EMERGENCY PETITION TO LIST THE PYGMY THREE-TOED SLOTH

(*Bradypus pygmaeus*)

AS ENDANGERED UNDER THE ENDANGERED SPECIES ACT

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Petitioner
Animal Welfare Institute

Submitted to:	U.S. Fish and Wildlife Service, Washington D.C. and International Affairs
Submitted by:	Animal Welfare Institute
Date:	November 15, 2013

EXECUTIVE SUMMARY

The Animal Welfare Institute (AWI) formally requests that the United States Fish and Wildlife Service (USFWS) list the pygmy three-toed sloth (*Bradypus pygmaeus*) as endangered under the federal Endangered Species Act (ESA) on an emergency basis. Alternatively, if the USFWS determines that an emergency listing is not warranted in this case, AWI requests that it process this listing petition pursuant to the standard timetable as required under the ESA.

Bradypus pygmaeus has been listed as Critically Endangered on the International Union for Conservation of Nature (IUCN) red list since 2006. This species is confined to Isla Escudo de Veraguas (Isla Escudo), a 5 km² island on the Mosquito Gulf coast of Panama. On that island, pygmy sloths have nearly exclusively been found in red mangrove forests. These forests comprise 1.67 hectares (4 acres) or 0.024% of the total island area. The IUCN reports that the pygmy sloth population is less than 500 individuals but the most recent surveys on Isla Escudo detected only 79 individuals located in five isolated patches of red mangrove forest, with no single population greater than 20 individuals.

Ongoing and pervasive threats to the pygmy sloth and its habitat include:

- Degradation and destruction of mangrove forests, further reducing the species' habitat and, hence, its area of occupancy.
- Opportunistic hunting of pygmy sloths for food by indigenous and local visitors to Isla Escudo.
- The cumulative impacts of habitat loss, degradation and fragmentation, and hunting further isolating the existing pygmy sloth populations on Isla Escudo.
- Increased genetic inbreeding and loss of genetic diversity due to existing low level of genetic heterozygosity, habitat loss, and population isolation.
- Minimal protection under Panama law for pygmy sloths or their habitat despite Isla Escudo being designated an Indigenous Reserve.

The magnitude and frequency of occurrence of threats to the species are rapidly increasing, primarily due to an increase in popularity of sloths in popular culture. This has contributed to an increase in the exploitation, including capture, of wild sloths for sale as pets or for use as tourist photo props (see, e.g., http://abcnews.go.com/International/hottest-selling-animal-colombias-illegal-exotic-pet-trade/story?id=19172620).

In addition, representatives of the Dallas World Aquarium (DWA) recently captured eight individuals from Isla Escudo with the intent to export six of these pygmy sloths into the United States (the other two animals were destined to remain in Panama for placement at Zoologico del Istmo in Colón, Panama). This export attempt was thwarted at the last minute by citizens that physically blocked DWA personnel from exporting the pygmy sloths from Panama. While those individual sloths were returned to the wild, at least two may have died prior to or immediately after release potentially as a result of the consequences of their prior capture and confinement.

Furthermore, it is unknown what long term damage this ill-fated capture and export plan could have done to the population if it were not stopped. Depending on the actual size of the population, the removal from the wild of eight pygmy sloths represented a potential loss of approximately 2%-10% of the species' global population. The DWA's capture, export, and captivity plans were not subject to review or endorsed by sloth scientists, did not adequately consider how to ensure survival of the animals in captivity, and failed to contemplate how it would impact the wild population of this species including the species genetic diversity

Due to the ongoing, escalating, and cumulative threats to this population, without immediate listing under the ESA, there will be virtually no safeguards to prevent the DWA or other entities from recklessly capturing pygmy sloths, importing them into the United States, and putting the remaining wild population on a nearly certain path to extinction.

NOTICE OF PETITION

Animal Welfare Institute
900 Pennsylvania Avenue SE
Washington, DC 20003
Phone: (202) 446-2148
Fax: (202) 446-2131
E-mail: tara@awionline.org

Petitioner Animal Welfare Institute formally requests that the U.S. Fish and Wildlife Service classify the pygmy three-toed sloth as an endangered species under the federal Endangered Species Act (ESA), 16 U.S.C. §§ 1531-1544. Petitioner further requests that the USFWS review whether the species warrants emergency listing, and if so, that the USFWS use its authorities to list the species as endangered on an emergency basis. The petition is filed pursuant to the authorities of 5 U.S.C. §553(e), 16 U.S.C. §1533(b)(7) and 50 C.F.R. part 424.14.

The U.S. Fish and Wildlife Service has the authority to promulgate an emergency listing rule for any species when an emergency exists that poses a significant risk to the species, under 16 U.S.C. §1533(b)(7). Such a rule shall take effect immediately upon publication in the Federal Register, and shall be effective for a maximum of 240 days. This petition sets in motion a specific administrative process as defined by §1533(b)(3) and 50 C.F.R. §424.14(b), placing mandatory response requirements on the U.S. Fish and Wildlife Service.

The pygmy three-toed sloth is currently listed as Critically Endangered on the IUCN Red List, but it has no designation under the ESA and is not presently listed under the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES). The critically low population size, highly restricted range and area of occupancy, continuing decline in habitat, and ongoing threat of capture for export demonstrate that the species should be listed as endangered. Evidence to support the listing presented in this petition includes: recent evaluations of the status of the pygmy three-toed sloths by researchers, analysis provided by the IUCN, and information published in peer-reviewed literature

Petitioner Animal Welfare Institute is a non-profit, charitable organization that seeks to alleviate the suffering inflicted on animals by people. The Animal Welfare Institute works to minimize the impacts of all human actions detrimental to wildlife, including the commercial trade that threatens endangered species and destruction of native habitat.

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VI. APPENDIX

I. NATURAL HISTORY AND STATUS OF THE PYGMY THREE-TOED SLOTH (*Bradypus pygmaeus*)

A. NATURAL HISTORY

1. Description

Pygmy sloths are approximately 40 percent smaller in body mass and 15 percent shorter in body length compared to the brown-throated sloths (*Bradypus variegatus*) found on the mainland in Panama. Adult pygmy sloths weigh 2.5 to 3.5 kilograms (5.5 to 7.7 lb) and measure 48 to 53 centimeters (19 to 21 in) including a tail length of 4.5 to 6.0 centimeters (1.8 to 2.4 in) (Anderson and Handley, 2002). Pygmy sloths are smaller than any other studied population of *Bradypus variegatus* in Central or South America.

Their external auditory meatus (ear canal) is conspicuously large for such a diminutive sloth. Discrete cranial characteristics separate pygmy sloths from all other species of the genus. Pygmy sloths differ from populations of brown-throated sloth in having external carotid foramen through which the carotid artery normally passes; a small stylomastoid foramen at the posterior external base of the auditory bulla; a concave ventral edge of the stylohyoid; and slender and strongly falcate coronoid process of the mandible (Anderson and Handley 2001). Pygmy sloths have eighteen teeth, ten in the upper jaw and eight in the lower. Two of the teeth in each jaw are incisor-like, although those in the upper jaw are small or may be absent. The incisor-like teeth in the lower jaw are compressed anteroposteriorly. Many of the features found in pygmy sloths are thought to be indicative of a relatively rapid evolution of a new species in an isolated, island habitat. Pygmy sloths are also 12–16 percent smaller in cranial dimensions compared to the mainland species (length: 6.75 to 7.22 centimeters (2.66 to 2.84 in); width: 3.88 to 4.57 centimeters (1.53 to 1.80 in) (Anderson and Handley 2002).

Externally, pygmy sloth may be separated from maned three-toed sloth (*B. torquatus*) by the lack of a black dorsal mane originating at the nape and by the presence of short, tan facial pelage with a black stripe lateral to the eye; and in adult males by possessing a dorsal speculum. Pygmy sloths may be separated from pale-throated sloths (*B. tridactylus*) by their tan facial and gular pelage and dark stripe lateral to the eye. The pygmy sloth differs externally from brown-throated sloth (*B. variegates*) by long hair projecting over the brow. This characteristic provoked C.O. Handley to refer to the pygmy sloth in the field as the “monk sloth” (Anderson and Handley 2001). No other sloth of the Bocas islands is hooded.

2. Taxonomy

Sloths belong to the Neotropical order Xenarthra. Two distantly related genera, *Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths) are in existence. *B. pygmaeus* is a relatively recently recognized species of *Bradypus* known only from Isla

Escudo de Veraguas, Panama (Anderson and Handley 2001), bringing the number of species known in the genus to four. This new species, *B. pygmaeus*, is closely related to *B. variegatus*, which is widespread in both Central and South America (See Figure 1). The other two species in the genus, *B. tridactylus* and *B. torquatus*, are restricted to South America (Anderson and Handley 2002).

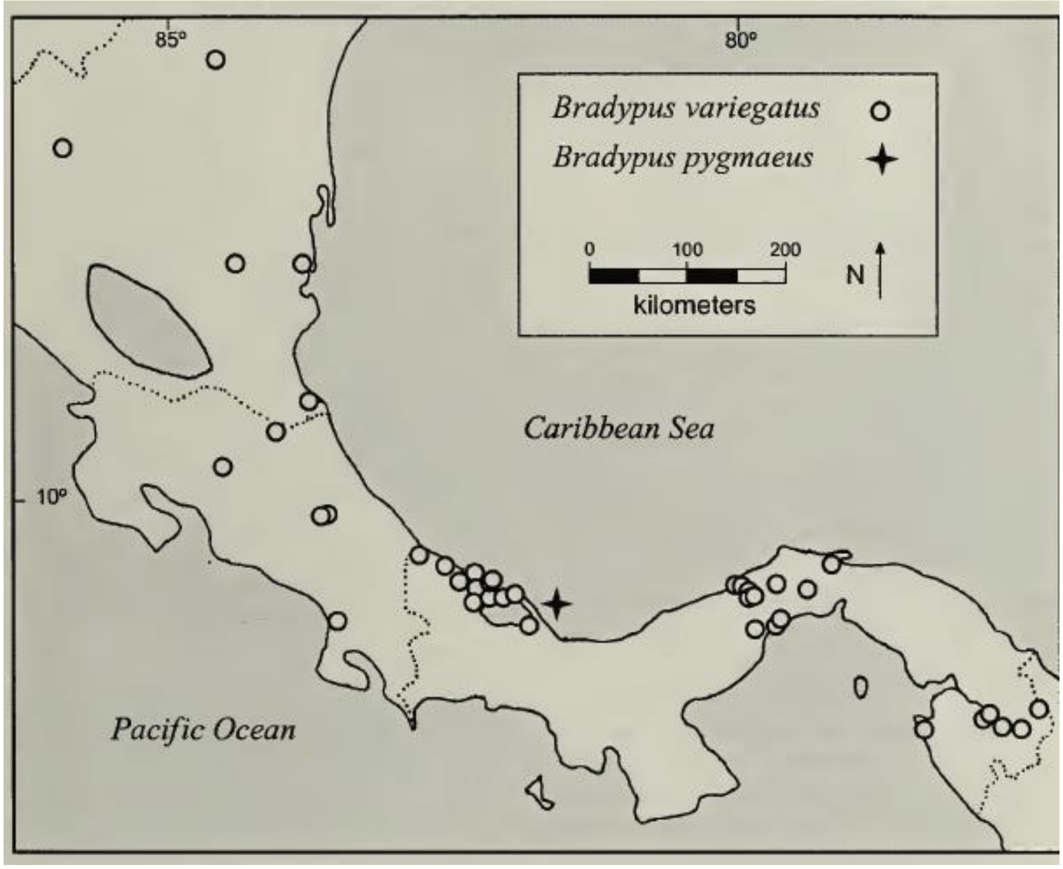

Figure 1. Distribution of brown-throated sloth (B. variegatus) and pygmy sloth (B. pygmaeus). From Anderson and Handley (2001).

3. Distribution

B. pygmaeus is known only from Isla Escudo, which is one of the islands within the Bocas del Toro archipelago. Bocas del Toro is a province of Panama. It consists of the mainland and nine main islands and a number of secondary islands including Isla Escudo. Sloths on the geologically younger islands are thought to remain conspecific with mainland populations of *B. variegatus* (Anderson and Handley 2001, 2002). On Isla Escudo – the oldest and most remote island of the archipelago – however, the three-toed sloth has differentiated to the species level, and is described as *B. pygmaeus.* Isla Escudo has an area of approximately 4.3 km² and is about 17.6 km from the mainland of Panama. The total amount of red mangrove habitat, the primary habitat in which pygmy sloths are known to occur, is estimated to be 106,699 m² which is .024% of the total island area. (Figure 2) (Kaviar 2012).

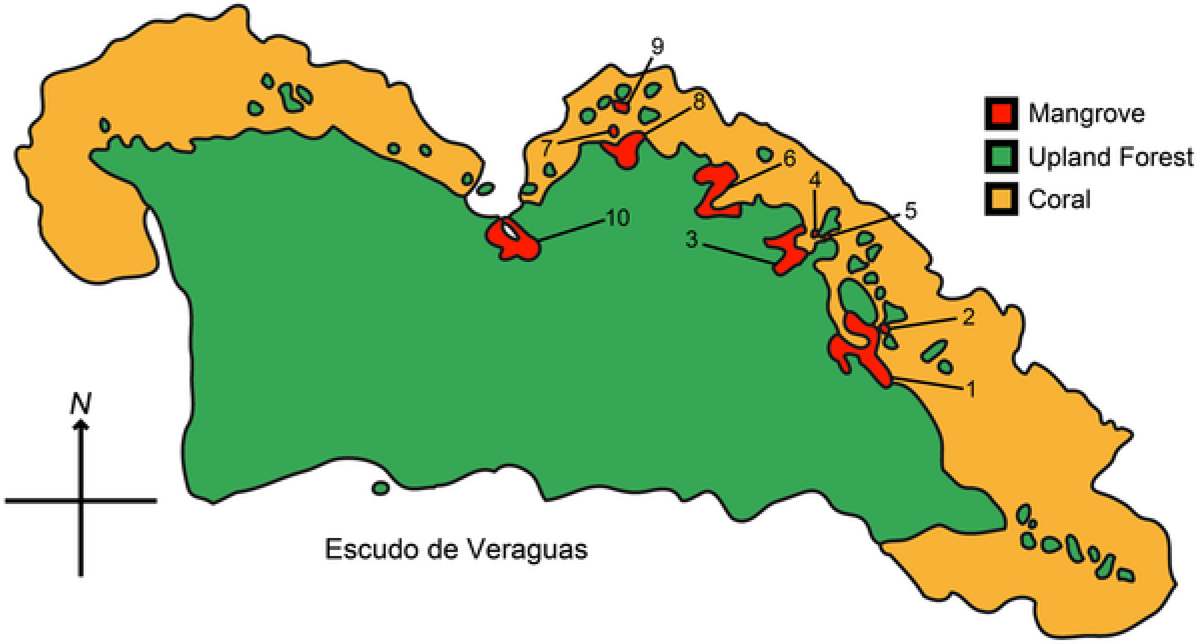

Figure 1. Map of all mangrove thicket locations found on Isla Escudo de Veraguas based on GPS data, showing thicket ID numbers. From Kaviar et al. (2012) (available at http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0049854).

4. Habitat Requirements

B. pygmaeus has been primarily recorded in the red mangrove forests surrounding the island (Anderson, Moraes-Barros, and Voirin 2011). The species has not been recorded in upland forest patches on the island (Anderson, Moraes-Barros, and Voirin 2011). They primarily, if not exclusively, feed on mangrove leaves (Anderson, Moraes-Barros, and Voirin 2011; Kaviar 2012; Superina et al. 2010). Because pygmy three-toed sloth locomotion is primarily arboreal, individual animals and ultimately the entire remaining population is at increased risk when remaining mangrove forests are logged and habitat is degraded and fragmented (Hayssen 2008).

5. Life History

The lifespan or longevity for *B. pygmaeus* has not been well studied. Other species of sloths have been known to live 30 to 40 years (Moraes-Barros, Silva, and Morgante 2011).

Little is known about the reproductive habits of *B. pygmaeus*. However, in other *Bradypus* species, there is evidence that males compete for access to mating opportunities with receptive females (Dias 2009). In *Bradypus torquatus*, for example, copulation occurs towards the end of the dry season and beginning of the wet season, which occurs from August through October, resulting in the gestation and lactation periods occurring when food is abundant. Births occur from February to April, marking the end to the wet season and start of the dry season. Pregnant females give birth to one infant after a gestation period of 6 months. The interbirth interval is one-year for maned sloths (Dias 2009).

6. Natural Mortality

Recent observations of *B. pygmaeus* have led experts to suspect a high rate of death due to disease, habitat loss, or natural causes (Kaviar et al. 2012). As an insular endemic species, *B. pygmaeus* may be adapted to a relatively high rate of inbreeding and, hence, have a diminished risk of deadly recessive allele expression (Kaviar et al. 2012). Nevertheless, loss of allelic diversity could negatively affect the ability of *B. pygmaeus* to adapt to changes in its environment such as novel pathogens and climate change (Kaviar, et al. 2012).

B. CHANGES IN DISTRIBUTION AND ABUNDANCE

1. Historic and Current Distribution

B. pygmaeus is known only from Isla Escudo (Anderson and Handley 2001). This 4.3-km² island separated from the mainland about 8,900 years ago (Anderson and Handley 2001).

2. Historic and Current Abundance

There is little information on the historic abundance of the pygmy sloth. The best scientific information available indicates that the current population is very small. The species is listed as critically endangered by the IUCN because its population is below the 500 individual threshold (Superina et al. 2010) used to justify this designation. The most recent population survey detected only 79 pygmy sloths, which suggests a total population significantly below 500 individuals in size (Kaviar et al. 2012). Of these 79 animals, 70 were observed in mangrove forests while 9 were found within 20 meters of mangrove forests (Kaviar et al. 2012). The population trend is decreasing (Anderson, Moraes-Barros, and Voirin 2011).

3. Population Trend and Extinction Risk Analysis

The pygmy sloth is decreasing as a result of habitat loss, exploitation for food, and other natural and anthropogenic threats. Although Isla Escudo is uninhabited, there are seasonal visitors (e.g., fishermen, lobster divers and indigenous people) who are known to opportunistically hunt the sloths. Preliminary studies suggest a low level of genetic diversity among pygmy sloths (Anderson, Moraes-Barros, and Voirin 2011 citing Silva et al. 2010 and N. Moraes-Barros, pers. comm. 2010), which could lead to endogamic depression if the (already low) population size decreases any further. (Superina et al. 2010).

The mangroves on Isla Escudo are fragmented into five clumps (containing ten mangrove thickets) separated by non-mangrove, mixed forest or sea water (Kaviar et. al 2012). Within these thickets, researchers noted many instances of anthropogenic cutting of mangroves that have interrupted the canopy layer between previously continuous mangrove forest habitat (Kaviar et. al 2012). Of the total area they surveyed, it was estimated that 30 percent of Isla Escudo's total mangrove forest habitat had been lost to logging and land clearing activities. The pattern and severity of logging and clearing varied between the ten identified mangrove forest thickets and may be a factor in declining *B. pygmaeus* density. The full range of effects of these cuts on the ecology and viability of *B. pygmaeus* are not fully understood, but it is assumed that this habitat disturbance, degradation, and fragmentation could contribute to a reduction in the population (Kaviar et al. 2012). The species ability to expand its range or to colonize any available habitat is extremely limited given the inability of any *Bradypus sp*. to move over ground.

Kaviar et al. (2012) noted that the deforested areas appear to be the result of logging by local people using hand tools. They observed numerous felled trees with machete and saw marks. The largest mangrove trees appeared to have been selectively felled and in numerous thickets the largest mangroves trees observed had been cut, but remained decomposing on the ground. Often the roots and branches of these trees were stripped away and the mangrove trunks were left behind. For *B. pygmaeus* to survive, protection of mangrove forests is required (Kaviar et al 2012).

Though unregulated cutting of mangrove forests represents a critical threat to the pygmy sloth, the presence of feral cats also poses a potential threat from predation and disease transmission (Kaviar et. al 2012).

