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Phyllostomus discolor.

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Phyllostomus discolor (Wagner, 1843)

Pale Spear-nosed Bat

Phyllostoma discolor Wagner, 1843:366. Type locality "Cuyaba," Mato Grasso, Brazil.

Phyllostoma innominatum Tschudi, 1844:62. Type locality "Peru."

Phyllostoma angusticeps Gervais, 1855:47. Type locality "Bahia, Brazil."

Phyllostoma verrucossum Elliot, 1905:236. Incorrect original spelling of *Phyllostoma verrucosus* Elliot, 1905; type locality "Niltepec, Oaxaca, Mexico."

Phyllostomus discolor: Miller, 1907:131. First use of current name combination.

Phyllostomus verrucosus: Miller, 1912:38. Corrected spelling of *Phyllostoma verrucossum* Elliot, 1905:236.

CONTEXT AND CONTENT. Order Chiroptera, suborder Microchiroptera, family Phyllostomidae, subfamily Phyllostominae, tribe Phyllostomini (Baker et al. 1989), genus *Phyllostomus*. Two subspecies of *Phyllostomus discolor* are recognized (Hall 1981; Handley 1980).

P. d. discolor (Wagner, 1843:366), see above: *angusticeps* Gervais and *innominatum* Tschudi are synonyms.

P. d. verrucosus (Elliot, 1905:236), see above.

DIAGNOSIS. *Phyllostomus discolor* (Fig. 1) can be distinguished from other members of genus by a weakly developed or absent sagittal crest and a calcar ca. one-half length of tibia in *P. discolor* (Dobson 1878). *P. discolor* resembles juvenile *P. hastatus*, but *P. discolor* can be distinguished by its much narrower muzzle and shorter calcar (Dobson 1878). *P. discolor* (mean length of forearm, 61.44 mm) is smaller than *P. hastatus* (mean length of forearm, 83.17 mm—Eisenberg 1989). *P. discolor* also differs from *P. hastatus* by having a long and narrow muzzle, glandular pads surrounding horizontal portions of nose leaf that do not extend in front, ears more broadly rounded at tips, projection from medial surface of pinna near termination of outer margin of ear is rounded, not square, and calcar shorter than foot (Dobson 1878). *P. elongatum* is slightly larger (mean length of forearm, 66 mm—Eisenberg and Redford 1999) than *P. discolor*, and has a much longer nose leaf, which is more narrow with an attenuated tip. *P. elongatum* also has an attenuated tragus and ears that are comparatively longer, broader, and more rounded because of much greater convexity of upper one-half of medial margin (Dobson 1878). *P. latifolius* is slightly smaller (length of forearm, 56–59 mm) than *P. discolor* and ranges only in northwestern Brazil and adjacent portions of Guyana and Colombia (Eisenberg and Redford 1999).

GENERAL CHARACTERS. *Phyllostomus discolor* is a medium-sized, robust bat with narrow pointed ears, short tail, large interfemoral membrane, and no facial stripes. Lower lip has V-shaped, naked pad bordered by row of elongate papillae. Interfemoral membrane is well developed and, when stretched, reaches ankles. Calcar is shorter than hind foot and less than one-half length of tibia. Tail is ca. one-third length of interfemoral membrane, its tip appearing on dorsal surface of that membrane. Skull (Fig. 2) is massive, with a broad, low rostrum, rounded braincase, and weak sagittal crest. Upper incisors completely fill space between canines; left and right i1 are simple and directed slightly forward. Left and right i2 are short and blunt. Length of 1st upper premolar shorter than 2nd; its crown is ca. one-half as high as that of 2nd; last upper molar is ca. one-third length of 2nd, but equal in breadth. Lower incisors form continuous arcuate row between canines, with i2 being slightly smaller than i1. Unworn cutting edges of i1 and i2 are faintly trifid. Cingulae of lower premolars are ca. equal in length. Crown of 1st premolar is broadly triangular and not as high as narrow triangular crown of 2nd premolar (Felten 1956; Goodwin and Greenhall 1961; Hall 1981; Husson 1962; Valdez 1970).

Ranges of measurements (in mm, sexes and subspecies combined, studies combined, total n = 1,213) are: total length, 75–109; length of tail, 9–22; length of hind foot, 12.0–17.7; length of ear, 18–24; length of tragus, 8–10; length of forearm, 55.4–66.0; greatest length of skull, 28.2–32.2; condylobasal length, 25.3–28.2; zygomatic breadth, 14.6–16.3; interorbital breadth, 6.5–7.4; and length of maxillary toothrow, 9.2–10.4. Nose leaf is well developed. Lancet is long (ca. 13 mm) and broad (ca. 7 mm), and pinna are relatively broad (ca. 12 mm) and reach apex of rostrum when extended forward (Davis and Carter 1962; Felten 1956; Hall 1981; Miller 1932; Sanborn 1936; Valdez 1970).

Mean values (in mm, and parenthetical ranges) for 185 male and 217 female, respectively, *P. d. verrucosus* from El Salvador (Felten 1956) are: total length, 99.1 (89–109), 98.7 (90–108); length from head to rump, 83.9 (75–90), 83.5 (76–91); length of tail, 15.2 (10–22), 15.2 (9–20); length of hind foot, 14.7 (12.0–16.5), 14.6 (12–16); length of ear, 23.3 (19.0–26.5), 23.5 (20–27); length of tragus, 8.7 (7–11), 8.8 (6–10); and length of forearm, 61 (57–66), 60.9 (57–66). Cranial measurements (in mm, mean and parenthetical range) from 35 male and 39 female, respectively, *P. d. verrucosus* from El Salvador (Felten 1956) are: total length, 30.2 (29.1–31.9), 29.6 (28.2–31.2); condylobasal length, 27.2 (26.2–29.1), 26.7 (25.8–28.0); mastoid breadth, 14.9 (14.1–15.6), 14.4 (13.7–15.2); breadth of braincase, 12.2 (11.8–12.6), 12.1 (11.6–12.7); height of braincase, 10.4 (9.8–10.9), 10.2 (9.7–10.9); zygomatic breadth 15.7 (15.0–16.2), 15.4 (14.6–16.3); breadth across canines, 7.2 (6.8–7.7), 6.8 (6.4–7.7); breadth across molars, 10.2 (9.7–10.7), 10.0 (9.3–10.6); length of maxillary toothrow, 9.8 (9.2–10.4), 9.6 (9.2–10.1); intertemporal breadth, 6.5 (6.1–6.9), 6.4 (6.0–6.8); and interorbital breadth 7.1 (6.7–7.3), 7.1 (7.0–7.4).

Mean external and cranial measurements combined from 8 females and 15 females (in mm, parenthetical range, n) of *P. d. discolor* from northwestern Venezuela (Valdez 1970) are: length of forearm, 62.0 (58.5–65.7, 23); length of skull, 30.4 (29.3–31.1, 22); condylobasal length, 27.1 (26.5–27.9, 22); zygomatic breadth, 15.8 (15.0–16.2, 20); length of maxillary toothrow, 9.8 (9.4–10.2, 13);

FIG. 1. Adult *Phyllostomus discolor* from a captive colony, Bronx Zoo, New York. Used with the permission of J. L. Maher and P. Thomas.

