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Tamandua tetradactyla (Pilosa: Myrmecophagidae)

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Abstract: *Tamandua tetradactyla* (Linnaeus, 1758), commonly called the southern tamandua, is 1 of 2 extant, primarily arboreal anteaters. It is distributed over northern and central South America east of the Andes and uses a diverse array of habitats including Chaco, grasslands, and transitional forests. Its diet is primarily one of social ants and termites. It is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources due to its wide distribution. Primary threats to *T. tetradactyla* are fire, habitat loss, highway mortality, and hunting.

Key words: anteater, Edentata, edentate, South America, Xenarthra

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Tamandua Gray, 1825

Myrmecophaga Linnaeus, 1758:35. Part.
Myrmecophagam Pallas, 1766:64. Part.
Tamandua Gray, 1825:343. No species mentioned; inferred (Gray 1821:305) type species *Myrmecophaga tamandua* G. Cuvier, 1798 = *Tamandua tetradactyla* (Linnaeus, 1758), by tautonomy.
Tamanduas F. Cuvier, 1829:501. Unavailable name, French vernacular.
Uroleptes Wagler, 1830:36. Type species *Myrmecophaga tetradactyla* Linneaus, 1758, by monotypy.
Dryoryx Gloger, 1841:112. No type species mentioned.
Uropeltes Alston, 1880:191. Incorrect subsequent spelling of *Uroleptes* Wagler, 1830.
Dryorix Cabrera, 1958:203. Incorrect subsequent spelling of *Dryoryx* Gloger, 1841.
Uropeltess Cabrera, 1958:203. Incorrect subsequent spelling of *Uropeltes* Alston, 1880.

CONTEXT AND CONTENT. Order Pilosa, suborder Vermilingua, family Myrmecophagidae. Synonymy is modified from Gardner (2005, 2007).

Tamandua tetradactyla (Linnaeus, 1758)
Southern Tamandua

[*Myrmecophaga*] *tetradactyla* Linnaeus, 1758:35. Type locality "America meridionali," restricted to "Pernambuco (= Recife)," Pernambuco, Brazil, by Thomas (1911:133).
M[*yrmecophagam*]. *myosura* (Pallas, 1766:64). Type locality "Brasil."
Myrmecophaga tamandua G. Cuvier, 1798:143. No type locality; identified as "L'Amérique méridionale" by É. Geoffroy Saint-Hilaire (1803:217).
Myrmecophaga nigra É. Geoffroy Saint-Hilaire, 1803:217. Type locality "La Guyane?" (= French Guiana according to Cabrera (1958:205).
Myrmecophaga bivittata Desmarest, 1817:107. Type locality "Brésil."
Uroleptes tetradactyla: Wagler, 1830:36. Name combination.
[*Myrmecophaga*] *crispa* Rüppell, 1842:179. Type locality "Guiana."
Tamandua tetradactyla: Gray, 1843:191. First use of current name combination.

Fig. 1.—An adult *Tamandua tetradactyla* from the Buffalo Zoo, Buffalo, New York. Used with permission of the photographer, Michael Noonan.

M[*yrmecophaga*]. *longicaudata* Wagner, 1844:211. Type locality "auf dem nördlichen Theil des tropischen Südamericas;" restricted to "al interior de Surinam" by Cabrera (1958:203).

Uroleptes bivittatus: Fitzinger, 1860:395. Name combination.

Tamandua bivittata: Gray, 1865:384. Name combination.

Tamandua longicaudata: Gray, 1865:384. Name combination.

Tamandua brasiliensis Liais, 1872:360. Type locality "Brasil" (= Recife, Pernambuco, Brazil according to Gardner (2007:176)).

[*Tamandua bivittata*] var. 1. *Opisthomelas* Gray, 1873:27. Type locality "Brazils."

Tamandua tamandua: Jentink, 1888:215. Name combination, not *Myrmecophaga tamandua* G. Cuvier.

Myrmecophaga bivittata straminea Cope, 1889:132. Type locality "at São João [Rio Grande do Sul] or at Chapada [Mato Grosso];" restricted to Chapada, Mato Grosso, Brazil by Gardner (2007:176).

Tamandua tridactyla: Matschie, 1894:63. Name combination in reference to *Myrmecophaga tetradactyla* Linnaeus, not *Myrmecophaga tridactyla* Linnaeus.

[*Tamandua*] *longicauda* Trouessart, 1898:1121. Incorrect subsequent spelling of *Myrmecophaga longicaudata* J. A. Wagner.

Tamandua tetradactyla nigra: Menegaux, 1902:494. Name combination.

Tamandua tetradactyla chapadensis Allen, 1904:392. Type locality "Chapada, Matto Grosso, Brazil."

[*Tamandua tetradactyla*] *straminea*: Trouessart, 1905:803. Name combination.