Although Isla Escudo is protected as a wildlife refuge under Panamanian law and is contained within the Comarca Indigenous Reserve, these designations appear to provide little protection to the island. There is a critical need to improve the enforcement regulations governing the management and protection of this refuge, which currently receives little attention from wildlife protection authorities (Anderson, Moraes-Barros, and Voirin 2011). Conservation of the species could be improved through local awareness programs, specifically those promoting sloths as conservation flagship species (Anderson, Moraes-Barros, and Voirin 2011).

II. CRITERIA FOR ENDANGERED SPECIES ACT LISTING

A. THE PYGMY THREE-TOED SLOTH IS A "SPECIES" UNDER THE ESA

A "species" may be defined as a true taxonomic species, a subspecies, or a distinct population segment vertebrate (16 U.S.C. § 1532(16)). The pygmy three-toed sloth is a clearly recognized taxonomic species for purposes of listing under the ESA.

B. THE PYGMY THREE-TOED SLOTH IS ENDANGERED UNDER THE ESA

A species is defined as "endangered" if the species is "in danger of extinction throughout all or a significant portion of its range . . . ." ESA § 3(6), 16 U.S.C. § 1532(6). [A species is defined as "threatened" if the species is "likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." ESA § 3(20), 16 U.S.C. § 1532(20).]

A species may be listed on the basis of any of these five factors:

(A) The present or threatened destruction, modification or curtailment of its habitat or range;
(B) Overutilization for commercial, recreational, scientific, or educational purposes;
(C) Disease or predation;
(D) The inadequacy of existing regulatory mechanisms; or
(E) Other natural or manmade factors affecting its continued existence.

[ESA § 4(a)(1), 16 U.S.C. § 1533(a)(1)]. The USFWS decision to list a species must be made "solely on the best scientific and commercial data available . . . after conducting a review of the status of the species and after taking into account those efforts, if any, being made by any State or foreign nation, or any political subdivision of a State or foreign nation, to protect such species . . . ." ESA § 4(b)(1)(A), 16 U.S.C. § 1533(b)(1)(A).

The pygmy three-toed sloth warrants immediate emergency listing under the ESA as an endangered species. This species is native to only a small island (Isla Escudo de Veraguas) off the coast of Panama. Its entire known range encompasses at most four acres and its total population size may not exceed 79 animals. The continued hunting of the sloth, ongoing destruction and fragmentation of its remaining habitat, a lack of sufficient protection for the sloth's habitat, and the potential for the capture and export of live pygmy sloths for public display threatens the species' continued existence.

An emergency ESA listing of the pygmy sloth as an endangered species would greatly reduce the potential for the export of the species to the United States, raise the profile of the species thereby generating greater attention to its protection and conservation, and potentially provide the government of Panama, scientists, and conservation organizations with access to funding to improve the protection and conservation of the species and its habitat.

1. Present or Threatened Destruction, Modification, or Curtailment of its Habitat or Range

Logging

As described previously, a recent increase in logging on the island could be a contributing factor to the decline of the pygmy three-toed sloth as this species relies on the mangrove forest ecosystem for its survival. According to Kaviar et al. (2012) the disturbance and fragmentation of pygmy sloth habitat, including through the cutting of existing occupied mangrove thickets "could contribute to a decline of their population," since this species survival is so reliant on forest mangrove habitat. Kaviar et al. (2012) also emphasized that the pygmy three-toed sloth can only survive in the wild if its mangrove habitat is protected.

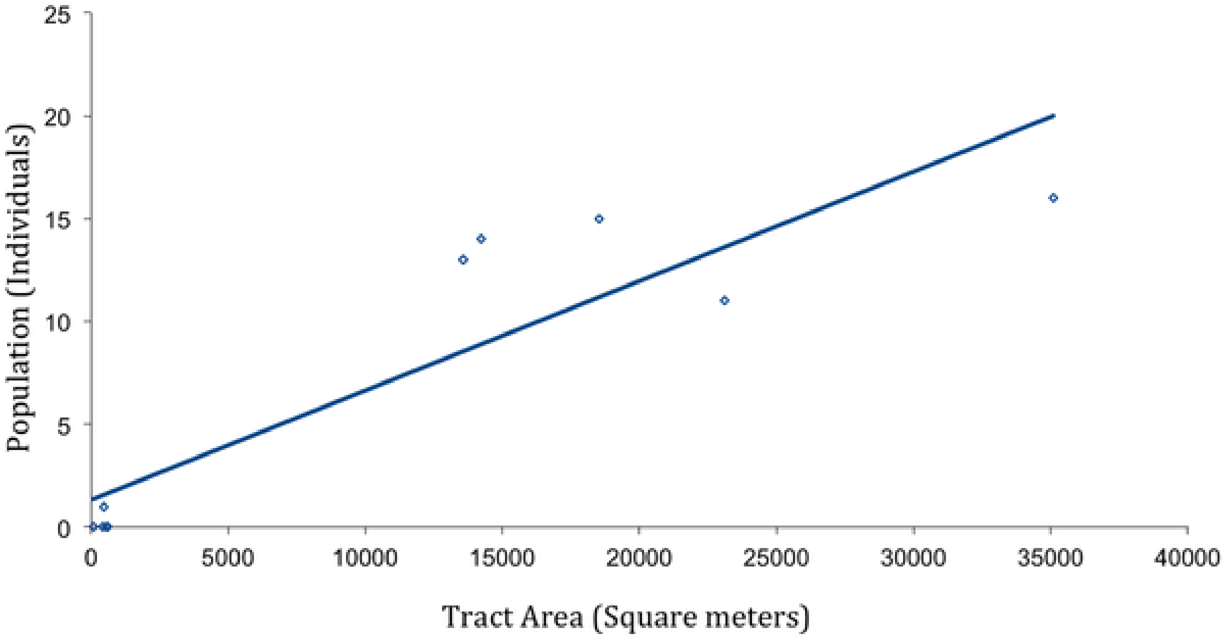

Figure 3. Regression analysis indicating the population of pygmy three-toed sloth as dependent on mangrove area, where y = 0.0005x+1 and R2 = 0.80493. From Kaviar et al.(2012) (available at http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0049854).

2. Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

In September 2013, Dallas World Aquarium (DWA) traveled to an island off the coast of Panama to collect several endangered pygmy three-toed sloths with the intent to export them to the United States. In total, eight sloths were taken from the wild and placed in crates awaiting export. DWA had been issued permits and certificates (i.e., research, export, veterinary health) to authorize the collection and export of six pygmy sloths to the United States while the other two sloths remained in Panama destined for Zoologico del Istmo in Colón, Panama (*See* permits and news articles in Appendix). Based on the most recent population surveys during which 79 sloths were counted, this capture and export scheme could have removed over 10 percent of the known population of pygmy sloths from the wild.

DWA claims that it was capturing and importing these imperiled sloths in order to ensure their survival (i.e., through captive breeding), in case they eventually disappear from the wild. However, the species does not survive well in captivity generally and there is no verifiable record of the conception, birth, or survival of a pygmy sloth in captivity or of a captive pygmy sloth being released back into the wild (See Max Planck Institute for Ornithology letter in Appendix). The DWA has also experienced significant mortality with imported three-toed sloths (an overall death rate of >85 percent) (*See* Max Planck Institute for Ornithology letter in Appendix). According to sloth experts, very little is known about these sloths and their diet, much less whether they can breed in captivity, and under what circumstances (*See* Max Planck Institute for Ornithology letter in Appendix). In addition, zoo breeding programs are typically conducted under the auspices of a species management plan, which doesn't exist for the pygmy sloth.

DWA also failed to consult with or subject its capture/export/captivity plan to review by those scientists working with pygmy sloths; Panamanian and international research entities, conservation organizations, and scientific associations involved in the study of sloths were all completely unaware of this planned export (*See* Max Planck Institute for Ornithology letter in Appendix). This includes the Smithsonian Tropical Research Institute, the IUCN, the Zoological Society of London, Conservation, Nature and Life (CONAVI), and the Max Planck Institute of Ornithology.

Fortunately, the export of these sloths was prevented prior to their transport from Isla Colón International Airport in Bocas del Toro, Panama to the United States as a result of local environmentalists, police, indigenous groups, and local Panamanian authorities who ultimately negotiated the surrender of these animals from DWA. The animals were then transported back to Isla Escudo de Veraguas and released. According to scientists and citizens who are knowledgeable about the incident, at least two of the captured sloths who were returned to the island may have died prior to or soon after release. There were also three other sloths who were captured but not removed from the island because they did not adapt well to captivity (their fate is unknown and not verifiable).

If not immediately protected under the ESA, DWA and/or another entity could attempt to capture and export pygmy sloths to the United States again without obtaining any permit from the USFWS or having its application for an import permit subject to USFWS and public review as would be required if designated as endangered under the ESA.

In addition to the potential adverse impact associated with any capture and export of this species, another significant threat to its survival is hunting. Although Isla Escudo de Veraguas was deemed a protected area in 2009, the species is often hunted by seasonal visitors to the island (Superina et al. 2010; *see also* Hance, J. 2013).

Sloths have also become increasingly popular in modern culture. For example, a December 21, 2011 article in the Washington Post declared "Sloths are the new kittens" (*See* http://www.washingtonpost.com/blogs/arts-post/post/sloths-are-the-new-kittens/2011/12/21/gIQANE2j9O_blog.html) while, in the same year, the Animal Planet aired a documentary called "Too cute!! Baby Sloths" (*See* http://animal.discovery.com/tv-shows/too-cute/videos/too-cute-baby-sloths.htm). More recently, celebrity Kristen Bell declared that the sloth was her spirit animal on the Ellen DeGeneres show in which a captive sloth was brought to her birthday party (*See* http://www.youtube.com/watch?v=t5jw3T3Jy70). In addition, in May 2013 the ABC News program Nightline investigated the illegal sale of sloths in Columbia (*See* http://abcnews.go.com/International/hottest-selling-animal-colombias-illegal-exotic-pet-trade/story?id=19172620). This increasing popularity of sloths as cute pets is leading to more exploitation of sloths in the wild, regardless of conservation status, to satisfy popular demands to possess and interact with these species.

3. Predation or Disease

Predators of pygmy three-toed sloths have not been reported although feral domestic cats have been seen on the island (Anderson and Handley 2001) and may pose a threat to the pygmy sloths as a result of predation or disease transmission (Kaviar et al. 2012). In addition, recent observations have led researchers to suspect a high rate of death through disease, habitat loss, or natural causes in the population (Kaviar et al. 2012).

4. Inadequacy of Existing Regulatory Mechanisms

The three-toed pygmy sloth is not currently afforded protection under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) or the ESA. The CITES Secretariat has recently determined, however, that the omission of *B. pygmaeus* from Appendix II is an oversight dating back to 2007 and that this oversight is to be corrected soon through a notification distributed to CITES parties (pers. comm. with J. Barzdo, CITES Secretariat, 2013).

Pygmy sloths have been known to exist only since 2001, when they were formally described as a separate species, occurring only on Isla Escudo de Veraguas (Anderson and Handley 2001). As a result, the capture and export of this species from Panama only requires permits and certificates issued by Panamanian authorities.

Although the sloth is technically living on a wildlife refuge that is contained within the Comarca Indigenous Reserve, we cannot find any evidence of regulations providing any specific protections for the island or the sloth's habitat and, even if these regulations do exist, it does not appear that they are adequately enforced by Panamanian wildlife protection authorities.

Because of the small size of the pygmy sloth population, there is an imminent need to improve conservation measures to preserve the pygmy three-toed sloth. The inadequacies in the current regulatory schemes could be curtailed through local awareness programs that promote this unique sloth as a conservation flagship species (Superina et al. 2010).

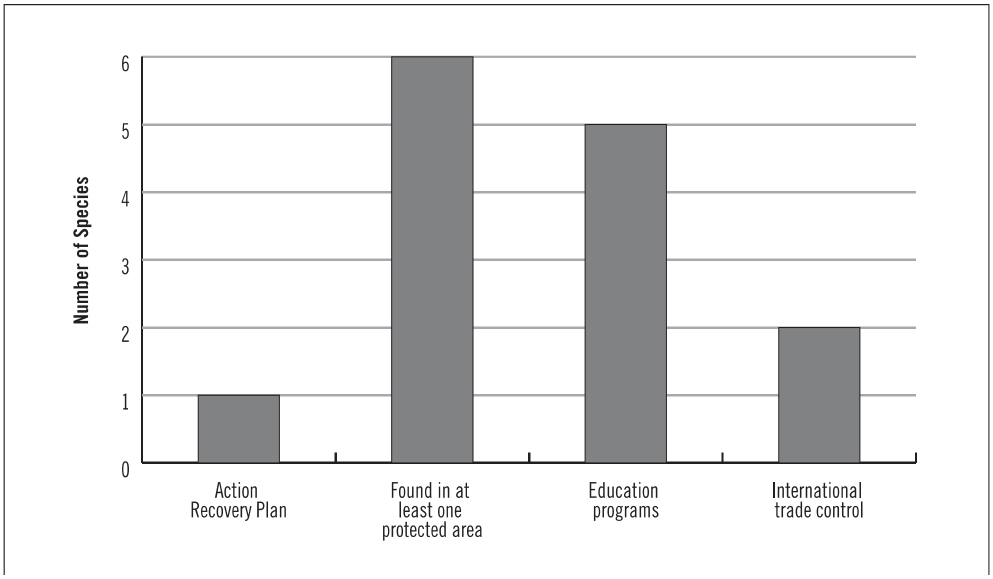

Figure 3. Existing conservation measures for sloths. From M. Superina, et al. (2010) (available at http://www.bioone.org/doi/full/10.5537/020.011.0202). This chart reflects recommended conservation measures for all sloth species evaluated by Superina et al. 2010.

5. Other Natural or Manmade Factors

Low Level of Genetic Diversity

Studies suggest that the pygmy three-toed sloth is subject to low levels of genetic diversity (Superina et al. 2010). This could lead to endogamic depression within the species if the already low number of sloths in the population declines even further (Superina et al. 2010).

III. CONCLUSION

The pygmy three-toed sloth has been listed as Critically Endangered on the IUCN Red List since 2006. The range of this species is highly restricted, being found only on one very small island off the coast of Panama. The estimated population of pygmy three-toed sloths in existence is fewer than 500 and, according to recent surveys, likely numbers less than 100 animals. There is an ongoing decline in the quality of habitat and area of occupancy due to habitat degradation and both logging of the mangrove forests and opportunistic hunting of the pygmy sloths are causing a major threat to the survival of the species. In addition, the pygmy three-toed sloth is subject to low levels of genetic diversity increasing the potential for inbreeding with a long-term adverse impact on productivity, heterozygosity, and allelic diversity. The combination of these factors presents an urgent need to protect and conserve this species.

The pygmy three-toed sloth is at a high risk of extinction. We urgently petition the USFWS to list the pygmy three-toed sloth as endangered on an emergency basis to afford the species with protections available under the ESA.

IV. SIGNATURE PAGE

Submitted this 15th day of November, 2013

Tara Zuardo

Tara Zuardo
Animal Welfare Institute
900 Pennsylvania Ave
Washington, DC 20002
Phone: (202) 446-2148
Fax: (202) 446-2131
E-mail: tara@awionline.org

LITERATURE CITED

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DWARFISM IN INSULAR SLOTHS: BIOGEOGRAPHY, SELECTION, AND EVOLUTIONARY RATE

Robert P. Anderson[1,2,3] and Charles O. Handley, Jr.[4,5]
[1]*Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024*
[2]*E-mail: rpa@amnh.org*
[3]*Natural History Museum and Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045*
[4]*Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560*

Abstract.—The islands of Bocas del Toro, Panama, were sequentially separated from the adjacent mainland by rising sea levels during the past 10,000 years. Three-toed sloths (*Bradypus*) from five islands are smaller than their mainland counterparts, and the insular populations themselves vary in mean body size. We first examine relationships between body size and physical characteristics of the islands, testing hypotheses regarding optimal body size, evolutionary equilibria, and the presence of dispersal in this system. To do so, we conduct linear regressions of body size onto island area, distance from the mainland, and island age. Second, we retroactively calculate two measures of the evolutionary rate of change in body size (haldanes and darwins) and the standardized linear selection differential, or selection intensity (*i*). We also test the observed morphological changes against models of evolution by genetic drift. The results indicate that mean body size decreases linearly with island age, explaining up to 97% of the variation among population means. Neither island area nor distance from the mainland is significant in multiple regressions that include island age. Thus, we find no evidence for differential optimal body size among islands, or for dispersal in the system. In contrast, the dependence of body size on island age suggests uniform directional selection for small body size in the insular populations. Although genetic drift cannot be discounted as the cause for this evolution in body size, the probability is small given the consistent direction of evolution (repeated dwarfism). The insular sloths show a sustained rate of evolution similar to those measured in haldanes over tens of generations, appearing to unite micro- and macroevolutionary time scales. Furthermore, the magnitude and rate of this example of rapid differentiation fall within predictions of theoretical models from population genetics. However, the linearity of the relationship between body size and island age is not predicted, suggesting that either more factors are involved than those considered here, or that theoretical advances are necessary to explain constant evolutionary rates over long time spans in new selective environments.

Key words.—*Bradypus*, body size, darwins, haldanes, island, selection differential, selection intensity.

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Islands have long attracted biologists' attention as windows into evolution and community ecology (e.g., Darwin 1859; Wallace 1880; MacArthur and Wilson 1967; Brown and Lomolino 1998). Usually relatively depauperate in species richness, insular faunas undergo a shuffling of community composition as species are lost due to extinction or gained through immigration and speciation (MacArthur and Wilson 1967; Simberloff 1974; Heaney 1986, 2000; Lomolino 1986, 2000). The community ecology of islands isolated from continental areas by rising sea level—landbridge islands—is typically dominated by extinction (faunal relaxation), rather than by a more even equilibrium of extinction and colonization, as on oceanic islands (Lawlor 1986; Patterson and Atmar 1986).

Following isolation, many mammals surviving on landbridge islands undergo evolutionary changes in physiology, behavior, and morphological features, such as size, cranial and dental characteristics, and coloration (e.g., Heaney 1978; Lomolino 1985; Kalko and Handley 1994). Models from population genetics can predict morphological shifts in quantitative characters (e.g., such as body size) under changing environmental conditions such as mainland versus insular environments (Lande 1980, 1986; Kirkpatrick 1982). Differentiation in body size, one of the most important predictors of life-history characteristics in mammals (Marquet and Taper 1998), follows a strikingly consistent pattern: Large species generally become dwarfed on islands, whereas small mammals commonly evolve larger size.

Reviews differ in which and how many mechanisms drive that change in body size and under what circumstances each is relevant. Some (Lomolino 1985; Roth 1992; McNab 1994) conclude that insular populations of small species become larger to use broader resource bases in the absence of former competitors (competitive release of Lomolino 1985), and large mammals are often resource-limited on islands, favoring smaller size (resource limitation of Lomolino 1985). Recently, Marquet and Taper (1998, p. 135) suggested that resource limitation may cause both dwarfism in large mammals and gigantism in small ones, due to changes in intraspecific competition that are related to home range size. In contrast, Adler and Levins (1994) put forward models invoking selection for larger body size in small species in response to higher intraspecific competition (see also Crowell 1983). Finally, Heaney (1978) proposed that island area determines which factor drives selection: resource limitation on small islands and competitive release on large islands. General models for the evolution of body size in insular terrestrial vertebrates have been proposed and a few notable exceptions investigated (e.g., Foster 1964; Case 1978; Lawlor 1982; Case and Schwaner 1993; Petren and Case 1997). Thus, while the overall causes of body size evolution in insular situations remain an open area of research, most reviews to date suggest

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[5] Charles O. Handley, Jr. passed away on June 9, 2000.

that selection for smaller size in large mammals on islands is caused by resource limitation and strong intraspecific competition (Heaney 1978; Lomolino 1985; Roth 1992).

Body size is but one of many morphological traits that have been examined in studies assessing evolutionary rates and selection intensities (Lynch 1990; Gingerich 1993; Hendry and Kinnison 1999; Hoekstra et al. 2001; Kingsolver et al. 2001). In studies where relative fitness, w, is known, the linear selection gradient, β, is defined as the slope of a regression of relative fitness on a continuously varying (quantitative) trait or character, z (Arnold and Wade 1984). In contrast, a selection differential measures evolutionary rate and can be calculated without data regarding fitness (see Materials and Methods). The islands of Bocas del Toro, Panama, provide a superb empirical opportunity to investigate differentiation and rates of morphological evolution in mammals, because the ages of the islands have been estimated, the sequence of their formation is known, and the mammalian fauna is well sampled.