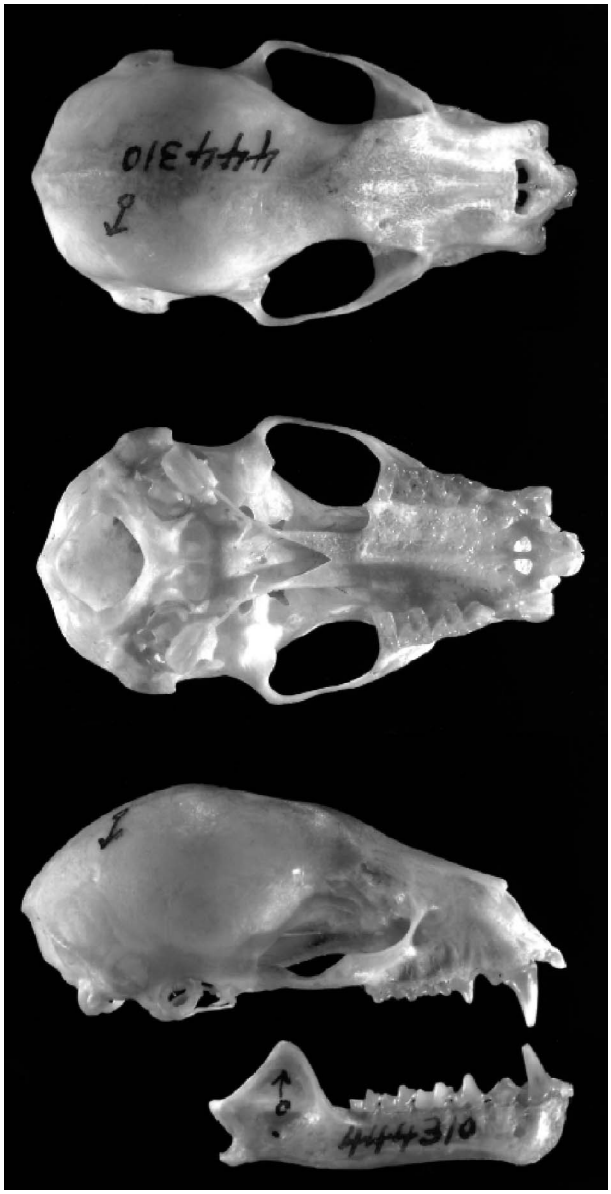

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Phyllostomus discolor* (United States National Museum 444310). Greatest length of skull is 29.7 mm.

FIG. 3. Geographic distribution of *Phyllostomus discolor*. Subspecies are: 1, *P. d. discolor* including Barro Colorado Island (Handley 1966:761); 2, *P. d. verrucosus*.

breadth across molars, 10.1 (9.7–10.5, 23); breadth across canines, 7.3 (6.7–7.6, 23); and length of dentary, 19.0 (18.4–19.8, 23).

Significant sexual dimorphism in size occurs in *P. discolor* from southern Brazil (Taddei 1975) and northeastern Brazil (Willig 1983). In southwestern São Paulo, males were larger than females in 17 external characters and 15 cranial characters (Taddei 1975). In northeastern Brazil, males were larger for 8 external characters and 8 cranial characters (Willig 1983). Body mass ($\bar{X} \pm SD$, in g) of 17 males (44.6 ± 3.6) was significantly larger than that of 10 females (39.7 ± 2.1) from Barro Colorado Island, Panama (Bonaccorso 1979). Gular glandular sac is distinct in males, but rudimentary in females (Krutzsch 2000; Valdivieso and Tamsitt 1964).

Phyllostomus discolor has short (3–4 mm), soft, dense hair that is variable in color. Dorsal hairs have a white basal band, followed by a darker band varying from dark blackish brown to mummy brown to Prout's brown to grayish brown to yellowish brown, whereas tips are whitish. Hairs of ventral surface are white basally, followed by a broad band that is grayish buff to cinnamon-brown to brown, and tipped with a narrow whitish to silvery band that gives ventral surface of body a distinctly whitish to light gray or frosted appearance (Felten 1956; Goodwin and Greenhall 1961; Hall 1981; Valdez 1970).

DISTRIBUTION. *Phyllostomus discolor* occurs from Vera Cruz, Mexico, south to northern Peru, eastward to northern Bolivia to western Paraguay to southeastern Brazil (Fig. 3—Eisenberg 1989; Eisenberg and Redford 1999; Hall 1981; Handley 1966). Inclusion of *P. discolor* in Salta Province, Argentina, is based on a single record (Olrog 1958) and is controversial (Barquez et al. 1993; Redford and Eisenberg 1992). Barquez et al. (1999:20) could not locate Olrog's specimen.

FOSSIL RECORD. A well preserved late Pleistocene or Holocene cranium of *P. discolor* was found in Quebrada Honda Cave in Aragus, San Sabastián, Venezuela (Linares 1968). Six partial mandibles were recovered from Pleistocene cave deposits at Toca da Boa Vista, Bahia, Brazil (Czaplewski and Cartelle 1998). Fragments of dentary from Quaternary deposits were recovered from limestone caves in Serra da Mesa, Goiás, Brazil (Fracasso and Salles 2005).

FORM AND FUNCTION. Vertebrae of *P. discolor* include 7 C, 12 T, 6 L, 5 S, 7 Ca, total 37 (Walton and Walton 1970). Morphology of scapula, sternum, humerus, and pelvis have been detailed (Walton and Walton 1968). Dental formula is i 2/2, c 1/1, p 2/2, m 3/3, total 32. Specimens (n = 103) of *P. discolor* from Mexico, Guatemala, Nicaragua, and Trinidad had no dental caries (Phillips and Jones 1970). Mean bite force (± *SD*, in newtons) was 21.61 ± 3.05 (n = 8—Aguirre et al. 2002).

Phyllostomus discolor had a mean wing span of 41.6 cm and mean wing area of 261.6 cm^2, resulting in a mean aspect ratio of 7.13 (n = 4—Lawlor 1973). Aspect ratio ranges from 6.6 to 7.32 (n = 21—Giannini and Brenes 2001; n = 6—Norberg and Rayner 1987; n = 2—Strickler 1978). Uropatagium area was 11.0 cm^2 and comprised 4.2% of total wing area (Lawlor 1973). Wing tips are relatively large and rounded, as indicated by a tip length ratio of 1.36, tip area ratio of 0.8, and tip shape index of 1.50 (n = 21—Giannini and Brenes 2001). A tip length ratio of 1.33, tip area ratio of 0.85, and tip shape index of 1.77 also have been reported (n = 6—Norberg and Rayner 1987). Wing loading has been reported as 0.162 g/cm^2 (n = 4—Lawlor 1973), 0.158 g/cm^2 (n = 6—Norberg

and Rayner 1987), and 13.6 pascal (n = 21—Giannini and Brenes 2001).

Phyllostomus discolor has an encephalization index of 266 (Stephan 1977) or 200 (Stephan et al. 1981). Relative progression indices show that *P. discolor* has a large neocortex with a neocorticalization index of 519 (Stephan and Pirlot 1970). Brain of *P. discolor* has large cerebral hemispheres that are elongate and anteriorly blunt with well-developed sulci and small secondary fissures (McDaniel 1976). Inferior colliculi are completely covered by cerebrum and cerebellum. Cerebellum contains secondary foliation at lateral edges of vermiform body, the latter being enlarged to form a pronounced medial crest to cerebellum. Measures of brain angles show lateral pole of cerebral hemispheres is rostrally placed (Schneider 1972). Mean brain measurements (in mm, n = 15, sex not indicated) are: total length, 18.2; length of hemisphere, 11.8; width of hemisphere, 12.0; height of hemisphere, 10.0; and length of corpus callosum (n = 3), 4.26 (Baron et al. 1996a). Mean brain weight (n = 15, sex not indicated) was 1,090 mg (Baron et al. 1996a). Total brain volume of *P. discolor* (n = 1) was 835.9 mm^3 and relative composition was 57.9% telencephalon, 9% diencephalon, 7% mesencephalon, 16.5% cerebellum, and 9.6% medulla oblongata (Stephan and Pirlot 1970). Net volume (in mm^3, n = 1) of brain was 1,031.0; ventricles, 7.3; and meninges, stumps of nerves, and hypophysis, 13.8 (Baron et al. 1996a). Measures of brain structures (Baron et al. 1996a, 1996b), absolute volumes of brain structures (Pirlot and Stephan 1970), and photoprints (McDaniel 1976; Stephan 1977) are available.