Tamandua longicaudata var. *nigra* Beaux, 1908:417. Type locality "Brasilien (?);" preoccupied by *Myrmecophaga nigra* É. Geoffroy Saint-Hilaire (1803:217).

[*Tamandua tetradactyla*] *bivittata*: Osgood, 1910:24. Name combination.

[*Tamandua*] *opisthomelas*: Osgood, 1910:24. Name combination.

[*Tamandua*] *straminea*: Osgood, 1910:24. Name combination.

Tamandua tetradactyla quichua Thomas, 1927:371. Type locality "Yurac Yacu," San Martín, Peru.

T[*amandua*] *tetradactyla longicaudata*: Pittier and Tate, 1932:255. Name combination.

Tamandua tetradactyla kriegi Krumbiegel, 1940:171. Type locality "Zanja Moroti," Concepción, Paraguay.

Tamandua kriegi: Lönnberg, 1942:42. Name combination.

T[*amandua*]. *quichua*: Lönnberg, 1942:43. Name combination.

Tamandua longicaudata mexianae Cabrera, 1958:203. Nomen nudum.

Tamandua tetradactila Rodrigues et al. 2009:330. Unjustified emendation of *tetradactyla* Linneaus.

Tamandua tetradctyla Rodrigues et al. 2009:330. Unjustified emendation of *tetradactyla* Linneaus.

CONTEXT AND CONTENT. Context as for genus. Synonymy is modified from Gardner (2005, 2007). *T. tetradactyla* has 4 subspecies. The subspecies name *opisthomelas* cannot be assigned because the origin of the type specimen is unknown (Gardner 2007).

T. tetradactyla nigra (Geoffroy Saint-Hilaire, 1803:217). See above; *crispa* (Rüppell), *longicauda* (Trouessart), *longicaudata* (Wagner), *mexianae* Cabrera, and *tamandua* Jentnik are synonyms.

T. tetradactyla quichua Thomas, 1927:371. See above.

T. tetradactyla straminea (Cope, 1889:132). See above; *chapadensis* J. A. Allen, *kriegi* Krumbiegel, and *tridactyla* Matschie are synonyms.

T. tetradactyla tetradactyla (Linnaeus, 1758:35). See above; *bivittata* (Desmarest), *bivittatus* (Fitzinger), *brasiliensis* Liais, and *myosura* (Pallas) are synonyms.

NOMENCLATURAL NOTES. The generic name, *Tamandua*, is Portuguese (tamanduá) from Tupi (a language of peoples from the Amazon River valley) meaning ant-catcher, tacy = ant plus monduar = to catch (Morris 1969). The species name, *tetradactyla* meaning four-toed, is in comparison with the three-toed anteater (giant anteater—*Myrmecophaga tridactyla*). Other common names are ant bear (Glerean and Marques de Castro 1965); little anteater (Rodrigues et al. 2009); collared anteater, lesser anteater, southern tamandua, tamandua, ourmilier á collier, tamandou tétradactyle, tamandou á quatre doigts, brazo fuerte, hormiguero de collar, tamandúa de collar (Abba et al. 2008); collared tamandua, yellow tamandua (Gray 1865); caguaré, oso melero, tamanduá-mirim (Wetzel 1985); fourmilier a deux bandes (Desmarest 1817); golden anteater (Montgomery and Lubin 1977); kleinen Ameisenbären, oso hormiguero, yurumí (Krieg 1944); and tamanduá collete (Strong et al. 1926). *T. mexicana* was separated from *T. tetradactyla* in 1975, thus prior literature may in fact be describing *T. mexicana*.

DIAGNOSIS

The following cranial features distinguish *Tamandua* from other xenarthrans: a transpromontorial internal carotid artery, a carotid foramen in the basisphenoid, a frontal diploic vein foramen visible in the dorsal view, and a posterior opening of the posttemporal canal between the squamosal and the parietal (Wible and Gaudin 2004). *T. tetradactyla* and *T. mexicana* (the northern tamandua) can be distinguished geographically because they have disjunct ranges with *T. tetradactyla* in South America and *T. mexicana* in Central America. Morphologically *T. tetradactyla* has a longer ear (50–54 mm versus 40–46 mm in *T. mexicana*), usually 3 pairs of orbital foramina (4 is usual in *T. mexicana*), and an incomplete crescent on the posterior border of the infraorbital foramen (distinctly crescent-shaped in *T. mexicana*—Wetzel 1985).