The Islands of Bocas del Toro

The province of Bocas del Toro is located on the Caribbean coast of northwestern Panama adjacent to Costa Rica (Fig. 1). Just off shore lies a group of landbridge islands that formed during the Holocene as a result of postglacial events, including rising sea level and continental submergence (Olson 1993; Kalko and Handley 1994; Anderson and Handley 2001). Rising sea levels isolated hilltops and ridges, first as peninsulae, and then eventually as islands. These islands vary in area, distance from the mainland, depth of surrounding water, and age—all contributing to the degree of isolation of the fauna of each island (Table 1).

Combining ocean-floor topography with studies of pollen and coral cores from the western Caribbean allowed C. O. Handley, Jr. and M. Varn (unpubl. ms.) to determine the sequence of island formation and to estimate the dates of separation for the various islands of Bocas del Toro (for details, see Anderson and Handley 2001). Assuming that the present-day submarine topography of Bocas del Toro is not very different from that of the terrestrial topography 10,000 years ago (before flooding), then the depths of water at which land bridges to various present-day islands disappeared should be apparent from current sea-floor maps. Thus, given estimates of sea level at various time intervals in the past, it is possible to estimate the approximate date of isolation of each island.

C. O. Handley, Jr. and M. Varn (unpubl. ms.) produced maps of bathymetric contours of Bocas del Toro for various depths below present sea level and used three models based on coral and pollen cores taken in the western Caribbean to estimate sea levels over the past 10,000 years. Radioisotope dating of *Acropora palmata*, a coral restricted to the upper 5 m of water, formed the bases of the curves of depth below current sea level versus time produced by Lighty et al. (1982) and Fairbanks (1989). Bartlett and Barghoorn (1973) used the pollen of *Rhizophora mangle* in deep-sea cores from the Gatún Basin in Panama to produce a similar curve. *Rhizophora mangle* is an obligate saltwater species and represents the major component of Neotropical coastal mangrove swamps. Using a composite curve with years before present and depth below current sea level as axes, Handley and Varn dated each of the bathymetric contours and thus estimated island ages from the dates of disappearance of land bridges between each island and the mainland (Table 1). Even if their absolute dates err in one direction or the other, relative dates of island formation will be correct to the extent that sea-floor contours in this region have remained constant through the Holocene.

Isla Escudo was the first of the islands to be separated from the mainland (Fig. 1). It fragmented from the eastern shore of the Península Valiente about 8900 years ago and is not directly related to any of the other islands. To the northwest of the Península Valiente and Isla Escudo, the islands of the Laguna de Chriquí are younger (Fig. 1A). They fragmented sequentially from the Península Tierra Oscura, which was once a long, J-shaped peninsula jutting out from the southwestern shore of the Laguna de Chiriquí (Fig. 1B). That peninsula was formed by the opening of the Boca del Drago Pass at the western end of the laguna. The outermost islands of the Laguna de Chriquí are about 5000 years old: Isla Colón, which was the first to split off of the Península Tierra Oscura (ca. 5200 years ago), and Isla Bastimentos, which separated from the peninsula along with what currently is Cayo Nancy (ca. 4700 years ago). Cayo Agua became isolated from the adjacent mainland (presently part of Isla Popa) about 3400 years ago. In the past 1000 years, Cayo Nancy split from Isla Bastimentos proper, and Isla Popa and Isla Cristóbal each separated from the mainland.

Biological interest in the islands of Bocas del Toro emerged only relatively recently (Handley 1959, 1993; Olson 1993; Kalko and Handley 1994; Anderson and Handley 2001). These studies generally assume that the fauna of the coastal plain of Bocas del Toro was relatively uniform as sea levels rose and populations were stranded on the forming islands. Despite significant climatalogical fluctuations, palynological data indicate that lowland tropical forests remained intact in Panama during the past 2 million years (Colinvaux 1997), lending support to this premise. Subsequent to isolation, numerous species of mammals, including bats, rodents, felids, and mustelids present on the nearby mainland, were extirpated from some or all of the islands (Handley 1993, unpubl. data). Additionally, a few relictual species are present on one or more of the islands but no longer on the adjacent mainland (Handley 1993; Olson 1993; García-París and Wake 2000). Several species surviving on the islands exhibit marked morphological differentiation from their mainland relatives. For example, a fruit-eating bat, *Artibeus incomitatus*, underwent rapid differentiation on Isla Escudo (Kalko and Handley 1994). Similarly, several populations of three-toed sloths (*Bradypus*) have become dwarfed following insularization (Anderson and Handley 2001), and here we further examine their evolution and biogeography.

Three-toed Sloths

Along with armadillos and anteaters, sloths belong to the Neotropical order Xenarthra (Gardner 1993; or magnorder Xenarthra sensu McKenna and Bell 1997). Two distantly related genera, *Choloepus* (two-toed sloths) and *Bradypus*

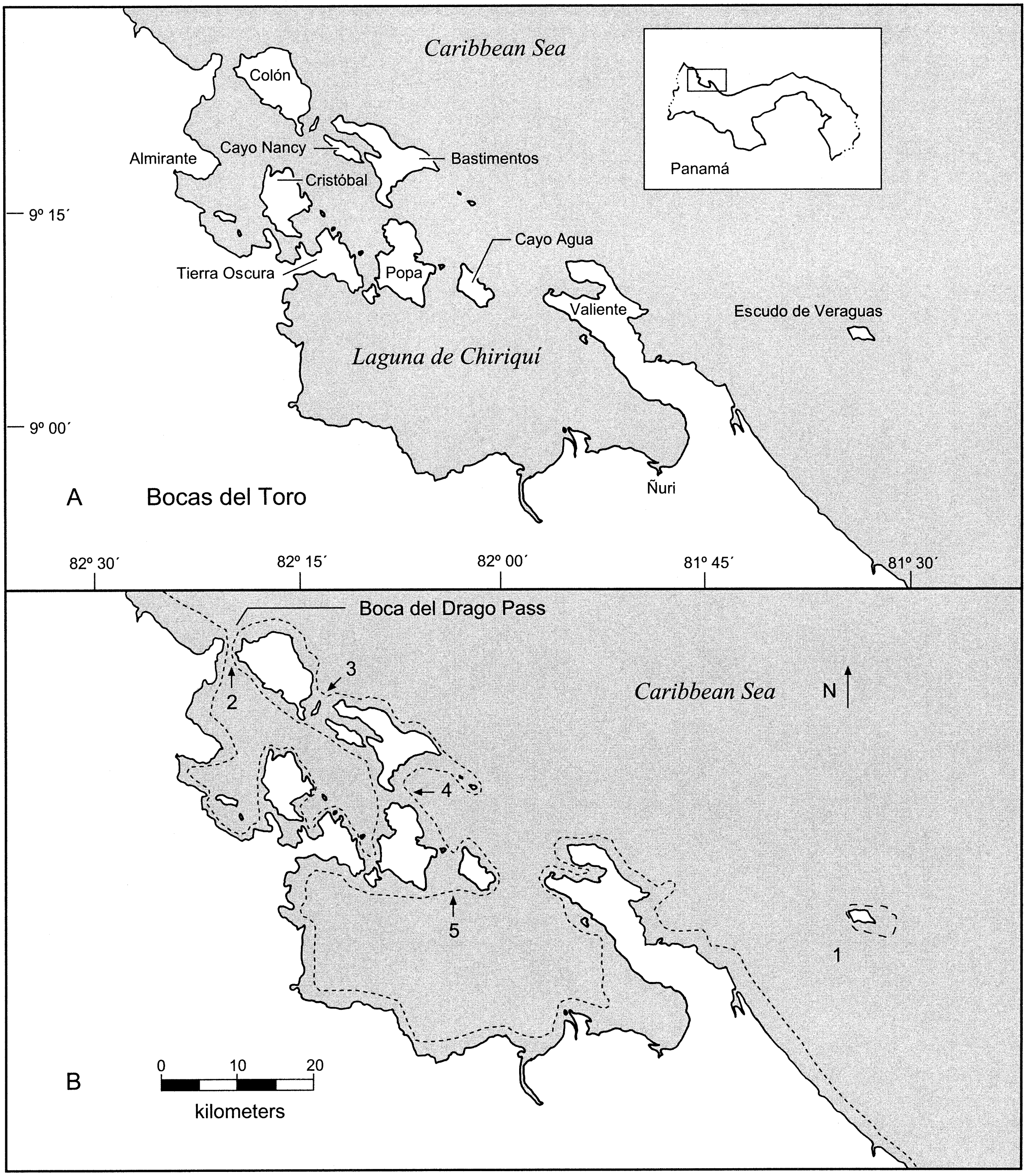

FIG. 1. Maps of Bocas del Toro showing major islands and place names on the mainland (A) and reconstruction of the sequence of island formation (B). In (B), the dashed line approximates sea level at 10 m below present. Major events in the formation of the islands (Anderson and Handley 2001; C. O. Handley, Jr. and M. Varn, unpubl. ms.) are as follows: (1) Isla Escudo separated from the southern coast of the province about 8900 years ago; (2) the Boca del Drago pass opened, creating a J-shaped peninsula in the Laguna de Chiriquí about 6300 years ago; (3) Isla Colón became isolated from the peninsula about 5200 years ago; (4) the superisland Bastimentos-Nancy became separated from what remained of the peninsula about 4700 years ago; and (5) Cayo Agua was formed about 3400 years ago. More recently (in the past 1000 years), Isla Cristóbal and Isla Popa each separated from the mainland, and Cayo Nancy split from Isla Bastimentos.

TABLE 1. Estimated age (since separation from the adjacent mainland), area, and distance from the mainland for the islands of Bocas del Toro, Panama. Data are from the Anderson and Handley (2001).

Island	Age (years ago)	Area (km²)	Distance from the mainland (km)
Isla Escudo	8900	4.3	17.6
Isla Colón	5200	59.0	1.5
Isla Bastimentos	4700	51.5	6.3
Cayo Nancy	4700	6.8	9.5
Cayo Agua	3400	14.5	6.6
Isla Popa	1000	53.0	1.8
Isla Cristóbal	1000	36.8	0.3

(three-toed sloths), are extant (Webb 1985; Patterson et al. 1992). Here we consider only the three-toed sloths, *Bradypus*. We recently described a new species of *Bradypus* from Isla Escudo (Anderson and Handley 2001), bringing the number of species known in the genus to four (Wetzel and Avila-Pires 1980; Wetzel 1985; Anderson and Handley 2001). This new species, *B. pygmaeus*, is closely related to *B. variegatus*, which is widespread in both Central and South America. The other two species in the genus, *B. tridactylus* and *B. torquatus*, are restricted to South America.

Three-toed sloths are arboreal folivores with low dispersal ability (Carvalho 1960; Montgomery and Sunquist 1975; Chiarello 1998b). Concomitant with their energy-poor diet, they have extremely low metabolic rates and are not fully homeothermic (Britton and Atkinson 1938). Sloths avoid predation largely by avoiding detection, moving very slowly in trees (Brattstrom 1966) throughout small home ranges, which average 1.6 ha (Montgomery and Sunquist 1975; see also Chiarello 1998a). Sloths move even more slowly on the ground than in trees, traveling on average 0.4 km per hour (Britton and Kline 1939; see also Mendel 1985), although they are known to swim well in rivers (Beebe 1926, pp. 7–9; Carvalho 1960). We have found no reference to their swimming in salt water, however; perhaps they have a behavioral aversion to salt water or to rough water and wave action. Their relatively large size, restricted diet, and low dispersal potential make sloths a model system for investigating the effects of isolation on body size in large insular mammals.

Body Size in Sloths from Bocas del Toro

In a morphological and morphometric study of the sloths of Bocas del Toro (Anderson and Handley 2001), we documented a repeated pattern of dwarfism in sloths from several of the islands. The populations of three-toed sloths of the outer (and older, Fig. 1, Table 1) islands of Bocas del Toro—Isla Colón, Isla Bastimentos, Cayo Nancy, Cayo Agua, and Isla Escudo—are significantly smaller in body size than the *Bradypus* from most or all of the four localities on the adjacent mainland (by Tukey's tests of multiple pairwise comparisons with a conservative familywide error rate of $\alpha = 0.05$; from Anderson and Handley 2001; see also Table 2). Furthermore, some of the populations on those five islands themselves vary in mean body size, with that from Isla Escudo clearly being the smallest (Anderson and Handley 2001; Fig. 2; Table 2; see Fig. 3; in addition to the statistical significance of the magnitudes of these differences in mean relative to within-group variation, the magnitudes are clearly biologically significant as well). In contrast, the samples from Isla Popa and Isla Cristóbal, young islands close to shore, are not significantly different in body size from any population on the adjacent mainland (Anderson and Handley 2001; Table 2; see Fig. 3).

TABLE 2. Descriptive statistics for greatest length of skull (mm) and scores on the first principal component (PC I) for adult *Bradypus* from Bocas del Toro, Panama. Measurements and scores are given as the mean ± two standard errors and the range of minimum to maximum. Sample size is given in parentheses. Data are from Anderson and Handley (2001). Islands are arranged from outermost to innermost; mainland localities from west to east.

Locality	Greatest length of skull	First principal component (PC I)
Isla Escudo	69.0 ± 1.34 67.5–72.2 (6)	−0.28 ± 0.05 −0.35 to −0.22 (5)
Isla Bastimentos	70.4 ± 1.53 68.3–73.4 (6)	−0.14 ± 0.07 −0.18 to −0.07 (3)
Cayo Agua	72.5 ± 1.18 68.7–74.9 (12)	−0.04 ± 0.03 −0.14–0.02 (11)
Isla Colón	73.4 ± 2.96 70.5–76.6 (4)	−0.08 ± 0.12 0.20–0.00 (3)
Cayo Nancy	76.0 ± 2.60 73.2–80.0 (5)	−0.05 ± 0.07 −0.15–0.05 (5)
Isla Cristóbal	79.3 ± 2.00 76.5–82.1 (5)	0.06 ± 0.08 −0.06–0.13 (4)
Isla Popa	80.0 ± 1.29 77.7–82.5 (6)	0.11 ± 0.03 0.09–0.16 (5)
Almirante	79.7 ± 2.88 75.9–82.5 (4)	0.09 ± 0.07 0.04–0.15 (3)
Tierra Oscura	80.5 ± 2.50 76.1–86.0 (7)	0.12 ± 0.05 0.02–0.19 (7)
Valiente	80.3 ± 1.99 77.7–83.5 (6)	0.09 ± 0.04 0.04–0.17 (6)
Ñuri	78.4 ± 1.13 77.0–80.6 (7)	0.06 ± 0.03 0.01–0.10 (5)

Although sloths from the five outer islands share small body size, pelage characters indicate similarities between insular and mainland populations that were once contiguous (Anderson and Handley 2001). Several pelage characters evaluated throughout the range of *B. variegatus* in Central and South America show that sloths from Bocas del Toro group most closely with those from nearby samples in central Panama and extreme northwestern Colombia (Anderson and Handley 2001). Furthermore, a few discrete pelage characters vary within Bocas del Toro, with geographically proximate populations there sharing the same character states. For example, there is a west-to-east cline from uniformly colored to blotchy dorsal pelage. Similarly, the only populations in Bocas del Toro with individuals lacking a dorsal stripe are found at Tierra Oscura and the adjacent islands of Isla Cris-

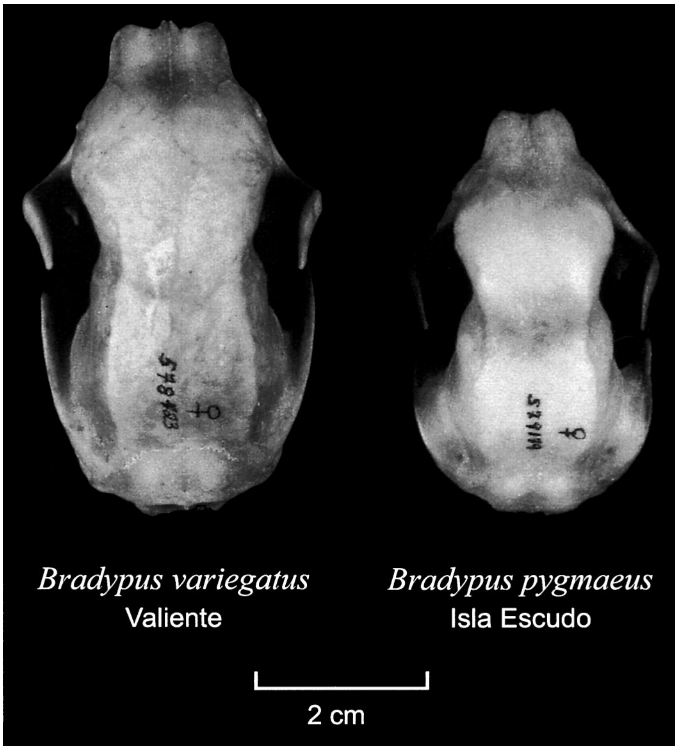

FIG. 2. Skulls of *Bradypus variegatus* from the Península Valiente on the mainland of Bocas del Toro (left) and *Bradypus pygmaeus* from Isla Escudo (right) showing the degree of size divergence of the sloth on Isla Escudo.

tóbal, Isla Popa, and Cayo Nancy (for other examples, see Anderson and Handley 2001).

This pattern of similar pelage traits being present in geographically proximate populations (without regard to whether they are mainland or insular) lies in stark contrast to the striking differences in body size between most insular populations and the nearest respective mainland samples. The few cranial characters common to the small sloths on various islands are all gracile traits associated with size reduction and ontogenetic truncation (e.g., thin zygomatic arches, weakly developed temporal crests). In fact, many cranial traits of adult individuals of the small insular sloths mimic those of immature individuals from the adjacent mainland (Anderson and Handley 2001), suggesting an evolutionary syndrome often described as or attributed to paedogenesis (Reilly et al. 1997). In contrast, the pelage traits provide data independent of size reduction, which is especially predisposed to convergence (Roth 1992). Because of the extreme differences in body size between mainland and insular samples, Anderson and Handley (2001) suggested that the distribution of pelage traits did not represent recent gene flow (via dispersal), but rather the relictual manifestation of previously continuous geographic variation that was subdivided into isolated populations when the islands formed.

This interpretation suggests that populations of *Bradypus* may have evolved smaller size four times subsequent to island formation in Bocas del Toro: independently on Isla Escudo, Isla Colón, and Cayo Agua (each of which formed separately) and once on the superisland Isla Bastimentos–Cayo Nancy together (they separated from the mainland as a unit and only recently separated from each other; see Fig. 1). Based on several unique cranial features (including some indicative of a divergent pattern of cranial circulation) and extremely small body size (well out of the variation found anywhere in the range of *B. variegatus*), Anderson and Handley (2001) considered that the population on Isla Escudo has evolved to represent a distinct species, *B. pygmaeus*, but that the sloths of other islands remain conspecific with *B. variegatus*, despite their moderate dwarfism. In any case, all insular three-toed sloths in Bocas del Toro are very closely related to populations of *B. variegatus* from the mainland of Panama (see Anderson and Handley 2001 and above). L. E. Olson and R. P. Anderson (unpubl. data) have begun DNA sequencing of part of the mitochondrial genome to elucidate the genetic relationships among populations of *Bradypus* in Bocas del Toro (after Brooks and McLennan 1991; Avise 1994; Matocq et al. 2000). Here, we test several biogeographic hypotheses based on morphological data and physical characteristics of the islands and compare the results with theoretical and empirical values from other evolutionary studies.

MATERIALS AND METHODS

Regressions

Hypotheses based on physical characteristics of the islands

Island area, distance from the mainland, and age represent the major physical variables potentially affecting evolution in insular mammals. Heaney (1978) showed that body size in tri-colored squirrels (*Callosciurus prevosti*) was related to island area (presumably because intra- and interspecific competitive relationships vary with island area and faunal richness, which is a function of area). Thus, in an archipelago with islands varying greatly in area, optimal body size may not be constant among all islands. In contrast, for groups of islands with generally similar areas and selective environments (related to community composition and resource availability) for a particular taxon, island area is not expected to be related to body size (see also Adler and Levins 1994).

