length of skull, 18.6; condylobasal length, 15.1; zygomatic breadth, 10.1; interorbital breadth, 2.6; breadth of braincase, 8.4; length of maxillary toothrow, 5.9; and length of mandibular toothrow, 6.9 (Jones 1971). Mean measurements (mm) for 7 females from Rio Muni were: greatest length of skull, 18.8; condylobasal length, 15.4; zygomatic breadth, 10.3; interorbital breadth, 2.6; breadth

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Hipposideros caffer angolensis* (Smithsonian National Museum of Natural History 172915) from Huxe, Bengula, Angola. Greatest length of skull is 17 mm.

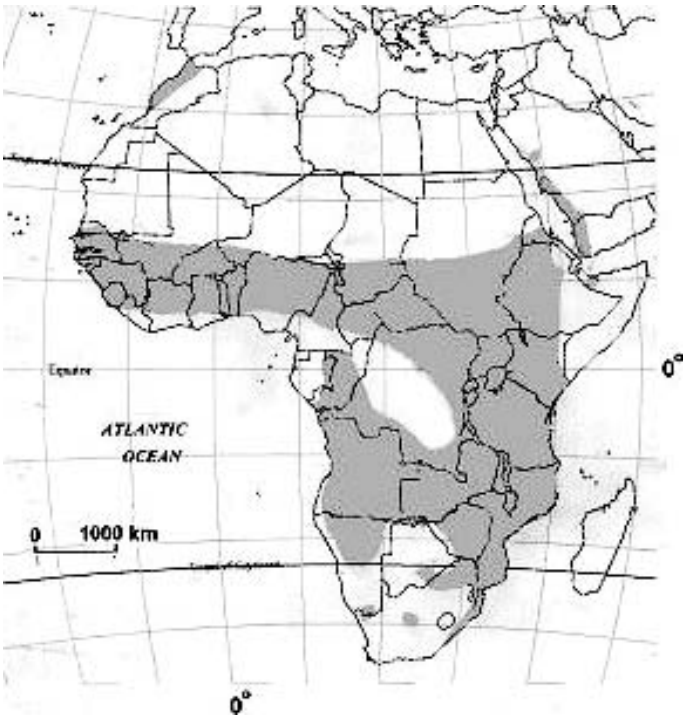

Fig. 3.—Geographic distribution of *Hipposideros caffer*. Map based on Skinner (2000) and Harrison and Bates (1991). Kingdon (1974) shows a somewhat larger distribution. Subspecies limits are unclear (Simmons 2005) and are therefore not designated on the map.

of braincase, 8.4; length of maxillary toothrow, 5.8; and length of mandibular toothrow, 7.0 (Jones 1971). Two males from the same location had mean measurements of (mm): greatest length of skull, 18.8; condylobasal length, 15.1; zygomatic breadth, 10.2; interorbital breadth, 2.5; breadth of braincase, 8.4; length of maxillary toothrow, 5.9; and length of mandibular toothrow, 6.9 (Jones 1971).

The condylocanine lengths for 7 female *H. caffer* from Kassala and Blue Nile ranged from 14.5 to 15.1 mm, and the width across the posterior molars ranged from 5.8 to 6.2 mm (Koopman 1975). The condylocanine lengths for 20 males from Darfur, Kordofan, Equatoria, ranged from 14.0 to 14.9 mm, and values for 15 females ranged from 14.1 to 14.8 mm (Koopman 1975). Widths across posterior molars of 23 males from the same location ranged from 5.5 to 5.9 mm and for 13 females ranged from 5.6 to 6.0 mm (Koopman 1975).

DISTRIBUTION

Hipposideros caffer is found in the southwestern Arabian Peninsula (including Saudi Arabia and Yemen), and in most of Africa south of the Sahara (Fig. 3), excluding the central forested region (Hayman and Hill 1971; Simmons 2005), and in Morocco, Zanzibar, and Pemba (Simmons 2005). This species is widespread and has been described as ''probably the commonest'' of its genus (Happold 1987:63). Subspecies limits are ''somewhat unclear'' (Simmons 2005:368). No fossils of *H. caffer* are known.

