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Anoura geoffroyi (Chiroptera: Phyllostomidae)

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Abstract: *Anoura geoffroyi* Gray, 1838, is a phyllostomid bat commonly referred to as Geoffroy's tailess bat. This bat is broadly distributed in the Neotropics from both versants of Mexico into northern and western South America and the Amazon Basin. *A. geoffroyi* eats mainly pollen, but also consumes fruit, nectar, and insects. It is not of special conservation concern because it is abundant throughout its range. DOI: 10.1644/818.1.

Key words: abundant species, Neotropics, phyllostomid bat, pollen-eater, widely distributed mammal

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Anoura geoffroyi Gray, 1838
Geoffroy's Tailess Bat

Anoura Geoffroyi Gray, 1838:490. Type locality "Brazil."
Ch[*oeronycteris*]. *peruana* Tschudi, 1844:71. Type locality "Peru."
Anoura ecaudata: Saussure, 1860:81. Not *Glossophaga ecaudata* Geoffroy, 1818:418.
Glossonycteris lasiopyga Peters, 1868:365. Type locality "Mexico;" restricted to the "State of Veracruz" by Arroyo-Cabrales and Gardner (2003).
Glossonycteris geoffroyi: Dobson, 1878:508. Name combination.
Glossophaga apolinari J. A. Allen, 1916:86. Type locality "Boqueron de San Francisco (altitude 2730 m = 8900 ft), near Bogotá, Colombia."
Anoura geoffroyi antricola Anthony, 1921:5. Type locality "Loja, Ecuador, altitude 9000 ft."

CONTEXT AND CONTENT. Order Chiroptera, suborder Microchiroptera, family Phyllostomidae, subfamily Glossophaginae, tribe Glossophagini. *A. geoffroyi* has 3 subspecies (Simmons 2005):

A. g. geoffroyi Gray, 1838:490; see above.
A. g. lasiopyga (Peters, 1868:365); see above.
A. g. peruana (Tschudi, 1844:70); see above; *antricola* Anthony and *apolinari* (J. A. Allen) are synonyms.

DIAGNOSIS

Anoura geoffroyi (Fig. 1) differs from *A. cultrata* in having a shortened bladelike p1, the smallest of the mandibular premolars (Nagorsen and Tamsitt 1981; Tamsitt and Nagorsen 1982). *A. geoffroyi* does not have a complete zygomatic arch, whereas *A. cultrata* does (Tamsitt and Valdivieso 1966). The skull of *A. geoffroyi* (Fig. 2) is smaller than that of *A. cultrata* and is characterized by a braincase that is less tapered anteriorly; a thinner rostrum; a posterior margin of the palate that is less deeply incised; no posterior palatal extension; and pterygoids that are not inflated posteriorly (Handley 1960). *A. geoffroyi* differs from *A. caudifer* in having a larger forearm (43–45 mm versus 34–38 mm), a larger cranium, and a less furred and narrower interfemoral membrane (Tamsitt and Nagorsen 1982; Tamsitt and Valdivieso 1966). *A. geoffroyi* is most like *A.*

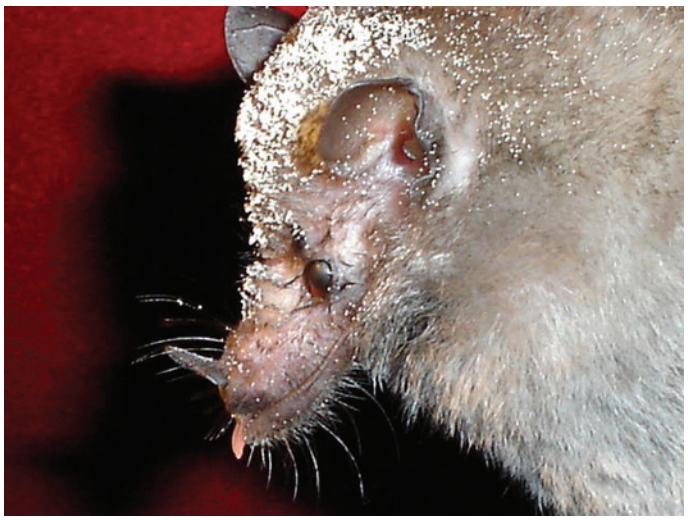

Fig. 1.—*Anoura geoffroyi* covered with pollen, from Cuernavaca, Morelos. Used with permission of the photographer, J. Guerrero.