Second, distance from the mainland is predicted to affect immigration rates, especially for more vagile taxa (MacArthur and Wilson 1967). Barring differences in ocean currents, prevailing winds, or opportunities for rafting (such as the outlet of a major river) among islands of an archipelago, immigration rates for a particular taxon should be a function of distance. Thus, for taxa and systems with appreciable immigration rates, distance from the mainland will influence rates of morphological evolution by differentially diluting in situ evolution on closer islands with colonists from the mainland. In contrast, where immigration is minimal or nonexistent (such as island archipelagos outside the dispersal potential of the species), distance would not be related to body size.

Finally, when directional selection is still occurring on an insular population, the population has not yet reached its optimal body size (evolutionary equilibrium). In such cases, islands of various ages present in the archipelago should show a relationship between body size and island age, with the

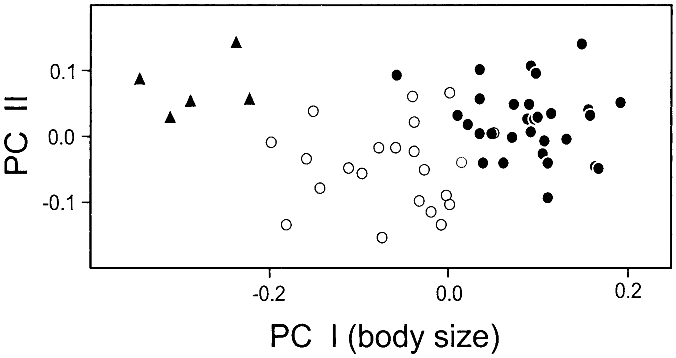

FIG. 3. Plot of specimen scores on the first two axes of a principal components analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panama, highlighting the divergence in body size of five insular populations. Specimens from Isla Escudo are marked with solid triangles, those from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles, and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. The first principal component (PC I) represents a measure of overall body size (Table 3). Data are taken from Anderson and Handley (2001).

most morphological evolution present in the oldest islands. On the contrary, once all insular populations have reached the equilibrium (optimal) body size, island age should no longer be related to body size.

Analyses

To test the above hypotheses regarding optimal body size, dispersal, and evolutionary equilibrium, we conducted a series of regressions. We used scores on the first principal component (PC I; Fig. 3; Table 3) of log-transformed morphological measurements from Anderson and Handley (2001) as a measure of overall body size in the present analyses. We regressed mean PC I scores for insular populations on the following independent physical predictor variables: island area (km^2), island distance from the mainland (km), and island age since separation from the mainland of Bocas del Toro (years). Next, for all localities in Bocas del Toro—both island and mainland—we regressed mean PC I scores on the same three predictor variables. In the second set of analyses, years since separation = zero and distance from the mainland = zero for mainland populations; island area was considered a missing value for mainland populations. For both sets of analyses, we conducted multiple linear regressions for those predictor variables that were significant by themselves in simple linear regressions. Likewise, when possible, we subjected significant linear models to lack-of-fit (pure-error) tests (Draper and Smith 1981, pp. 33–42). All statistical analyses were performed in Minitab (1998).

However, not all sloth populations may be considered strictly independent (see Felsenstein 1985). As mentioned above, the geological evidence regarding the sequence of island formation indicates that Isla Bastimentos and Cayo Nancy separated from the mainland together (ca. 4700 years ago) and only recently separated from each other (in the last 1000 years; Anderson and Handley 2001). Thus, if present-day sloth populations derive directly from the founder populations stranded on the superisland Bastimentos-Nancy when it was formed, then the two populations do not represent independent derivations of dwarfism. Likewise, the four mainland localities represent repetitive estimates of the body size of mainland sloths (which we use as the original body size of the insular sloths at time of isolation).

TABLE 3. Loadings, eigenvalues, and percent variance explained for the first two axes of a principal components analysis of 57 three-toed sloths (*Bradypus*) from Bocas del Toro, Panama, using the covariance matrix of $\log_{10}$-transformed values of 14 cranial and three external measurements. PC I represents general size, which is uncorrelated with external auditory meatus diameter. Data are taken from Anderson and Handley (2001).

	PC I	PC II
Total length	0.786	0.302
Tail length	0.331	0.788
Hind foot length	0.801	0.141
Greatest length of skull	0.878	0.221
Anterior zygomatic breadth	0.905	0.049
Posterior zygomatic breadth	0.895	−0.010
Postorbital breadth	0.682	0.129
Squamosal process length	0.874	−0.062
Maxillary tooth row length	0.610	0.164
Postpalatal length	0.839	0.269
Palatal breadth	0.712	0.236
Braincase depth	0.794	0.054
Antorbital bar breadth	0.866	−0.092
Descending jugal process length	0.354	0.348
External auditory meatus diameter	−0.044	0.481
Squamosal process breadth	0.689	−0.477
Ascending mandibular ramus breadth	0.842	−0.191
Eigenvalue	**0.0164**	**0.0046**
Variance explained	51.2%	14.3%

Considering these issues, we repeated the regression analyses using all geologically independent populations (mainland, Cayo Agua, Isla Colón, Isla Cristóbal, Isla Escudo, Isla Popa, and superisland Bastimentos-Nancy). The mainland and Bastimentos-Nancy represent the two geologically independent populations that are composed of more than one locality. For those two composite samples, we calculated pooled estimates of PC I scores by the grand mean of the constituent populations. For the Bastimentos-Nancy predictor variables, we used the lesser distance from the mainland (that of Bastimentos) and summed the areas of the two islands. These regressions do not assume that the geologically independent populations are independent genetically (i.e., with no current gene flow [dispersal] among them). Given only a moderate number of discrete morphological characters available (Anderson and Handley 2001), molecular analyses are necessary to evaluate that hypothesis from phylogeographic and population-genetic perspectives (L. E. Olson and R. P. Anderson, unpubl. data; see above). Rather, the current, more conservative, approach allows for the possibility of detecting patterns different from those found in the overall regressions of all populations. Furthermore, in the case that the insular populations have been isolated (or effectively so) since separating from the mainland, these analyses permit a more appropriate modeling of their evolution.

Despite its widespread use, simple linear (least-squares) regression is most strictly applicable to cases in which the independent (predictor) variable is measured without error.

Therefore, for those predictor variables that were significant in multiple regressions (i.e., with significant partial sums of squares), we conducted separate reduced-major-axis regressions to produce an unbiased estimate of the slope for further analyses (Sokal and Rohlf 1995).

Furthermore, island area, distance from the mainland, and island age may have nonlinear effects (e.g., Heaney 1978). To consider this possibility, plots of mean PC I scores versus area, versus distance, and versus age for geologically independent populations were examined visually for curvilinear or step (threshold) functions. We did the same for the residuals of regressions onto island age (i.e., plotting residuals from that regression vs. area and vs. distance).

Genetic Drift

Genetic drift, along with mutation, can cause the evolution of quantitative characters in the absence of selection (Lynch 1990; Futuyma 1998, pp. 437–438). To compare the observed differentiation in body size evolution with the maximum phenotypic response expected due to drift, we used a neutral rates test (Lande 1977; Lynch 1990). This test compares observed rates of divergence in quantitative traits with expectations under the null hypothesis of only mutation and drift (for calculations see Lynch 1990; Schluter 2000, pp. 91–92). Using divergence between samples, the number of elapsed generations, and the phenotypic variance, it is possible to calculate an evolutionary rate, Δ, used in such tests. Δ is a per generation ratio of between-species phenotypic variance to within-species phenotypic variance (Lynch 1990). Based on population-genetic theory and empirical data regarding the mutational rate of input of genetic variance, the neutral expectation for Δ lies within the range of 0.01–0.0001 (Schluter 2000). Here we compared divergence in PC I scores for the Isla Escudo population with the grand mean of the four mainland populations.

Complementarily, we then tested for a consistent pattern in the direction of body size evolution by a one-tailed signs test (see Lande 1977, p. 442). We compared the mean PC I score of each of the five insular populations that were significantly different from mainland populations (from Anderson and Handley 2001) with the grand mean of mainland populations, testing whether the sign of change was consistently negative (Zar 1996). Then, we combined Cayo Nancy and Isla Bastimentos into a singe datum and repeated the test for the four geologically independent populations with body size significantly different from that of the mainland samples.

Evolutionary Rates and Selection Intensity

To compare the evolution of body size in the sloths of Bocas del Toro with other known cases of rapid evolution under directional selection (which was implicated by the results of the regressions), we conducted a retrospective selection analysis (Lande 1979; Endler 1986, pp. 171–175; Arnold 1988; Hartl and Clark 1989, pp. 441–446). We first calculated the phenotypic change for the population of *Bradypus* on Isla Escudo (*B. pygmaeus*) by subtracting the grand mean of PC I scores for the four mainland populations in Bocas del Toro (z_1) from the mean PC I score for the Escudo population (z_2) and dividing that difference by the pooled standard deviation (s_p, square root of the mean square error from an ANOVA of the five populations), thus expressing body size change in standard deviation units,

$$\text{body size change} = (z_2 - z_1)/s_p. \tag{1}$$

Dividing phenotypic change (in standard deviation units) by the number of generations (g) produces a common measure of evolutionary rate, the haldane (Haldane 1949; Gingerich 1993; Hendry and Kinnison 1999; see also Lynch 1990). Although age at first reproduction (~3 years) and birth frequency (approximately annually) for *Bradypus* are known, data regarding longevity and survivorship remain deficient (Taube et al. 2001 and references therein). Nevertheless, based on available demographic data for *Bradypus* (Montgomery and Sunquist 1978; Hayssen et al. 1993; Pinder 1993; Richard-Hansen and Taube 1997; Taube et al. 2001) and more complete data for *Choloepus* where necessary (summarized in Nowak 1999), we approximated an average generation time of 6 years for *Bradypus* in the wild. We then calculated the number of generations (g) of *Bradypus* since the formation of Isla Escudo (8900 years ago). It follows that,

$$\text{evolutionary rate in haldanes} = \text{body size change}/g. \tag{2}$$

The standardized linear selection differential, or selection intensity (i) is equal to the evolutionary rate in haldanes divided by heritability of the trait (Hendry and Kinnison 1999). Heritability (h^2) of body size typically ranges from 0.2 to 0.7 in mammals (Leamy 1985, 1988; Mavrogenis and Constantinou 1990; Yamaki and Sagae 1991; Ahlborn and Dempfle 1992; Beniwal et al. 1992). Dividing the evolutionary rate in haldanes by h^2 estimates (0.2–0.7) yielded a range of estimates for the average per generation net selection differential (S),

$$i = S = \text{evolutionary rate in haldanes}/h^2. \tag{3}$$

Because we converted to standard deviation units in calculating haldanes, the selection differential (S) is equal to the per generation selection intensity (i; or standardized linear selection differential) often reported in the literature (e.g., Endler 1986; Kingsolver et al. 2001). These analyses (calculation of haldanes and selection differentials) are based on the following assumptions: (1) constant selection pressure and heritability; (2) a nearly constant body size in mainland populations since the formation of Isla Escudo; and (3) that sloths on Isla Escudo had the same average body size as adjacent mainland populations at the time of isolation.

When time series are present, such as several independent cases of dwarfism, evolutionary rates are best calculated based on the overall relationship between morphological change and time (rather than based only on the endpoints). The rate is estimated from the slope of the regression of morphological change in standard deviation units onto number of generations, following Hendry and Kinnison (1999). This approach takes advantage of all available information and therefore is less vulnerable to errors in estimates of morphological change caused by small sample sizes. Thus, after calculating haldanes and selection intensity for the Escudo population compared with the mainland populations, we recalculated the same values from the slope of the relevant

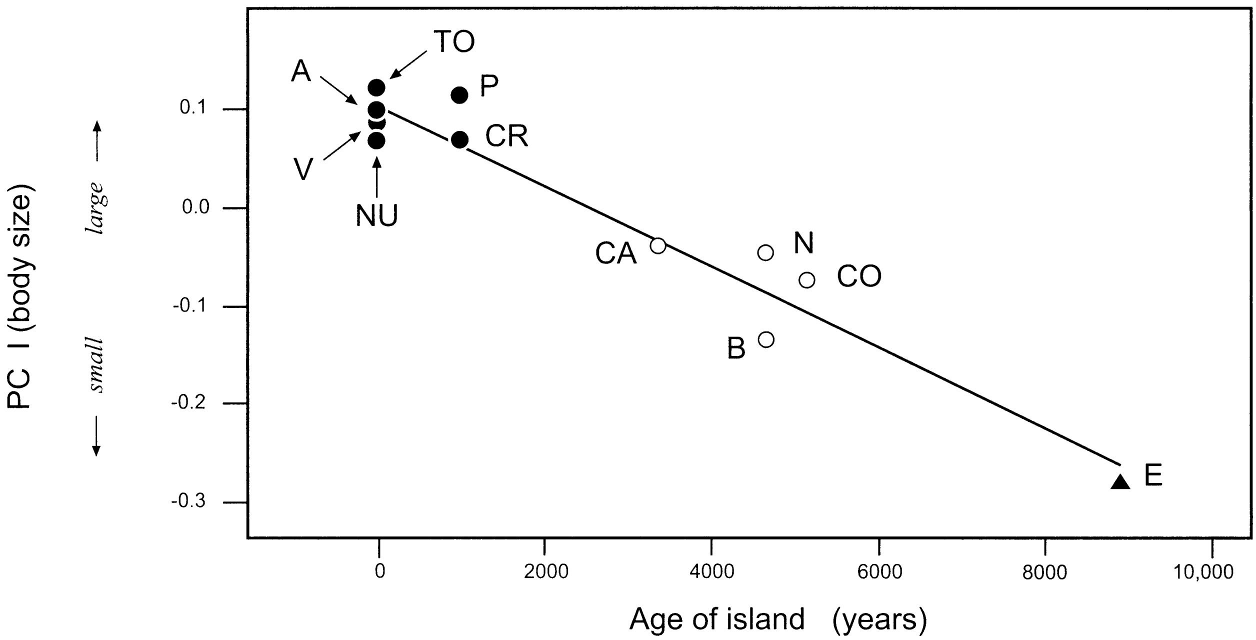

FIG. 4. Regression of general body size (mean PC I score for each locality) on island age (years since isolation) for populations of *Bradypus* from Bocas del Toro, Panama, explaining 94% of the variation in body size among locality means. Isla Escudo is marked with a solid triangle; the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and mainland localities and the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. A, Almirante; B, Isla Bastimentos; CA, Cayo Agua; CR, Isla Cristóbal; CO, Isla Colón; E, Isla Escudo; N, Cayo Nancy; NU, Ñuri; P, Isla Popa; TO, Tierra Oscura; V, Península Valiente.

regression of all geologically independent populations (see above).

To compare our results with other examples of evolutionary change where haldanes are not given (e.g., Gingerich 1983), we calculated the evolutionary rate of change of the Isla Escudo population in darwins (Haldane 1949, p. 55; Futuyma 1998, p. 159). In contrast to haldanes, darwins are calculated per years elapsed between samples, rather than by number of generations; furthermore, they are not expressed in standard deviation units. One darwin is equal to a change by a factor of e (2.718) per million years. Over t years elapsed between samples, the rate of evolutionary change of the continuously varying (quantitative) trait z in darwins is equal to $10^6(\log_e z_2 - \log_e z_1)/t$. Despite these drawbacks and special sensitivity to the interval over which it is measured (see Gingerich 1993, 2001; Hendry and Kinnison 1999), the darwin can be used when the standard deviation and generation time are not known (especially common with fossil taxa) and to compare with such cases. For these calculations, we used greatest length of skull measurements as a measure of overall body size (GLS, from Anderson and Handley 2001) instead of scores on PC I because darwins are based on logarithmic ratios and are thus not amenable to negative numbers, such as in standardized principal component scores. Furthermore, darwins cannot be calculated on traits measured on interval scales (where the zero point is arbitrary; Hendry and Kinnison 1999, p. 1644). We again compared the mean for *B. pygmaeus* on Isla Escudo with the grand mean of the four mainland localities in Bocas del Toro.

RESULTS

Regressions

For insular populations, separate regressions of mean PC I scores on island age and on distance from the mainland were significant ($P < 0.001$, $P = 0.019$, respectively), but a regression on island area was not ($P = 0.337$). Of the two significant regressions, the percent of variation explained (R^2) for the regression on island age was much higher (93.8%) than for the regression on distance (70.0%). The regression on island age passed a pure-error (lack-of-fit) test for linearity ($P = 0.892$), whereas the same test for the regression on distance from the mainland could not be performed due to a lack of true repeats (Draper and Smith 1981). In a multiple linear regression of mean PC I scores on both island age and distance from the mainland, island age was significant ($P = 0.017$), but distance was not ($P = 0.793$).

Including both mainland and insular populations, regressions of PC I on island age and distance were each significant ($P < 0.001$). R^2 was once more higher for island age (93.8%) than for distance (78.6%). The regression on area was not significant ($P = 0.337$). The regression on island age passed a pure-error (lack-of-fit) test for linearity ($P = 0.621$), but the regression on distance did not ($P = 0.036$). In a two-variable multiple regression, island age was significant ($P = 0.002$), but distance was not ($P = 0.571$). The linear regression of mean PC I scores on island age (PC I = 0.103 − 0.000041 [island age]) shows a clear decrease in body size with island age (Fig. 4).

Regressions for all geologically independent populations showed the same patterns. The regressions of mean PC I scores onto island age and distance from the mainland were significant ($P < 0.001$, $P = 0.006$, respectively), but that onto island area was not ($P = 0.289$). The regression onto island age passed a pure-error test for linearity ($P = 0.726$), in contrast to the one on distance ($P = 0.006$). In the multiple regression, age was significant ($P = 0.005$) but distance was not ($P = 0.245$). The simple linear regression onto age explained 96.9% of the variation among means of independent populations, compared to an R^2 of 81.3% for distance from the mainland. No step functions or curvilinear relationships were evident in visual examinations of PC I scores versus island age, area, or distance from the mainland or between residuals of the regression on island age versus area or distance.

Genetic Drift

The rate Δ calculated comparing mean PC I scores for the Escudo population versus the grand mean of the mainland populations was 0.0055. The range of values under the neutral expectation is 0.01 to 0.0001, bracketing the observed result. Thus, the magnitude of the observed rate could be due to drift. In contrast, regarding the direction of morphological evolution in the five islands with sloth populations different from the mainland on PC I, the probability of all being smaller in body size was significant ($P = 0.0312$; one-tailed binomial). Likewise, the probability of all four geologically independent populations being smaller was of marginal significance ($P = 0.0625$; one-tailed binomial).

Selection Intensity and Evolutionary Rates

The average body size (PC I) of the population of *B. pygmaeus* on Isla Escudo is 7.02 standard deviations smaller than mainland sloths ($z_2 = -0.2811$, $z_1 = 0.0899$, $s_p = 0.0528$). Given an estimated generation time of 6 years and the 8900-year existence of Isla Escudo, that morphological change equals an evolutionary rate of -0.00473 haldanes. Using the slopes of the regressions of body-size change in standard deviation units onto number of generations for the seven geologically independent populations yielded similar estimates. Least-squares regression gave an evolutionary rate of -0.00428 haldanes, and the reduced-major-axis regression produced an estimate of -0.00434 haldanes ($s_p = 0.0604$ for both). The 95% confidence interval for the slope of the least-squares regression did not include zero (lower limit -0.00333; upper limit -0.00522). Even a 99.9% confidence interval on the slope (rate in haldanes) failed to include zero, firmly rejecting the hypothesis of no evolution in body size. Using a range of 0.2–0.7 for heritabilility, these three regression approaches yielded similar ranges for the standardized linear selection differential (i; average per generation selection intensity) of -0.0068 to -0.0237 (Escudo vs. mainland populations); -0.0061 to -0.0214 (least-squares regression); and -0.0062 to -0.0217 (reduced-major-axis regression) standard deviations.