GENERAL CHARACTERS

Pelage varies from pale tan to black and may or may not have the collar or vest (Fig. 1; Wetzel 1985). Mean external measurements (mm or kg; *SD*, range, *n*) for adults of mixed sex from Venezuela to Argentina were: total length, 1,105 (71, 955–1,300, 83); length of tail, 511 (58, 402–672, 83); length of hind foot, 100 (8, 80–118, 71); length of ear, 49.4 (4.6, 41.0–57.0, 53); body mass, 4.83 (0.90, 3.42–7.00, 41—Wetzel 1985). External measurements (mm) for 47 adults of mixed sex (*SD*, range) from French Guiana were: length of head and body, 561 (48, 345–650); length of tail, 569 (58, 370–670); height at shoulder, 301 (31, 250–380); length of hind foot, 96 (8, 78–108); length of head, 148 (13, 121–180); length of ear, 53 (5, 40–63); body mass (kg, $n = 43$), 4.80 (0.80, 3.28–6.20—Richard-Hansen et al. 1999). Mean measurements (mm; range) for 17 female and 5 male adults, respectively, from Bolivia and Brazil were: total length, 1,056.2 (945–1,160), 1,046.0 (960–1,205); length of head and body, 547.4 (432–601), 539.0 (460–635); length of tail, 508.8 (440–570), 507.0 (470–570); tail as percent of head and body, 94.3 (71.9–126.4), 94.9 (81.0–98.1—Lönnberg 1942). The external measurements (mm) of a young female were: length of head and body, 580; length of tail, 240; length of hind foot, 60; length of ear, 29 (Jenkins 1970). Body length of 22 animals of mixed sex was 550–820 mm with ear length of 26–40 mm (Krumbiegel 1940). Tail as a percent of head and body for 35 animals of mixed sex was 42–94 (Krumbiegel 1940). Six captive adults weighed 3–8.4 kg (Meritt 1975). No sexual dimorphism in size was present in 47 animals from French Guiana (Richard-Hansen et al. 1999).

Cranial (Fig. 2) measurement ranges (mm) of 5 *Tamandua tetradactyla straminea* from Brazil and 3 *T. t. nigra* from Venezuela, respectively, were: occipitonasal length, 121–133, 124–131; basal length without premaxillaries, 121–133, 121–128; antorbital breadth, 33–37, 33–35; interorbital breadth, 25–28, 23–26; width of braincase, 41–43, 39–43; width across bullae, 36–39, 35–36; length of nasals, 41–45, 45–48; width at front border of nasals, 7–9, 7–9; least width of nasals, 6–7, 7–9; width at posterior border of nasals, 11–15, 11–13 (Allen 1904). Mean and range (mm) of cranial measurements from 19 adults (13 females, 4 males, 2 unknown sex) from Bolivia and Brazil were: occipitonasal length, 121.6 (112–133); least rostral breadth in front, 13.1 (12–17); least interorbital width, 23.6 (21.5–27.5); mesial length of nasals, 40.2 (34–45); mesial length of frontals, 48.6 (39–58); mesial length of parietals, 21.5 (17–25); breadth across middle of auditory meatus, 33.9 (30–37); least palatal width below orbits, 15.3 (14–18); width of braincase, 40.2 (38–42—Lönnberg 1942). The skull of an unsexed Colombian animal had the following dimensions (mm): greatest length, 134; width of braincase, 45.9; greatest length of mandible, 112 (Tamsitt and Valdivieso 1964).

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult female *Tamandua tetradactyla* (American Museum of Natural History 96265) from Ilha do Taiuna, Rio Tocantins, Brazil. Greatest length of skull is 133.64 mm.

DISTRIBUTION

Tamandua tetradactyla (Fig. 3) occurs from sea level to 1,600 m east of the Andes from Colombia, Venezuela, Trinidad, and the Guianas (French Guiana, Guyana, and Suriname), south to northern Uruguay and northern Argentina (Gardner 2005; Wetzel 1985). Following Reeve (1942), the International Union for Conservation of Nature and Natural Resources Web site (Abba et al. 2008) suggests that *T. tetradactyla* also occurs in 2 disjunct pockets in Colombia, but these animals are *T. mexicana* (Gardner 2007).

FOSSIL RECORD

Tamandua is present in the Pleistocene in South America and Holocene in Central America (McDonald et al. 2008; Simpson 1945). Coprolites have been found in Brazil (Ferreira et al. 1989).