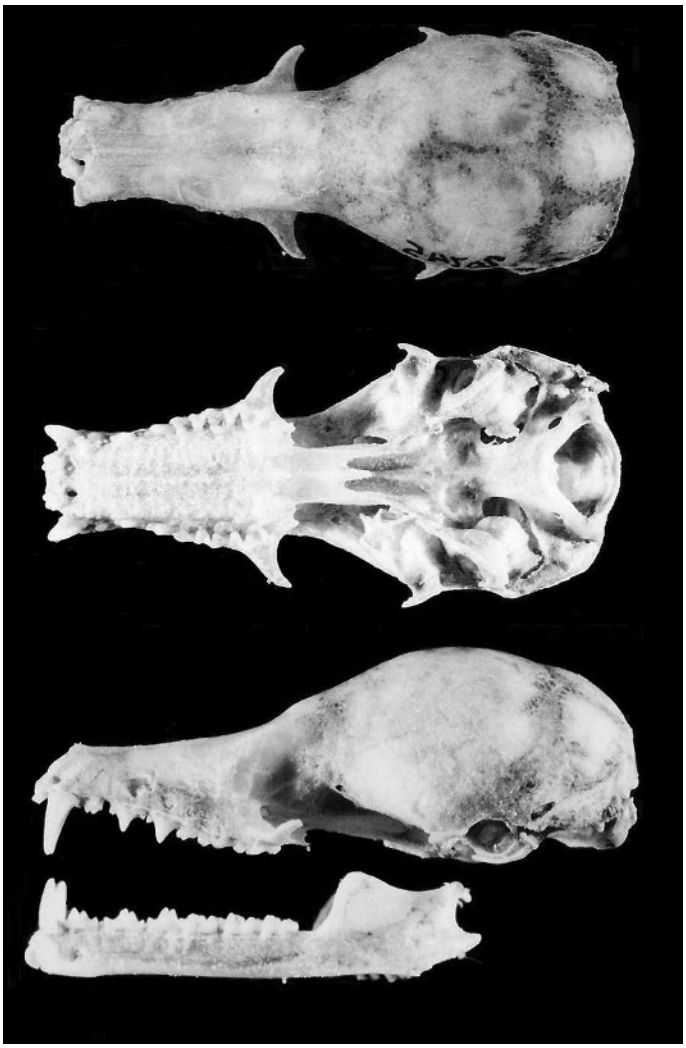

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Anoura geoffroyi* (Instituto de Biología, Universidad Nacional Autónoma de México, 20745). Greatest length of skull is 67.5 mm. Used with permission of the photographer, L. Mirón.

latidens but has a p3 and p4 that are thinner and less robust; the lingual cusp of p4 not enclosed within the triangular basal outline of the tooth; a crescent-shaped p4; and a larger rostrum. *A. latidens* also has slightly smaller canines that are less bulging at their base and a more pale dorsal coloration (Handley 1984).

GENERAL CHARACTERS

Anoura geoffroyi is a medium-sized neotropical bat without a tail. The interfemoral membrane is small and hairy, and the heel bone is very short (Gray 1838). The dorsal pelage is dark to gray-brown with the base of individual hairs more pale. The pelage of the ventral torso is gray-brown, becoming silvery gray over the sides of the neck and shoulders (Hall 1981). Wing and tail membranes are black or blackish brown (Emmons and Feer 1997). Ears are short, rounded, and fused over the forehead. The muzzle is elongated and the lower jaw extends well beyond the upper jaw (Emmons and Feer 1997). Bases of forearms, legs, and toes are hairy; sides of feet are covered with very short hair (Reid 1997).

The skull (Fig. 2) is small and sturdy with a rudimentary and incompletely ossified zygomatic arch (Tamsitt and Nagorsen 1982). The braincase tapers anteriorly; the rostrum is thickened. The posterior margin of the palate is barely incised on the posterior palatal extension; pterygoids are inflated posteriorly, narrowing the elongated mesopterygoid fossa (Handley 1960). External morphological and cranial measurements (mean ± 2 *SE* in mm or g; $n = 46$, sexes combined) are: total length, 69.2 ± 1.2; length of forearm, 43.3 ± 1.4; length of ear, 11.3 ± 1.4; length of foot, 12.3 ± 1.7; body mass, 12.8 ± 2.4; greatest length of skull, 25.3 ± 1.4; condylobasal length, 24.8 ± 2.1; zygomatic width, 10.8 ± 1.5; length of postorbital constriction, 4.9 ± 0.9; greatest width of braincase, 9.8 ± 1.6; length of maxillary toothrow, 9.7 ± 0.9; width across upper molars, 3.6 ± 0.4; width of mastoid, 10.5 ± 0.4; interorbital width, 5.1 ± 0.6; length of digit III, 1.4 ± 0.1; length of digit IV, 1.0 ± 0.1; length of digit V, 0.8 ± 0.1 (Anderson 1957, 1997; Goodwin 1946; Goodwin and Greenhall 1961; Hall 1981; Matson and Patten 1975; Sanborn 1933; Smith and Starrett 1979; Swanepoel and Genoways 1979).