FORM AND FUNCTION

Dental formula is i 1/2, c 1/1, p 2/2, m 3/3, total 30 (Koopman 1994). The m 3/3 is partially reduced (Tate 1941). The deciduous dentition in *H. caffer* disappears before birth and is never functional, and there is a high level of coordination in development of upper and lower teeth (Gaunt 1967). *H. caffer*, which primarily feeds on soft-bodied insects, has lower values for enamel thickness than at least 1 congener (*H. commersoni*) known to prey on hard-bodied insects (Dumont 1995).

Rather than employing hibernation, *H. caffer* has been observed to use short-term torpor during winter cold spells (Bernard and Meester 1982). Males and females show different patterns of fat accumulation, with heavier females reported during the wet months and lighter ones found during dry months, whereas the masses of males fluctuate less consistently (Kingdon 1974). The length of the baculum is 1.28 mm (Hosken et al. 2001). In females, the caudal ends of the uterine horn and the corpus uteri are lined with stratified epithelium, which is atypical for mammals (Bernard and Meester 1982). Females possess false pubic teats, which can be about 4 cm (Mutere 1970) long but are not well developed in all females (Rosevear 1965). These teats may be present to provide a place for pups to hold on to their mothers (Mutere 1970). Pubic teats are present but vestigial in males (Rosevear 1965).

Hipposideros caffer is a high–duty-cycle echolocator, with echolocation calls dominated by narrowband components (Bell and Fenton 1984; Fenton 1986; Heller 1992). The echolocation calls of *H. caffer* in Zimbabwe were reported as about 8 ms long and dominated by a constant-frequency component (about 6 ms) followed by a steep frequency-modulated sweep downward (Fenton 1986) and are emitted nasally. Calls are intermediate in intensity and can be detected at 2 m when a bat is flying toward a sensitive broadband microphone (Fenton 1986). The constant-frequency component is about 140 kHz (137.4–147.1 kHz, depending on location), with frequency-modulated sweep bandwidths of about 20.7–27.7 kHz, and interpulse interval of about 7.5 ms during the search phase and about 4.7 ms when approaching a target. Individuals from Kenya, Uganda, and Nigeria were reported to have a constant-frequency component of 130–160 kHz (Pye 1972). The average echolocation frequency with maximum energy was reported as 144 kHz $\pm$ 0.5 *SD* ($n = 6$) for South African *H. caffer* (Jacobs 2000), and the constant-frequency component of the calls of 2 females and 1 male from Zaire ranged from 154.9 kHz to 157.0 kHz (Heller 1992).

ONTOGENY AND REPRODUCTION

Ontogeny.—*Hipposideros caffer* is a widespread species, and timing of copulation and parturition, and length of gestation, vary by location. During gestation in *H. caffer* from Natal, South Africa, the zygote was present for about 21 days, the embryo for 123 days, and the fetus for 76 days (Bernard and Meester 1982). In Shagunu, Nigeria, fetuses measured in early March (about 3 months after the trophoblast formed and 2 months before birth) were 9.1–11.9 mm from crown to rump (Menzies 1973). Pups are born with hairless ventrums and eyes closed (Mutere 1970). Pups from a Ugandan population had a mean forearm length of 26 mm at birth ($n = 17$), 38 mm at about 1.5 months of age ($n = 13$), and the approximate adult length of 48 mm by about 3 months after birth (Mutere 1970).

Females have been reported to carry their young while flying for a brief period after birth (Menzies 1973). About 1 month after parturition began, all mature females from a Nigerian cave were lactating but did not carry young when flying (Menzies 1973). When females were disturbed, they carried their pups with them to seek safety (Bell 1987). Young nurse for 3.5 months in Gabon (Brosset and Saint Girons 1980), and those in equatorial Uganda nurse for 3 months, but they are not carried by their mothers for the entire duration (Kingdon 1974). Young bats begin flying at around 1 month of age (Menzies 1973).