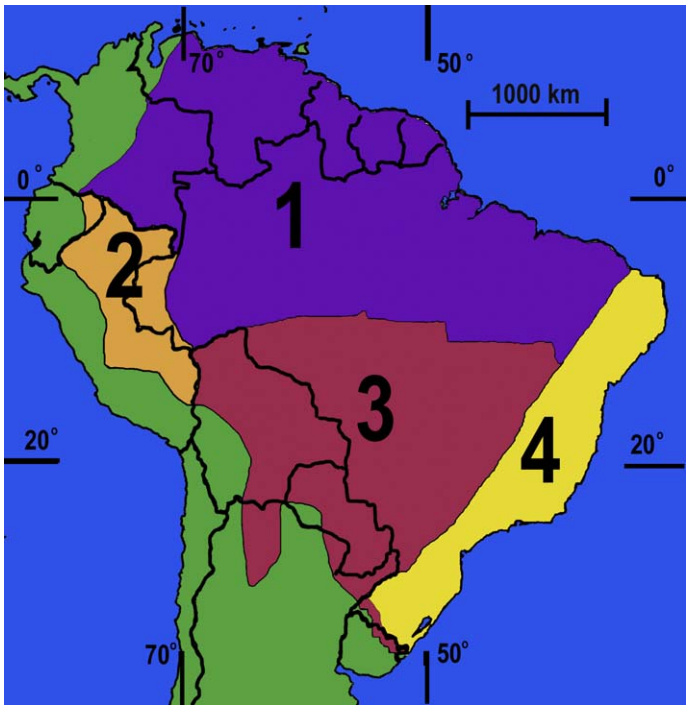

Fig. 3.—Geographic distribution of *Tamandua tetradactyla*. Subspecies are: 1, *T. nigra*; 2, *T. t. quichua*; 3, *T. t. straminea*; and 4, *T. t. tetradactyla*. Map modified from Gardner (2007).

FORM AND FUNCTION

Form.—*Tamandua tetradactyla* has no teeth (Barlow 1984). The muzzle curves downward "so that the nose is below the level of the eyes" and the mouth has a short gape (Pocock 1924:996). Ears are oval and stand away from the head, with fur outside but not inside (Menegaux 1902; Pocock 1924). A well-defined intertragal notch occurs between the tragus and an antitragal lobe (Pocock 1924). *T. tetradactyla* has a prehensile tail (Jenkins 1970).

Length of hair is 17–40 mm at middle of back and 25–90 mm at root of tail (Lönnberg 1942). Forelimb lengths (mm) for 5 animals with spinal lengths of 383–433 were 158.9–190.0 or 40.6–45.5% of spinal length (Krumbiegel 1940). Limb and torso measurements (mm) from a melanistic animal 590 in head and body length were: neck, 160; front leg, 180; thigh, 210; hind leg, 125; chest, 310; venter, 410 (Menegaux 1902). No underfur was present on this melanistic animal (Menegaux 1902).

Of the 4 digits on the forefoot, 1 is longer and stouter with a large, compressed, falcate claw (Pocock 1924). The outside of the forefoot is protected by a thick, naked, granular pad that supports a portion of the animal's mass during locomotion on the ground (Pocock 1924). The hind foot has 5 short digits, 4 of equal size and 1 shorter, all with moderately long, curved, sharp claws (Pocock 1924). The sole is naked, narrower at the heel, and about twice as long as broad (Pocock 1924). Details of the leg and foot muscles (gastrocnemius medialis, gastrocnemius lateralis, soleus, popliteus, flexor tibialis, flexor fibularis, tibialis posterior, flexor digitorum brevis, quadratus plantae, and lumbricales) are available (Vuori 1931). The carpal bones are figured in Yalden (1972).

The skull opening for the eustachian tube is variable in shape (Patterson et al. 1992). The internal carotid artery enters the tympanic cavity through a posterior carotid foramen, crosses the promontory in a sulcus, then exits anteriorly through the promontory foramen (Bugge 1979). The external carotid artery system takes over the blood supply of the dura (Bugge 1979). The horizontal process of the palatine has 6 or so anteriorly directed foramina (Wible and Gaudin 2004). The caudal palatine is posterior to the sphenopalatine foramina, and they both occur in a palatine depression but are separated by a septum (Wible and Gaudin 2004). The perilymphatic ducts enter the petrosal bones via the cochlear canaliculus in the rostal edge of the jugular foramen (Wible and Gaudin 2004). A craniopharyngeal canal, piriform fenestra, and ventral condyloid foramina are absent (Wible and Gaudin 2004). Tiny dorsal condyloid foramina are present (Wible and Gaudin 2004). One ethmoidal foramen occurs between the frontal and the orbitosphenoid and 3 formina occur above the supraorbital margin of the frontal (Wible ane Gaudin 2004). The foramen magnum is formed by the basioccipital, the paired exoccipitals, and the supraoccipital (Wible and Gaudin 2004). A single hypoglossal foramen is posterolateral to, and level with, the jugular foramen within the exoccipital (Wible and Gaudin 2004). An elongate (half the length of the premaxilla) incisive foramen is mostly within the premaxilla but the maxilla forms the posterior border (Wible and Gaudin 2004). The infraorbital canal is primarily in the maxilla but the palatine and lachrymal contribute (Wible and Gaudin 2004). The jugular foramen occurs between the exoccipital and the petrosal (Wible and Gaudin 2004). Two lacrimal foramina are ventrally directed (Wible and Gaudin 2004). The maxilla has dozens of tiny and 1 small foramina (Wible and Gaudin 2004). The mandibular foramen is anterior to the coronoid process (Wible and Gaudin 2004). The musculotubal canal is in the medial bullar wall (Wible and Gaudin 2004). The optic canalis is between the orbitosphenoid and the palatine (Wible and Gaudin 2004).