Olfactory organ consists of 3 endoturbinals and 2 ectoturbinals (Kämper and Schmidt 1977). Morphology and histology of nasal cavities revealed a total area of 20.0 mm^3, of which 6.9 mm^3 were perforated by 92 foramina (Bhatnagar and Kallen 1974). Endoturbinalia 1 (8 mm) is largest (Kämper and Schmidt 1977). A well-developed vomeronasal organ is present (Kämper and Schmidt 1977) and is associated with accessory olfactory bulb (Frahm and Bhatnagar 1980). Volume of main olfactory bulb was 39.8 mm^3 (Baron et al. 1996a), and volume of accessory olfactory bulb was 0.616 mm^3 (Frahm 1981). Accessory olfactory bulb reaches ventricular ependyma, has well-developed glomeruli, mitrial cells, and internal granular cells, but internal and external plexiform layers are not well represented (Frahm and Bhatnagar 1980). Olfactory thresholds (in molecules/cm^3) were low, including propionoic aldehyde at 6×10^8–2×10^9, butyric acid at 9×10^9–9×10^{10}, and butyric methyl ester at 1.8×10^9 (Schmidt 1975). Ability to orient by olfactory cues decreased in low relative humidity (Laska et al. 1986).

Echolocation calls of *P. discolor* are pulses with multiple harmonics and frequency modulation (Esser and Kiefer 1996; Pye 1967; Rother and Schmidt 1985). Calls are have a steep downward-directed frequency modulation at a faint sound pressure level (86 dB sound pressure level maximum) in stationary animals (Esser and Daucher 1996; Rother and Schmidt 1985). In flight, echolocation pulses (0.3–2.5 ms duration) consist of 5 or 6 harmonics, with frequency of 3rd or 4th harmonic containing the main energy (3rd harmonic range is 70–45 kHz—Rother and Schmidt 1985). In flight, orientation sounds were 45–100 kHz, reached a peak intensity of 124 dB sound pressure level (calculated at 10 cm in front of nose), and fell in intensity to 75 dB sound pressure level when animals approached a landing site (Rother and Schmidt 1982). *P. discolor* can detect wires no smaller than 0.25-mm diameter, a threshold that was not improved by visual information. In above-threshold detection range, repetition rate of orientation calls was significantly lower when wires could be localized visually (Rother and Schmidt 1982).

Nose leaf of *P. discolor* produced interference between 2 nostril sources and acted as a filter whose frequency response curve was directionally dependent (Pye 1986). Highest interaural intensity difference was 25–30 dB and located at low-frequency border of echolocation calls (40 kHz), and highest gain of pinna was 10 dB located at 45 kHz (Obrist et al. 1993). Measurements (central, 400–800 μm; radial, 1,400–1,700 μm) made at one-half cochlear turns indicated cochlea was conical, with mean (n = 5) height of cochlea at 2 mm (Pye 1967). Width of basilar membrane varied from 75 μm at base to 150 μm at apex and thickness varied from 20 μm at base to <5 μm at apex. Greatest height (600 μm) and width (200 μm) of the spiral ligament occurred at base and diminished linearly to minimum height (300 μm) and width (75 μm) at apex. Cochlear efferent cells (olivocochlear neurons) originate at ipsilateral superior olive nucleus and bilaterally at trapezoid body (Aschoff and Ostwald 1987). As measured for frontal hemispheres, sound pressure transformation by head and pinnae is directionally dependent. As frequency of sound increases, pinnae increase angle of elevation (aim higher) to optimize sound pressure with highest pinnae gain occurring at midsagittal plane. This is generally true to ca. 55 kHz, when pressure drops abruptly (spectral notch). Above 55 kHz, increases in elevation of pinnae with increasing frequency for highest sound pressure gain continues. Some frequencies have a fairly large interaural intensity difference. Tragi influence position of pinnae axes and introduce spectral changes in sound reaching eardrums that are used in target location (Firzlaff and Schuller 2003). In *P. discolor*, optokinetic nystagmus occurs up to 100–160 °/s (Burghardt and Schmidt 1993).

In 2-choice experiments for a food reward, *P. discolor* preferred visual to auditory stimuli (Schmidt et al. 1988). For *P. discolor*, visual cues (if available) are important during detection phases of orientation, but the complicated motor performance of landing is dependent on echolocation (Joermann et al. 1988; Schmidt et al. 1988).

Brain sites from which vocalizations could be experimentally elicited in *P. discolor* are in periaqueductal gray of midbrain (Fenzl and Schuller 2002). Communication call–like vocalizations and echolocation calls could be elicited at dorsal and ventral edges of periaqueductal gray. The paralemniscal area is located in a restricted ventral region rostral and medial to dorsal nucleus of lateral lemnicsus and only echolocation calls were emitted upon electrical or pharmacological stimulation of this area (Fenzl and Schuller 2002). Respiration is similarly influenced by stimulation of periaqueductal gray and paralemniscal area. Periaqueductal gray and paralemniscal area interact differently with the final common pathway for vocalization and offer different functional organization in vocal controlling pathways for communication and echolocation calls.

Males and females have sebaceous glands. A sexually dimorphic, holocrine, sebaceous, gular gland occurs in males superficial to sternum and throat (Krutzsch 2000; Valdivieso and Tamsitt 1964). When squeezed, a viscous white secretion is exuded that is responsible for characteristic odor of *P. discolor*. These secretions (and odor) serve in olfactory communication (Höller and Schmidt 1993).

Stomach is tubular and has a relatively abrupt, pylo-fundic transition zone, a well developed and dilated fundic cecum, an elongate terminal stomach, and a relatively thin muscular pyloric sphincter. Pyloric portion is elongated with a prominent constriction in front of gastroduodenal junction. A small, but perceptible, cardiac vestibule occurs between lesser curvature and gastroesophageal junction. Muscularis externa and muscularis interna are uncommonly thick. Measurements (in mm, n = 3, sex not indicated) of stomachs of *P. discolor* from Nicaragua ranged: greatest length, 12.1–12.4; greatest breadth, 5.0–5.2; gastroesophageal junction to pyloric valve, 3.5–3.6; gastroesophageal junction to apex of fundic cecum, 4.1–4.4; and breadth of pylorus at sphincter, 1.9–2.0 (Forman 1972). Upper portions of cardiac and pyloric gastric glands stained intensely with periodic acid–Schiff reaction for mucopolysaccharides (Forman 1972; Forman et al. 1979). Cardiac and fundic glands stained positively for acid mucopolysaccharides (Forman 1971, 1972).

Peyer's patch nodules of small intestine have unusually well-developed apices that project far into intestinal lumen, and subepithelial zones are large and extremely elongate. These nodules are rarely of uniform shape, increase in size from duodenum to ileum, and germinal centers within nodules were large at 50–70% of nodular volume. Abundance of lymphoid tissue underscores importance of immunological competency in this species (Forman 1974).