It is generally accepted that *H. caffer* can 1st conceive at 2 years of age (Brosset 1968, 1969), but 98% of females in a cave in Nigeria that were not pups were breeding, suggesting that female *H. caffer* may be reproductively mature in their 1st year (Menzies 1973). Males probably do not breed until their 2nd year, as evidenced by testis size (Menzies 1973). Testis size increases with age, with older males (showing some tooth wear) displaying the largest testis sizes (Menzies 1973).

Reproduction.—*Hipposideros caffer* gives birth to a single young once a year. *H. caffer* in the Northern Hemisphere typically follows a boreal cycle (parturition around March–April), whereas Southern Hemisphere bats follow an austral cycle (parturition around October–November); however, equatorial colonies may have either cycle (Brosset 1968). This distinction, as well as differences in age structure and body size, has been reported even for colonies living as close as 5 km apart (Brosset 1968; Brosset and Saint Girons 1980). Because the male's period of sexual activity is short and synchronized with female estrus, it has been suggested that sexual isolation may occur between such colonies in Gabon (Brosset 1968). This breeding difference may be the result of populations arising from 2 separate origins (Nowak 1994). During the breeding season in Nigeria, males disperse, whereas females remain at the colony's current roost (Menzies 1973).

Females of a South African population were monestrous and monotocous (Bernard and Meester 1982), as were individuals at 10.5°N (Bernard and Cumming 1997). *H. caffer* may be bimodally polyestrous or breed year-round between 13°N and 15°S (Bernard and Cumming 1997). The annual breeding cycle, which includes pregnancy and lactation, lasts about 6 months for *H. caffer* in Gabon (Brosset and Saint Girons 1980). The species is not reproductively active from August to October in northern Nigeria. During this time, follicles in the left ovaries enlarge, and spermatogenesis peaks in preparation for copulation in November (Menzies 1973). The corpus luteum was extruded from the ovary and was gone within 1 month after ovulation (Bernard and Meester 1982).

In *H. caffer* from northern Nigeria, spermatogenesis began between March and May, but the seminiferous tubules remained empty and were not enlarged at that time (Menzies 1973). Males captured in Rio Muni in February had testis lengths and widths of 1 by 1 mm; in June, 2 by 2 mm; in August, 2 by 1 mm and 1 by 1 mm; and in November, 2 by 1 mm (Jones 1971). Males in Nigeria were at a minimum weight in May and a maximum weight in November, when testes were at a maximum size, spermatozoa were present, and seminiferous tubules were at maximum size (twice previous size and full of spermatozoa—Menzies 1973). By December, the testes were completely inactive, and tubules began shrinking back toward a resting state (Menzies 1973). In the same colony, copulation occurred in November, when no pregnant bats were found, but females in all but the youngest age group (no tooth wear; probably bats up to about 2 years old) had enlarged nipples and false nipples and unequal uterine horns (6 mm across). At this time, sperm was found in the vagina and fallopian tubes, and bats possessed enlarged follicles in the ovaries. No bats had ovulated at this time and none were pregnant (Menzies 1973). In July, some individuals from a Nigerian cave were still molting, and males were returning to the colony (Menzies 1973).

In some regions there is immediate ovulation and implantation, and gestation is reported to be about 3.5–4 months (Brosset 1968; Brosset and Saint Girons 1980). Gestation can be as short as 90 days (Brosset 1968, 1969) or >200 days as in Natal, South Africa (Bernard and Meester 1982). In Gabon, breeding seasons for *H. caffer* are well defined, but members of some colonies give birth in March and some in October (Brosset 1968). In other regions, such as northern Nigeria, there is a 2-month delay between copulation and further trophoblast development, resulting in a gestation period of about 5 months (Menzies 1973).