The mean cochlear height is 4.7 mm and the width at the base of the cochlea is 3,000 μm (Pye 1979). The width does not decrease linearly from the base to the apex but is broadest at the 4th half-turn (Pye 1979).

The tongue has 2 vallate papillae (Sonntag 1923). Facial muscles include the platysma myoides, musculus auriculo-occipitalis, m. orbicularis auriculae, m. helicis, m. orbito-auricularis, m. auricularis superior, m. orbicularis oculi, m. levator labii superioris alaeque nasi, m. levator labii inferioris, m. zygomatico-labialis, m. sphincter colli, m. orbicularis oris, m. nasalis, m. maxillo-labialis, m. buccinator, and m. mandibulo-auricularis (Uekermann 1912).

Facial nerves include nervus facialis, ramus maxillaris, ramus buccinatorius, and ramus mandibularis (Uekermann 1912). In the sublingual gland the secretory endpieces and intralobular ducts are surrounded by cholinergic nerve fibers (Rossoni et al. 1981). Dorsal, lateral, ventral, and mesial surfaces of the brain are figured in Elliot Smith (1899). A female over 6 years of age, with a body mass of 7.0 kg, had a brain mass of 30 g (Sherwood et al. 2009). Estimated volumes of brain regions are (mm^3): medulla, 1,287.84; cerebellum, 3,420.48; mesencephalon, 720.00; diencephalon, 1,439.52; striatum, 1,505.76; septum, 94.56; amygdala, 216.48; paleocortex, 1,189.92; hippocampus, 1,070.40; schizocortex, 425.28; isocortex, 8,075.52 (Reep et al. 2007). The motor region is located at the posterior part of the brain and reaches to the occipital region (Dias 1945). The claustrum is fairly well developed. In horizontal sections, the claustrum is broader anteriorly than posteriorly. It rises to the head of the caudate nucleus and extends to the most anterior portion of the thalamus (Kaelber and Ingram 1962). The nuclear configuration of the diencephalon is detailed in 25 photomicrographs (Kaelber 1966). In the neocortex 4.33% of interneurons are calbindin immunoreactive, 2.99% are calrectin immunoreactive, 7.19% are parvalbumin immunoreactive, and 3.12% are neuropeptide Y immunoreactive (Sherwood et al. 2009).

The pituitary gland lies in a troughlike depression of the sphenoid bone with a thick sheath of deeply pigmented dura (Wislocki 1938). The pars intermedia is extensive and complex (Wislocki 1938).

The heart is oblong, with a rounded apex formed by the left ventricle. The long axis of the heart deviates from the midline by 30–35° (Rowlatt 1980). The right atria is larger than the left and is triangular, whereas the left atrium is rectangular with a narrow neck and crenated edge (Rowlatt 1980). Epicardial fat, if present, is deposited along the main coronary vessels (Rowlatt 1980). The hearts of *T. tetradactyla* with a mean body mass of 2,646 g had the following measurements, mean ± *SD* in cm or g (*n*): mass (18), 10.0 ± 6.4; length (12), 4.6 ± 0.78; breadth (10), 3.2 ± 0.76; depth (11), 2.6 ± 0.51; right ventricle mass (18), 1.6 ± 1.1; left ventricle and septum weight (18), 6.8 ± 4.6; right ventricle thickness of sinus (18), 0.16 ± 0.05; right ventricle thickness of conus (18), 0.14 ± 0.03; left ventricle thickness (18), 0.44 ± 0.14; right inflow tract length (18), 2.4 ± 0.51; right outflow tract length (18), 2.4 ± 0.78; left inflow tract length (18), 2.5 ± 0.58; left outflow tract length (18), 2.6 ± 0.54 (Rowlatt 1980).

Ventral musculature of an adult female is figured in Zeiger (1925). The foramen esophagicum of the diaphragm is limited by the left pillar (Locchi 1940).

Anteroposteriorly expanded ribs occur in *T. tetradactyla*. The posterior flanges of the ribs are moderately developed and anterior flanges are lacking. An incipient secondary expansion occurs at the distal end of the ribs (Jenkins 1970). The external intercostal muscle fibers attach along the posterior margin of each rib and along the anterolateral surface of the next posterior rib. The external intercostal is triangular in cross section (Jenkins 1970). "The right lung has dorsal, lateral, medial, and ventral bronchiole systems whereas the left lung lacks the ventral bronchiole system" (Nakakuki 1996:1). *T. tetradactyla* has 17 or 18 thoracic vertebrae and 2 or 3 lumbar vertebrae (Jenkins 1970).