Organ weights (as % of body mass; $\bar{X} \pm SE$, n = 4 males) were: heart, 0.94 ± 0.08; kidneys, 1.57 ± 0.06; liver with gall bladder, 5.98 ± 0.3; and spleen, 0.38 ± 0.12 (Jürgens et al. 1981). Heart rate in a handheld bat was 600 beats/min (Jürgens et al. 1981). Hematological values for *P. discolor* from Colombia (Valdivieso and Tamsitt 1971) for an adult male and an adult female, respectively, were: erythrocytes ($\times 10^6$/mm^3), 6.40, 6.37; leukocytes (per mm^3), 4,050, 4,100; hematocrit (%), 46.0, 32.0; and hemoglobin (g/100 ml), 13.0, 13.4. Mean values (and parenthetical ranges) for leukocytes (%) for 4 adult males and 4 adult females were: basophils, 0, 0.5 (0–2); eosinophils, 1.3 (0–2), 3.0 (0–6); lympho-

cytes, 50.5 (33–74), 49.0 (34–72); monocytes, 0.8 (0–2), 2.5 (0–4); and neutrophils, 46.8 (25–65), 45.0 (22–63). Mean values (and parenthetical range) for 2 lactating females and 1 gravid female, respectively, were: erythrocytes ($\times 10^6$/mm^3), 6.35 (6.00–6.70), 5.6; leukocytes (per mm^3), 6,575 (5,800–7,350), 4,350; hematocrit (%), 52.5 (50–55), 50; hemoglobin (g/100 ml), 15.6 (14.8–16.4), 15.0 g/100; and leukocytes (%), basophils, 1, 2; eosinophils, 1.5 (1–2), 5; lymphocytes, 72.5 (72–73), 79; monocytes, 4.5 (3–6), 1.0; and neutrophils, 20.5 (19–22), 13.0. Total protein in serum (g/100 ml) from an adult male and an adult female, respectively, were 6.55 and 5.12, and relative proportions (% total protein) of some serum fractions were: albumin, 3.70; alpha$_1$ globulin, 0.47; alpha$_2$ globulin, 0.64; beta globulin, 0.83; and gamma globulin, 0.92 (Valdivieso and Tamsitt 1974). Hematological values also are provided by Jürgens et al. (1981).

Response of *P. discolor* (4 males and 7 females) to different CO_2 levels were a 30% increase in mean ventilation, 15% increase in ventilatory frequency, and 15% increase in tidal volume at 3% CO_2; a 70% increase in mean ventilation, 50% increase in ventilatory frequency, and 60% increase in tidal volume at 5% CO_2; and a 108% increase in mean ventilation, 65% increase in ventilatory frequency, and 30% increase in tidal volume at 7% CO_2 (Walsh et al. 1996). Ventilatory responses (4 males and 7 females) to low oxygen were a 10% reduction in metabolic rate (ml O_2 min^{-1} g^{-1}) at 12% oxygen, a 30% reduction in metabolic rate at 10% oxygen, and a 55% reduction in metabolic rate at 8% oxygen (Walsh et al. 1996). *P. discolor* has high-affinity hemoglobin. Whole blood (37°C, pH 7.4) of 4 males had an O_2-binding affinity of 28.6 torr and −0.55 Bohr factor (Jürgens et al. 1981), for 4 males and 7 females an O_2-binding affinity of 27.5 torr (Walsh et al. 1996), and for 2 females and 1 male an O_2-binding affinity of 27.5 torr (Boggs et al. 1999). For 2 females and 1 male the in vivo O_2-binding affinity normoxic condition of 30.8 torr (37.4°C, pH 7.31) fell to 21.8 torr (33.6°C, pH 7.46) upon exposure to 8% atmospheric O_2 (Boggs et al. 1999). Examination of blood gas data for 2 females and 1 male revealed progressive and substantial decreases in arterial O_2 when exposed to low atmospheric O_2, but high-affinity hemoglobin, hypoxia-induced hypothermia, and respiratory alkalosis maintained blood oxygen saturation at levels from 0.64 to 0.70 (Boggs et al. 1999).

Period length of the circadian rhythm of free-running activity under constant conditions in *P. discolor* was unimodal with main activity in 1st half of activity phase. Period length was positively correlated with illumination intensity (Erkert and Kracht 1978). In the applied range of illumination from 10^{-1} to 10^{-6} lx, day to day variation was 24.2–24.5 h and smallest day to day variation occurred at 10^{-4} lx. Under continuous illumination, maximum variation of period length was 1.0–1.6 h (Erkert et al. 1980). After a phase shift by +8 h (advance shift by a single shortened L-phase) and −8 h (delay shift by a single elongated L-phase), resynchronization took 12 days and 5.5 days, respectively (Erkert and Kracht 1978). Interindividual variability occurred in response to constant ambient temperatures, with no clear dependence of amount of activity per day on ambient temperature (Erkert and Rothmund 1981). Among 6 individuals, 3 were most active at 20°C, 1 at 25°C, and 2 at 30°C. At 20°C, animals were most active during 2nd half of their period whereas at 25 and 30°C total activity was greater during 1st half of activity period. *P. discolor* made negligible responses to temperature changes during free-running activity under constant illumination. One *P. discolor* in free-running conditions at 20 and 25°C exhibited a splitting phenomenon in which the activity phase, at first clearly delimited, suddenly split into several bouts after the 7th free-running period and these became grouped into a rhythm that shifted by 180° from original rhythm. When temperature was increased to 30°C, activity returned to original phase (Erkert and Rothmund 1981).

Daily body temperature (T_b) cycles indicated minima at 35.3°C and maxima at 38.8°C. Responses to cold ambient temperatures varied: some animals maintained normal resting body temperature down to ambient temperature of 12°C, others showed marked cooling, but no animal was able to maintain its body temperature below an ambient temperature of 12°C (Morrison and McNab 1967). Over an ambient temperature range of 10–30°C, body temperature had a mean of 34.6°C, basal metabolic rate (M_b) was 1.43 cc O_2/g-h, and thermal conductance (C) was 0.21 cc O_2/g-h°C for "many" *P. discolor* (McNab 1969). Body temperature was given by the relationship $T_b = 3.33(M_b/C)_r W^{0.26} + 27.0$, where $(M_b/C)_r = M_b(100 \text{ mean}/3.4\ W^{-0.25})/C(100 \text{ mean}/1.02W^{-0.51})$ where W is body weight. When individual *P. discolor* were cooled to low ambient temperature, colonic temperature dropped upon return to warm ambient temperatures by as much as 2–3°C, because of return to core of blood cooled in peripheral tissues (McNab 1969). *P. discolor* reduced core body temperature at mild environmental temperatures, but had higher core temperatures at low ambient temperatures. Mean body temperature and minimal rate of metabolism fell as number of pale spear-nosed bats making up a roosting cluster increased. Pale spear-nosed bats nearest center of cluster allow their body temperatures to drop further than do those near periphery of cluster (McNab 1969).

For *P. discolor* ($n = 6$), the medulla to cortex ratio of the kidney was 2.9 and inner medulla to cortex ratio was 1.8 (Studier and Wilson 1983). Values ($\bar{X} \pm SE$, parenthetical range, n) for urine include: osmotic pressure (mOsm/kg), 728 ± 80 (428–911, 5); sodium (mEq/l), 4.8 ± 1.0 (3.0–6.5, 3); and urinary potassium (mEq/l), 34.7 ± 15.9 (3.0–53.0, 3 (Studier et al. 1983). Additional measurements ($\bar{X} \pm SD$, $n = 2$) of kidney are: relative medullary thickness, 6.13 ± 0.85; medulla to cortex ratio, 4.61 ± 1.81; and nitrogen isotope composition, 7.6 ± 0.1 (Herrera et al. 2001).