DISTRIBUTION

Anoura geoffroyi is distributed from northern Mexico (Sinaloa, Nayarit, Durango, Jalisco, Colima, Michoacán, San Luis Potosí, Tamaulipas, and Veracruz states) through central and southern Mexico (Estado de México, Guerrero, Puebla, Tlaxcala, Morelos, Oaxaca, and Chiapas states), excluding the Yucatan peninsula and the southern Pacific coast, and both versants (Fig. 3). *A. geoffroyi* occurs through Central America (Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama) and northern South America (Ecuador, Colombia, Venezuela, Guyana, French Guiana, and Suriname) to southwestern Peru, Bolivia, and into much of southeastern Brazil south of the Amazon Basin (Eisenberg 1989; Eisenberg and Redford 1999). It also occurs on Trinidad and Grenada (Eisenberg and Redford 1999). It is distributed from 400 m (Iñiguez 1993) to 2,500 m in elevation (Reid 1997; Tamsitt et al. 1964). No fossils are known.

FORM AND FUNCTION

The aspect ratio of the wings of *A. geoffroyi* is 6.50 mm. Other wing characteristics are (mean ± *SE* cm): tip index, 2.20 ± 0.03; aspect ratio of wing tip, 4.98 ± 0.06; and aspect

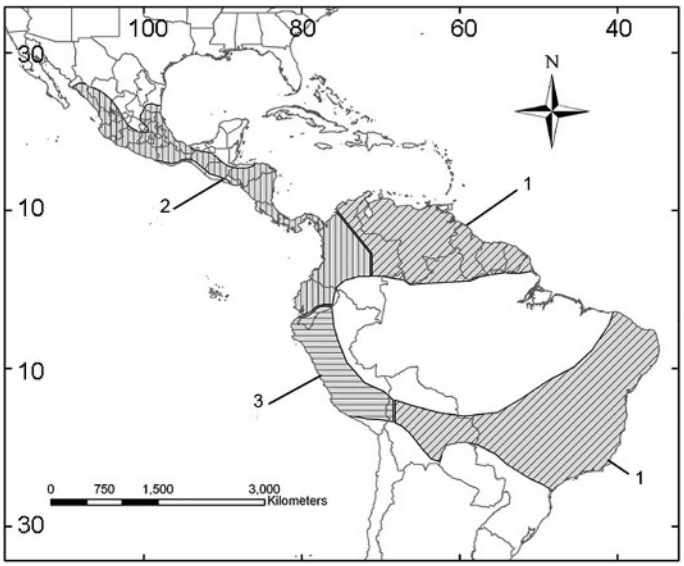

Fig. 3.—Distribution of *Anoura geoffroyi* in Central and South America (Eisenberg 1989; Hall 1981): 1, *A. g. geoffroyi*, 2, *A. g. lasiopyga*, and 3, *A. g. peruana*.

ratio of plagiopatagium, 1.47 ± 0.01 (Smith and Starrett 1979).

The cerebrum of *A. geoffroyi* is elongated and smooth with shallow pseudocentral sulci. Cerebral hemispheres are the largest in any member of the subfamily. The olfactory bulbs are large and pseudotemporal lobes are shallow. The interhemispheric sulcus that bulges to form a shallow cingulated sulcus terminates above the corpus callosum. There is no callosal sulcus. Substantia alba and cortical cells together form a thicker layer than the overlying cortex. Lateral thalamic nuclei are situated slightly above the habernular. Amygdaloid nuclei are small and thalamic nuclei form a wide, shallow body. A dense layer of cell bodies occurs along the external margin of interhemispheric sulcus. The pons is wide and shallow and has a flat ventral surface. Inferior olivary nuclei are small; superior olivary nuclei are large (McDaniel 1976). Other histological and morphological details of the brain are presented in McDaniel (1976).

