

Bradypus variegatus (Pilosa: Bradypodidae)

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Abstract: *Bradypus variegatus* Schinz, 1825 (the brown-throated three-toed sloth), is 1 of 4 extant three-toed sloths. A high-canopy folivore, *B. variegatus* is distributed over southern Central America and northern and central South America and is listed as Least Concern by the International Union for Conservation of Nature and Natural Resources because of its wide distribution. Males have a middorsal speculum. *B. variegatus* has a commensal relationship with the algae and invertebrates that live in its thick pelage. It does not adapt well to zoo settings. DOI: 10.1644/850.1.

Key words: commensal, Edentata, edentate, folivory, sloth, South America, Xenarthra

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Bradypus variegatus Schinz, 1825 Brown-throated Three-toed Sloth

Bradypus variegatus Schinz, 1824:251. Nomen nudum.
Brad[ypus]. variegatus Schinz, 1825:510. Type locality “Südamerika,” restricted to “Brasilien (wahrscheinlich Bahia) [Brazil, probably Bahia]” by Mertens (1925:23).
Bradypus ai Wagler, 1831:610. Preoccupied by *Acheus ai* Lesson, 1827:306 (= *Bradypus tridactylus* Linnaeus).
Bradypus infuscatus Wagler, 1831:611. Type locality “Brasilia versus Peru” restricted to “la confluencia del Solimões y el Iça,” Amazonas, Brazil by Cabrera (1958:209).
Bradypus tridactylus brasiliensis de Blainville, 1840:64, pls. 3, 4, 6. Type locality “Bresil;” restricted to “Rio Janeiro” by Thomas (1917:354).
[*Bradypus* (*Acheus*)] *ustus* Lesson, 1840:271. Type locality “Le Brésil, la province de Rio de Janeiro.”
B[radypus]. pallidus Wagner, 1844:143. Type locality “Ostküste von Brasilien;” restricted to “Sapitiba” [= Sepetiba], Rio de Janeiro, or “Ypanema,” São Paulo, Brazil by Pelzeln 1883:97; not “Rio Janeiro” (Thomas 1917:354) or “Ipanema, São Paulo” (Vieira 1955:401; Wetzel and Kock 1973:28).
B[radypus]. infumatus Tschudi, 1845:205. Incorrect subsequent spelling of *Bradypus infuscatus* Wagler.
B[radypus]. rufuscatus Cornalia, 1849:12. Incorrect subsequent spelling of *Bradypus infuscatus* Wagler.
[*Bradypus*] *trivittatus* Cornalia, 1849:4. Type locality “prope Gurupe ad Amazonum ripas,” Pará, Brazil.
Arctopithecus marmoratus Gray, 1850:71. Type locality “Brazil;” restricted to “Pará” by Cabrera (1958:210).
Arctopithecus problematicus Gray, 1850:73. Type locality “Para,” Brazil.

Bradypus brachydactylus Wagner, 1855:173. No type locality; based on *Bradypus infuscatus* Var. β ., which Wagner (1844:149) described from a male specimen Natterer acquired at Borba, Rio Madeira,



Fig. 1.—An adult male *Bradypus variegatus* from São Vicente, São Paulo, Brazil (23°57'35"S, 46°23'15"W). Used with permission of the photographer, M. Motta.

- Amazonas, Brazil (Wagner 1844:150; Pelzeln 1883:97).
- Bradypus problematicus*: Gerrard, 1862:290. Name combination.
- Bradypus ephippiger* Philippi, 1870:267. Type locality “das Vaterland nicht genau angeben ... aus den Wäldern von Ostabhang der Republik Ecuador oder des nördlichsten Peru's stammt;” restricted to “N. W. Colombia” by Thomas (1917:355); further restricted to “Río Atrato” by Cabrera (1958:209).
- Bradypus dorsalis* Fitzinger, 1871:355. Type localities “Süd-Amerika, Nordost-Brasilien, woselbst diese Art nicht nur zwischen dem Rio San Francisco und der Provinz Rio Grande angetroffen wird, sondern auch noch weiter nordwärts bis in die Provinz Pará hinaufreicht;” restricted to “Pernambuco,” Brazil, by O. Thomas (1917:354).
- Bradypus unicolor* Fitzinger, 1871:362. Type locality “Süd-Amerika, Nordost-Brasilien, woselbst diese Form in der Provinz Pará.”
- Bradypus marmoratus*: Fitzinger, 1871:367. Name combination.
- Bradypus speculiger* Fitzinger, 1871:372. Nomen nudum.
- Arctopithecus griseus* Gray, 1871a:302. Type locality “Costa Rica;” corrected to Cordillera del Chucu, Veragua, Panama, by Alston (1880:183–184).
- A[rctopithecus]. boliviensis* Gray, 1871b:439, 443. Type locality “Bolivia,” restricted to “Buena Vista, departamento de Santa Cruz,” Bolivia by Cabrera (1958:208).
- Arctopithecus castaneiceps* Gray, 1871b:444. Type locality “Javali gold-mine in the Chontales district of Nicaragua” (B. Seemann, in litt.; Gray 1871b:429).
- Arctopithecus griseus* Gray, 1871a:302. Type locality “Costa Rica.”
- Bradypus ustus*: Liais, 1872:341. Name combination.
- B[radypus]. castaneiceps*: Alston, 1880:182. Name combination.
- Bradypus griseus*: Allen, 1891:216. Name combination.
- [*Bradypus infuscatus*] Var. *brachydactylus*: Trouessart, 1898:1095. Name combination.
- [*Bradypus tridactylus*] Var. *boliviensis*: Trouessart, 1898:1096. Name combination.
- [*Bradypus tridactylus*] Var. *ephippiger*: Trouessart, 1898:1096. Name combination.
- [*Bradypus tridactylus*] Var. *marmoratus*: Trouessart, 1898:1096. Name combination.
- Bradypus (Arctopithecus) marmoratus*: Goeldi and Haggmann, 1904:90. Name combination.
- Bradypus ignavus* Goldman, 1913:1. Type locality “Marra-gantí (about 2 miles above Real de Santa Maria), near the head of tide-water on the Rio Tuyra,” Darién, Panama.
- [*Bradypus*] *brasiliensis*: Thomas, 1917:354. Name combination.
- Bradypus macrodon* Thomas, 1917:356. Type locality “Sar-yacu, Upper Pastasa River, Oriente of Ecuador.”
- Bradypus violeta* Thomas, 1917:357. Type locality “Balzar Mountains, Guayas, W. Ecuador.”
- Bradypus griseus castaneiceps*: Goldman, 1920:57. Name combination.
- Bradypus gorgon* Thomas, 1926:309. Type locality “Gorgona Island, off the coast of Colombia.”
- Bradypus ecuadorianus* Spillmann, 1927:317. Type locality “Santo Domingo de los Colorados,” Pichincha, Ecuador.
- Bradypus nefandus* Spillmann, 1927:317. Type locality “Provincia de Los Ríos,” Ecuador.
- Bradypus [(Eubradypus)] tocantinus* Lönnberg, 1942:5. Type locality “Cametá, Rio Tocantins, [Pará,] Brazil.”
- Bradypus [(Eubradypus)] miritibae* Lönnberg, 1942:8. Type locality “Miritiba at the northern coast of Brazil;” Maranhão, Brazil.
- Bradypus [(Neobradypus)] marmoratus codajazensis* Lönnberg, 1942:15. Type locality “Codajaz, N. of Rio Solimões, W. of Rio Negro.”
- [*Bradypus (Neobradypus) infuscatus*] *subjuruanus* Lönnberg, 1942:21. Type locality “Lago Grande,” Rio Juruá, Amazonas, Brazil.
- Bradypus (Neobradypus) beniensis* Lönnberg, 1942:22. Type localities “Victoria, Dept. Beni, Bolivia” and “Confluencia de Rio Madre de Dio, Rio Beni, Dept. Beni, Bolivia.”
- B[radypus]. brasiliensis* Sanderson, 1949:783. Incorrect subsequent spelling of *brasiliensis* Blainville.
- Bradypus griseus ignavus*: Hall and Kelson, 1952:315. Name combination.
- Bradypus tridactylus infuscatus*: Vieira, 1955:401. Name combination.
- Bradypus tridactylus miritibae*: Vieira, 1955:402. Name combination.
- Bradypus tridactylus tocantinus*: Vieira, 1955:402. Name combination.
- Bradypus [(Bradypus)] boliviensis*: Cabrera, 1958:208. Name combination.
- Bradypus [(Bradypus)] infuscatus brasiliensis*: Cabrera, 1958:208. Name combination.
- Bradypus [(Bradypus)] infuscatus ephippiger*: Cabrera, 1958:209. Name combination.
- Bradypus [(Bradypus)] infuscatus infuscatus*: Cabrera, 1958:209. Name combination.
- Bradypus [(Bradypus)] infuscatus gorgon*: Cabrera, 1958:209. Name combination.
- Bradypus [(Bradypus)] infuscatus marmoratus*: Cabrera, 1958:210. Name combination.
- Bradypus variegatus ephippiger*: Hall, 1981:280. First use of current name combination.
- B[radypus (Bradypus)]. v[ariegatus]. boliviensis*: Wetzel, 1982:353. Name combination.
- B[radypus (Bradypus)]. v[ariegatus]. brasiliensis*: Wetzel, 1982:353. Name combination.
- B[radypus (Bradypus)]. v[ariegatus]. castaneiceps*: Wetzel, 1982:353. Name combination.