Body size in *B. pygmaeus* showed a raw change of -10.69 mm in mean GLS measurements (79.72 mm to 69.03 mm; from Anderson and Handley 2001), corresponding to a change of -0.144 in natural-log units ($\log_e 69.03 - \log_e 79.72$). Such a shift over the approximate 8900-year history of Isla Escudo yielded a rate of 16.18 per million years on a natural-log scale, or 16.18 darwins. Using just the specimens for which PC I scores are also available produced a raw change of -11.19 mm in mean (79.59 mm to 68.40 mm), corresponding to a change of -0.152 in natural-log units, or 17.02 darwins.

DISCUSSION

Biogeographic Hypotheses

Island age explained an overwhelming 94–97% of the variation in body size among populations and revealed a linear relationship (e.g., Fig. 4). Although regressions on distance from the mainland were also significant, pure-error tests indicated that the relationship was not linear. Furthermore, multiple regressions showed that distance from the mainland had no independent effect (nonsignificant partial sums of squares). Distance was significant in simple linear regressions (by itself) only because of its high correlation with island age ($r = 0.845$ for insular populations; $r = 0.891$ for all populations; $r = 0.865$ for independent populations). Island area was never a significant predictor of sloth body size. These patterns were consistent for analyses of the insular populations, all populations, and all geologically independent populations.

Thus, we find no evidence for differing optimal body sizes on different islands. No linear, curvilinear, or step functions were evident between body size and island area. This suggests that the islands are similar enough in size that selective environments for sloth body size do not vary appreciably among the islands. The islands of Bocas del Toro possess areas that are similar to the smallest of those examined by Heaney (1978). The empirical values corresponding to his theoretical curvilinear relationship between optimal body size and island area are taxon and system specific, and a large range of island areas would be necessary to detect such a pattern. Thus, although we cannot discount area as a possible predictor of optimal body size in *Bradypus* on hypothetical islands of a larger range of areas, the data do not support its importance in this particular system, simplifying further interpretations.

Likewise, we fail to detect any true effect of distance from the mainland on sloth body size. As mentioned above, the multiple regressions indicate that the significance of distance in linear regressions of body size onto distance derives not from the independent predictive power of distance but rather to its high—although imperfect—correlation with island age. On average, more distant islands tend to be smaller in area, but the exceptions serve to separate the effects of distance and age. For example, Isla Colón (an old island close to the mainland) harbors small sloths, whereas Isla Popa (a young island close to the mainland) has large ones (both are of similar area). Thus, the current data provide no evidence that the evolution of smaller body size in these populations has been diluted by differential immigration of large-bodied sloths from the mainland (more immigration on closer islands). Although the resolution of the available data is not fine enough to reject dispersal events categorically, these results are not consistent with the expectations of a system with higher immigration rates for closer islands. Dispersal events may occur, but if so, they are evidently rare.

In contrast to the negative results for island area and distance from the mainland, a clear and easily interpretable pattern is revealed regarding island age. Time since isolation seems to explain the evolution of body size in these sloths: Populations on older islands show smaller average body size. The relationship between body size and age is linear and very tight. It explains 97% of the variation in mean body size among geologically independent populations, with similar values for the other regressions (insular populations and all populations).

Arguments for Selection

We interpret that natural selection drove the evolution of these sloths, for several reasons. Although reductions in body size in insular sloths may have begun as ''stunting'' (sensu Roth 1992), such a purely phenotypic response to insufficient resources cannot explain the magnitude and diversity of dwarfism found on these islands. The Isla Escudo sloth has diverged in body size much more (seven standard deviations) than seems plausible by stunting alone. Furthermore, the strong relationship between island age and sloth size (Fig. 4) is consistent with directional selection—with each geologically independent island representing a snapshot in time. In contrast, a phenotypic response would be evident in even the youngest islands.

Likewise, although genetic drift can cause the evolution of quantitative characters in the absence of selection (Futuyma 1998, pp. 437–438), the uniform direction of the evolution of body size is not predicted by such models. Although the divergence found here lies within the range possible due only to drift and mutation, failure to reject selection using this test provides only weak evidence against it (Hendry and Kinnison 1999, p. 1648). Indeed, many well-known cases attributed to selection fall below the maximum rate possible under neutral (drift) hypotheses (Schluter 2000). Finally, if all five islands with significantly smaller sloths are considered, we can reject the hypothesis that the consistent direction of body size change (dwarfism in each case) has occurred by chance. With the geologically independent populations, the probability of four events of dwarfism remains small, although only marginally significant. This consistent direction of body size evolution is not predicted under genetic drift.

Selection Intensity and Evolutionary Rates

Empirical comparisons

Interpreting evolutionary rates.—For the reasons outlined above, it seems reasonable to compare the present evolutionary rates and selection differentials to theoretical models and other known empirical cases. The values that we report for body size in *Bradypus* are averages over the roughly 9000-year existence of Isla Escudo (or over the various intervals of existence of the islands). The pattern of smaller sloths with increasing island ages suggests a uniform selection regime, but given the coarse resolution afforded by this study, other scenarios could produce the same pattern. For example, weak or no selection on size in most intervals, but occasional extreme selection for small size, such as in episodes of aberrant weather, could produce an overall pattern of smaller sloths over time that could not be distinguished from the observed one (see fig. 2 of Hendry and Kinnison 1999). Nevertheless, uniform directional selection pressure for small body size remains the most parsimonious explanation for the observed pattern of dwarfism in the sloths of Bocas del Toro.

Two important factors should be considered in comparisons of evolutionary rates: (1) the interval over which the estimates were measured; and (2) the confidence in the estimate. Several review articles have shown that estimates of evolutionary rate tend to decrease with the interval over which they are measured (Gingerich 1983, 1993, 2001; Kinnison and Hendry 2001). This phenomenon may be due to: (1) exponential assumptions in the calculation of the darwin; (2) mathematical artifacts of plotting a rate versus the time interval over which it was measured; and/or (3) undetected interspersed periods of stasis that dilute estimates measured over longer time intervals (Hendry and Kinnison 1999; see also Schluter 2000, pp. 61–62). Rates in haldanes are not subject to the first problem, and it is thus desirable to separate the effects of intervening periods of stasis from artifactual ones when comparing rates in haldanes. Toward this end, Gingerich (1993, 1994, 2001) proposed log rate versus log interval (LRI) analyses. LRI regressions establish a scaling factor that holds potential for allowing valid comparisons of rates measured over differing time scales. Although the debate regarding evolutionary rates is not yet fully resolved, it currently appears prudent to compare only rates measured over similar time intervals or to take into account a scaling factor in making comparisons of rates measured over differing intervals. Even then, rates in darwins may be difficult to interpret.

Second, the error associated with estimates of evolutionary rates may often be high, but the precision of the estimates can seldom be evaluated because confidence intervals are generally not reported (Hendry and Kinnison 1999). Here, we present confidence intervals for our estimate of evolutionary rate in haldanes (based on the slope of the regression line through all geologically independent populations). Although the precision of that estimate is fairly high (and the rate is certainly greater than zero), all of our estimates are based on a generation time of 6 years for *Bradypus* in the wild. As previously mentioned (see Materials and Methods) *Bradypus* reach sexual maturity at approximately 3 years of age, and birth frequency is about 12 months, but data regarding longevity and survivorship are lacking (Taube et al. 2001). A change in estimated generation time of only one year (e.g., to 5 years), would decrease the resulting evolutionary rate to nearly the lower limit of the confidence interval (to -0.00356 haldanes). However, even with extremely low survivorship and longevity, the plausible generation time should be no lower than 4 years, which yields a rate of -0.00285 haldanes; similarly, a generation time of 8 years would correspond to -0.00570 haldanes. Thus, given the uncertainty regarding generation time, a reasonable range for evolutionary rate (including consideration of the confidence interval of the slope), varies less than a half degree of magnitude (from -0.00191 to -0.00664 haldanes). Furthermore, the precision of the estimates of island age is not known but should be investigated (C. O. Handley, Jr. and M. Varn, unpubl. ms.). With these caveats, we proceed to compare with recent reviews.

Comparisons.—Unfortunately, few studies measuring evolutionary rates over similar intervals of time are available. Although examples of fossil vertebrates (measured over millions of years) ranged from zero to 26.2 darwins in Gingerich's (1983) review of evolutionary rates, most were low (geometric mean = 0.08 darwins). The evolutionary rate of over 16 darwins in *Bradypus* also greatly surpasses average rates reported for body size in Cenozoic horses, which did not exceed 0.28 darwins (also measured over millions of years; MacFadden 1986). In contrast, the present rates in darwins lie within the range of the few studies for other post-Pleistocene mammals considered by Gingerich (1983; rates in haldanes not available). Gingerich (1983) plotted $\log_e$ rate (in darwins) versus $\log_e$ measurement interval (in years) for the studies he considered, yielding a roughly linear pattern and revealing an apparent scaling factor for such studies. The Bocas del Toro sloths would fall nicely into that relationship. Thus, when measured in darwins, they represent a typical value for the interval of measurement.

In contrast, several recent reviews of evolutionary rates from studies reported in the literature consider only microevolutionary time scales. Interestingly, comparisons of the Bocas del Toro sloths with rates calculated in haldanes differ from comparisons with rates in darwins. For example, Hendry and Kinnison (1999) surveyed rates measured over 1–125 years (1–140 generations). Despite being measured over a much longer time interval, the absolute value (0.00434 haldanes) of the evolutionary rate of sloths in Bocas del Toro lies near the center of the cluster of magnitudes they report in haldanes. In contrast, all but a few of those studies showed a rate in darwins faster than that of the sloths. Reconstructed rates for the sloths of Bocas del Toro are also similar to the median of absolute values of rates reported in haldanes (0.00580) in a subsequent, larger review of studies measured over 300 generations or less (Kinnison and Hendry 2001). In contrast, when measured in darwins, the rate of evolution of sloths (16.18–17.02 darwins) pales in comparison with their median of 1151.3 darwins. Likewise, rates measured over about 50 years for insular populations of rodents showed estimates in haldanes similar to the sloths of Bocas del Toro but much larger ones in darwins (Pergams and Ashley 2001). These differences derive partially from the relatively long generation time of sloths (taken into account in calculating haldanes but not darwins), but also highlight the difficulty of interpreting rates measured in darwins (Gingerich 1993; Hendry and Kinnison 1999; see above). Extending the regression line of evolutionary rate (in $\log_{10}$ haldanes) on $\log_{10}$ generations from Kinnison and Hendry (2001)—potentially correcting for the interval over which the rates were measured—the case of *Bradypus* in Bocas del Toro would lie above the regression line, but no farther above it than many of the points used to make the line. Thus, after taking into account a scaling factor, the present rates appear typical, or perhaps even strong, when measured in haldanes.

Our reconstructed selection intensity (i), of -0.0062 to -0.0217 (from reduced-major-axis regression) standard deviations for body size in the Bocas del Toro sloths is weak compared with some strong selection intensities that have been measured in the field in short-term studies. For example, the selection intensity on corporal measurements of one of the Galápagos finches, *Geospiza fortis*, ranged 0.21–0.30 during an intense drought, but was less or even opposite in trend direction in other years (Grant 1986; Futuyma 1998). Selection intensities of one or two standard deviations per generation in quantitative traits under natural conditions are not uncommon (Endler 1986, pp. 208–211), but such strong directional selection is seldom maintained for many generations (Hendry and Kinnison 1999).

Clearly, scaling of evolutionary rates remains a controversial area of much current research. Perhaps the most salient feature of the present analyses regards the consistency of the pattern. Because the time series of sloths of Bocas del Toro provides an example of linear decease in body size with increasing island age, they likely represent a system whose estimates of evolutionary rates and selection intensity are not diluted by intervening periods of stasis. Similar rates in haldanes have been reported over short time intervals (<100 years; Pergams and Ashley 2001). What is noteworthy is that such rates are evidently sustained in the sloths of Bocas del Toro. We detected no slowing of evolutionary rates in the four geologically independent populations of dwarf sloths (regression of $\log_e$ haldanes on $\log_e$ island age following Gingerich 1993, 2001; $P = 0.692$, $R^2 = 9.5\%$). Thus, this example may represent continuity between micro- and macroevolutionary processes, as the differentiation in body size has been an integral part of the speciation process in the oldest insular population (see Anderson and Handley 2001). The archipelago of Bocas del Toro clearly constitutes an outstanding system for similar studies of other taxa, as well as complementary work examining genetic differentiation among the various populations.

It is noteworthy that sustained strong selection would likely lead to population extinction, especially in small populations (Bürger and Lynch 1995). If compared with selection intensities and evolutionary rates in haldanes measured over very short time frames, selection on the sloths of Bocas del Toro was not especially strong (but note complications of comparing across intervals of measurement). The empirical rates here, at least as measured over thousands of years between samples, lie well below what are considered maximal sustainable rates (Bürger and Lynch 1995; Hendry and Kinnison 1999).

Finally, the dependence of body size in sloths on time (years since isolation) highlights the fact that when more than one case of dwarfism or gigantism is present in the same taxon, the largest absolute divergence (rather than the average divergence) best reflects the evolutionary potential of that taxon for change in body size. Unfortunately, such an estimate may suffer from higher error because of smaller sample sizes. However, when possible, we suggest that synthetic treatments of the evolution of body size on islands (e.g., Lawlor 1982; Brown et al. 1993) should use maximal divergence in body size for each taxon in further analyses.

Comparisons with theory

Models from population genetics describing the evolution of quantitative characters predict a morphological shift under changing environmental conditions such as those experienced by the sloths of Bocas del Toro (Lande 1980, 1986; change in the ''individual fitness function'' of Kirkpatrick 1982). Furthermore, environmental change that fosters a change in selection pressures can promote a morphological shift of several standard deviations in a small, isolated population within ''a few thousand generations'' (Lande 1980, p. 476). The shift of seven standard deviations in body size in the *Bradypus* of Isla Escudo probably occurred in approximately 1500 generations, falling within the predictions of theory.

However, the linearity of the response does not fulfill theoretical expectations. If a particular smaller body size is optimal on islands, then selection should be strongest immediately after island formation, when the population is farthest from the new adaptive peak. Body size would then asymptotically approach the equilibrium (optimal body size) over time, as selection intensity decreased. This is clearly not the case in the *Bradypus* from Bocas del Toro, where sloths from the youngest islands (Isla Popa and Isla Cristóbal) are not significantly different in body size from mainland samples. Skulls of sloths from those islands do appear slightly more gracile than those of mainland individuals, however (Anderson and Handley 2001). One possible explanation is that the basis for changes in optimal body size lies with the disappearance of other species in the community, which does not occur immediately upon island formation. Alternatively, the adaptive peak for optimal body size might shift as a function of the population's average body size (presumably by some frequency-dependent mechanism; see Bürger and Lynch 1995). Because of these discrepancies, future work is necessary to reconcile the present results with theory or perhaps develop theoretical models regarding conditions under which morphological divergence would be linear for thousands of generations in new selective environments.

Possible Selective Forces

Changes in diet, resource limitation, and absence of mainland predators may all have contributed to selection for smaller size. Many small sloths on the islands, and all from Isla Escudo, were collected in mangroves, a habitat that *Bradypus* usually does not inhabit on the mainland. Thus, some sloths on the outer islands, and certainly those on Isla Escudo, probably eat primarily *R. mangle* leaves, which are coarse and leathery (Everett 1981). Mainland sloths eat the leaves of many terra firma forest trees, especially those of *Cecropia*, a short-lived successional tree with tender leaves protected by ants rather than by chemicals or lignin (Carroll 1979; Everett 1981). Therefore, a poorer food source may have interacted with evolutionary processes in these sloths.

Based on what is known of folivore biology, however, one would not necessarily predict smaller body size given a poorer food source. Principles of energetics and allometry of body proportions (Grand 1978; McNab 1978) demonstrate that in primates, for example, the largest species must acquire protein from leaves because they cannot gather enough insects (which are high in protein) and fruits are too low in protein (Hladik 1978). Furthermore, the relatively large storage capacity of herbivore intestines is related to their need to retain large volumes of plant matter for long periods of time, to accommodate the fermentation process (Parra 1978). Smaller herbivores, in fact, ''are faced with a paradox, that is as their size is decreased their energy requirements per unit weight are increased and their fermentation contents per unit weight are decreased'' (Parra 1978, p. 208).

Even though an energetically poorer food source might favor larger body size, a smaller sloth's absolutely lower energy requirements could allow survival and successful reproduction with less total resources (Roth 1992). Large mammals are often resource limited on islands, favoring smaller size (Heaney 1978; Lomolino 1985; Roth 1992). Conversely, larger size may be advantageous for greater digestive efficiency and in antipredator defense on the mainland (see also discussion in Alder and Levins 1994). Several species of felids that prey on *Bradypus* are present on the mainland but have not been observed on the outer islands of Bocas del Toro and are assumed to have been extirpated subsequent to isolation (Handley 1993, unpubl. data). Additional studies are clearly called for, investigating possible relationships between optimal body size and metabolism, diet, and community composition.

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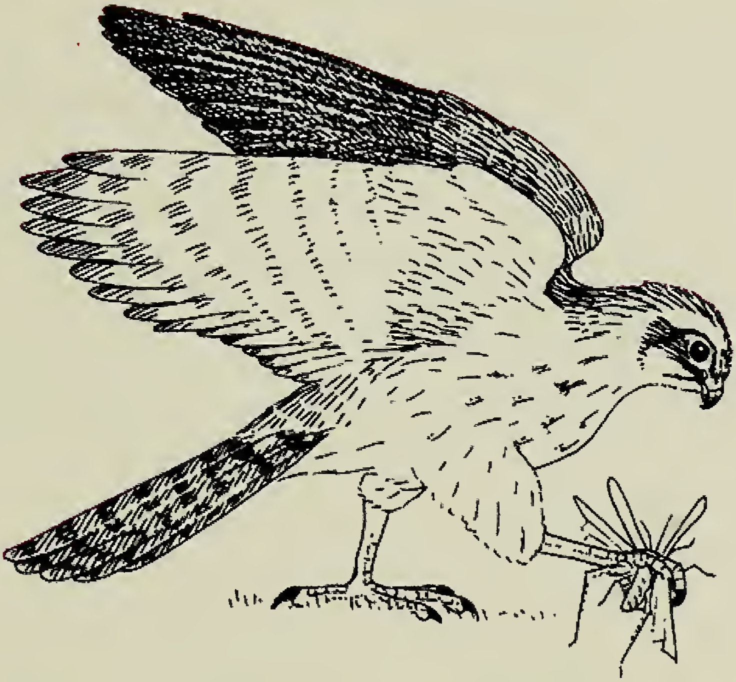

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A new species of three-toed sloth (Mammalia: Xenarthra) from Panamá, with a review of the genus *Bradypus*

Robert P. Anderson and Charles O. Handley, Jr.

(RPA) Natural History Museum & Biodiversity Research Center, and Department of Ecology & Evolutionary Biology, 1345 Jayhawk Blvd., University of Kansas,
Lawrence, Kansas 66045-7561, U.S.A.;
(COH, Jr.—deceased) Division of Mammals, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—Morphological and morphometric analyses of three-toed sloths (*Bradypus*) from the islands of Bocas del Toro reveal rapid differentiation of several populations during the Holocene. These islands, lying off the Caribbean coast of western Panamá, were separated from the adjacent mainland by rising sea levels during the past 10,000 years. The sequence of island formation and the approximate ages of the islands are known. In at least four independent events, sloths on five of the islands evolved smaller size following insularization. Sloths on the younger islands remain conspecific with mainland populations of *Bradypus variegatus*. On Isla Escudo de Veraguas—the oldest and most remote island of the archipelago—however, the three-toed sloth has differentiated to the species level, and we here describe it as *Bradypus pygmaeus*. We provide updated diagnoses and distributions for the species of *Bradypus*, including a key to the genus.