The dental formula for *A. geoffroyi* is i 2/0, c 1/1, p 3/3, m 3/3, total 32 (Hall 1981). The upper incisors are reduced and separated by a gap. The coronal portion of the dentin is characterized by distinct tubules that follow an S-shaped path from the pulpal chamber to the dentino-enamel junction. The pulp is simple and the cementoid layer is thin.

The tongue is narrow, elongate, and highly extensible, with a pointed apex, but without lateral grooves. The anterior one-third of the tongue has rows of vertical hairlike papillae that function to load nectar by capillary action. In the tongue, muscle fibers form a system of longitudinal, vertical, and transverse bundles that reduce its depth and diameter (Phillips 1971; Phillips et al. 1977). The genioglossus is highly developed into a leaflike form and contributes to extensibility of the tongue.

Anoura geoffroyi prefers sucrose over glucose, fructose, and a glucose–fructose mixture (Herrera 1999). *A. geoffroyi* also is highly effective in extracting pollen grains from flowers (46–90% of all pollen present in a flower). Pollen is retained in the gut for 105–127 min (minimum retention time = 50 min—Herrera and Martínez del Río 1998). A highly effective pyloric sphincter in *A. geoffroyi* improves the efficiency of gastric closure, and thus delays gastric emptying and improves digestion in nectar feeders (Forman et al. 1979). Villi in the intestine of *A. geoffroyi* are tightly compact in some areas. Villi are digitate or club-shaped and may be interspersed among transverse folds (Forman et al. 1979).

Spermatozoids of *A. geoffroyi* have rounded heads, slightly convex bases, and asymmetrical, pointed acrosomes. The acrosome is shorter and broader than the nucleus and contributes imperceptibly to the total length of the sperm head. Apices and nuclei of spermatozoids are usually broadly rounded. The junction of the neck of the sperm with the head is slightly off-center. The midpiece of the sperm is wide at its anterior end, but tapers abruptly by the posterior end. Dimensions of spermatozoa (in μm) are (mean ± 2 *SE*; n = 13): length of head, 3.9 ± 0.2; length of acrosome, 2.2 ± 0.03; length of nuclear region, 3.1 ± 0.2; width of head, 3.1 ± 0.1; total length, 5.6 ± 0.4 (Forman and Genoways 1979).

ONTOGENY AND REPRODUCTION

Embryos of 1.5 weeks were 24 mm in total length and weighed 1.0 g (Álvarez-Castañeda 1992). The sex ratio of neonates was 1:1 in central Brazil (n = 16). Neonates (up to 2 weeks of age) gained 1 g/week during early development. Young become volant when they reach 50% of adult body mass and 90% of adult forearm length (Baumgarten and Vieira 1994; Goodwin and Greenhall 1961). Pregnant *A. geoffroyi* captured on Trinidad carried embryos with a crown–rump length of 8.7 ± 0.3 mm (mean ± 2 *SE*; n = 8) in September, 16.8 ± 0.4 mm in October, and 24.0 ± 0.9 mm in November (Heideman et al. 1992).

A discrete monestrous reproductive cycle may occur late in the rainy season (Wilson 1979). Sexually segregated colonies of *A. geoffroyi* occur during part of the year (July–September) in Michoacán, Mexico (Álvarez and Ramírez-Pulido 1972), Brasilia, Brazil (Baumgarten and Vieira 1994), and in Tamana Caves, Trinidad (Goodwin and Greenhall 1961). However, mixed-sex groups occupy Tamana Caves in late November (Goodwin and Greenhall 1961).

Females with advanced-stage fetuses have been reported in November in Trinidad (n = 56—Goodwin and Greenhall 1961) and in Serrania de las Pavas, Argentina (n = 1—Barquez 1988). Histological examinations indicated that

females become pregnant in July or August and give birth in late November, in Trinidad, West Indies (Heideman et al. 1992). Two females, each with 1 embryo, were captured in June in southern Bolivia (Anderson 1997), and pregnant females were captured from May to August in eastern lowlands and Andean highlands of Peru (Graham 1987; Tuttle 1970). In July, nonreproductive adult females were caught in Sinaloa, Mexico, and Nicaragua (Wilson 1979). During the Costa Rican dry season (March–June), 2 pregnant females were captured (Mares and Wilson 1971). Births occurred in central Brazil during the dry season (late February through April), and lactation was synchronous with flowering (Baumgarten and Vieira 1994; Zortéa 2003).

Testes and epididymides were small from September to mid-April in bats collected in Trinidad, increased in mass in late May, and reached peak mass in July, which corresponded to histological evidence for impregnation of females in July. Spermatogenesis occurred from May to August (Heideman et al. 1992).