B[radypus (Bradypus)]. v[ariegatus]. gorgon: Wetzel, 1982:353. Name combination.

B[radypus (Bradypus)]. v[ariegatus]. griseus: Wetzel, 1982:353. Name combination.

B[radypus (Bradypus)]. v[ariegatus]. infuscatus: Wetzel, 1982:353. Name combination.

B[radypus (Bradypus)]. v[ariegatus]. marmoratus: Wetzel, 1982:353. Name combination.

B[radypus (Bradypus)]. v[ariegatus]. variegatus: Wetzel, 1982:353. Name combination.

CONTEXT AND CONTENT. Order Pilosa, suborder Folivora, family Bradypodidae. Synonymy is modified from Gardner (2005, 2008). Although Wetzel (1982) lists 9 subspecies, *B. variegatus* is wide-ranging, highly variable, and without clearly differentiated forms (Anderson and Handley 2001). Nevertheless, Gardner (2005, 2008) recognized 7 subspecies:

B. v. boliviensis (Gray, 1871b:439, 442). See above.

B. v. brasiliensis de Blainville, 1840:64, pls 3, 4, 6. See above.

B. v. ephippiger Philippi, 1870:267. See above.

B. v. gorgon Thomas, 1926:309. See above.

B. v. infuscatus Wagler, 1831:611. See above.

B. v. trivittatus Cornalia, 1849:4. See above.

B. v. variegatus Schinz, 1825:510. See above.

NOMENCLATURE NOTES. The generic name, *Bradypus*, is from the Greek for slow-footed. The species name, *variegatus*, refers to the wide diversity of colors and patterns within the taxon. Many researchers refer to *B. variegatus* as *B. tridactylus*, thus much literature that reportedly concerns *B. tridactylus* actually pertains to *B. variegatus*. *B. tridactylus* is less common and is restricted to northeast South America (Hayssen 2009). For this account, if animals or researchers were based in areas where *B. variegatus* but not *B. tridactylus* occurs, I assumed the work was about *B. variegatus*. Other common names are ai, ai-ai, preguiça, and marmota (Wetzel and de Avila-Pires 1980); ai a dos brûle (Liais 1872); Bolivian three-toed sloth, ai de Bolivie, bradype, paresseux tridactyla, perezoso grisaceo, perezoso tridáctilo, and perico ligero (Chiarello and Members of the Edentate Specialist Group 2008); perezoso de tres dedos (Genoways and Timm 2003); camaleon (B. Seemann, in litt.; Gray 1871b); siwaiku (Miskito Indian—Jones 1965); preguiça da beira (Lönnerberg 1942); bicho preguiça (Oliver and Santos 1991); preguiça bentino (Vieira 1955); and dreifinger faultier, freizehen-faultier, bradipo variegato, and preguiça marmota (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2008).

DIAGNOSIS

In different parts of its range, *Bradypus variegatus* (Fig. 1) is sympatric with both two-toed sloths, Linnaeus's

two-toed sloth (*Choloepus didactylus*) and Hoffmann's two-toed sloth (*Choloepus hoffmanni*). The faces of the 2 genera have striking visual differences: the face of *Choloepus* is much more elongated, with a more-prominent fleshy nose, whereas that of *Bradypus* is much blunter. *B. variegatus* has 3 digits on the manus that are partially fused and hairy volar pads, whereas both *Choloepus* have only 2 unfused digits and hairless volar pads (Mendel 1985). In addition, *B. variegatus* has 8 or 9 cervical vertebrae compared with 6 in *C. hoffmanni* (Mendel 1985). Compared with the pale-throated sloth (*B. tridactylus*), *B. variegatus* has a brown throat (that of *B. tridactylus* is yellow) and lacks distinct foramina in the anterodorsal nasopharynx (present in *B. tridactylus*—Wetzel and Avila-Pires 1980). The color differences are variable and in areas of overlap (especially northern Brazil) the 2 species are difficult to distinguish. *B. variegatus* lacks the black mane on the neck and shoulders of the maned sloth (*B. torquatus*—Wetzel and Avila-Pires 1980). *B. variegatus* is generally larger in size (total length >535 mm) than the pygmy three-toed sloth (*B. pygmaeus*—total length <535 mm) and has a more robust skull. The coronoid process of the mandible (Fig. 2) for *B. variegatus* is thick, whereas that of *B. pygmaeus* is thin and falcate (Anderson and Handley 2001). *B. variegatus*, *B. tridactylus*, and *B. torquatus* are broadly similar in size.

GENERAL CHARACTERS

Throat and sides of face are brown and the color is continuous with that on chest and shoulders. Forehead is dark brown. A suborbital stripe outlines the paler color of the ocular area (Wetzel 1985). Overall the hair parts ventrally and meets dorsally (Grand 1978).