By December, all females examined in a Nigerian colony exhibited uteri with unimplanted trophoblasts, and in January the trophoblast remained unattached. The trophoblast resumed development in early February, when actual gestation commenced (Menzies 1973). By March, the embryos were half grown, and the bats gave birth in late April–early May (Menzies 1973). In a Ugandan population,

actual gestation was from December to March, with fetuses developing rapidly after the 2nd month of gestation (Mutere 1970). Bats from Natal, South Africa, followed another pattern, with follicular development beginning in February and copulation and ovulation taking place in late April (early winter at this location—Bernard and Meester 1982). Embryos develop in the left uterine horn (Menzies 1973; Mutere 1970).

In northern populations, parturition generally occurs in late April or early May (Menzies 1973). Bats from a cave in northern Nigeria copulated in November, ovulated in December, experienced a brief period of delayed implantation, and gave birth from late April (by which time most males had left the colony) to early May (Menzies 1973). This breeding cycle was identical to that of a population of *Rhinolophus landeri* (Lander's horseshoe bat) inhabiting the same cave. In equatorial Ugandan populations, births occur during February–March, between the 2 rainy periods (Kingdon 1974).

Females in Zambia were observed carrying newborn pups in late September (Cotterill 2002). *H. caffer* from Natal, South Africa, gives birth in early December. In this location, there is no delay between fertilization and implantation, but embryonic development is slowed during the winter (Bernard and Meester 1982). Although the bats were anestrous during lactation in December and January, there was no separate anestrous period (Bernard and Meester 1982).

In Rio Muni, West Africa, pregnant females were found during August–October, and lactating females were reported in November (Jones 1971). Breeding of *H. caffer* is correlated with rainfall peaks (Mutere 1968). In Uganda, pregnancies were reported from December through March with births occurring in April, just before the primary rainfall peak of the year (rainfall peaks are April–May and October–November—Mutere 1968). This timing may be related to low humidity levels being harmful to young bats, rather than to food abundance, at least in northern Nigeria (Menzies 1973).

ECOLOGY

Space use.—*Hipposideros caffer* is generally considered a savanna-dwelling species. Examples of habitat types from which the species has been reported include a sparsely wooded savanna in Nigeria (Menzies 1973); a sand thicket forest populated mainly by *Acacia*, *Albizia*, and *Dichrostachys* trees (generally <5 m high) and grass in South Africa (Bowie et al. 1999); and a mopane woodland in northwestern Zimbabwe (Bell 1987).

Hipposideros caffer uses a variety of roost types, including caves (Jacobs 2000; Menzies 1973), mines (Bernard and Meester 1982), rock shelters (Jones 1971), tree hollows (Bell 1987), house rooftops (Kingdon 1974), basements of human dwellings (Lawrence 1964), and deserted buildings and attics (Cotterill 2002; Cowles 1936; Dunning and Kruger 1996). This species uses night roosts that are different from their day roosts, and although day roosts typically have a balance of sexes, single-sex associations have been reported at night roosts (Kingdon 1974). Individuals hang close together but without touching each other and have been observed roosting in association with hornet nests in Uganda (Kingdon 1974). *H. caffer* surveyed in Namibian caves in May and June preferred warm, humid cave locations and roosted in caves with an average temperature of 26°C and mean relative humidity of 94% (Churchill et al. 1997).

Hipposideros caffer sometimes roosts in very large groups, and 1 cave in Gabon is reported to have housed 500,000 individuals (Brosset 1968). A cave high in a cliff in northern Nigeria housed an estimated 1,000 *H. caffer* and another 1,000 *R. landeri* (Menzies 1973). *H. caffer* also commonly shares roosts with other bat species, including *Nycteris thebaica* (Egyptian slit-faced bat—Bowie et al. 1999), *Coleura afra* (African sheath-tailed bat—Kingdon 1974), *H. ruber* (Lawrence 1964), and *Rhinolophus denti* (Dent's horseshoe bat—Churchill et al. 1997). In a cave in northeastern South Africa, *H. caffer* roosted with 4 other species, all aerial feeders (Jacobs 2000).