Resumen.—Se realizaron análisis morfológicos y morfométricos de los perezosos de tres dedos (*Bradypus*) de las islas de Bocas del Toro, que mostraron una diferenciación rápida de varias de las poblaciones durante el Holoceno. Estas islas, que se ubican en la costa caribeña del occidente de Panamá, se separaron de tierra firme debido a aumentos en los niveles del mar durante los últimos 10.000 años. Se conoce la secuencia de formación de las islas y sus edades aproximadas. Los perezosos de cinco de las islas evolucionaron hacia un tamaño corporal menor en por lo menos cuatro eventos independientes, siguiendo el proceso de insularización. Consideramos que tanto los perezosos de tierra firme como los de las islas jóvenes son representantes de la especie *Bradypus variegatus*; sin embargo en la Isla Escudo de Veraguas, la más vieja y más remota del archipiélago, el perezoso de tres dedos ha logrado el nivel de especie y lo describimos acá como una especie nueva, *Bradypus pygmaeus*. Presentamos caracteres diagnósticos y distribuciones para las especies de *Bradypus*, incluyendo una clave de las especies del género.

Together with armadillos and anteaters, sloths make up the Neotropical order Xenarthra (Gardner 1993, or magnorder Xenarthra sensu McKenna & Bell 1997). Two distantly related genera of sloths, *Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths) are extant. Over much of their ranges, one species of *Choloepus* and one species of *Bradypus* occur together in the same habitat, exhibiting biotic sympatry (= syntopy; Sunquist & Montgomery 1973, Wetzel 1985, Taube et al. 1999). The two genera are easily distinguished by the number of clawed digits on their forelimbs (two for *Choloepus*; three in *Bradypus*), by the blunter muzzle of *Bradypus,* and by dentition—stronger and more complex in *Choloepus,* while simple and peg-like in *Bradypus* (Naples 1982, Wetzel 1985). Here we consider only the three-toed sloths, *Bradypus.*

The three nominal species of *Bradypus* can be distinguished both externally and cranially (Wetzel & Avila-Pires 1980, Wetzel 1985). The maned sloth (*Bradypus torquatus*) of southeastern Brazil has a distinctive plume or mane of long, jet-black hair from its nape to the middle of its back, and its skull is characterized by inflated pterygoid sinuses (illustrated by Wetzel 1985:10). Both the pale-throated sloth, *Bradypus tridactylus* (Guianas, eastcentral Venezuela, and northcentral Brazil), and the brown-throated sloth, *B. variegatus* (Honduras to Argentina), lack the mane and inflated pterygoids. Adult males of these two species also have a large orange patch (speculum) on the dorsum. They may be distinguished from each other by the bright golden-yellow throat and face in *B. tridactylus,* whereas the throat is brownish, at least at the base of the hairs, in *B. variegatus.* Most *B. variegatus* also possess a facial stripe not present in *B. tridactylus.* A single pair of large foramina in the anterodorsal nasopharynx in *B. tridactylus* are lacking in *B. variegatus* (illustrated in Wetzel 1985:10). Emmons & Feer (1997) provided external color illustrations of these sloths.

Three-toed sloths are arboreal folivores. They eat leaves of a variety of trees, including, but by no means limited to, *Cecropia* spp., which is a common early successional tree in Neotropical rainforests (Carvalho 1960, Montgomery & Sunquist 1975, Chiarello 1998b). Concomitant with their energy-poor diet, they have low metabolic rates and are not fully homeothermic (Britton & Atkinson 1938). Interestingly, temperature regulation is more effective in pregnant females (Morrison 1945). The percent of body weight made up of muscle in *Bradypus* is about half that of most mammals (Britton & Kline 1939); its muscle mass to surface area ratio may not be enough to create sufficient heat to maintain a constant body temperature. Clearly, the low level of energy expenditure by three-toed sloths for both movement and thermoregulation directly relates to their diet of leaves.

The natural history of *Bradypus* indicates a low potential for dispersal. Sloths avoid predation largely by avoiding detection, moving very slowly in trees (Brattstrom 1966). Their small home ranges average 1.6 ha (Montgomery & Sunquist 1975, see also Chiarello 1998a). Furthermore, their outer fur harbors an alga, which grows in grooves in the surface of the hair (Alston 1879:183, Aiello 1985), giving the pelage a green tint and providing camouflage. Sloths move even more slowly on the ground than in trees, traveling on average 0.4 km per hour (Britton & Kline 1939). Surprisingly, they are known to swim well in rivers (Beebe 1926:7–9, Carvalho 1960), but we have found no reference to their swimming in salt water. Perhaps they have a behavioral aversion to salt water or to rough water and wave action. Their relatively large size, restricted diet, and low dispersal potential make sloths a model system for investigating the evolution of body size in large insular mammals.

The islands of Bocas del Toro.—The province of Bocas del Toro is located on the Caribbean coast of northwestern Panamá adjacent to Costa Rica (Fig. 1). Just off the coast lies a group of continental islands that were formed during the Holocene as a result of postglacial events, including rising sea level and continental submergence due to meltwater loading and redistribution of the Earth's magma. Rising sea levels isolated hilltops and ridges, first as peninsulae, and then eventually completely separated them as islands. The islands of Bocas del Toro have low elevations and occupy a Tropical Moist Forest life zone, *bosque húmedo tropical* (OEA 1959). They vary in age, size, distance from the mainland, and depth of surrounding water. Mangrove swamps (primarily red mangroves, *Rhizophora mangle*) fringe parts of the shoreline of Bocas del Toro and the coasts of some of the islands, possibly acting as added barriers to the dispersal of some species.

Combining ocean floor topography with studies of pollen and coral cores from the western Caribbean allowed Handley and M. Varn (in litt.) to determine the sequence of island formation and to estimate the dates of separation events for the various islands of Bocas del Toro. We present their general conclusions as an introduction to this island system and to interpret the evolution of three-toed sloths in Bocas del Toro. Assuming that the present-day submarine topography of Bocas del Toro is not very different from that of the terrestrial topography 10,000 years ago (before flooding), then the depths of water at which land bridges to various present-day islands disappeared should be apparent from current sea-floor maps. Thus, given estimates of sea level at various time intervals in the past, it is possible to estimate the approximate date of isolation of each island. Handley and Varn obtained sea-floor data from maps of Bocas del Toro produced by the U.S. Army Map Service. Using geographic information systems (GIS) software, they digitized data points from isobars below present sea level. With a program produced by the Morphometrics Laboratory of the National Museum of Natural History, they converted the data points to a database transferable to Surfer 4 and then connected them to produce maps of bathymetric contours of Bocas del Toro for various depths below present sea level.

To estimate sea levels over the past 10,000 years, Handley and Varn utilized three models based on coral and pollen cores taken in the western Caribbean. Radioisotope dating of *Acropora palmata,* a coral restricted to the upper 5 m of water, formed the bases of the curves of depth-below-current-sea level vs. time produced by Lighty et al. (1982) and Fairbanks (1989). Bartlett & Barghoorn (1973) used the pollen of *Rhizophora mangle* in deep-sea cores from the Gatún Basin in Panamá to produce a similar curve. *Rhizophora mangle* is an obligate saltwater species and represents the major component of Neotropical coastal mangrove swamps. Handley and Varn then created a composite curve with years-before-present and depth-below-current-sea-level as axes. Using this curve, they roughly dated each of the bathymetric maps and thus estimated island ages from dates of disappearance of land bridges between islands and the mainland. Even if their absolute dates err in one direction or the other, relative dates of island formation will be correct to the extent that sea-floor contours in this region have remained constant through the Holocene.

Isla Escudo de Veraguas (= Isla Escudo) occupies a position well outside the Laguna de Chiriquí (Fig. 1a), and was the first of the islands to be separated from the mainland of Bocas del Toro (ca. 8900 years B.P.). It fragmented from the eastern shore of the Península Valiente and is not directly related to the other islands (Fig. 1b). To the northwest of the Península Valiente and Isla Escudo, the islands of the Laguna de Chiriquí are much younger (Fig. 1a). They fragmented sequentially from the Península Tierra Oscura, which was once a long, *J*-shaped peninsula jutting out from the southwestern shore of the Laguna de Chiriquí. The peninsula was formed by the opening of the Boca del Drago Pass at the western end of the Laguna (Fig. 1b). These islands are related to each other, but not to Isla Escudo. The outermost, facing the ocean, are about 5000 years old: Isla Colón, which was the first to split off of the Península Tierra Oscura (ca. 5200 years B.P.), and Isla Bastimentos, which separated from the peninsula along with what now is Cayo Nancy (ca. 4700 years B.P.). Cayo Agua became isolated from the adjacent mainland (now part of Isla Popa) about 3400 years B.P. Cayo Nancy recently split from Isla Bastimentos proper (<1000 years B.P.), and

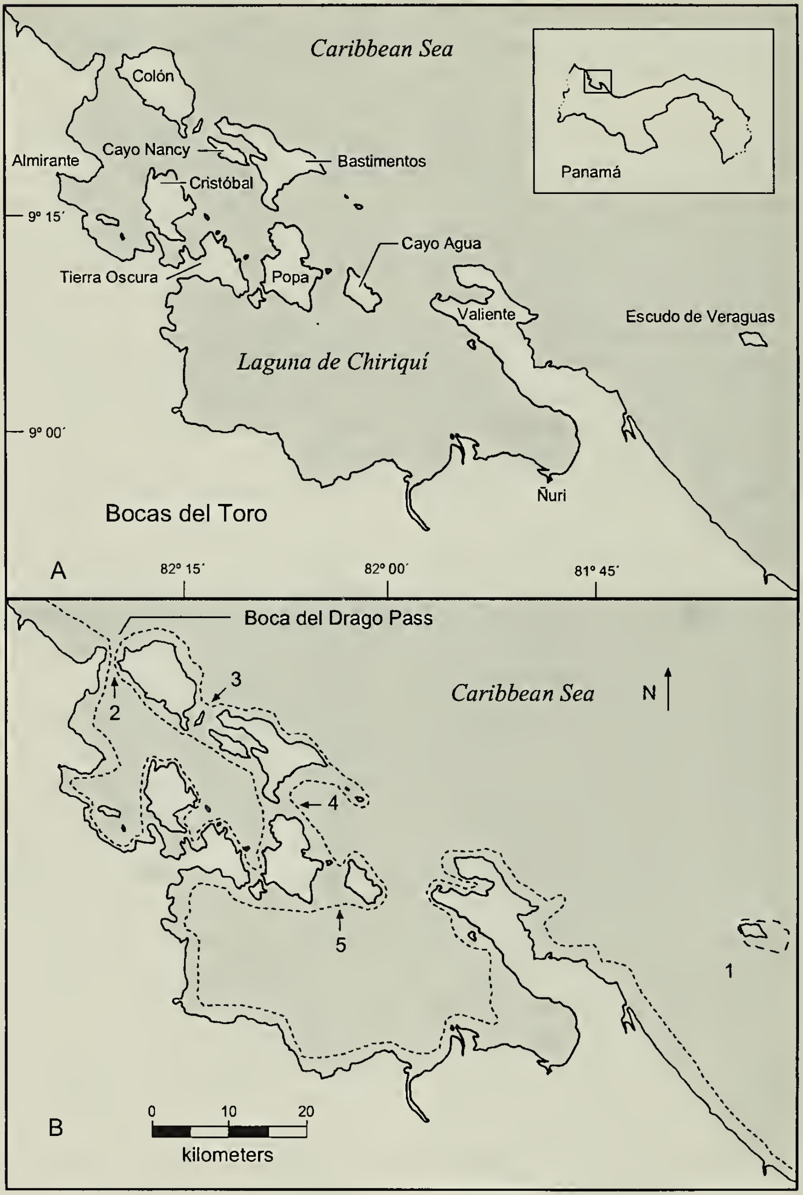

Fig. 1. Maps of Bocas del Toro showing major islands and place names on the mainland (A, upper) and reconstruction of the sequence of island formation (B, lower). In B, the dashed line approximates sea level at 10 m below present. Major events in the formation of the islands (Handley & Varn, in litt.) are as follows: 1) Isla Escudo separated from the southern coast of the province, ca. 8900 years B.P.; 2) the Boca del Drago pass opened, creating a *J*-shaped peninsula in the Laguna de Chiriquí, ca. 6300 years B.P.; 3) Isla Colón became isolated from the peninsula, ca. 5200 years B.P.; 4) the superisland Isla Bastimentos-Cayo Nancy became separated from what remained of the peninsula, ca. 4700 years B.P.; and 5) Cayo Agua was formed, ca. 3400 years B.P. More recently (in the past 1000 years), Isla Cristóbal and Isla Popa separated from the mainland, and Cayo Nancy split from Isla Bastimentos.

mangroves fringe the shallow channel between it and Isla Bastimentos. Isla Popa and Isla Cristóbal each separated from the mainland in the past 1000 years. They are isolated from the mainland only by narrow, shallow channels through mangroves. Island area and distance from the mainland follow, for each of the major islands: Cayo Agua—14.5 km^2, 6.6 km; Cayo Nancy—6.8 km^2, 9.5 km; Isla Bastimentos—51.5 km^2, 6.3 km; Isla Colón—59.0 km^2, 1.5 km; Isla Cristóbal—36.8 km^2, 0.3 km; Isla Escudo—4.3 km^2, 17.6 km; Isla Popa—53.0 km^2, 1.8 km. Further discussion of the history of Bocas del Toro and surrounding regions can be found in Jackson et al. (1996).

Biological interest in the islands of Bocas del Toro emerged recently (summarized in Handley 1959, Olson 1993, Kalko & Handley 1994). Early collecting took place from 1958 to 1967 and intensified from 1987 to 1993, when scientists from the Smithsonian Institution sampled the biota on all of the islands and at several sites on the adjacent mainland. The major mainland collecting sites of sloths were Almirante and Tierra Oscura in the west, and Ñuri and the Península Valiente in the east (Fig. 1a). Smaller collections of *Bradypus* were made at Sibube and Changuinola in western Bocas del Toro. We assume that the fauna of the coastal plain of Bocas del Toro was relatively uniform as the islands sequentially became isolated from the mainland (Handley 1959, Olson 1993, Kalko & Handley 1994). Colinvaux (1997) has shown that despite significant climatological fluctuations, the vegetation of lowland tropical forests in Panamá remained intact during glacial times, lending support to this premise. Subsequent to their isolation, numerous species—including bats, rodents, cats, and weasels present on the nearby mainland—have been extirpated from some or all of the islands. Conversely, a few apparently relict species no longer found on the adjacent mainland are present on the islands. Many of the species that have survived on the islands exhibit marked morphological differentiation from their mainland relatives. For example, a fruit-eating bat, *Artibeus incomitatus,* underwent rapid differentiation on Isla Escudo (Kalko & Handley 1994).

Collectors found three-toed sloths (*Bradypus*) on all of the major islands, as well as at the mainland sites. The *Bradypus* on several of the islands were notably small, and some lived in the red mangroves rather than in upland forest trees as elsewhere. On Isla Escudo, *Bradypus* was found only in mangroves. Except for one purchased at Tierra Oscura from a local boy who claimed to have caught it in a mangrove, no three-toed sloths were found in mangroves on the mainland of Bocas del Toro. The 1993 expedition searched in vain for sloths in extensive areas of mangroves near Ñuri. This ecological separation, coupled with the observed size differences, spawned the current study.

Materials and Methods

Museum specimens.—We examined a total of 531 specimens of the genus *Bradypus* in 13 natural history collections (see Specimens examined) identified as follows: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BM, now Natural History Museum of London); Field Museum, Chicago (FMNH); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); Instituto del Desarrollo de Recursos Naturales Renovables, INDERENA, Bogotá (IND-M; specimens now part of the collection of the Instituto Alexander von Humboldt, Villa de Leiva); Michigan State University Museum, East Lansing (MSU); Museo del Instituto La Salle, Bogotá (MLS); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); United States National Museum of Natural History, Washington, DC (USNM; * denotes specimens returned to Panamá-INRENARE); Universidad del Cauca, Popayán (UC); Universidad del Valle, Cali

(UV), University of Kansas Natural History Museum, Lawrence (KU); and University of Michigan Museum of Zoology, Ann Arbor (UMMZ). Information provided by any source other than the collector is placed in [brackets]. Numbers in (parentheses) after the country name indicate the total number of specimens examined for that country.

In the Specimens examined sections, latitude and longitude are given after the place name to which the coordinates belong. Coordinates provided by the collector appear in parentheses. We provide latitude and longitude in brackets for localities that appear in the following standard references: Brazil—Paynter & Traylor (1991); Bolivia—Paynter et al. (1975); Colombia—Paynter (1997), except where more exact coordinates are given by Hershkovitz (1947) or in original sources cited in Anderson (1999), as noted; Costa Rica—McPherson (1985); Ecuador—Paynter (1993); French Guiana, Guyana, and Suriname—Stephens & Traylor (1985); Nicaragua—USBGN (1956), except where more exact coordinates appear in Genoways (1973); Panamá—Fairchild & Handley (1966); Peru—Stephens & Traylor (1983); and Venezuela—Paynter (1982); additional coordinates for localities in several countries were taken from Hershkovitz (1977), and are so noted.

Pelage analyses.—We analyzed geographic variation in pelage characters in the *Bradypus* from Bocas del Toro and in *B. variegatus* from other regions, principally from Nicaragua, central Panamá, and Colombia. Pelage analyses were based on specimens in the ICN, IND-M, KU, MLS, USNM, UC, and UV collections. Because different methods of field preparation or tanning can affect the color of fur, we did not consider subtle color differences. We focused on striking differences in color and color pattern. We eliminated juvenal and immature animals from the pelage analyses by including only individuals whose skulls indicated them as adult (see Cranial analyses) if skull was available, or that had clearly reached adult size if only a skin was present, based on the total length of specimens in that population verified as adult by their cranial characters.

We found seven pelage characters that varied among populations. Overall facial color is either tan (off-white to pale brown) or yellow (golden). Orange around the eyes is present to various degrees, or absent. Brow-color categories are: dark brow (a terminal band of 2–3 cm of dark brown or black hair), some dark hair on brow (a narrow terminal band of only about 1 cm of dark brown hair), or dark hair not present (in which case the brow is generally pale brown, with no dark terminal band). A distinct boundary line on the brow between the dark hair of the brow and the longer, paler hair of the crown is visible in some specimens, but in others the color of the brow hair blends in with that of the crown. Some individuals have a stripe down the midsagittal plane of the back. Dorsal underfur always appears blotchy, with pale and dark patches, but the surface coloration varies. Overall dorsal appearance is blotchy with brown and beige patches when the outer fur color corresponds to the color of the underfur in that particular area of the dorsum. In other animals, the surface color is uniformly pale, regardless of the color of the underfur. The color of the underfur can be observed by pushing aside the outer fur and examining the shorter underfur. In some specimens, the fur of the crown and the sides of the head is extremely long, overhanging the forehead and sides of the face and creating the aspect of a hood. In other specimens, the fur of the crown and sides of the head is shorter and not noticeably overhanging the face.

Cranial analyses.—For cranial analyses, we included only sloths that had reached adult size (Age classes 2 and 3, as defined below). Because no explicit standards exist for aging *Bradypus* skulls (but see Naples 1982:6–7), we developed the following system of age categories.

Age class 0, newborn and juvenile: all sutures open; size small; anterior skull elements small and poorly developed; masseter-temporal fossa smooth; postmastoid fossa not indicated; frontal sinuses little, if at all, swollen; lambdoidal crest not formed.

Age class 1, immature: all sutures open; size intermediate; anterior skull elements nearing adult proportions; masseter-temporal fossa usually smooth; postmastoid fossa may be indicated; frontal sinuses somewhat swollen; lambdoidal crest present (immatures may retain some juvenal characters).

Age class 2, young adult: all sutures open; size large; anterior skull elements at adult proportions. Young adults must also have some of the following: masseter-temporal fossa rugose to the touch; postmastoid fossa prominent; frontal sinuses swollen; lambdoidal crest sharp-edged.

Age class 3, full adult: some or all sutures closed; size large; anterior skull elements fully developed. Fully adult sloths have most or all of the following: masseter-temporal fossa visibly rugose; postmastoid fossa prominent; frontal sinuses swollen; lambdoidal crest sharp-edged.

Individuals reach adult size by Age class 2 in *Bradypus*. Skulls with all cranial sutures closed clearly represent adults, but closure of even one suture signifies full-adult status. The nasal (internasal) and interparietal sutures are usually the last to close. Closure of the basioccipital-basisphenoid suture represents a good indicator of maturity in bats and rodents, but this suture closes late in *Bradypus* after adult size is attained. Its lack of closure should not be used alone to judge adulthood.