Mean external measurements (mm; with parenthetical *SE*, range, and *n*) for Nicaraguan male and female *Bradypus variegatus*, respectively, were total length, 594 (28.1, 540–750, 7), 590 (8.2, 530–632, 14); length of tail, 55 (7.2, 25–70, 6), 55 (4.1, 20–65, 13); length of hind foot, 111 (5.4, 85–132, 8), 120 (6.9, 90–145, 14); length of ear, 12.5 (0.9, 10–15, 6), 12.8 (1.2, 7–22, 14—Genoways and Timm 2003). Average external measurements (mm or kg; with parenthetical *SD*, range, and *n*) of adults of mixed sex from Nicaragua to Brazil were: total length, 578 (59, 420–800, 108); length of tail, 58 (14, 38–90, 101); length of hind foot, 122 (16, 90–180, 101); length of ear, 13 (3, 8–22, 41); mass, 4.34 (0.85, 2.25–5.50, 25—Wetzel 1985). External measurements (mm or kg) with parenthetical range and sample size for adults of mixed sex averaged across 10 locations in Panama were: total length, 570.9 (485–657, 61); length of tail, 51.5 (37–71, 59); length of hind foot, 124.2 (105–148, 59); length of ear, 12.6 (8–18, 61), mass, 4.3 (3.1–6.3, 51—Anderson and Handley 2001). One captive male weighed 5.2 kg (head–body length, 615 mm) and a captive female weighed 6.2 kg (head–body length, 650 mm—Herbig-Sandreuter 1964). Five males had



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult female *Bradypus variegatus* (United States National Museum 545921) from Santarém, Mojui dos Campos, Para, Brazil. Greatest length of skull is 70.00 mm.

a mean mass of 4.1 kg (*SD* 0.6 kg—Pedrosa et al. 2002). Mean mass of 10 adults was 3.9 kg (*SD* 0.28 kg—Valentinuzzi et al. 1984). Four captive females had a mean mass of 2.6–3.9 kg (Mühlbauer et al. 2006). Mean mass of 20 adults of both sexes was 4.7 kg (range, 3.2–6.1 kg—Genoways and Timm 2003). Assuming gut contents are 30% of

body mass, mean body mass (95% confidence interval) without gut contents is 2.78 kg (\pm 0.42 kg) for 17 adult males and 3.18 kg (\pm 0.74 kg) for 18 adult females (Montgomery and Sunquist 1975).

X-ray computed tomography coronal scans of the skull and mandible of a male are available (American Museum of Natural History 95105—Digimorph 2003). Mean cranial measurements (mm; with parenthetical range and *n*) for adults of mixed sex averaged across 10 locations in Panama were: greatest length of skull, 76.7 (68.3–86.0, 62); anterior zygomatic breadth, 47.1 (40.4–53.7, 61); posterior zygomatic breadth, 44.4 (37.0–51.4, 62); postorbital breadth, 23.9 (19.8–26.6, 60); length of squamosal process, 27.0 (22.4–30.6, 62); breadth of squamosal process, 6.0 (4.5–7.9, 61); length of maxillary toothrow, 24.8 (22.0–27.4, 61); postpalatal length, 38.9 (33.2–45.2, 62); palatal breadth, 17.6 (15.6–20.7, 62); depth of braincase, 26.9 (23.8–29.3, 62); breadth of antorbital bar, 4.1 (2.6–5.3, 62); length of descending jugal process, 15.8 (10.3–19.9, 62); diameter of external auditory meatus, 5.4 (4.6–6.1, 61); breadth of ascending mandibular ramus, 16.5 (13.4–19.5, 60—Anderson and Handley 2001). Mean cranial measurements (mm; with parenthetical *SE*, range, and *n*) for male and female *B. variegatus*, respectively, were greatest length of skull, 80.3 (0.78, 77.2–85.0, 9), 78.7 (0.69, 75.3–86.5, 15), anterior zygomatic breadth, 46.8 (0.32, 45.4–48.3, 8), 46.9 (0.56, 44.4–50.4, 13); posterior zygomatic breadth, 44.5 (0.51, 41.3–46.2, 9), 43.9 (0.64, 39.5–48.1, 15); postorbital breadth, 25.4 (0.40, 23.7–26.8, 9), 24.9 (0.41, 23.2–29.3, 15); length of squamosal process, 29.9 (0.38, 27.9–31.5, 9), 29.2 (0.62, 24.7–33.4, 15); length of maxillary toothrow, 26.5 (0.38, 25.1–28.8, 9), 25.8 (0.62, 23.9–29.2, 15); postpalatal length, 41.7 (0.80, 39.3–46.4, 9), 41.2 (0.50, 38.0–45.6, 15); palatal breadth, 17.9 (0.18, 17.3–18.7, 8), 18.1 (0.27, 15.9–19.8, 15); depth of braincase, 28.3 (0.36, 27.0–30.5, 9), 28.1 (0.28, 26.5–29.6, 15); breadth of antorbital bar, 4.5 (0.14, 3.7–5.1, 9), 4.8 (0.17, 4.1–6.2, 15); length of descending jugal process, 15.2 (0.45, 13.4–16.8, 9), 15.8 (0.53, 13.4–19.5, 15—Genoways and Timm 2003). Mean greatest length of skull for 107 adults was 75.8 mm (*SD*, 4.9 mm; range, 65.1–87.4 mm) and mean length of mandibular spout of 108 animals was 1.4 mm (*SD*, 1.0 mm; range, 0.04–3.6 mm—Wetzel 1985). Sexual dimorphism in size is not apparent (Genoways and Timm 2003), but males have a dorsal speculum (Wislocki 1928).

DISTRIBUTION

Bradypus variegatus ranges from Nicaragua and Honduras (Fig. 3; McCarthy et al. 1999) south into Ecuador, Colombia, Venezuela (except the Río Orinoco delta and the Guiana highlands), east of the Andes into forested regions of Ecuador, Peru, and Bolivia to northern Argentina and Brazil (except Amapá to Paraná and Rio Grande do Sul—Wetzel

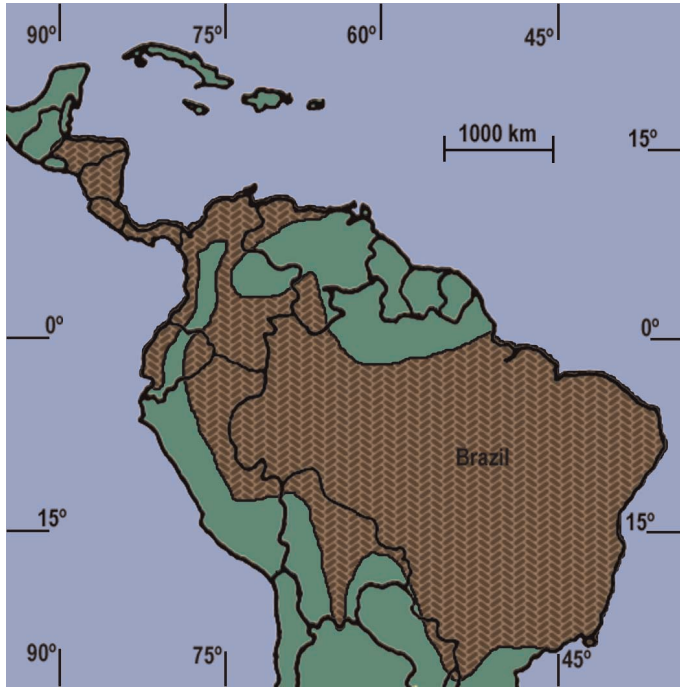


Fig. 3.—Geographic distribution of *Bradypus variegatus* (modified from Emmons and Feer [1990] and Gardner [2008]).