Paneth cells of the small intestine are numerous and larger than intestinal and goblet cells (Glerean and Marques de Castro 1965). They occur from the gastroduodenal transition to the ileo-caecal passage (Marques de Castro et al. 1959).

Females have a simplex uterus and males have abdominal testes (Hayssen et al. 1993). A pregnant, simplex uterus measured 8 by 13 cm and had a whitish discoidal plaque. The hemochorial placenta is discoidal and lobulated (Lash et al. 2009). The anogenital areas of both sexes are similar in profile (Pocock 1924). The simple, undivided clitoris of a young female was covered by a thick pair of hairy valvular labia (Pocock 1924). One female had 2 pairs of pectoral mammae (Enders 1930). The short penis of males has a small preputial orifice (Pocock 1924).

Function.—The carpus can be hyperextended up to 80° with flexion to 60° (Yalden 1972). Rectal temperature was 30°C (Wislocki 1933), 33.7–34.6°C (Wislocki and Enders 1935), or 35°C (Enders and Davis 1936). Two zoo-acclimatized, postabsorptive *Tamandua tetradactyla*, with an average mass of 3.50 kg, had a basal rate of metabolism of 0.253 ml O_2 g^{-1} h^{-1}, a minimal thermal conductance of 0.022 ml O_2 g^{-1} h^{-1} $°C^{-1}$, a body temperature of 35.0°C, and a lower limit of thermoneutrality at 23.0°C (McNab 1984). Hematologic values from a moribund *T. tetradactyla* were: red blood cells, 2.8 × 10^6 mm^3; hemoglobin concentration, 11.3%; hematocrit, 37.0%; mean corpuscle volume, 132 μm^3; reticulocytes, 0.167%; mean diameter of red blood cells, 8.947 μm; sedimentation rate, 20.25 mm/60 min; leukocytes, 3.7 × $10^3/mm^3$ of which J neutrophils, 1%; stab neutrophils, 22%; segmented neutrophils, 32%; eosinophils, 3%; lymphocytes, 39%; monocytes, 3%; and 37 erythroblasts/ml (Rosenfeld and Hoehne 1953). Feces of *T. tetradactyla* have cholesterol and 9 bile acids including lithocholic acid and deoxicolic acid but not chenodeoxycholic, cholic, or dehydrocholic acids (Araujo et al. 2007). On a dry matter basis, the stomach contents contained 4.58 kcal/g gross energy, 50.9% crude protein, and 11.2% fat (Oyarzun et al. 1996). Semen (10–20 μl) from 1 *T. tetradactyla* averaged 37.5 sperm cells with normal morphology that had an approximate head length of 14 μm, a width of 6 μm, and a tail length of 140 μm (Hay et al. 1994).

ONTOGENY AND REPRODUCTION

Litter size is 1 (Hayssen et al. 1993). The estrous cycles of 1 female averaged 42.5 days, range 38–46 days. Luteal

phase was 21.3 days. A 2nd female had a 7- to 12-day bloody vaginal discharge every 40 days (Hay et al. 1994). Gestation may be 130–190 days (Hayssen et al. 1993). Pelage color does not differ between immature and adult animals, but young animals have longer dorsal hair (Wetzel 1975).

ECOLOGY

Tamandua tetradactyla is common and uses diverse habitats (Chaco, grasslands, and transitional forests—Mares et al. 1996). In Suriname, *T. tetradactyla* accounts for 2.2% of the nonvolant, terrestrial mammalian biomass (Walsh and Gannon 1967 [not seen, cited in Eisenberg and Thorington 1973: table 1]). In Venezuela animals were caught in trees (64%) and on the ground (36%); most captures were in dry areas (64%) rather than moist areas or near streams (36%); the habitat distribution was: thorn forest, 44%; evergreen forest, 30%; deciduous forest, 5%; and savanna and cropland, 21%; and 83% were caught below 500 m (Handley 1976). In the Chaco of Paraguay, *T. tetradactyla* was more common in moister areas (Meritt 2008). In captivity, a *T. tetradactlya* lived 9.5 years (Jones 1982).

In Brazil, mean home-range size of 7 animals was 100 ha (Rodrigues et al. 2008), whereas in Venezuela, mean home-range size was 375 ha and mean daily movement was 3,000 m (Montgomery 1985; Montgomery and Lubin 1977). Home ranges of *T. tetradactyla* overlap those of *Myrmecophaga tridactyla* in Venezuela but are 20 times smaller (Montgomery 1985). Dietary overlap also occurs because *T. tetradactyla* and *M. tridactyla* eat the same species of ants (Montgomery 1985); however *Myrmecophaga* does not climb (Rodrigues et al. 2008).