Measurements.—We recorded external measurements—total length (TOTAL); tail length (TAIL); hind foot length (HF); and ear length (EAR)—in mm and body mass in kg from museum labels. Using dial calipers to the nearest 0.1 mm, we took 14 measurements on all adult-sized skulls of *Bradypus* (Age classes 2 and 3) from Bocas del Toro (Fig. 2). To examine geographic variation in size in *B. variegatus* from other parts of its range, we measured only greatest length of skull (GLS) on series of *B. variegatus* of Age classes 2 and 3, using either dial or digital calipers to the nearest 0.1 mm. We chose GLS because preliminary morphometric analyses indicated that it was most highly correlated with general size in *Bradypus*. Specimens from the American Museum of Natural History were not included in the quantitative analyses, but we report them as additional confirmed distributional records. Cranial nomenclature follows Naples (1982). We here define and illustrate (Fig. 2) our measurements for *Bradypus*.

Greatest length of skull (GLS): Distance between the anteriormost point of the nasals and a line connecting the posteriormost surfaces of the occipital condyles.

Anterior zygomatic breadth (AZB): Greatest breadth across the jugal (anterior) zygomata.

Posterior zygomatic breadth (PZB): Greatest breadth across the squamosal (posterior) zygomata.

Postorbital breadth (POB): Least breadth across the constriction of the frontals, posterior to the postorbital processes.

Squamosal process length (SPL): Distance between anteriormost point of the squamosal process of temporal (posterior zygomata), and the notch formed by the junction of the posterior border of the bulla and the mastoid process.

Maxillary toothrow length (MTRL): Greatest alveolar length from the anteriormost edge of the anterior chisel-shaped tooth to the posteriormost edge of the last molariform tooth in a maxillary toothrow.

Postpalatal length (PPL): Distance between the anteriormost margin of the mesopterygoid fossa and the anteriormost margin of the foramen magnum.

Palatal breadth (PB): Greatest alveolar breadth across the lateral margins of the first molariform teeth.

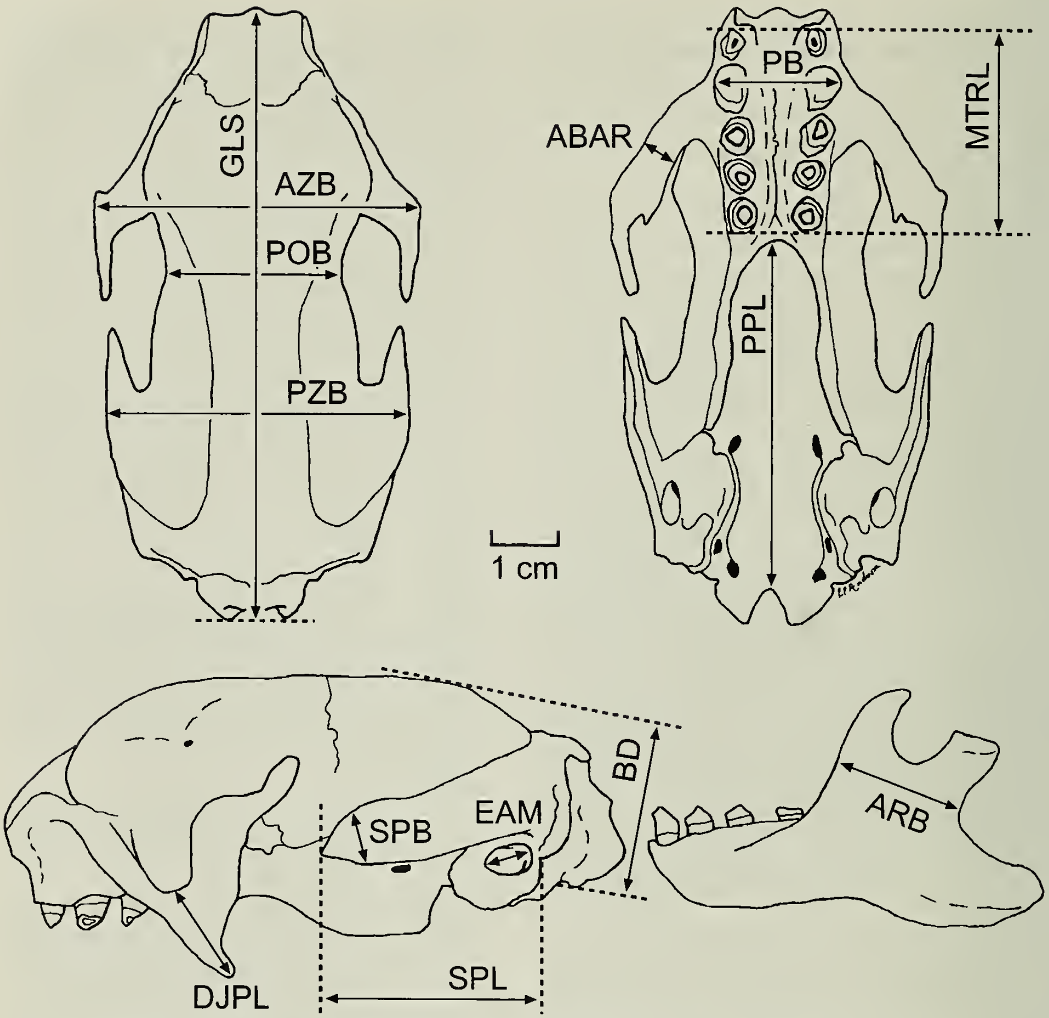

Fig. 2. Dorsal, ventral, and lateral views of a cranium and lateral view of a mandible of *Bradypus variegatus,* illustrating method of taking cranial measurements. Abbreviations and measurements are defined in the text.

Braincase depth (BD): Greatest distance between the medioventral surface of the basioccipital and the dorsalmost point of the braincase.

Antorbital bar breadth (ABAR): Least breadth across the flattened antorbital bar (jugal process of zygomata) anterior to its division into the ascending and descending jugal processes, taken in ventral view.

Descending jugal process length (DJPL): Distance between the ventralmost point of the descending jugal process and the nearest point on the dorsal border of the jugal process.

Greatest external auditory meatus diameter (EAM): greatest internal diameter of the external auditory meatus.

Squamosal process breadth (SPB): Breadth of the squamosal process, taken 5 mm posterior to the anterior tip of the process.

Ascending mandibular ramus breadth (ARB): Least distance between the anteriormost point of the angular notch of the mandible, between the condylar and angular processes, and the nearest point on the anterior margin of the ascending ramus below the coronoid process.

Statistics.—We calculated descriptive statistics and performed analyses of variance (ANOVAs) using MINITAB 11.12 software for personal computers (MINITAB 1996) and used SAS 6.12 for UNIX (SAS 1990) to examine the data using multivariate statistics. We used a Type-I error rate of $\alpha = 0.05$ for all tests. The probability levels that we report should be considered approximate, however, because our sample sizes were too small to test adequately for departures from multivariate normality.

We conducted a multiple-group discriminant function analysis (DFA) on the *Bradypus* of Bocas del Toro using $\log_{10}$-transformed measurements. Collection locality denoted group membership. Ear length and body mass were excluded from the DFA because few individuals carried those measurements. We tested for multivariate differences among localities by F-statistics for Mahalanobis distances between pairs of group centroids using Holm's (1979) modification of the Bonferroni correction for multiple comparisons. We then conducted multiple unplanned comparisons between all pairs of localities for scores on the first two canonical axes, using Tukey's test with a family-wide error rate of $\alpha = 0.05$.

Additionally, we performed a principal components analysis on the same data matrix without regard to collection locality. The first principal component (PC I) of the covariance matrix of $\log_{10}$-transformed measurements was used as the best measure of overall sloth size in further analyses. For the two populations with several individuals of both Age classes 2 and 3 (Cayo Nancy and Isla Escudo), we tested for a difference in mean PC I scores between age classes while controlling for locality, using a general linear model. Likewise, for those localities with multiple individuals of each sex—Cayo Agua, Cayo Nancy, Isla Popa, Península Valiente, and Tierra Oscura—we tested for a difference in mean PC I scores between sexes, again controlling for locality in a general linear model. Finally, we tested for differences between all pairs of localities on PC I, with the same protocols as in the comparisons of scores on the first two canonical axes.

We used measurements of greatest length of skull (GLS) to compare the small sloths from Bocas del Toro with *Bradypus variegatus* from mainland localities outside Bocas del Toro, as preliminary analyses indicated that GLS correlated highly with PC I, and thus represented a good measure of overall size. Series from Bonanza, El Recreo, and Tepeyac (Nicaragua); Bajo Calima-Río Raposo and Tumaco (Colombia); and Mojui dos Campos (Brazil) were our six mainland localities outside of Bocas del Toro, as few specimens were available from other sites. We conducted an ANOVA on GLS measurements of the six mainland samples outside Bocas del Toro and our samples from the five islands with small sloths in Bocas del Toro (Cayo Agua, Cayo Nancy, Isla Bastimentos, Isla Colón, and Isla Escudo), using a Tukey's test with a family-wide error rate of $\alpha = 0.05$.

Results

Pelage.—Externally, the *Bradypus* of Bocas del Toro resemble specimens from central Panamá more closely than they do those of Nicaragua or South America (Table 1). All Central American specimens have tan faces, whereas faces of most South American sloths have a yellowish cast. In addition, while the sloths of Bocas del Toro, central Panamá, and many localities in Colombia have at least some orange coloring around their eyes, Nicaraguan specimens lack this trait. Most individuals from Bocas del Toro have either some (~1 cm) or much (2–3 cm) black or dark brown brow hair. Specimens from central Panamá and extreme NW Colombia match those from Bocas del Toro in this trait, but Nicaraguan and most other South American sloths lack a dark brown brow. A distinct brow line is found in specimens from central Panamá, extreme NW Colombia, and in some localities in Bocas del Toro, but not in specimens from Nicaragua or elsewhere in Central America or western Colombia. Thus, the *Bradypus* from Bocas del Toro group with other Central American and western Colombian three-toed sloths, with closer affinity to those from central Panamá and extreme NW Colombia to the east rather than with sloths from Nicaragua to the northwest.

Within Bocas del Toro, geographically proximate populations share discrete pelage characters, often linking island populations with nearby populations on the mainland (Table 1; Fig. 1). For example, the only populations in Bocas del Toro with individuals lacking a dorsal stripe are found at Tierra Oscura and on the adjacent islands of Cristóbal, Popa, and Cayo Nancy. For dorsal appearance, there is a west-to-east cline from uniform to blotchy. The populations with the highest frequencies of individuals with a distinct brow line are two proximate localities in the west (Isla Colón and the adjacent mainland at Almirante) and two in the east (Isla Escudo and Ñuri, the nearest site on the mainland). Finally, while sloths from most localities in Bocas del Toro have orange eye patches, those of four central localities (Almirante, Isla Cristóbal, Isla Popa, and Península Valiente) have little if any orange. Overall, pelage of specimens from Isla Escudo closely matches pelage characters found at Ñuri. However, characters variable in the Ñuri population appear to be fixed on Isla Escudo. Sloths from Isla Escudo were unique in possessing long hair on the crown and sides of the head, giving the impression of a hood.

Quantitative measurements.—Both univariate and multivariate statistics documented the smaller overall size of *Bradypus* on the five outer islands (the older islands) of the archipelago of Bocas del Toro—Cayo Agua, Cayo Nancy, Isla Bastimentos, Isla

Table 1.—Discrete pelage characters for *Bradypus* from Bocas del Toro as well as from other selected regions throughout the range of *Bradypus variegatus.* Character abbreviations are as follows: face color, tan (T) or yellow (Y); orange on face, yes (Y), slight (slt), or no (N); dark on brow, yes (Y), some (S), or no (N); line on brow, yes (Y) or no (N); dorsal stripe, yes (Y) or no (N); dorsal appearance, uniform (U) or blotchy (B); and hood, yes (Y) or no (N). If samples are mixed for a character, both states are given with the most common state before the slash. Geographic groupings are arranged from NW to SE, with abbreviations as follows: NIC, Nicaragua; A, Almirante; CO, Isla Colón; N, Cayo Nancy; B, Isla Bastimentos; CR, Isla Cristóbal; TO, Tierra Oscura; P, Isla Popa; CA, Cayo Agua; V, Península Valiente; NU, Ñuri; E, Isla Escudo; CP, Central Panamá; SAW, South America west of the Andes; SAE, South America east of the Andes. Refer to Fig. 1 for geographic locations within Bocas del Toro.

Character	Locality														
	NIC	A	CO	N	B	CR	TO	P	CA	V	NU	E	CP	SAW	SAE
Face color	T	T	T	T	T	T	T	T	T	T	T	T	T	Y/T	Y/T
Orange on face	N	Y	Y	Y	Y	Y/slt	Y	Y/slt	Y	slt/N	Y	Y	Y	Y/N	N/Y
Dark on brow	N	S/Y	Y/S	S/N	S	S	S	N	S/Y	S	S/Y	Y	Y	N/Y	N/Y
Line on brow	N	N/Y	Y	N	N	N	N	N	N/Y	N	N/Y	Y	Y/N	N/Y	N/Y
Dorsal stripe	Y	Y	Y	N/Y	Y	N	N	Y/N	Y	Y	Y	Y	Y	Y	Y
Dorsal appearance	B	U/B	U	U/B	U	U	U/B	B/U	U/B	B/U	B/U	B/U	U/B	B	B
Hood	N	N	N	N	N	N	N	N	N	N	N	Y	N	N	N

Table 2.—Descriptive statistics for external and cranial measurements (mm), mass (kg), and scores on multivariate axes of *Bradypus* of Age classes 2 and 3 from Bocas del Toro, Panamá, showing small body size of several insular populations. Each measurement or score is given as the mean ± 2 standard errors, minimum–maximum, and sample size. See text and Fig. 2 for methods of taking cranial measurements, Hall (1962) for external measurements, and Materials and Methods for details of the multivariate analyses (C 1 & PC I). Islands are arranged from outermost to innermost; mainland localities from west to east.

Locality	Total length	Tail length	Hind foot length	Ear length	Mass	Greatest length of skull	Anterior zygomatic breadth	Posterior zygomatic breadth
Isla Escudo	505.4 ± 11.42	49.7 ± 4.26	102.4 ± 3.92	10.0 ± —	2.9 ± 0.37	69.0 ± 1.34	41.5 ± 2.30	39.5 ± 2.04
	485–530	45–60	94–110	10–10	2.5–3.5	67.5–72.2	38.3–45.7	36.5–42.9
	(7)	(7)	(7)	(1)	(7)	(6)	(6)	(6)
Isla Bastimentos	513.2 ± 18.04	42.8 ± 4.72	114.0 ± 2.76	12.2 ± 0.95	3.2 ± 0.20	70.4 ± 1.53	42.6 ± 1.93	39.1 ± 1.23
	485–540	37–50	110–118	11–14	3.1–3.3	68.3–73.4	40.4–45.2	37.0–41.6
	(6)	(6)	(5)	(6)	(2)	(6)	(5)	(6)
Cayo Agua	547.8 ± 11.26	45.1 ± 1.25	114.5 ± 3.52	12.5 ± 0.58	3.8 ± 0.19	72.5 ± 1.18	45.3 ± 0.75	44.0 ± 0.68
	520–575	40–47	105–127	11–14	3.3–4.2	68.7–74.9	43.5–47.8	42.1–45.9
	(12)	(11)	(12)	(12)	(10)	(12)	(12)	(12)
Isla Colón	547.7 ± 14.44	49.7 ± 8.36	121.3 ± 8.52	11.0 ± 1.15	3.7 ± 0.48	73.4 ± 2.96	45.5 ± 2.42	42.8 ± 1.88
	535–560	45–58	113–127	10–12	3.2–4.0	70.5–76.6	42.6–48.5	40.2–44.6
	(3)	(3)	(3)	(3)	(3)	(4)	(4)	(4)
Cayo Nancy	565.4 ± 15.84	55.2 ± 3.76	117.4 ± 7.14	13.0 ± 2.60	3.6 ± 0.37	76.0 ± 2.60	44.2 ± 1.90	42.5 ± 2.26
	542–585	49–60	106–128	11–18	3.1–4.2	73.2–80.0	42.1–47.1	39.3–45.2
	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Isla Cristóbal	582.4 ± 16.28	56.6 ± 2.42	124.5 ± 4.80	10.6 ± 1.96	4.1 ± 0.47	79.3 ± 2.00	47.6 ± 1.81	44.8 ± 1.93
	555–605	53–60	120–131	8–14	3.4–4.8	76.5–82.1	44.4–49.8	41.3–47.0
	(5)	(5)	(4)	(5)	(5)	(5)	(5)	(5)
Isla Popa	591.5 ± 18.28	57.7 ± 2.90	128.0 ± 6.04	11.5 ± 1.00	4.4 ± 0.31	80.0 ± 1.29	48.9 ± 1.76	45.6 ± 1.13
	562–618	52–61	116–138	10–13	3.9–5.0	77.7–82.5	46.3–52.3	43.8–47.4
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Almirante	581.5 ± 57.80	67.3 ± 5.46	135.0 ± 12.56	14.5 ± 1.00	— ± —	79.7 ± 2.88	48.6 ± 1.74	45.6 ± 1.41
	531–657	62–71	118–148	14–16	—	75.9–82.5	46.8–50.5	44.2–47.4
	(4)	(3)	(4)	(4)	(0)	(4)	(4)	(4)
Tierra Oscura	591.4 ± 28.20	48.7 ± 3.60	134.4 ± 4.40	13.3 ± 1.36	5.2 ± 0.56	80.5 ± 2.50	50.0 ± 1.60	47.2 ± 1.57
	538–645	42–55	126–140	10–15	4.5–6.3	76.1–86.0	47.5–53.7	45.5–51.4
	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)
Valiente	585.7 ± 23.60	51.5 ± 4.70	128.7 ± 4.78	15.0 ± 0.89	4.6 ± 0.23	80.3 ± 1.99	49.9 ± 1.98	46.6 ± 1.28
	545–634	47–62	120–137	13–16	4.5–5.2	77.7–83.5	47.3–53.4	44.9–49.1
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Ñuri	608.4 ± 16.44	54.6 ± 4.54	130.4 ± 4.32	12.0 ± 1.31	4.7 ± 0.53	78.4 ± 1.13	48.3 ± 1.27	45.3 ± 1.19
	572–632	45–64	122–136	10–14	3.7–5.5	77.0–80.6	46.1–50.6	43.8–47.9
	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)

Table 2.—Extended.