and Avila-Pires 1980) from 0 to 1,200 m (Alberico et al. 2000), although animals have been found above 2,400 m (Ureña et al. 1986). *B. variegatus* does not occur north of the Amazon and east of the Rio Negro where *B. tridactylus* occurs. *B. tridactylus* also does not overlap with the distribution of *B. torquatus* in the southeastern portion of Brazil. *B. variegatus* and *B. pygmaeus* do not co-occur. No fossils are known (Patterson and Pascual 1968).

FORM AND FUNCTION

Form.—Long, coarse guard hairs lie over short, dense, and silky underfur (Wislocki 1928). The direction of the hair on the body facilitates shedding rain (Wislocki 1928). Hairs of *Bradypus variegatus* have neither a medulla nor pigment granules (Aiello 1985). Individual hairs have transverse cracking that increases with age (Aiello 1985). Algae invest the overhair but not the underfur and occur between the cuticular scales (Aiello 1985). A red alga (*Rufusia pilicola*) and 2 green algae (*Dictyococcus bradypodis* and *Chlorococcum choloepodis*) live on hairs of *B. variegatus* (Wujek and Timpano 1986). Hair of young animals is white to black and lacks deep transverse cracks with little algae; middle-aged hair has larger algal colonies in deeper, wider cracks; very old hair may lose the spongy cuticle and thus has no algae (Aiello 1985). Numerous specialized guard hairs lack medullary cores and have a dense central cortical layer and a multilayer cuticle, which can peel off in layers; both central cortex and cuticle are pigmented (Chernova 2000). Cellular

production of these specialized hairs has been described (Chernova 2000). Scanning micrographs of hair are available (Chernova 2000).

Sweat glands are small and infrequent (Wislocki 1928). Skin is thick (mm; throat, 3; back of neck, 3; back, 2.5; back of head, 2; limbs, 2–2.5; abdomen, 2; sacrum, 1.5), tough, and closely connected to the musculature (Wislocki 1928).

Bradypus variegatus has 8 or 9 cervical vertebrae (Mendel 1985). The forelimbs are longer than the hind limbs (10:7—Wislocki 1928). The humerus is 153 mm and the femur 91.9 mm in length (no sample size or variability—Viveros et al. 2004). The calcaneus is large to support the resting posture (Wislocki 1928). Both fore- and hind feet have nonfunctional metapodials for digits I and V as well as 3 functional digits that are hairy, syndactylus to the level of the distal interphalangeal joint, and tipped by strongly curved, long, narrow claws (Mendel 1985). Fore claws are 70–80 mm in length; hind claws are 50–55 mm (Britton 1941).

Incisors and canines are absent; premolars and molars are indistinguishable thus dental formula is $i\ 0/0, c\ 0/0, p-m\ 5/4-5$, total 18–20. The central portion of teeth of *B. variegatus* is a modified orthodontine with numerous vascular canals and few or no dentinal tubules (Ferigolo 1985).

Circulation in the limbs consists of extensive rete mirabile and distinct brachial or femoral veins do not exist (Johansen et al. 1966). In the eye, the area centralis and visual streak in the retina of *B. variegatus* are situated for visualizing branches directly above the animal's head (Costa et al. 1987).

Relative to total body mass (3.6 kg) of 1 female, skin was 15.8%, muscle was 23.6%, and bone was 13.1% (Grand 1978). Proximal portions of the limbs are primarily muscular whereas the extremities are primarily bone (Grand 1978). Ranges of organ masses (g) of 3 adults were heart, 10.9–12.5; pancreas, 4.7–6.3; spleen, 3.5–5.1; paired kidneys, 16.9–19.6; paired adrenals, 0.55–0.65; and thyroids of 5 adults, 0.38–0.65 (Wislocki 1928). Mean (*SD*, *n*, body mass in kg, *SD* body mass) heart mass (in g) was from 5.98 (0.38, 5, 2.60, 0.16) to 10.64 (0.87, 5, 4.28, 0.72—Oliveira et al. 1980). Three livers weighed 50.65, 65.00, and 77.70 g in adults of 3,121, 4,674, and 4,316 g, respectively (Wislocki 1928). Adrenal glands were on average 0.0105% (*SD* = 0.00373%; range, 0.0060–0.0167%) of the adult mass of 5 female and 2 male *B. variegatus* (average mass, 3,354.3 g—Hartman 1959). The adrenals have much connective tissue (Hartman 1959). Stomach contents and urine (200–400 g) constitute a large share of body mass (Wislocki 1928). Contents of 2 stomachs weighed 493 and 662 g in adults of 3,121 g and 4,316 g, respectively (Wislocki 1928). Blood volume in 1 animal was 6.5% of body mass (Johansen et al. 1966).

The pituitary is ovoid, 4 by 5.5 mm in diameter, and 2 mm thick (Wislocki 1928). Body fat is cream in color

(Wislocki 1928). The gall bladder, cecum, appendix, and anal glands are lacking (da Mota et al. 1989; Wislocki 1928). Mean total length of the intestinal tract of 4 animals was 1,985 mm (da Mota et al. 1989). Inner surface of the duodenum has longitudinal and circular folds, whereas that of the small intestine has long, leaf-shaped villi (da Mota et al. 1989). The large intestine, with its short colon and large rectal pouch, has longitudinal and sinuous folds but lacks villi (da Mota et al. 1989). The pancreas has a thick connective tissue capsule; pancreatic islets are not conspicuous (Pinheiro et al. 1981).

Figures and descriptions of histological sections of skin, adrenal, ovary, pituitary, seminal vesicle, spleen, thymus, and thyroid (Wislocki 1928) as well as small and large intestine (da Mota et al. 1989) and pancreas (Abrahamsohn et al. 1981; da Mota et al. 1992; Pinheiro et al. 1981) are available.

In nongravid females, the uterus is pear-shaped with a single cavity; ovaries are bilobed, and the lower one-third of the vaginal canal is double (Wislocki 1927). Ovulation occurs from either ovary (Wislocki 1928). The placenta is deciduate with labyrinthine lobules and intermediate between endotheliochorialis and syndesmochorialis (Wislocki 1925, 1927). Testes are abdominal and spherical (Wislocki 1928, 1933). Seminal vesicles are rudimentary (Wislocki 1928). A prostate is present (Wislocki 1928).