Diet is social ants and termites (Wetzel 1985) at about a 50:50 ratio; mimics of social insects also are ingested (Montgomery 1985), along with occasional fruit (Meritt 1976). Detritus is not present in stomach contents (Montgomery 1985). All 21 samples of stomach contents and 9 fecal samples contained *Nasutitermes* termites (Lubin and Montgomery 1981). A single sample of stomach contents contained 69% ants, 22% termite workers, and 9% termite soldiers. A 2nd sample contained 77% termite workers, 18% soldiers, 5% ants, and a substantial quantity of nest material (Oyarzun et al. 1996). *T. tetradactyla* eats fewer termites during the wet season (Montgomery 1985). *T. tetradactyla* in Venezuela fed on a nest containing *Caponotus* ants for 1.2 min and a nest containing termite nymphs for 24 min (Lubin and Montgomery 1981). Of 5 *T. tetradactyla*, 1 ate army ants (*Dorylinae*—Montgomery and Lubin 1977). During a series of interrupted feeding bouts totalling 63 min, *T. tetradactyla* consumed ants 72% of the time, termites 20% of the time, and unknown prey 8% of the time (Montgomery and Lubin 1977). Termites (*Nasutitermes*) in nests are not preferred but are eaten when found in wood (Montgomery and Lubin 1977).

Ectoparasites include ticks: *Amblyomma cajennense* (Labruna et al. 2002), *A. calcaratum* (Martins and Guglielmone 1995), *A. göldii*, *A. maculatum*, *A. nodosum* (Amorim and Serra-Freire 1994; Aragão 1936; Bitencourth et al. 2007; Dantas-Torres et al. 2010; Labruna et al. 2002), and *A. rotundatum* (Barros and Baggio 1992); mites: *Psoralges libertus* (Fain 1965); and fleas: *Pulex irritans* and *Tunga bondari* (Hopkins and Rothschild 1953). *Staphylococcus* and *Streptococcus* bacteria were found in purulent skin (Diniz et al. 1997).

Endoparasites include acanthocephalans: *Gigantorhynchus echinodiscus* (Strong et al. 1926; Travassos 1917) and *G. ungriai* (Antonio 1958); chiggers: *Rhinibius tamandua* (Brennan and Yunker 1969); coccidians: *Cryptosporidium* (da Silva et al. 2008), *Eimeria corticulata*, *E. marajoensis*, and *E. tamanduae* (Lainson 1968; Lainson and Shaw 1990, 1991); hemoflagellates: *Leishmania amazonensis* (Mimori et al. 1989), *L. braziliensis panamensis*, *Trypanosoma cruzi*, *T. legeri* (Deane 1967; Lianson 1965; Shaw 1985; Sousa 1972), and *T. rangeli* (Dereure et al. 2001; Miles et al. 1983); nematodes: *Aspidodera lacombeae* (Vicente 1964), *Bradypostrongylus panamensis*, *B. inflatus*, *Filicapitis longicollis*, *Graphidiops major*, *G. ruschii* (Travassos 1949), *Caenostrongylus splendidus*, *Fontesia fontesi*, *F. secunda*, *Graphidiops costalimai*, and *G. inaequalis* (Lent and Teixeira de Freitas 1938); and protozoans: *Trichomonas aragaoi* (da Cunha and Muniz 1927). Unidentified round worms were found in the stomach of 1 animal (Enders 1930) and *Ascaris* occurs in feces (Meritt 1975).

Seven animals from Nicaragua were negative for leptospirosis (Clark et al. 1966). Of 32 animals, 9 were positive for *Salmonella* (Loureiro 1985). Two of 14 Panamanian animals were positive for the St. Louis encephalitis virus but none of the animals was positive for the Bussaquara, Illhéus, Mayaro, or yellow fever viruses (Seymour et al. 1983). *T. tetradactyla* can be experimentally infected with *Schistosoma mansoni* (Barbosa et al. 1958). The species is susceptible to infection by the cowpox virus after 5 days of incubation (Moreira 1956).

Predators of *T. tetradactyla* include harpy eagles (*Harpia harpyja*—Rettig 1978). Indigenous peoples hunt *T. tetradactyla* for diverse purposes (Noss et al. 2008), but its meat was not for sale in the Chaco of Paraguay (Meritt 2008). The Kayapó, a group of seminomadic hunter–gatherers of southeastern Amazonia, killed 1 *T. tetradactyla* between November 1994 and June 1996 (Peres and Nascimento 2006). Body parts are sold for diverse purposes in the La Pampa market in the city of Cochabamba, Bolivia (Romero-Muñoz and Pérez-Zubieta 2008).

HUSBANDRY

Tamandua tetradactyla can be immobilized for the attachment of radiocollars with CI-744 at 48 mg/kg (Montgomery 1985). For radiography and blood sampling,

T. tetradactyla can be anesthetized with ketamine (11 mg/kg) and xylazine (0.8 mg/kg) intramuscularly (Crawshaw and Oyarzun 1996). A combination of 20 mg/kg ketamine hydrochloride and 1 mg/kg xylazine hydrochloride immobilizes the animals for longer than 30–40 min (Fournier-Chambrillon et al. 1997).