Hipposideros caffer has been observed roosting in a hollow baobab tree with a cavity about 2 m across at base and 4–5 m high with 1 ground-level entrance 80 cm across. This roost contained 7 females, each with a single young, and 1 adult male, and was apparently used by different bats during day and night. The same 15 bats remained at the roost until mid-January, but by March, the majority of bats present at the roost were different individuals than had previously occupied the roost (Bell 1987). At a cave in northern Nigeria, the numbers of males and females were approximately even in July, August, and December, but fewer males were present in March and November, and very few males were present in May, when pups had just been born (Menzies 1973). The range of *H. caffer* is mostly mutually exclusive of the range of *Asellia* species (Koopman 1975).

Diet.—*Hipposideros caffer* is considered a moth specialist (Bell and Fenton 1984), and mixed reports suggest it may prefer moths of certain taxonomic distinctions (Dunning and Kruger 1996) or of medium size (Bell and Fenton 1984). Lepidopteran remains were found in the stomach contents of 100% of 90 *H. caffer* from a cave in Zambia during the winter months (May to September), with adult Lepidoptera comprising 92.7% of the bats' diet by volume during this season (Whitaker and Black 1976). Likewise, lepidopteran scales were found in 100% of fecal pellets sampled from South African *H. caffer* in November and December, and 92.4% of insect fragments from these pellets were lepidopteran (Dunning and Kruger 1996). During summer months (November–March), the bats consumed a greater variety of

prey items, with moths still most frequently consumed (65.2% of volume, and found in the stomachs of 82.1% of bats studied), and Coleoptera comprising 21.4% of prey by volume (Whitaker and Black 1976). At least 12 different prey items were found in stomach contents in summer, compared with 9 during the winter (Whitaker and Black 1976), and a total of 15 prey items were taken overall. A population of South African *H. caffer* ate significantly fewer arctiid moths capable of clicking than arctiid species that do not click (Dunning and Kruger 1996). Stomach contents of 10 Zambian *H. caffer* revealed 75.5% Lepidoptera by volume, followed by much smaller amounts of Coleoptera, Diptera, and other insects (Findley and Black 1983).

For a sample of *H. caffer* from South Africa, their diet in August was 79.5% Lepidoptera, 10% Trichoptera, 7.9% Coleoptera, and very small amounts of other prey items (n = 11—Bowie et al. 1999). The prey consumed by percentage across a different sample of 6 bats captured in South Africa was: 65.6 ± 46.3 *SD* Lepidoptera; 19.1 ± 40.0 Coleoptera; 14.5 ± 35.6 Isoptera; 0.5 ± 1.2 Hemiptera; 0.3 ± 0.6 unknown. No Hymenoptera, Diptera, or Mantodea were eaten by these bats (Jacobs 2000). This species is reported to have a narrow food-niche breadth (e.g., 1.94 in Fenton [1985] and 1.56 in Whitaker and Black [1976]). *H. caffer* may take more moths than bats using high-intensity, frequency-modulated echolocation calls (Fenton and Fullard 1979).

Miscellaneous.—*Hipposideros caffer* is preyed upon by bat hawks (*Macheirhamphus alcinus*) in Zimbabwe (Fenton et al. 1977). The endoparasite *Trypanosoma leleupi*, which is related to the parasite causing African sleeping sickness in humans, has been reported to infect *H. caffer* (Rodhain 1951). *H. caffer* also is a host for the batflies *Nycteribia schmidlii*, *Pthiridium scissa*, *P. integra*, *P. ovalis*, *P. tecta*, *Penicillidia allisoni*, *P. fulvida*, *P. senegalensis*, and *P. pachymela* (Crouch 1999). Additionally, *H. caffer* has been reported as a host for other arthropod ectoparasites including *Acomatacarus polydiscum*, *Gahrliepia nana*, *Periglischrus moucheti*, *Trombicula minutissima*, *Trombigastia ascoschongastoides*, *T. berghei*, *T. laarmani*, *T. minor*, *T. scapularia*, *T. vinckei*, *Whartonia atracheata*, *W. oweni*, and possibly *Myotrombicula bidentipalpis* (Zumpt 1961).