Details of the ear region (Patterson et al. 1992), facial musculature (Naples 1985), voluntary musculature (Wislocki 1928), somatotopic organization of the cerebral cortex (Saraiva and Magalhães-Castro 1975), and vasculature including plexiform arteries and lymphatic system (Bielik 1935; Wislocki 1928) are available.

Function.—Modifications of the hyoid region and palate facilitate feeding upside down (Naples 1986). The ratio of muscle to bite points at the distal, middle, and mesial tooth, respectively, are 1.13, 0.89, and 0.72 (Bargo 2001). The moment arms of jaw muscles (mm standardized to a 110-mm mandible) are: temporalis, 44; massetericus, 24 (Bargo 2001). Teeth of *Bradypus variegatus* are not pointed but nearly flat on the occlusal surface; characteristics not suited to piercing bites or defense against predators (Montgomery and Sunquist 1978).

Modifications of limb and trunk muscles and joints facilitate suspensory posture and locomotion (Böker 1937; Grand 1978; Jouffroy et al. 1961; Vassal et al. 1962). The hooklike claws on the fore- and hind feet suspend *B. variegatus* under branches (Mendel 1985). During terrestrial locomotion, the animals usually support themselves on the soles of their feet and on the ulnar and volar aspects of their forearms and hands and use lateral-sequence, single-foot, or diagonal-couplets gaits (Mendel 1985). They do not drag themselves across the ground (Mendel 1985). Other details of climbing and arboreal locomotion are available (Mendel 1985).

Esophageal pressure profiles for *B. variegatus* are available (Gilmore et al. 2001). *B. variegatus* has a large sacculated stomach. The intestine of 2 male and 2 female animals averaged 198.5 cm in length and was uniform in diameter, but dilated in the rectal area. The duodenum averaged 9.5 cm in length with a thicker wall. The wall of the intestine included mucosa, submucosa, tunica muscularis, and serosa (da Mota et al. 1989). Details of adrenal (Carneiro Filho [1953] as *B. tridactylus*) and intestinal (da Mota et al. 1989) histology are available. Adrenalectomized animals lived on average 28 h (range, 20–58 h; $n = 14$ —Britton et al. 1938).

Feeding increases respiration rate from 5 to 10 breaths/min but does not change arterial pH (mean, SD ; rest, 7.42, 0.05; feeding, 7.45, 0.03), partial pressure of CO_2 (rest, 35.2, 5.3; feeding, 33.3, 4.4 mm Hg), or partial pressure of O_2 (rest, 77.5, 8.2; feeding, 78.4, 5.2 mm Hg—Pedrosa et al. 2002). Other measures of average respiration rate range from 6.1 to 8.6 breaths/min. Under sodium pentobarbital anesthesia, respiration rate was 3 breaths/min with a tidal volume of 57.6 ml, an inspiration time of 3.8 s, and an expiration time of 15.9 s (Gilmore et al. 2000). Other measures of pulmonary capacity relative to total lung volume are: tidal volume, 13.5%; inspiratory reserve volume, 52.6%; expiratory reserve volume, 9.7%; inspiratory capacity, 66.2%, vital capacity, 75.8%; and functional residual capacity, 33.9% (Gilmore et al. 2000, 2008).

Heart rate (beats per minute [bpm]) under anesthesia is 91–94, compared with 90 for conscious animals under restraint, and 76–80 in unrestrained animals (Gilmore et al. 2000). Mean heart rate (bpm) in free-roaming but captive animals was 88 and was lower (66) during daylight (Gilmore et al. 2000). Atropine raises and propranolol lowers heart rate (Gilmore et al. 2000). For 9 animals (mean body mass of 4 kg), mean cardiac output was 0.24 l/min (SD 0.033 l/min), mean arterial blood pressure was 144.3 mm Hg, and mean heart rate was 89.7 bpm (Cabral et al. 1980). The ventricular fibrillation threshold is 2.3 mA/g of heart (SD 0.4 mA/g of heart—Valentinuzzi et al. 1984). Mean blood pressure (mm Hg, parenthetical SD) rose from 97 (19) at rest to 105 (12) during locomotion, and to 119 (17) during feeding; similarly, heart rate (bpm) rose from 84 (15) at rest to 96 (15) during locomotion, and remained at 96 (10) during feeding (Duarte et al. 2004). Mean blood pressure (mm Hg, parenthetical SD) was 97 (17) during the dark, 100 (17) during the light, and 90 (19) during behavioral sleep (Duarte et al. 2003). Arterial blood pressure (mm Hg) and heart rate (bpm) did not differ in unanesthetized, minimally restrained animals (125/85, 83.6) compared with unrestrained animals (133/87, 78.1—Duarte et al. 1982). Postural change from erect to supine or supine to erect increases blood pressure and has variable effects on heart rate (Duarte et al. 1982). Intravenous injection of 1 μ g/kg of epinephrine or norepinephrine increases systolic pressure by 80–90% (Duarte et al.

1987). Other details of cardiovascular function are available (Cabral et al. 1980; Chaves et al. 1960, 1963; Cingolani et al. 1979; Duarte et al. 1982, 1983, 1987, 1989a, 1989b; Gilmore et al. 2000, 2008; Oliveira et al. 1980), including electrocardiograms (Johansen et al. 1966; Silva et al. 2005). Details of blood pressure in the extremities (Johansen et al. 1966) and the role of baroreceptors in the control of blood pressure are available (Duarte et al. 2007).

Mean blood values (*SD*) for 3 *B. variegatus* include: hematocrit, 35.7% (3.1%); hemoglobin, 9.6 g/100 ml (1.3 g/100 ml), blood volume, 54.9 ml/kg body mass (6.1 ml/kg body mass); red cell volume, 19.5 ml/kg body mass (1.4 ml/kg body mass); plasma volume, 35.4 ml/kg body mass (5.2 ml/kg body mass); plasma iron 74.3 µg/100 ml (74.3 µg/100 ml—Bozzini et al. 1978). For 3 animals mean hematocrit was 40% and mean hemoglobin was 13.4 g/100 ml (Johansen et al. 1966). Mean values for 2 animals were: red blood cells, 3.3×10^6 /ml; hemoglobin, 104 g%; hematocrit, 39%; corpuscular volume, 116 µm³; sedimentation rate, 39 mm in 60 min; diameter, 8.2 µm; reticulocytes, 1.12%, leucocytes, 5.2×10^6 /ml; and leucocyte differential: young neutrophils, 0.5%; stab neutrophils, 13%; segmented neutrophils, 38%; eosinophils, 4%; basophils, 0%; lymphocytes, 37%; monocytes, 7.5% (Hoehne and Rosenfeld 1954). Neutrophils have a large hyaline cytoplasm with little granulation; eosinophils have much granulation; monocytes have a lobulated nucleus (Hoehne and Rosenfeld 1954). Amino-acid sequence data are available for α-crystallin (de Jong et al. 1985) and for hemoglobin from Panamanian *B. variegatus* (Kleinschmidt et al. 1989).