ONTOGENY AND REPRODUCTION. Hair follicles and vibrissae emerge in utero along with distinct pigment on dorsal side of head and body and on forearms, thumbs, shanks, and feet. Shortly before birth, minute hairs emerge on face, thumbs, feet near base of claws, and in a patch in sacral region. At birth, young appear naked, except for long vibrissae and distinct hairs on dorsal sides of thumbs, forearms, feet, shank, knees, and uropatagium (Tamsitt and Valdivieso 1963). Postnatal pelage appears 1st on limbs, from dorsal to ventral and from cranial to caudal regions. Two generations of hair occur; the 2nd (adult) generation emerges late in postnatal development (Klíma and Gaisler 1968).

Growth of captive neonates followed a logistic growth model for weight, with growth constants (g/day) of 0.055 ($n = 36$—Kwiecinski et al. 2003) and 0.053 ($n = 6$—Rother and Schmidt 1985). As young reached weaning, growth approached an asymptotic mass that was not reached until past weaning. Mean age (± *SE* in days) at weaning was 88.7 ± 1.9 ($n = 30$—Kwiecinski et al. 2003). Mineral and nitrogen concentrations in milk ($\bar{X} \pm SE$, in mg/g dry mass, $n = 40$) from mothers of known-age young were: calcium, 3.32 ± 0.25; iron, 0.18 ± 0.02; magnesium, 1.00 ± 0.09; potassium, 9.26 ± 0.55; sodium, 2.99 ± 0.29; and nitrogen, 67.27 ± 3.65. All minerals in milk, except calcium, were in concentrations that exceeded needs of developing young; calcium concentration equaled amount needed for developing young (Kwiecinski et al. 2003).

Orientation calls and isolation calls develop independently in *P. discolor* (Rother and Schmidt 1985). Young *P. discolor* ($n = 9$) were identified by their isolation calls and from olfactory cues (Esser and Schmidt 1989). Dual-choice experiments demonstrated that mothers of *P. discolor* are able to discriminate acoustically between their young and an alien young when both are presented at the same time ($n = 6$ mothers, 9 young—Rother and Schmidt 1985). The directive call of each mother contains her vocal signature in a distinctive frequency–time structure (Esser and Schmidt 1989). Isolation calls of young occur from birth, are individually distinct, progressively turn into adult directive calls, and may be recorded up to postnatal day 100 (Esser 1994; Esser and Schmidt 1989). Four isolation call types with different temporal characteristics and changes in frequency of each call type occur during development (Esser and Schmidt 1989). Isolation calls of newborn pups have almost no sinusoidal frequency-modulation pattern, but as the pup ages the sinusoidal frequency-modulation pattern becomes dominant (Esser and Schmidt 1989). Regular acoustic mother–infant exchanges, together with gradual changes in calls during the infant's development, assist in the mother's recognition of current modulation pattern of her own infant's isolation call (Esser and Schmidt 1989). Spontaneously emitted echolocation sounds occur from 10 days of age (Rother and Schmidt 1985). Durations of these echolocation sounds are initially 5–12 ms and decrease to ca. 1 ms (adult level) in the 4th week of development. In younger bats, lower harmonics are relatively more intense than in older bats; as young begin to become volant (5–6 weeks of age), their echolocation sounds become indistinguishable from those of adults (Rother and Schmidt 1985).

Mating occurs in harem groups that usually contain 1 male

and 1–15 females, with female composition changing frequently (Bradbury 1977; McCracken and Wilkinson 2000). Geographic variability occurs in mating, pregnancy, and birth (Krutzsch 2000). Seasonal polyestry was described for females from Colombia, Costa Rica, and Panama (Bonaccorso 1979; Fleming et al. 1972; Rasweiler and Ishiyama 1973). Pregnant or lactating animals were caught only during August and September in a 5-year study in Guatemala (Dickerman et al. 1981). Pregnant females were found only in June and November in Peru (Graham 1996), and only in February and October in Colombia (Tamsitt and Valdivieso 1963). Males with descended testes were found in February, June, August, September, and December in Brazil (Taddei 1976).

Uterus of *P. discolor* is externally simplex, with tubular to pear-shaped form, and a prominent rounded fundus. Internally, uterus consists of a large common lumen and narrow tubular segments that constitute the intrauterine cornua. Oviducts are coiled, regionally differentiated, and have been histomorphologically described (Hood and Smith 1983). Oviducts enter uterine body on lateral (mesometrial) border. Unilateral reactions of the oviduct (ipsilateral to corpus luteum) were observed in preovulatory and early-pregnant specimens. Ovarian histomorphology was typical for eutherian mammals, with a partial ovarian bursa, a laterally recurved oviduct, and a medium to large slitlike peritoneal opening (Hood and Smith 1983). Ovarian follicular growth patterns were confined to a small area on ovary and when follicular rupture occurred, released follicles traveled across inside part of this zone (Rasweiler and Badwaik 2000). Implantation occurs at intramural uterine cornua and embryonic mass of blastocyst is oriented toward uterotubal junction (Hood and Smith 1983).

ECOLOGY. *Phyllostomus discolor* is common at lower elevations and up to 610 m (Handley 1966). It is associated with agriculturally developed areas, forested lowlands, streams and other moist areas, dry sites, and fruit orchards, yards, croplands, pastures, evergreens, thorn, deciduous, and cloud and swamp forests (Handley 1966; Valdez 1970; Willig 1983). Pale spear-nosed bats roost in hollows of trees (Bradbury 1977; Enders 1930; Felten 1955, 1956), commonly in silk-cotton wood trees (*Ceiba pentandra*) in Trinidad (Goodwin and Greenhall 1961) and El Salvador (Felten 1955), *Brosimum terrabanum* in El Salvador (Felten 1955), and *Chorisia* sp. (Bombacaceae) in Brazil (McNab and Morrison 1963). *P. discolor* was encountered in dimly lit and dark caves in El Salvador (Felton 1956) and in the mouth of a cave in Venezuela (Linares 1968). Three specimens were found roosting in leaves of a palm tree in Paraguay (Podtiaguin 1944). *P. discolor* roosted in hollow trees with *Carollia perspicillata*, *Micronycteris megalotis*, *Noctilio leporinus*, and *Saccopteryx bilineata* (Enders 1930; Goodwin and Greenhall 1961); in caves with *Phyllostomus hastatus* (Linares 1968); and in trees or caves with *Chilonycteris psilotis* (= *Pteronotus personatus*), *Glossophaga soricina*, *Lonchorhina aurita*, *Mormoops megalophylla*, *Peropteryx kappleri*, *Pteronotus davyi*, and *Pteronotus suapurensis* (= *P. gymnonotus*—Valdez 1970).

Phyllostomus discolor displayed a restricted temporal range of activity 1–2 h after dark, based on recaptures of banded bats (LaVal 1970), but was active all night based on mistnetting (Brown 1968). In gallery forest, 20% of banded bats were recaptured and 4% were recaptured in wet forest (LaVal 1970). Recaptures within 30 m of original banding site occurred with frequencies similar to those of recaptures >30 m from original capture site. Pale spear-nosed bats have a large home range, based on low recapture rates (4%), and a mean recapture distance of 400 m (Fleming et al. 1972). *P. discolor* was placed in a guild of gleaning nectarivorous bats that forages in highly cluttered space and feeds on large flowers of trees, shrubs, or vines in open or forest habitats (Kalko et al. 1996).