Captive enclosures need abundant branches to allow climbing, soil flooring, and heated shelters in cold areas (Superina et al. 2008). Captive diets include water, canned milk, multivitamins, protein powder, meat, and mink chow in a soupy gruel (Meritt 1970, 1975). The recommended levels of vitamin A and vitamin D in the diet are <8,000 IU/ kg dry matter and <800 IU/ kg, respectively. The level of calcium should be 1.0% or less (Crawshaw and Oyarzun 1996). The diet and feeding schedules of adult and juvenile *T. tetradactyla* are available (Meritt 1976).

In captivity, *T. tetradactyla* is prone to developing hyperostosis of the axial skeleton (Crawshaw and Oyarzun 1996). Captive animals also are susceptible to taurine deficiency, which can be reversed by amino acid supplementation (Luppi et al. 2008). The number of *Cryptosporidium* oocysts in *T. tetradactyla* can be significantly reduced after treatment with trymetroprim–sulphametoxazol (da Silva et al. 2008). A case study of the amputation of the left pelvic member is available (Rodrigues et al. 2009). The claws of *T. tetradactyla* can inflict harmful wounds on humans (Dao 1968).

BEHAVIOR

Tamandua tetradactyla is nocturnal to diurnal–crepuscular (Montgomery 1985; Wetzel 1985) but captive animals may be active during the day (Krieg 1944; Meritt 1975). *T. tetradactyla* sleeps in trees (Montgomery 1985) or in burrows of *Euphractus sexcinctus* (six-banded armadillo—Rodrigues et al. 2008) during the day. When active, *T. tetradactyla* is scansorial and uses branches rather than lianas for moving and foraging (Montgomery 1985). It feeds from both small and large nests of ants or termites both on the ground and in tress (Montgomery 1985). Prey are located by scent (Montgomery 1985). While feeding on *Nasutitermes* termites, *T. tetradactyla* brushes its nose and ears and scratches repeatedly (Montgomery and Lubin 1977). Captive animals urinate daily and defecate every 2–6 days (Meritt 1975).

During an activity period between 1903 and 0230 h, 1 female *T. tetradactyla* in Venezuela rested 94 min, moved 290 min (over 1,927 m), and fed for 63 min. Gross movement rate was 6.4 m/min. The longest feeding bout was 5 min, and 82% of feeding bouts were 1 min or less (Montgomery and Lubin 1977). *T. tetradactyla* often uses the same paths on different days (Montgomery and Lubin 1977:119).

Plantigrade locomotion involves placing the outside of the front feet in contact with the substrate so that the large claw will not injure the foot (Pocock 1924). In walking, the heel of the hind foot is raised slightly (Pocock 1924). *T. tetradactyla* exhibits a bipedal position as a means of defense (Jenkins 1970).

GENETICS

Tamandua tetradactyla has a diploid number (2n) of 54 chromosomes and a fundamental number (FN) of 104. The karyotype contains 16 metacentric and 10 submetacentric autosomal pairs; X is metacentric and Y is acrocentric (Hsu 1965; Jorge et al. 1985; Jorge and Pereira 2008; Pereira et al. 2004; Svartman et al. 2006). The karyotype of a Brazilian specimen with 56 chromosomes has been described (Pereira et al. 2004). C- and G-banded karyotypes are available (Dobigny et al. 2005; Jorge et al. 1977).

An analysis of the 16S mitochondrial DNA sequence estimates a split between *T. tetradactyla* and *Myrmycophaga tridactyla* at 12.9 million years ago (Barros et al. 2003). The sequence of a partial 16S ribosomal RNA is available (Höss et al. 1996). The αA-crystallin of a putative *T. tetradactyla* (Van Dijk et al. 1999) is probably for *T. mexicana* (de Jong et al. 1984).

CONSERVATION

Tamandua tetradactyla is not in Convention on International Trade in Endangered Species of Wild Fauna and Flora (2009) and is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources (Abba et al. 2008), but is protected in Argentina (Mares et al. 1996). It has a low density over a wide distribution (Arita et al. 1990). In 1983, 1 *T. tetradactyla* was introduced on a land-bridge island, Anchieta Island, Brazil. In 2005, a follow-up study found 3 *T. tetradactyla* on the island, 2 of which were dead (Bovendorp and Galetti 2007). Of 8 translocated *T. tetradactyla*, all but 1 remained within 2.17 km of the release sites, and all appeared to thrive (Rodrigues et al. 2001). Primary threats are fire, habitat loss, highway mortality, and hunting (Aguiar and da Fonseca 2008). Along a 572-km stretch of road in Venezuala roadkills are estimated to be 129 *T. tetradactyla* during the rainy season (Pinowski 2005).

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