Values for blood chemistry from 1 animal were: magnesium, 4.35 mEq/l; calcium, 4.50 mEq/l; phosphorus, 6 mg/100 ml; glucose, 75 mg/100 ml; blood urea nitrogen, 63 mg/100 ml; uric acid, 5.1 mg/100 ml; cholesterol, 171 mg/100 ml; total protein 7.8 g/100 ml; bilirubin, 0.3 mg/100 ml; alkaline phosphatase, 24 µg/100 ml; lactate dehydrogenase, 186 µg/100 ml; and thyroxine (T₄), 1.5 µg/100 ml (Toole 1972). For 3 animals, plasma electrolytes (mEq/l, parenthetical *SD*) were sodium, 140.30 (9.05); calcium, 5.53 (0.96); and potassium, 4.50 (0.62); pH was 7.69 (0.06) and osmolarity was 301.67 (7.64—Oliveira et al. 1980). Serum chemistry for 13 animals of mixed sex was (mean with parenthetical range): sodium, 128.2 mEq/l (118.1–142.4 mEq/l); potassium, 5.7 mEq/l (3.6–10.3 mEq/l); chloride, 101.8 mEq/l (94.8–110.8 mEq/l); urea, 81 mg% (53–129 mg%); sugar 84 mg% (63–100 mg%—Britton et al. 1938). The mean oxygen capacity was 12.3% ($n = 6$ —Irving et al. 1942) to 17% ($n = 3$ —Johansen et al. 1966). For 3 animals, plasma partial pressure of O₂ and partial pressure of CO₂ (mm Hg, *SD*) were 108.33 (1.53) and 30.67 (4.04), respectively (Oliveira et al. 1980). Mean percent glycogen with parenthetical range from 13 animals was: liver, 0.54 (0.30–0.98); muscle, 0.47 (0.23–0.69); and heart, 0.61 (0.28–0.95—Britton et al. 1938). For 13 animals, muscle was 74.7%

water on average (range, 70.0–77.7%—Britton et al. 1938). The activities of myosin and glycolytic enzymes from the pectoralis major, adductor magnus, and soleus are available from animals reported to be *B. tridactylus* but that more probably were *B. variegatus* (Toole and Bullock 1973).

Body temperature of *B. variegatus* was 24–33°C (Britton and Atkinson 1938; Wislocki 1933), 28–35°C (Gilmore et al. 2000), 31–33.5°C (McNab 1978), or 30.0–37.2°C (Enders and Davis 1936; Nagy and Montgomery 1980), and is correlated with environmental temperature (Gilmore et al. 2000); but pregnant *B. variegatus* have a more constant body temperature (Morrison 1945). Four captive females had a mean body temperature of 32°C (*SD* = 1°C—Mühlbauer et al. 2006). The thermalneutral zone is from 11°C (7–18°C) to 35°C (McNab 1978). *B. variegatus* regulates its metabolism by varying body temperature rather than metabolic rate (McNab 1978). Rainfall, especially during the day, reduced body temperature (Montgomery and Sunquist 1978). Behavioral thermoregulation, via exposure to sunlight but not via activity, substantially alters body temperature (Montgomery and Sunquist 1978). Thermal conductance is 15.1 mlO₂ g⁻¹ h⁻¹ °C⁻¹ (McNab 1978).

Estimated field energy expenditure per day is 330.8 kJ for homeostasis and 75.9 kJ for activity, yielding a total of 406.7 kJ (McNab 1978). Rates (*SE*) of water influx (ml kg⁻¹ day⁻¹), water efflux (ml kg⁻¹ day⁻¹), metabolism (kJ kg⁻¹ day⁻¹), and feeding (g dry food kg⁻¹ day⁻¹) for 2 males, 2 females with young, and 1 female without young, respectively, were 40.6 (7.1), 41.0 (5.1), 166 (43), 16.0 (4.1); 40.1 (1.6), 40.4 (2.2), 154.0 (27.0), 16.4 (2.5); and 29.7 (2.0), 31.2 (3.9), 116 (8), 11.2 (0.8—Nagy and Montgomery 1980).

Rates of digestion for leaves of 12 tree species ranged from 0.20% to 9.32% digested per day (Montgomery and Sunquist 1978). Young leaves are digested faster than old leaves (Montgomery and Sunquist 1978). Colored beads (3 mm in diameter) passed through individuals at an average rate of 1.9% per day (range, 0.25–4.61% per day—Montgomery and Sunquist 1978).

Bacterial counts from the 2 forestomach chambers (pouch and diverticulum) were 10¹¹–10¹⁷ colony-forming units. The proportion of gram-negative to gram-positive bacteria was 1.3:1 with rod bacteria dominant to cocci bacteria (81% versus 19%). Lysozymes were present in all 4 stomach compartments (pouch, diverticulum, glandular prepyloric, and muscular prepyloric). Fermentation takes place in the pouch and diverticulum, whereas conventional digestion takes place in the prepyloric stomach (Pacheco et al. 2007).

Four captive sloths defecated on average every 2.4 days (*SD* = 0.4 days) over 94–184 days (Mühlbauer et al. 2006). Mean dry weight of fecal mass was 56 g (range 45–68 g, $n > 26$ —Montgomery and Sunquist 1975). Average (*SE*) manganese (µg/g dry matter) and energy levels (kJ/g dry food) from stomach contents and feces, respectively, were stom-

ach: 84 (12), 19.0 (0.5); feces: 233 (30), 20.3 (1.2—Nagy and Montgomery 1980).

Pancreatic cells are immunoreactive individually for glucagon, insulin, somatostatin, and serotonin but not pancreatic polypeptide (da Mota et al. 1992). Glucagon cells are especially frequent (da Mota et al. 1992).

ONTOGENY AND REPRODUCTION

Litter size is 1 (Enders 1935) although 2 young have been observed with a single female (Bezerra et al. 2008). Based on fetal development in 41 females from Panama, the peak for mating occurs in January–March and that for birth in August–September for a 4- to 6-month gestation (Enders 1935; Heuser and Wislocki 1935; Taube et al. 2001; Wislocki 1927). Gestation in a captive female was >7 months (Mühlbauer et al. 2006). The interbirth interval is 10–12 months (Taube et al. 2001). Copulation was observed in Pernambuco, Brazil, on 20 July and 13 November; a preweaned juvenile remained on its mother's abdomen during the November copulation (Bezerra et al. 2008; Gilmore et al. 1994). No active spermatogenesis was observed in 4 males in Pernambuco, Brazil, from November to early February (Gilmore et al. 1994).

Details of fetal development are available (Heuser and Wislocki 1935; Wislocki 1926, 1927, 1928). Neonates can cling to their mother's ventrum (Wislocki 1927) as do young animals (Soares and Carneiro 2002). Young are carried for about 5.5 months (Montgomery 1983), although rarely for 23 months (Herbig-Sandreuter 1964). A late-term embryo weighed 260 g, was fully furred, and had fully developed claws (Gilmore et al. 1994). A captive male neonate weighed 340 g with a head–body length of 190 mm at birth and was fully furred with open eyes (Herbig-Sandreuter 1964). First solid food was at 4 days (Herbig-Sandreuter 1964) or 2 weeks (Montgomery 1983). The end of lactation is at 4–5 weeks (Taube et al. 2001; Wislocki 1927) or 6 weeks (Montgomery 1983).