Based upon pollen loads, *P. discolor* was an important pollinator of *Caryocar coriaceum* in Brazil (Willig 1983). Number of captured specimens increased 4-fold when *C. coriaceum* flowered. Variable visitation patterns of *P. discolor* and spatial distribution of flowers on *Bauhinia ungulata* were main factors allowing spatial and temporal partitioning of nectar (Fischer 1992). *P. discolor* visits *B. ungulata* soon after sunset and arrived before *Anoura caudifer* and *G. soricina*. *P. discolor* foraged at flowers above 2.5 m, whereas *A. caudifer* and *G. soricina* foraged at flowers below 2.5 m. Each flower was visited for 1–2 s by *P. discolor* for each foraging bout. After having visited most flowers on a shrub, *P. discolor* visited an adjacent shrub, sometimes following the same sequence of shrubs from earlier foraging bouts.

In general, *P. discolor* is omnivorous and most often a consumer of plant material with high levels of nectarivory (Dobat and Peikert-Holle 1985). Pale spear-nosed bats consume nectar, pollen, and flowers in Brazil (de Carvalho 1961). On Barro Colorado Island, Panama, *P. discolor* ate 82.1% pollen and nectar and 17.9% fruit (Kalko et al. 1996), 70.4% pollen and 29.6% fruit (Giannini and Kalko 2004), and was described as primarily a nectarivore (Giannini and Kalko 2005). Stomach contents were 99% insects and 1% plants in Panama and Costa Rica (Fleming et al. 1972). Diet included insects (Coleoptera, Diptera, Hymenoptera, and Lepidoptera), vesiculate plant material, fruit, and pollen in Costa Rica (Howell and Burch 1974). In Panama, *P. discolor* ate only nectar and pollen in the dry season, and switched to fruit and insects in the wet season (Bonaccorso 1979). Fruit and insects were found in the stomach of a Colombian specimen (Arata et al. 1967). *P. discolor* likely feeds on frogs (Uieda and Hayashi 1996).

Plant families and species visited by *P. discolor* as pollinator include: Anacardiaceae, *Mangifera indic* (Dobat and Peikert-Holle 1985); Bignoniaceae, *Cresentia alata* and *C. cujete* (Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985); Bombacaceae, *Bombacopsis fendleri* (Dobat and Peikert-Holle 1985; Heithaus et al. 1975), *Ceiba aesculifolia* (Dobat and Peikert-Holle 1985; Heithaus et al. 1975), *C. pentandra* (Butanda-Cervera et al. 1978; de Carvalho 1961; Dobat and Peikert-Holle 1985; Gardner 1977; Heithaus et al. 1975), *Chorisia speciosa* (Dobat and Peikert-Holle 1985), *Ochroma lagopus* (Bonaccorso 1979; Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985; Gardner 1977; Heithaus et al. 1975; Helversen 1993), *O. pyramidale* (Kalko et al. 1996), *Pseudobombax grandiflorum* (Dobat and Peikert-Holle 1985), and *P. septenatum* (Bonaccorso 1979; Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985; Gardner 1977; Heithaus et al. 1975); Cactaceae, *Pilosocereus tillianus*, *Stenocereus griseus*, and *Subpilocereus repandus* (Simmons and Wetterer 2002); Caesalpiniaceae, *Bauhinia pauletia* (Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985; Fleming 1982; Gardner 1977; Heithaus et al. 1974; Helversen 1993; Ramírez et al. 1984; Sazima and Sazima 1977), *B. rufa* (Dobat and Peikert-Holle 1985; Helversen 1993; Sazima and Sazima 1977), *B. ungulata* (Dobat and Peikert-Holle 1985; Fischer 1992; Heithaus et al. 1975; Helversen 1993; Ramírez et al. 1984), and *Hymenaea courbaril* (Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985; Dunphy et al. 2004; Fleming 1982; Gardner 1977; Heithaus et al. 1975; Helversen 1993; Sazima and Sazima 1977); Capparidaceae, *Crataeva tapia* (Dobat and Peikert-Holle 1985; Heithaus et al. 1975); Caryocaraceae, *Caryocar brasiliense* (Gribel and Hay 1993; Willig et al. 1993), *C. coriaceum* (Gribel and Hay 1993), and *C. villosum* (Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985); Chrysobalanaceae, *Couepia longipendula* (Baker 1970; Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985); Lythraceae, *Lafoensia glyptocarpa* (Dobat and Peikert-Holle 1985; Fleming 1982; Sazima and Sazima 1977) and *L. punicifolia* (Kalko et al. 1996); Mimosaceae, *Inga vera* (Dobat and Peikert-Holle 1985; Heithaus et al. 1975), *Parkia auriculata* (Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985; Fleming 1982; Sazima and Sazima 1977), *P. cachimboensis* (Hopkins 1984), *P. gigantean* (Fleming 1982), *P. gigantocarpa* (Butanda-Cervera et al. 1978; de Carvalho 1961; Dobat and Peikert-Holle 1985; Gardner 1977; Hopkins 1984, 1986), *P. igneiflora* (Hopkins 1984), *P. nitida* (Hopkins 1984; Hopkins and Hopkins 1982), *P. pendula* (Butanda-Cervera et al. 1978; de Carvalho 1960, 1961; Dobat and Peikert-Holle 1985; Gardner 1977; Hopkins 1984, 1986), and *P. platycephala* (Hopkins 1984); Musaceae, *Musa* sp. (Dobat and Peikert-Holle 1985); Sapotaceae, *Manilkara zapota* (Butanda-Cervera et al. 1978; Dobat and Peikert-Holle 1985; Gardner 1977; Heithaus et al. 1975); and Strelitziaceae, *Phenakospermum guyannense* (Kress and Stone 1993).

Plant families and species visited by *P. discolor* as a disperser include: Anacardiaceae, *Mangifera indica* (Heithaus et al. 1975) and *Spondias purpurea* (Gardner 1977; van der Pijl 1957); Cecropiaceae, *Cecropia exima* (Bonaccorso 1979), *C. peltata* (Fleming 1988; Fleming and Williams 1990), and *Cecropia* (Giannini and Kalko 2004); Clusiaceae, *Vismia guianensis* (Reis and Peracchi 1987); Cucurbitaceae, *Gurania spinulosa* (Kalko 1998); Ebenaceae, *Diospyros ebenaster* (Gardner 1977); Moraceae, *Chlorophora tintoria* (Fleming 1988) and *Ficus* (Gardner 1977; Giannini and Kalko 2004; Villa-R. 1966); Musaceae, *Musa* (Gardner

1977; Howell and Burch 1974; Willig et al. 1993); Piperaceae, *Piper* (Gardner 1977; Howell and Burch 1974; Willig et al. 1993); Sapotaceae, *Achras sapota* (Gardner 1977; Reis and Peracchi 1987); and Solanaceae, *Acnistus* (Howell and Burch 1974), *Solanum gradiflorum* (Reis and Peracchi 1987), and *S. salviifolium* (Reis and Guillaumet 1983; Reis and Peracchi 1987).