Annual reproduction has been reported to be synchronized with daylight. *A. geoffroyi* maintained continuously in light : dark cycles of 12 h 19 min light : 11 h 41 min dark exhibited an active testicular cycle with a period of 7.2–7.7 months (Phillips et al. 1977).

Other studies have failed to demonstrate a circannual rhythm of reproduction of male *A. geoffroyi*. Seasonal and endogenous reproductive cycles are not regulated by photoperiod because testis growth patterns in the laboratory are the same as those in a wild population (Heideman and Bronson 1994).

The birthing process in *A. geoffroyi* lasts 2 h and 10 min. The time of year for parturition in 1 female that gave birth in a laboratory was similar to that of bats in the field (Heideman et al. 1992).

ECOLOGY

Space use.—*Anoura geoffroyi* roosts in a variety of refuges that include caves and tunnels (Reid 1997) near streams and in orchards, croplands, evergreen pine forests, deciduous *Quercus* forests, and cloud forests (Ceballos and Galindo 1984; Handley 1976). They roost alone or in colonies of 20–75 (Tuttle 1970); a roosting colony of 300 individuals is the largest reported (Ramírez-Pulido et al. 2001). A roosting colony of both sexes was reported in a temperate cave of Mexico (Galindo-Galindo et al. 2000). *A. geoffroyi* prefers to roost in the portions of caves receiving some daylight (Villa-R. 1966).

Anoura geoffroyi roosts in mixed-species colonies with *Artibeus amplus*, *A. azteca, A. hirsutus*, *A. lituratus*, *Carollia perspicillata*, *Corynorhinus mexicanus*, *Desmodus rotundus*, *Glossophaga soricina*, *Leptonycteris curasoae*, *L. nivalis*, *Lonchorhina aurita*, *Lonchophylla robusta*, *Mormoops megalophylla*, *Myotis velifer*, *Natalus tumidirostris*, *Peropteryx kappleri*, *P. macrotis*, *Phyllostomus hastatus*, *Platyrrhinus vittatus*, *Pteronotus davyi*, *P. parnellii*, and *Tadarida brasiliensis* (Ceballos and Galindo 1984; Goodwin and Greenhall 1961; Muñoz-Saba et al. 2000; Ramírez-Pulido et al. 2001; Roemer 2000; Sánchez et al. 1999). It also shares roost caves with oil birds (*Steatornis caripensis*—Goodwin and Greenhall 1961).

Diets.—*Anoura geoffroyi* is considered to be insectivorous and facultative nectarivorous throughout its range (Gardner 1977), although a strictly nectar diet was reported for *A. geoffroyi* on Granada (McNab 1971). Variable amounts of fruit and pollen also are consumed (Gardner 1977; Howell and Burch 1974; Iñiguez 1993). Stomach contents of *A. geoffroyi* ($n = 30$) from the northern part of its distribution contained 90% (by volume) Lepidoptera, 6% nectar, and 4% pollen (Howell 1974). Fecal samples ($n = 38$) from *A. geoffroyi* collected from August to July in central Brazil contained primarily fruit pulp and arthropods, with pollen less abundant (Zortéa 2003), and stomachs ($n = 4$) of individuals from southeastern Brazil contained nectar, pollen, thrips (Thysanoptera), ants (Hymenoptera), beetles (Coleoptera), and moths (Lepidoptera). The thrips and ants were presumably consumed incidentally to nectar feeding, but the beetles and moths were probably too large (ca. 10–15 mm in length) to have been consumed accidentally, thus *A. geoffroyi* was labeled as a foliage gleaner (Sazima 1976). Pollen of *Acacia*, *Agave*, *Alnus*, *Bombax*, *Bombacopsis squamigera*, *Burmeistera sodiroana*, *B. truncata*, *Calliandra*, *Caryocar brasiliense*, *Ceiba*, *Clusia*, *Cobaea aschersoniana*, *Ficus*, *Geranium*, *Hibiscus*, *Ipomea*, *Marcgravia coriaceae*, *Markea*, *Meriania pichinchensis*, *Myrtillocactus*, *Pasiflora*, *Pinus*, *Pitcarnia brogniartiana*, *Purpurella grossa*, *Quercus*, *Salvia*, *Symbolathum latifolius*, and *Vochysia* are consumed by *A. geoffroyi* in Brazil, Ecuador, and Mexico (Álvarez and González 1970; Caballero-Martínez 2008; Fisher et al. 1992; Gardner 1977; Gribel and Hay 1993; Ippolito and Suarez 1998; Muchhala and Jarrín-V. 2002).