Average (*SE*) rates of water (ml/day, ml kg⁻¹ day⁻¹) and energy (kJ day⁻¹, kJ kg⁻¹ day⁻¹) from milk in a 470-g and a 636-g young, respectively, were: 9.5 (2.0), 20.2 (4.2), 79.0 (17.0), 169.0 (35.0); 6.4 (1.4), 10.0 (2.2), 53.0 (12.0), 84.0 (18.0—Nagy and Montgomery 1980). On Barro Colorado Island, Panama, mid- to late-stage pregnant females tend to use the tree *Cecropia eximia*, but females with young do not exhibit this tree preference (Montgomery and Sunquist 1978).

Plasma estradiol is 2–6 pg/ml; fecal estradiol is 200–1,500 pg/g feces (Mühlbauer et al. 2006). Fecal progesterones vary from 0 to 3,500 ng/g wet feces (Mühlbauer et al. 2006). Ovulation can be hormonally detected by fecal estradiol levels (Mühlbauer et al. 2006).

Testicular Sertoli cells contain bundles of crystalloid filaments (Toyama et al. 1990). Micrographs of the testis are available (Gilmore et al. 1994). Injections of luteinizing

hormone–releasing hormone increase plasma luteinizing hormone and testosterone levels (Gilmore et al. 1991). Neither naloxone nor anti–luteinizing hormone–releasing hormone altered serum luteinizing hormone in 7 males ($\bar{X} \pm SE$ in ng/ml; before injection, 0.98 ± 0.16 ; 4 h after injection, 0.96 ± 0.19); testosterone generally remained below 2 nmol/l (Gilmore et al. 1994).

ECOLOGY

Bradypus variegatus is a high-canopy folivore and is a major vertebrate primary consumer in moist Neotropical forests (Montgomery 1983). It is sympatric with *B. torquatus* in the eastern coastal areas of Brazil below 1,500 m but is the only three-toed sloth above 1,500 m (Oliver and Santos 1991) and is sympatric with *B. tridactylus* along both banks from the Rio Negro to the Rio Tapajós and along the left bank to the mouth of the Amazon (Wetzel and Avila-Pires 1980).

Diet is varied because stomach contents or direct feeding observations include material from at least 51 plant species in at least 13 families (Carvalho 1960 [as *B. tridactylus*]; Goffart 1971; Montgomery and Sunquist 1975; Urbani and Bosque 2007). Young leaves account for 67% of the diet (Urbani and Bosque 2007). An individual chose only young leaves to eat not old ones and did not eat the entire leaf (Luederwaldt 1918). Estimated leaf removal for *B. variegatus* is 5.1 g of leaf per kilogram of sloth per day (Montgomery and Sunquist 1975). In Costa Rica, *B. variegatus* visited 71 tree species and used 15 species as food (Vaughan et al. 2007).

Sex ratio is 1:1 in Panama (Meritt and Meritt 1976) and Brazil (Jorge et al. 1985). In an organic cacao farm in Costa Rica, mean home-range size (ha, *SD*) for 7 males and 8 females, respectively, was 9.18 (53.07), 6.45 (9.26) but median home-range size for all 15 animals was 5.2 ha (Vaughan et al. 2007). In Panama, mean home-range size is 1.59 ha (*SD* 1.066 ha, *n* = 9 animals, range 0.5–3.7 ha) and overlaps with conspecifics, although individual animals do not use the same tree (Montgomery and Sunquist 1975). Estimated density is 8.5 animals/ha (Montgomery and Sunquist 1975). *B. variegatus* accounts for 40–48% of the nonvolant, terrestrial mammalian biomass on Barro Colorado Island, Panama (Eisenberg and Thorington 1973).

Within a home range *B. variegatus* uses an average of 41.4 trees (*SD* 12.02 trees, *n* = 9) from an average of 24.4 species (*SD* 4.67 species, *n* = 9—Montgomery and Sunquist 1975). Individuals are found 9–21% of the time in a single tree, but the species of tree differs among individuals (Montgomery and Sunquist 1975). As a species, *B. variegatus* is a generalist regarding the use of particular tree species, but individuals specialize on a few species (Montgomery and Sunquist 1978). *B. variegatus* tends to use trees with crowns that are exposed to sunlight (Montgomery and

Sunquist 1978). Individuals are most visible in *Cecropia* trees (Montgomery 1983).

Ectoparasites include mange or scabies mites: *Edentalges bradypus* (Fain 1965), *Lobalges trouessarti*, and *Sarcoptes scabiei* (Fonseca 1954; Oliveira et al. 2000); other mites: *Liponissus iheringi* = *Bdellonyssus bursa* (Fonseca 1935; Fonseca 1957–1958); ticks: *Amblyomma aureolatum* = *A. striatum* (Aragão and Fonseca 1961), *A. gertschi* (Christensen and Herrer 1976), *A. varium* (Luederwaldt 1918; Marques et al. 2002), *Boophilus microplus* (in captivity—Aragão 1936); fleas: *Polygenis atopus* (Tipton and Machado-Allison 1972); mosquitoes: *Deinocerites epitedeus*, *D. melanophyllum*, and *D. pseudes* (Tempelis and Galindo 1970); sand flies (Diptera, Psychodidae): *Phlebotomus gomezi*, *P. sanguinarius*, and *P. trapidoi* (Thatcher and Hertig 1966); and blattids (Luederwaldt 1918).

Commensal invertebrates include the sloth moth, *Cryptosis choloepi*, which lives in the fur of *B. variegatus* and deposits eggs in the dung, which its larvae eat (Waage and Montgomery 1976); and coprid beetles, *Trichillum bradyporum* (Balthasar 1939), *Uroxys gorgon* on a Colombian *B. variegatus* (Arrow 1933), and a *Uroxys*-like species on a Panamanian *B. variegatus* (Waage and Best 1985). Yellow-headed caracaras (*Milvago chimachima*) can forage on invertebrates in the fur of *B. variegatus* (Krakauer and Krakauer 1999).

Endoparasites include *Endotrypanum* (Shaw 1985), *Leishmania braziliensis* sensu lato (in 1 of 77 Panamanian animals—Herrer and Telford 1969), *Leishmania braziliensis* (in 8 of 47 Costa Rican animals—Zeledón et al. 1975), *Leishmania herreri* (in 3 of 86 animals—Shaw 1985), *Leishmania (Viannia) shawi* (in viscera—Lainson et al. 1989), a *Pneumocystis*-like protozoan (in 1 Panamanian female—Yonushonis et al. 1986), *Trypanosoma cruzi* (in 1 of 7 animals—Pipkin 1968; Shaw 1985), and *Trypanosoma leuwenhoekii* (Shaw 1985). A captive animal died of toxoplasmosis (*Toxoplasma gondii*—Túry et al. 2001). No leptospirae were found in 5 animals in Nicaragua (Clark et al. 1966). The nematode *Leiuris decodontus* parasitizes the duodenum (Enders 1935; Wislocki 1928).