Endoparasites found in *P. discolor* include the following families and species: Lecithodendriidae, *Limatulum aberrans* (Nicaragua); Porocephalidae, *Porocephalus crotali* (Brazil, Cumana, and Venezuela); Trichostrongylidae, *Histiostrongylus cornatus* (Brazil); and Trypanosomatidae, *Trypanosoma cruzi* and *T. cruzi*–like (Colombia—Marinkelle 1966; Sambon 1922; Ubelaker et al. 1977). Ectoparasites found on *P. discolor* include the following families and species: Labidocarpidae, *Pseudoalabidocarpus secus* (Venezuela); Myobiidae, *Eudusbabekia phyllostomi* (Nicaragua); Spinturnicidae, *Periglischrus acustisternus* (Trinidad and Venezuela) and *Periglischrus torrealbai* (Venezuela); Streblidae, *Apsidopter buscki* and *Megistopoda aranea* (Panama), *Euctenodes mirabilis* (Trinidad), *Strebla consocius* (Colombia), *S. hertigi* (Colombia, Panama, Peru, Suriname, Trinidad, and Venezuela), *S. mirabilis* (Brazil, Panama, and Trinidad), *Trichobiodes perspicillatus* (Colombia, Panama, and Trinidad), *Trichobius costalimai* (Colombia, El Salvador, Guatemala, Panama, Peru, Trinidad, and Venezuela), *T. longipes*, *T. mixtus*, and *T. perspicillatus* (Trinidad); and Trombiculidae, *Beamerella autoascuta* (Nicaragua), *Eutrombicula goeldii* (Venezuela), *Hooperella vesperuginis* (Nicaragua), *Trombicula carmenae* (Trinidad), and *Microtrombicula carmenae* (Costa Rica, Nicaragua, and Trinidad—Brennan and Jones 1960; Jobling 1949; Webb and Loomis 1977).

HUSBANDRY. *Phyllostomus discolor* has been maintained in the laboratory for short periods in small groups in rectangular wire cages (0.38 by 0.38 by 0.61 m) on mixed fruits (bananas, papayas, and zapotes) and "bat glop" (Morrison and McNab 1967). Captive *P. discolor* did not eat meat (Goodwin and Greenhall 1961), but McNab (1969) stated that *P. discolor* requires "a small, but regular intake of meat" and these bats were fed fruit, meat, and fish in captivity. A group of 41 *P. discolor* was maintained on a banana-based diet for 4–18 months (Rasweiler and Ishiyama 1973). *P. discolor* was housed in wood and wire cages (0.9 by 0.7 by 0.7 m) that included a 0.28 by 0.67 by 0.30 m, removable, roosting box similar to Wimsatt vampire cages (Rasweiler 1977). In these cages, young were born and raised in the laboratory and all laboratory-reared females became pregnant. Other formulations of mixed-fruit and liquid diets with protein and vitamin supplements have been used, but a shortcoming of liquid diets was souring before animals were satiated, leading to chronic underfeeding (Rasweiler 1977; Rasweiler and Ishiyama 1973). A successful breeding colony was maintained (7.3 by 2 by 2.4 m) for 5 years on artificial nectar (15% corn syrup and 10% honey in baby formula), fresh fruit, and mealworms (Kwiecinski et al. 2003). In captivity, fruit alone may not meet all nutritional requirements.

BEHAVIOR. *Phyllostomus discolor* lives predominantly in hollow trees on Trinidad where colonies of up to 400 individuals were found (Bradbury 1977). Sometimes entire colonies change roost sites (Wilkinson 1987). Adult sex ratio was ca. equal, but colonies were divided into 5–10 groups of small harems of 1–15 females per male and small all-male clusters (Bradbury 1977; Wilkinson 1987). Within a colony, different social clusters were spatially segregated, but within harems or all-male groups, individuals roost in close contact with one another (Bradbury 1977). Females within groups frequently groom each other (Wilkinson 1987). *P. discolor* does not form female groups that are age cohorts (McCracken and Wilkinson 2000; Wilkinson 1987). Harem formation was active and ongoing, with males performing elaborate displays to both sexes. Female composition of harems changed frequently although the same male may roost in a given location for extended periods. Interfemale aggression was high when females moved between adjacent harems; strange or infrequent females are chased out by resident females, despite attempts by harem males to keep new females. Associated with female movement into and out of harems, both sexes showed olfactory, tactile, motor (wing shaking), and complicated vocal displays to gain entry into groups (Bradbury 1977).

Copulation may occur within the harem during the day, or a receptive female may be chased about the roost by a harem or nonharem male and inseminated. Young are carried by mothers when foraging for the first few days and then left behind at the roost for several hours. Males are tolerant of young and harem males were often seen with an infant asleep on their back. Allogrooming between males and females frequently occurs (Bradbury 1977).

When 2-week-old young are separated from their mothers for several hours and released near their harem group, they rapidly approach adults and perform solicitations (Bradbury 1977). There is an intense exchange of mother directive and infant isolation calls with modulation frequency, modulation depth, carrier frequency, and number of modulations per call contributing to mother's vocal signature (Esser and Kiefer 1996). When hand-reared infants of *P. discolor* ($n = 5$) were exposed to a digitally stored directive call and a set of different call parameters, young adapted their isolation calls to an external reference signal, providing the 1st evidence for audio-vocal learning in a terrestrial, nonhuman mammal (Esser 1994). Natural and digitally modified directive calls were used as acoustic stimuli to determine response selectivity in pups. In digitally modified calls, 1 or more acoustic features were subtracted from the natural call. On postnatal day 5, the pups were unable to distinguish different stimuli types. Day 11 pups could distinguish some calls but not among original maternal directive call and 2 modifications (maternal directive call with amplitude modulation removed and modulation frequency reduced 50%). By day 16, pups distinguished maternal directive calls from all others. Ability to recognize own mother's maternal directive call develops earlier than ability to respond to maternal call characteristics (Esser 1998). *P. discolor* has considerable auditory spectrotemporal resolution (average [$\pm$ *SD*] difference limen for modulation frequency of 2.42 $\pm$ 0.29 Hz, $n = 3$) for labeling individuals (Esser and Lud 1997). For *P. discolor* ($n = 10$), a nonhuman primate–like repertoire of 20 structurally defined call types has been identified (Pistohl and Esser 1998). Female dialects were demonstrated when directive calls of 2 laboratory breeding colonies (1 from Costa Rica and 1 from Colombia, $n = 19$ for colonies together) were analyzed for number of frequency minima and maxima per call, carrier frequency, and modulation frequency (Esser and Schubert 1998).

Behavioral audiograms for 6 adult male *P. discolor* revealed responses to pure tones throughout tested range of 5–142 kHz (Esser and Daucher 1996). Mean audiogram was characterized by 2 peaks of sensitivity and an insensitive region at 55 kHz. First sensitivity peak (>10 and <55 kHz) from audiogram is probably adapted to bandwidth of isolation and directive calls used for individual communication. Second sensitivity peak, centered around 85 kHz, is associated with bandwidth for species' echolocation calls. *P. discolor* has a pronounced ability for frequency discrimination (Esser and Kiefer 1996). For 4 adult male *P. discolor* with a carrier frequency of 18.5 kHz, mean frequency modulation limens increased from 95 Hz at a modulation frequency of 10 Hz to 820 Hz at a modulation frequency of 2,000 Hz, resulting in Weber ratios ($2\Delta f/f$) of 0.005 and 0.044, respectively. Difference limens increased linearly in proportion to carrier frequency throughout a major part of the species' hearing range (9–74 kHz) and are related to use of individual frequency-modulated communication calls and audio-vocal learning (Esser and Kiefer 1996). For 7 female and 1 male adult *P. discolor* frequency tuning properties of cochlea revealed broad filter bandwidths with Q10dB values between 3.4 and 10.7 and no frequency-specific specializations of cochlear tuning (Wittekindt et al. 2005). Characteristic patterns of threshold maxima and minima at high frequencies observed in behavioral studies (Esser and Daucher 1996) are shaped by transfer characteristics of outer ear, by neuronal processing in ascending auditory pathways, or both, and not by cochlear mechanics (Wittekindt et al. 2005).