In edaphic Cerrado of northeastern Brazil, stomachs of *A. geoffroyi* (all 23 with identifiable contents) contained arthropods, including representatives from 3 orders and 7 families. This diet was similar to that of other members of an insectivorous feeding guild that included *Phyllostomus discolor*, *P. hastatus*, and *Molossus molossus*. Because *A. geoffroyi* can hover in flight and is known to feed on nectar and pollen, it is likely that this guild segregates vertically while feeding (Willig et al. 1993).

Diseases and parasites.—Streblid batflies found on *A. geoffroyi* are *Anastrebla mattadeni*, *A. modestini*, *Exastinion clovisi*, *Strebla harderi*, and *Trichobius propinquus* (Graciolli and Cunha Coelho 2001; Komeno and Linhares 1999). Other ectoparasites reported for *A. geoffroyi* are mesostigmatid mites, *Androlealaps laviculus*, *Macrocheles*, *Periglischrus paracutisternus*, and *P. vargasi* (Bassols 1981), and *Alabidocarpus furmani*, *Aspidoptera phyllostomatis*, *Basilia speiseri*, *Chirorhynchobia matsoni*, *Ixodes downsi*, *Loomisia desmodus*, *Nycternastes primus*, *N. secundus*, *Paradyschiria*

parvuloides, *Paraeuctenodes longipes*, *Radfordiella anourae*, *R. oricola*, *Speiseria ambigua*, *Speleochir aitkeni*, *Strebla wiedemanni*, *Trichobius dugesii*, and *T. longipes* (Vargas 1980; Webb and Loomis 1977). Nematodes such as *Litomosoides brasiliensis* also are reported for *A. geoffroyi* (Cuartas-Calles and Muñoz-Arango 1999).

BEHAVIOR

Under controlled laboratory conditions, *Anoura geoffroyi* can use visual cues to escape but uses echolocation in the absence of visual cues (Chase 1981, 1983). While navigating through a laboratory obstacle course, *A. geoffroyi* emitted pulses of 0.5–2 ms duration at pulse rates up to 30/s, depending on proximity to vertically strung wires and to the diameter of the wires (Howell 1974). Hearing sensitivity has been measured by recording cochlear potentials at different sound frequencies. Hearing is most sensitive in the 65- to 75-kHz range, although 1 individual displayed maximal sensitivity at 95 kHz. Hearing was very poor at low frequencies (low frequency cutoff = 20 kHz—Howell 1974).

Nightly activity by *A. geoffroyi* starts 1 h after sunset as groups of 5–8 individuals leave the roost in the Aripo Cave, Trinidad, at intervals of about 2 min. In flight, the species is swift and can hover, but it also does a quick backflip when alighting (Goodwin and Greenhall 1961).

GENETICS

In *Anoura geoffroyi*, fundamental number = 56 and diploid number = 30. The Y chromosome is acrocentric, and the X chromosome is submetacentric (Baker 1979). The karyotype contains a large pair of submetacentrics, 6 pairs of small near metacentrics, and 1 large pair and 6 medium to small pairs of subtelocentrics or near subtelocentrics (Baker 1967). An analysis of allelic frequenicies and heterozygosity values for *A. geoffroyi* is included in a protein electrophoretic study of the Phyllostomidae (Straney et al. 1979).

CONSERVATION

Anoura geoffroyi has been collected regularly in the Cerrado region of Brazil and was reported to be the 2nd most abundant species among the Phyllostomidae in the region in 2000–2001 (Zortéa 2003; Zortéa and Alho 2008). *A. geoffroyi* is broadly tolerant of human disturbance (Handley 1976). In Mexico, it is very abundant with a wide distribution; thus, it is not considered a species of special concern (Arita and Ceballos 1997). It is rated by the International Union for the Conservation of Nature and Natural Resources as lower risk (lr), least concern (lc—Chiroptera Specialist Group 1996).

REMARKS

Anoura is informally grouped with *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, *Lichonycteris*, and several other genera as 1 of the 2 subgroups within the tribe Glossophagini (Carstens et al. 2002). The genus name *Anoura* is derived from the Greek *a*, meaning without, and *oura*, meaning tail, and therefore, literally means bat without a tail (Álvarez-Castañeda and Álvarez 1996). This species was named after E. Geoffroy Saint-Hilaire, its 1st collector (Gray 1838).

ACKNOWLEDGMENTS

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