Experimental inoculation with yellow fever, Venezuelan encephalitis, and St. Louis encephalitis produce long viremias (up to 23 days) but no symptoms (Seymour 1985). Two of 21 *B. variegatus* had antibodies to a South American subtype of Venezuelan encephalitis (Seymour 1985). None of 21 Panamanian *B. variegatus* tested positive for Mayaro virus nor did any of 70 animals test positive for the yellow fever virus, but 8–16% (of 58–167 individuals) were positive for the St. Louis encephalitis virus, 1 of 167 was positive for the Ilheus virus, and 61% of 23 were positive for Utinga virus (Seymour 1985). The Utinga virus was isolated from a male from central Panama and 3 of 35 animals were seropositive (Seymour 1985). A strain of the Punta Toro virus was isolated from a female and 8 of 106

animals were seropositive (Seymour 1985). The Changuinola virus was isolated from 3 animals and 5 of 96 animals were seropositive (Seymour 1985). Animals from Belém, Brazil (reported as *B. tridactylus*), exhibited hemagglutination inhibition antibodies for Mayaro (1 of 7 animals) and Ilheus (4% of animals) viruses, and 2 types of simbu viruses also were isolated from their blood (Woodall 1967).

Harpy eagles (*Harpia harpyja*) prey on *B. variegatus* (Galetti and de Carvalho 2000; Touchton et al. 2002) as do jaguars (*Panthera onca*—Garla et al. 2001). On Barro Colorado Island, >60% of mortality is during the rainy season (October–December), which coincides with the fewest human visits to the island (Montgomery and Sunquist 1978).

HUSBANDRY

Three captive *Bradypus variegatus* lived for at least 3 years on freshly cut branches of *Cecropia*, *Clusia*, and *Ficus* and successfully bred (Herbig-Sandreuter 1964). *B. variegatus* are resistant to ether (Enders 1935). Anesthesia sufficient for blood collection can be achieved with intraperitoneal chloralose at 60–100 mg/kg (Chaves et al. 1960). A fungal infection is common in captive juveniles (Superina et al. 2008).

BEHAVIOR

Bradypus variegatus can swim well (Carvalho 1960 [as *B. tridactylus*]; Tirlor 1966; Viveros et al. 2004). *B. variegatus* is arboreal and travels with its body perpendicular to the branch it is climbing (Enders 1935). *B. variegatus* does not seek shelter during rains (Luederwaldt 1918).

Adult animals usually sleep 15–18 h per day (Tirlor 1966), often holding onto the limb of a tree or sitting in the crotch of a tree (Enders 1935). The usual posture is a sitting or squatting position (Urbani and Bosque 2007; Wislocki 1928). When sleeping, the hind limbs are used for support, the head lies on the chest or abdomen, and the forelimbs curl over the abdomen (Wislocki 1928). This posture also is used during rainstorms (Brattstrom 1966). Electroencephalograms of asleep and awake *B. variegatus* are available (Galvão de Moura Filho et al. 1983).

Bradypus variegatus is active during the day and at night with a dawn lull in activity (Janzen 1983; Sunquist and Montgomery 1973). In Panama, 15 *B. variegatus* were active an average of 10.1 h (*SD* 2.17 h, range 7.0–15.5 h; *n* = 38 diels—Sunquist and Montgomery 1973). Most (66%) of activity bouts were <1 h, but 55% of active time was in bouts >2 h (Sunquist and Montgomery 1973). Activity increases when *B. variegatus* is excited, exposed to sun, or injected with adrenalin (Britton and Kline 1939). Activity is greatest from 1200 to 1600 h (Urbani and Bosque 2007). An individual changed trees every 1–3 days (Luederwaldt 1918).

Six adult males moved more at 2100–2400 h than at other times of the day (Gilmore et al. 2001). One animal moved 3 m in 1 min at the onset of a sudden rainstorm (Brattstrom 1966).

Bradypus variegatus descends to the ground to defecate on average every 8 days (Montgomery and Sunquist 1975). It digs a shallow depression with its tail into which it deposits a mass of fecal pellets (Montgomery and Sunquist 1978).

Except for mother–young pairs, *B. variegatus* is solitary. Young animals learn food preferences initially by licking leaf fragments from their mother's lips and subsequently by eating what the mother eats (Montgomery 1983). At social weaning (6 months after birth), females leave the portion of their home range in which they had raised their young. Mothers return to that area with the birth of each succeeding young (Montgomery 1983). In this manner, young inherit part of the home range of their mothers (Montgomery and Sunquist 1978) and lineages of *B. variegatus* have food preferences that differ from those of other lineages in the same area (Montgomery 1983).

Calls of young *B. variegatus* when separated from their mothers are whistles that rise slightly from 1.9 to 2.6 kHz. Energy is concentrated in a shallow band with no sidebands. The average length of 22 calls was 0.882 s (Montgomery and Sunquist 1974).

The behavior and vocalizations of 2 acclimated animals have been described (Tirler 1966). An adult male clung to an adult female for several hours over the course of 2 days in captivity (Enders 1935). A 3-min agonistic interaction between 2 males included striking at each other with their forefeet and short, high-pitched vocalizations (Greene 1989).

GENETICS

Bradypus variegatus has a diploid number (2n) of 54–55 and a fundamental number (FN) of 56–58, with 4 metacentric or submetacentric and 48–50 acrocentric autosomal pairs; X is submetacentric and Y is metacentric (Jorge et al. 1985). XYY karyotypes are known from Manaus, Rio de Janeiro, and Teofilo Otoni (Jorge et al. 1985; Jorge and Pereira 2008). Populations of *B. variegatus* have low levels of genetic variability (Moraes et al. 2002). In 47 animals from 3 regions, a 362-base pair (bp) mitochondrial DNA (mtDNA) fragment from the control region yielded 6 haplotypes with 10 polymorphic sites (Moraes-Barros et al. 2006). Similarly, a 387-bp mtDNA fragment in 28 animals represented 6 phylogroups (Moraes-Barros et al. 2007). A 1,147-bp sequence from mitochondrial rDNA is available (Höss et al. 1996), as is the cytochrome-*b* sequence (Greenwood et al. 2001). The 16S mtDNA from 3 *B. variegatus* and 2 *B. torquatus* estimates a split between the lineages 7.7 million years ago, whereas the split between the 3 *B. variegatus* and 1 *B. tridactylus* is estimated at 0.4 million years ago (Barros et al. 2003).

CONSERVATION

Bradypus variegatus is in Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (2008) and is listed as Least Concern by the International Union for Conservation of Nature and Natural Resources because of its wide distribution, presumed large population, and occurrence in protected areas (Aguiar and da Fonseca 2008; Chiarello and Members of the Edentate Specialist Group 2008). With a wide distribution and high density, *B. variegatus* is generally not rare (Arita et al. 1990) although some populations are rare (Oliver and Santos 1991). *B. variegatus* is more vulnerable to habitat disturbance than other sloths (Moreno and Plese 2006). *B. variegatus* is used for meat, medicine, and crafts by indigenous Bolivians (Noss et al. 2008).

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