Phyllostomus discolor often forages in groups of 2–12 bats around flowering trees (Heithaus et al. 1974; Sazima and Sazima 1977). From 2 to 6 *P. discolor* flew in single file and visited flowers in turn (Heithaus et al. 1974). Upon reaching a flowering tree, each animal drank from, and often drained, a flower that was not visited subsequently (Heithaus et al. 1974; Wilkinson 1987). Such groups spent 5–15 min at each tree, disappeared for 1 h or more, and then returned to feed from that tree again (Heithaus et al. 1974). As a flower-visitor in captivity, *P. discolor* ($n = 21$) exhibited a behavior intermediate between hovering and landing, by landing very briefly and flying back and forth to the same flower, and in the process, drained 75% of available nectar (Giannini and Brenes 2001). Simultaneous radiotracking of 8 male and 2 female *P. discolor* from 1 colony in Costa Rica revealed that females foraged nonrandomly

(Wilkinson 1987). The 2 females flew together over a 20-km circuit and visited the same 7 flowering trees on at least 3 successive nights. At a large balsa tree (*Ochroma lagopus*), the 2 radiotagged females and 4 unmarked *P. discolor* visited flowers while flying in single file.

Consistent with an intermediate behavior between typical hovering and landing bats, *P. discolor* displayed an agile foraging behavior, by landing briefly and flying back and forth to the same flower or by changing flowers in each contact (Fischer 1992; Giannini and Brenes 2001; Heithaus et al. 1974). *P. discolor* may sit on flowers (Heithaus et al. 1975). Pale spear-nosed bats turn around easily without landing, fly and land securely in complete darkness, and use echolocation and vision to locate objects (Joermann et al. 1988; Schmidt et al. 1988). In flight tunnel experiments, 6 male and 3 female *P. discolor* avoided obstacles more efficiently when visual information was available (Rother and Schmidt 1982). If several cues were available, actual mode of orientation depended on their relative conspicuousness, but *P. discolor* preferred visual information at distances >40 cm, demonstrating visual cues are more important in far and medium ranges (Joermann et al. 1988; Schmidt et al. 1988).

Naive hungry males presented with finding 1–16 cups containing accessible food in a large flight cage made fewer exploratory flights and located food in less time if a knowledgeable individual was present (Wilkinson 1987). Time to find food was further decreased if 2 experienced individuals were present, demonstrating *P. discolor* learns location of food from other individuals (Wilkinson 1987). *P. discolor* (based on 8 females) is capable of imitative learning, as evidenced by observations that infants produced isolation calls that converged on maternal directive calls (Esser and Schmidt 1989).

Gular glands serve as a means of recognition and for marking territory (Esser 1994; Esser and Schmidt 1989). Females of *P. discolor* sniff the gular gland of males, which open their glands while flapping in front of females (Müller-Schwarze 1983). Males are able to distinguish between their own odor and that of another male (Höller and Schmidt 1993). When a strange male marked another male's preferred roosting site, the latter responded by increasing time spent at the preferred roosting site, but not at alternative sites where a strange male also marked. Females reacted to a non–harem male's odor at their roosting site by increased motor activity, not time spent there, whereas odor of a familiar harem male did not evoke an obvious behavioral response (Höller and Schmidt 1993).

GENETICS. *Phyllostomus discolor* has 15 pairs of autosomal chromosomes that display a smooth size gradation from large to small; 2n = 32 and FN = 60 (Baker 1967; Rodrigues et al. 2000). All autosomes are biarmed, and either submetacentric or metacentric (Baker 1967). The sex-determining mechanism of *P. discolor* has been reported as XX/XY_1Y_2, with Y_1 and Y_2 different sizes (Hsu et al. 1968; Yonenaga et al. 1969). X chromosomes are medium-sized and submetacentric; Y chromosomes are acrocentric (Baker 1967). Blocks of constitutive heterochromatin were visible after C-banding staining with Giemsa, except in Y chromosomes, which were almost completely heterochromatic (Santos and de Souza 1998). Complementary reverse banding occurs after chromosomes are triple stained with base-specific fluorochromes (Santos and de Souza 1998). A pair of nuclear organizer regions (NORs) occurs on terminal regions of autosomal short arms (Morielle and Varella-Garcia 1988). Chromosome 15 was altered by a pericentric inversion with Ag-NOR labeling at distal region (Rodrigues et al. 2000). Of 8 pairs of biarmed chromosomes in the single primitive genome (belonging only to *Macrotus waterhousii*), 7 pairs are found in *P. discolor*, indicating genome of *P. discolor* is primitive for phyllostomid karyotype (Baker 1979; Rodrigues et al. 2000).

REMARKS. In the original description of *Phyllostoma verrucossum* from Niltepec, Oaxaca, Mexico (Elliot 1905), specific epithet was spelled with a double "s". Derivation of the name was not stated, it was used only once, and was most likely referring to *verrucosum*, Latin for warty. In a subsequent publication (Elliot 1907), the specific epithet was spelled with a single "s". Subsequent authors spelled *verrucosum* with a single "s". Therefore, the original *verrucossum* usage was most likely a misspelling (misprint?). Citing Article 32 (a) (ii) of the 1961 *International Code of Zoological Nomenclature*, which states that the original spelling must remain unchanged if an inadvertent error cannot be proven, Husson (1962) stated that proof that Elliot had made an inadvertent error was not possible and the original spelling should stand. Valdez (1970) stated that because Elliot subsequently spelled *verrucosum* with a single "s", this proves that Elliot recognized an "inadvertent error" and the correct spelling should be *verrucosum* with single "s".

Sanborn (1936) assigned 2 specimens from Venezuela to *discolor* based on shorter forearm (55.4 and 61.1 mm) and shorter condylobasal length (25.3 and 26.2 mm) and those from Guatemala and Mexico to *verrucosus* based on forearm length (57.7 and 65.6 mm) and condylobasal length (25 and 27.8 mm), which from available measurements for *discolor*, placed them closer to *verrucosus*. Sanborn (1936) suggested 5 males from Panama assigned to *discolor* by Miller (1932) should be *verrucosus* based on long forearm (64–66 mm) and longer condylobasal length (28 mm). He concludes "from present material *verrucosus* seems to average larger than *discolor*." Felten (1956) assigned 429 specimens from El Salvador to *verrucosus* based on larger size. Davis and Carter (1962) examined 1 specimen from Costa Rica and 2 from Trinidad, reviewed available literature, and found no geographic pattern for recognizing 2 subspecies; these authors concluded all specimens of *P. discolor* belong to a single subspecies and that measurements of geographic variation are measurements of individual variation. Power and Tamsitt (1973) measured 1 limb bone and 8 cranial characters of 223 specimens from 21 localities and found pronounced phenetic heterogeneity among populations within and west of the Andes Mountains, through Central America, and into southern Mexico, but populations east of the Andes were more heterogeneous. Power and Tamsitt (1973) concluded, "Thus recognition of two subspecies offers curatorial advantages but does not really represent phenetically tractable intraspecific differentiates." When variation in cranial and external measurements of 77 specimens from Sao Paulo, Brazil, was analyzed and compared to values in the literature, Taddei (1975) concluded that evidence (individual variation) did not justify the designation of 2 geographic races of *P. discolor*.

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