Researchers typically capture this species using mist nets (e.g., Jones 1971; Menzies 1973) or hand nets (e.g., Bowie et al. 1999). Individuals of this species can be marked using a plastic split-ring run through a small incision made on the anterior side of the forearm (the incision is necessary because *H. caffer* has a wide propatigium, and the band could otherwise cause damage—Bell 1987).

BEHAVIOR

Hipposideros caffer is a flexible forager that is maneuverable in flight and approaches prey quickly and directly whether catching prey in the air or gleaning it from surfaces (Bell and Fenton 1984). *H. caffer* generally takes flying prey in the air but also can glean prey from a variety of surface types (including cluttered surfaces) and may even briefly touch down with wrists and feet to capture prey (Bell and Fenton 1984; Fenton 1986). *H. caffer* can hover briefly (Bell and Fenton 1984) and forage in cluttered habitats (Aldridge and Rautenbach 1987). This species has been grouped with species of low mass, wing loading, aspect ratio, and flight speed; with high maneuverability; and with echolocation calls that are resistant to cluttered conditions (''clutter-resistant'' calls—Aldridge and Rautenbach 1987:771). *H. caffer* seems to depend upon prey flapping its wings for successful capture (whether prey is flying or stationary), most likely because it uses the Doppler-shifted information in the echoes of its vocalizations to detect and capture prey (Bell and Fenton 1984). Evidence suggests that *H. caffer* always uses echolocation calls in prey capture and does not rely on visual cues or the sound of fluttering wings to locate prey (Bell and Fenton 1984). There may be differences between the sexes in hunting behavior, at least seasonally (Kingdon 1974).

The calls of *H. caffer* are typically of higher frequency than those of *H. ruber*, particularly when the species are sympatric (Heller 1992). The calls of *H. caffer* also are broader band than most Rhinolophidae species (Pye 1972). The constant-frequency component of echolocation calls of *H. caffer* from Zaire was reported as >154 kHz (Heller 1992). The frequency of these calls was higher than those recorded from Zimbabwe bats (Fenton 1986), but similar to some calls recorded from other East African populations (Pye 1972). The calls of this species vary geographically, with calls of *H. caffer* from East and Central Africa about 10 kHz higher than *H. caffer* from South Africa (Heller 1992). Pinnae of *H. caffer* are mechanically tuned to the frequency dominated by its own echolocation calls (Obrist et al. 1993).

A harem social system has been suggested for *H. caffer*, with resource defense as a proposed reason for polygyny (Bell 1987). *H. beatus*, sometimes considered a sister species of *H. caffer*, is monogamous in Gabon (Brosset 1982). In at least some areas, roosts may be limited. *H. caffer* in Zimbabwe were observed vying for access to 1 tree, and in this area, few hollow baobab trees were present, and the many small caves around were nearly all occupied by bats, mostly *H. caffer* (Bell 1987). When disturbed, individual *H. caffer* may jerk their heads ''with sharp and regular motions'' (Cowles 1936:123).

GENETICS

The diploid chromosome number (2n) for *Hipposideros caffer* is 32, based on a single female specimen from Uganda (Dulic and Mutere 1974). The fundamental number (FN) is 60, and all chromosomes are biarmed (Dulic and Mutere 1974). Ten pairs of chromosomes were metacentric, and 6

pairs were submetacentric (Dulic and Mutere 1974). The chromosomal characteristics of *H. caffer*, including diploid number and fundamental number, closely resemble those of speciemens of *H. ater* (dusky leaf-nosed bat) and *H. fulvus* (fulvus leaf-nosed bat) from India (Dulic and Mutere 1974).

CONSERVATION

Hipposideros caffer is not considered endangered or threatened and is listed as a species of "Least Concern" by the World Conservation Union (International Union for Conservation of Nature and Natural Resources—Kock et al. 2008). *H. caffer* sometimes roosts in man-made structures, such as attics, rooftops, and deserted buildings (Cotterill 2002; Cowles 1936; Dunning and Kruger 1996; Kingdon 1974).

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