Locality	Postorbital breadth	Squamosal process length	Maxillary toothrow length	Postpalatal length	Palatal breadth	Braincase depth	Antorbital bar breadth	Descending jugal process length	External auditory meatus diameter
Isla Escudo	21.2 ± 0.79	21.5 ± 0.81	23.3 ± 0.76	34.8 ± 1.20	16.3 ± 0.49	24.5 ± 0.39	3.2 ± 0.27	16.2 ± 0.92	5.9 ± 0.45
	20.2–22.4	20.3–22.9	22.3–24.7	33.3–37.0	15.5–17.2	23.7–25.0	2.8–3.7	14.7–18.0	5.3–6.7
	(6)	(7)	(6)	(6)	(7)	(6)	(7)	(7)	(7)
Isla Bastimentos	21.9 ± 0.90	24.3 ± 1.25	23.9 ± 0.82	35.4 ± 0.99	16.6 ± 0.56	24.8 ± 0.48	3.1 ± 0.28	13.2 ± 1.83	5.2 ± 0.29
	20.4–22.9	22.4–27.0	22.5–25.0	34.0–36.9	15.7–17.4	23.8–25.6	2.6–3.5	10.3–17.1	4.6–5.5
	(5)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Cayo Agua	22.3 ± 0.66	26.4 ± 0.75	23.9 ± 0.71	36.0 ± 0.81	16.6 ± 0.41	26.1 ± 0.27	3.9 ± 0.24	16.0 ± 0.96	5.2 ± 0.20
	19.8–24.2	23.2–28.0	22.0–26.8	33.2–38.0	15.6–18.0	25.0–26.8	3.2–4.6	13.4–18.4	4.7–5.8
	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
Isla Colón	23.0 ± 1.17	25.3 ± 1.55	25.3 ± 1.33	36.4 ± 2.96	17.0 ± 0.74	25.2 ± 1.15	3.9 ± 0.57	15.7 ± 1.25	5.7 ± 0.34
	21.7–24.2	23.2–26.6	23.5–26.7	33.7–39.8	16.2–17.9	23.8–26.6	3.2–4.6	14.2–16.9	5.3–6.1
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Cayo Nancy	24.2 ± 0.60	26.2 ± 1.13	25.2 ± 0.91	38.0 ± 2.08	17.2 ± 0.82	26.0 ± 0.85	3.4 ± 0.22	15.3 ± 1.46	5.7 ± 0.43
	23.6–25.3	24.3–27.8	24.0–26.5	35.1–40.3	16.6–18.8	24.9–26.8	3.2–3.8	13.1–17.4	4.9–6.1
	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Isla Cristóbal	24.9 ± 1.01	27.2 ± 1.41	25.5 ± 0.92	40.0 ± 0.93	18.3 ± 0.59	27.3 ± 0.89	4.0 ± 0.45	15.9 ± 0.94	5.1 ± 0.19
	23.8–26.5	25.2–29.5	23.7–26.2	38.9–41.7	17.6–19.1	26.2–28.7	3.2–4.4	14.1–16.9	4.9–5.4
	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Isla Popa	23.8 ± 1.09	28.4 ± 1.05	24.6 ± 0.35	41.0 ± 1.79	17.4 ± 0.48	27.6 ± 0.59	4.5 ± 0.35	16.3 ± 1.58	5.1 ± 0.36
	21.3–25.1	26.4–30.0	23.9–25.1	37.1–42.7	16.6–17.9	26.4–28.2	4.0–5.2	14.1–19.9	4.5–5.5
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(5)
Almirante	24.6 ± 1.12	28.1 ± 1.66	25.5 ± 1.41	40.7 ± 1.62	18.3 ± 0.54	27.0 ± 0.46	4.4 ± 0.21	17.1 ± 2.22	5.6 ± 0.26
	23.2–25.8	26.7–30.5	23.8–26.8	39.3–43.0	17.8–19.0	26.7–27.7	4.2–4.6	14.3–19.4	5.3–5.8
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Tierra Oscura	25.0 ± 1.20	28.6 ± 1.15	25.1 ± 0.86	41.4 ± 1.33	18.7 ± 0.77	27.9 ± 0.72	4.8 ± 0.35	16.5 ± 1.11	5.6 ± 0.28
	22.0–26.4	26.7–30.6	23.9–27.4	38.9–43.9	17.7–20.7	26.3–28.7	4.0–5.3	14.6–19.0	5.1–6.1
	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)
Valiente	25.0 ± 1.02	27.7 ± 0.64	25.1 ± 0.77	41.9 ± 1.77	18.3 ± 0.81	28.5 ± 0.33	4.6 ± 0.36	16.3 ± 1.35	5.5 ± 0.27
	23.9–26.6	27.0–28.8	23.7–26.0	39.8–45.3	16.8–19.6	28.0–29.0	4.1–5.3	13.2–17.9	5.1–6.0
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Ñuri	25.1 ± 0.44	27.4 ± 1.02	25.3 ± 0.69	40.1 ± 0.86	18.4 ± 0.71	28.2 ± 0.55	4.3 ± 0.29	15.4 ± 1.79	5.6 ± 0.16
	24.4–26.0	25.6–29.1	24.3–26.7	38.9–41.8	16.5–19.3	27.3–29.3	3.8–4.7	12.3–18.8	5.2–5.8
	(6)	(7)	(6)	(7)	(7)	(7)	(7)	(7)	(7)

Table 2.—Extended.

Locality	Squamosal process breadth	Ascending mandibular ramus breadth	First canonical axis (C 1)	First principal component (PC I)
Isla Escudo	4.3 ± 0.47	13.2 ± 0.92	−7.32 ± 0.71	−0.28 ± 0.05
	3.5–5.0	11.9–14.9	−8.03–−6.34	−0.35–−0.22
	(7)	(7)	(5)	(5)
Isla Bastimentos	5.4 ± 0.64	16.4 ± 0.62	−4.70 ± 0.63	−0.14 ± 0.07
	4.9–7.0	15.3–17.4	−5.33–−4.36	−0.18–−0.07
	(6)	(6)	(3)	(3)
Cayo Agua	6.3 ± 0.39	15.9 ± 0.60	−2.41 ± 0.72	−0.04 ± 0.03
	5.5–7.5	14.0–17.5	−4.46–−0.43	−0.14–0.02
	(12)	(12)	(11)	(11)
Isla Colón	5.3 ± 0.60	15.8 ± 1.22	−4.34 ± 1.79	−0.08 ± 0.12
	4.5–5.9	14.7–16.8	−6.14–−3.39	0.20–0.00
	(4)	(3)	(3)	(3)
Cayo Nancy	6.0 ± 1.02	16.0 ± 1.50	−2.05 ± 0.46	−0.05 ± 0.07
	4.9–7.9	13.4–17.7	−2.78–−1.39	−0.15–0.05
	(5)	(5)	(5)	(5)
Isla Cristóbal	6.4 ± 0.73	17.2 ± 1.39	3.38 ± 0.75	0.06 ± 0.08
	5.0–7.0	15.5–18.8	2.66–4.18	−0.06–0.13
	(5)	(5)	(4)	(4)
Isla Popa	6.6 ± 0.23	16.8 ± 0.65	4.26 ± 0.37	0.11 ± 0.03
	6.3–6.9	15.6–17.5	3.67–4.68	0.09–0.16
	(5)	(5)	(5)	(5)
Almirante	6.0 ± 0.76	16.9 ± 0.26	3.16 ± 1.01	0.09 ± 0.07
	4.9–6.7	16.6–17.2	2.57–4.17	0.04–0.15
	(4)	(4)	(3)	(3)
Tierra Oscura	5.9 ± 0.39	17.6 ± 0.83	3.06 ± 0.91	0.12 ± 0.05
	5.0–6.5	16.3–19.5	1.41–4.76	0.02–0.19
	(7)	(7)	(7)	(7)
Valiente	5.7 ± 0.64	16.7 ± 0.87	3.36 ± 1.09	0.09 ± 0.04
	5.0–7.1	15.7–18.0	1.49–5.55	0.04–0.17
	(6)	(6)	(6)	(6)
Ñuri	5.8 ± 0.47	16.1 ± 0.49	2.91 ± 0.49	0.06 ± 0.03
	5.0–6.9	15.1–17.0	2.27–3.76	0.01–0.10
	(7)	(7)	(5)	(5)

Table 3.—Approximate statistics for morphometric separation among populations of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá. *F*-statistics with 17 and 30 degrees of freedom are given for Mahalanobis distances between pairs of group centroids, with an asterisk (*) signifying significant differences, using Holm's (1979) correction for multiple tests. Below the *F*-statistic, pairs are marked by PC I (Principal component I), C 1 (Canonical axis 1), or C 2 (Canonical axis 2) if their mean scores on those respective axes were significantly different by Tukey's tests of multiple comparisons with family-wide error rates of α = 0.05. Note that the sloth of Isla Escudo is morphometrically distinct from all other samples in Bocas del Toro, and that the samples from Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón are significantly smaller than most or all mainland localities (*F*-statistics, PC I, and C 1). Significance levels attached to all tests must be regarded as approximate due to small sample sizes. Locality abbreviations are given in Table 1.

	E	B	CA	CO	N	CR	P	TO	V	A
B	5.18*									
	C 1, 2									
CA	7.65*	3.22								
	PC I, C 1, 2	C 1								
CO	3.49*	2.00	1.96							
	PC I, C 1, 2									
N	4.41*	3.00	2.15	1.54						
	PC I, C 1, 2	C 1, 2	C 2							
CR	11.55*	6.74*	5.37*	5.41*	3.32*					
	PC I, C 1, 2	PC I, C 1, 2	C 1, 2	C 1	C 1					
P	14.68*	8.46*	7.44*	7.19*	5.29*	0.84				
	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1	PC I, C 1					
TO	14.94*	6.92*	6.55*	5.39*	4.46*	2.12	2.69			
	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1	PC I, C 1	PC I, C 1					
V	13.23*	7.17*	7.19*	6.04*	4.19*	1.51	1.72	0.70		
	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1	PC I, C 1					
A	9.08*	6.13*	4.90*	4.39*	2.62	1.05	1.30	1.74	1.41	
	PC I, C 1	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1, 2	C 1			C 2		
NU	11.67*	6.67*	5.99*	5.00*	3.03	1.67	2.29	1.09	0.91	0.80
	PC I, C 1, 2	PC I, C 1, 2	C 1, 2	C 1	C 1					

Colón, and Isla Escudo—in comparisons with those from the younger islands (Isla Popa and Isla Cristóbal) and sites on the adjacent mainland (Tables 2 and 3). The discriminant function analysis showed differences in both size and shape. In the DFA, 32 of 55 comparisons between pairs of group centroids were significantly different and followed a clear pattern (Table 3, Fig. 3). The sloths on Isla Escudo were morphometrically distinct from all other populations. Furthermore, sloths on the outer islands were generally distinct from those of Isla Popa and Isla Cristóbal as well as from those from all mainland sites in Bocas del Toro. The first canonical axis accounted for most (63%) of the variation among groups, and the first and second together encompassed 76% of the variation (Table 4). The first canonical axis may be interpreted as general size, with smaller sloths having lower scores. Most measurements loaded strongly and positively on this axis; external auditory meatus diameter (EAM) had a negative loading, but its magnitude was small enough to be negligible, indicating that EAM diameter did not correlate with general size. The second canonical axis contrasted tail length and EAM diameter to squamosal process breadth and ascending mandibular ramus breadth (Table 4). Sloths with relatively long tails, large EAMs, narrow squamosal processes, and narrow rami scored high on this axis.

In the principal components analysis of overall variation in the sloths of Bocas del Toro, the first component (PC I) accounted for 51% of the variation among individuals, without regard to locality (Table 5). Specimens from Isla Escudo again plotted far from all other specimens from Bocas del Toro (Fig. 4). The loadings on PC I indicate that it represents overall size, with EAM loading so slightly as to be immaterial. No difference between Age classes 2 and 3 or age-locality interaction was detected for PC I scores in a general linear model ($F_{\text{age } 1,6} = 0.23$, $P = 0.650$; $F_{\text{age*locality } 1,6} = 0.00$, $P = 0.981$). Similarly, the difference between the sexes and the sex-locality interaction also were nonsignificant ($F_{\text{sex } 1,23} = 1.32$, $P = 0.262$; $F_{\text{sex*locality } 4,23} = 1.04$, $P = 0.408$). These tests suggest that our pooling of the sexes and Age classes 2 and 3 was justified. Scores on PC I, however, were significantly different among localities in a one-way ANOVA ($F_{10,46} = 21.79$, $P < 0.001$). Patterns of localities differing significantly on PC I paralleled the results for the first canonical axis (Table 3). PC II and PC III represent shape differences, but given the multiple groups involved they probably do not represent the most appropriate way to examine shape.

In comparing the small sloths from Bocas del Toro with six series of *Bradypus variegatus* from its range outside Bocas del Toro, only the population on Isla Escudo is significantly smaller than all mainland samples (Table 6) in the greatest length of skull. Sloths from the other differentiating populations in Bocas del Toro—Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón—fall within the size variation in *B. variegatus* from Colombia and Brazil.

Discussion

The three-toed sloths of the outer islands of Bocas del Toro—Isla Colón, Isla Bastimentos, Cayo Nancy, Cayo Agua, and Isla Escudo—are significantly smaller than the *Bradypus* of the adjacent mainland of Bocas del Toro, as evidenced by Canonical axis 1, Principal component I, and univariate statistics. Furthermore, sloths on those five islands themselves vary in mean size, with those from Isla Escudo being the smallest (Tables 2 and 3). The samples from Isla Popa and Isla Cristóbal, which are young islands close to shore, are not significantly different in size from sloths on the mainland of Bocas del Toro (Table 3).

Sloths on Isla Escudo display differences in cranial shape when compared with other populations of *Bradypus* from Bocas del Toro. The position of specimens from Isla Escudo on the second canonical axis (Fig.

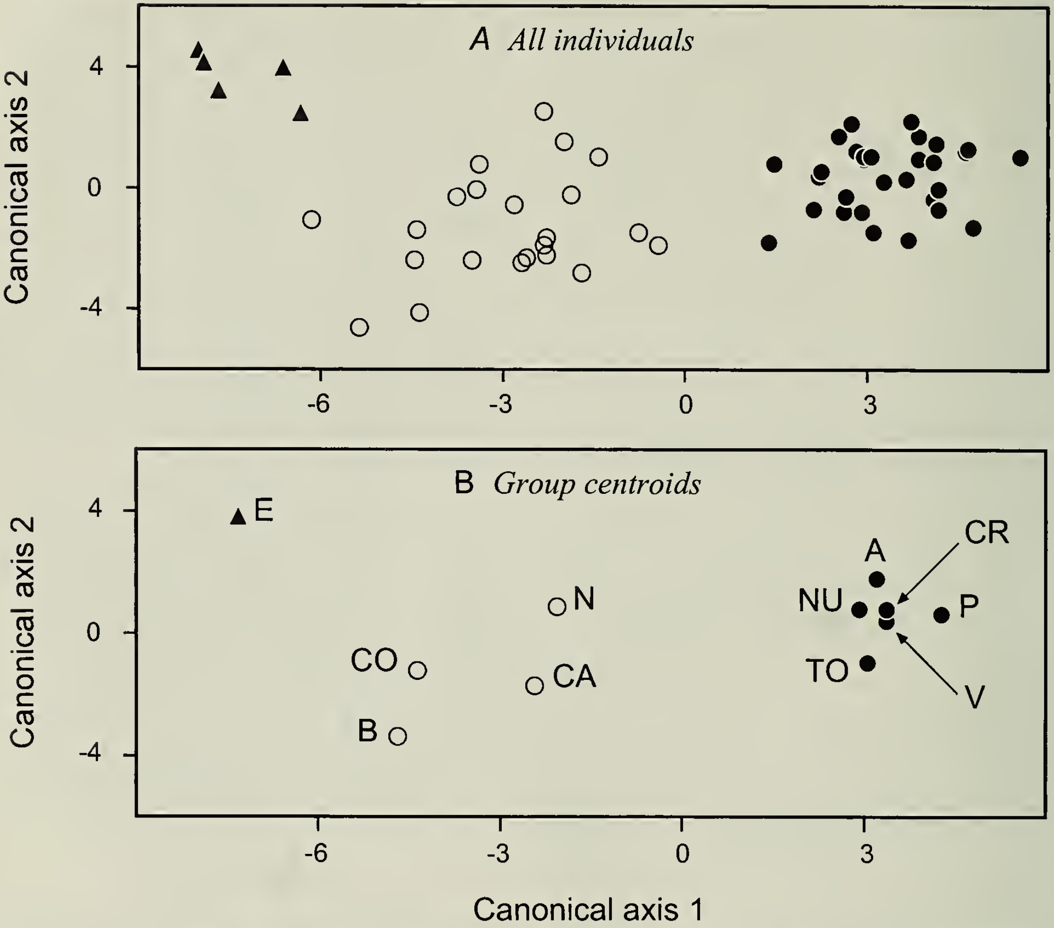

Fig. 3. Plot of specimen scores (A, upper) and locality centroids (B, lower) on the first two canonical axes from a multiple-group discriminant function analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, showing morphometric distinctiveness of sloths of Isla Escudo and moderate dwarfing on four other islands. In A, specimens from Isla Escudo are marked with solid triangles; specimens from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. Abbreviations for locality centroids in B follow, with symbols following the same scheme as in A: A, Almirante; B, Isla Bastimentos; CA, Cayo Agua; CR, Isla Cristóbal; CO, Isla Colón; E, Isla Escudo; N, Cayo Nancy; NU, Ñuri; P, Isla Popa; TO, Tierra Oscura; V, Península Valiente.

3) is due primarily to their large external auditory meatus, narrow squamosal process, and narrow ascending mandibular ramus (Table 2, Table 4). For the other island and mainland populations in Bocas del Toro, variation in shape is minimal as compared with differences in size.

Although the sloths from the outer islands share small size, our examinations of pelage show similarities between island and mainland populations that were once contiguous (Table 1, Fig. 1). These analyses show that the small sloths on the outer islands share no discrete pelage characters. The pelage traits are independent of body size, which is notably predisposed to convergence (Roth 1992). The few cranial characters common to the small sloths on various islands are all gracile traits associated with size reduction and ontogenetic

Table 4.—Loadings (correlation coefficients) of three external and 14 cranial measurements (log$_{10}$-transformed) on the first three canonical axes of a multiple-group discriminant function analysis of three-toed sloths (*Bradypus*) from 11 localities in Bocas del Toro, Panamá. Eigenvalues and the corresponding cumulative percent of total dispersion explained are given for each axis. For the analysis, specimens were grouped by collection locality. See Materials and Methods for variable abbreviations. The first canonical axis represents a measure of general size.

	C 1	C 2	C 3
TOTAL	0.804	0.026	0.081
TAIL	0.423	0.620	−0.136
HF	0.822	−0.158	0.252
GLS	0.895	0.046	0.132
AZB	0.856	−0.141	0.096
PZB	0.797	−0.178	−0.004
POB	0.742	0.027	0.268
SPL	0.795	−0.324	−0.058
MTRL	0.452	0.009	0.202
PPL	0.862	0.124	0.202
PB	0.716	0.027	0.398
BD	0.885	−0.027	0.136
ABAR	0.760	−0.258	0.107
DJPL	0.236	0.160	−0.199
EAM	−0.152	0.437	0.515
SPB	0.477	−0.467	−0.355
ARB	0.681	−0.481	0.070
Eigenvalue & (cumulative % of total dispersion)	17.7800 (63.3%)	3.6367 (76.3%)	2.2703 (84.4%)

truncation (e.g., thin zygomatic arches, weakly developed temporal crests). The geographic distribution of the pelage traits apparently represents the relictual manifestation of previously continuous geographic variation that was subdivided into isolated populations when the islands formed. Movement of sloths between islands or to or from the mainland probably has been insignificant. We propose that those populations independently underwent selection for smaller size when separated from the mainland, under a vicariant model consistent with the patterns of island formation elucidated by Handley & Varn (see Introduction). This hypothesis of strict vicariance is currently being tested by Anderson and L. Olson by comparing a population-level phylogeny produced from DNA sequence data, with an area cladogram based on the sequence of island formation derived from sea level mapping (Brooks & McLennan 1991:197–198, Avise 1994).

Thus, we suggest that the evolution of smaller body sizes occurred at least four times in Bocas del Toro: independently on Isla Escudo, Isla Colón, and Cayo Agua—each of which formed separately—and once on Cayo Nancy and Isla Bastimentos together (they became isolated from the mainland as a unit and only recently have become separated from each other). The sloths from the outer islands are not linked by a common ancestry as might be presumed because of their small size, but rather they adapted separately as isolated populations while experiencing similar environmental changes following insularization, in an instance of parallel evolution. The sloth of Isla Escudo has clearly reached the species level, but we consider that the populations on Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón remain conspecific with *Bradypus variegatus.* Future work will evaluate the factors that may have led to these instances of dwarfism.

We have documented the extremely small size of the three-toed sloth on Isla Escudo, as well as its unique cranial and pelage characters relative to other known species of the genus. For these reasons, we here formally describe this endemic insular population as:

Bradypus pygmaeus, new species

Fig. 5

Holotype.—USNM 579179, adult female, skin and skull (Fig. 5), collected on 27 Mar 1991 by Charles Handley and Penny Nelson, from Panamá: Bocas del Toro: Isla Escudo de Veraguas, West Point. Original number EPN 166. Also examined: nine paratypes from Isla Escudo: USNM 578413, 579171–579175, 579176 (returned to Panamá-INRENARE), 579177–579178.

Etymology.—From the Latin *pygmaeus,*

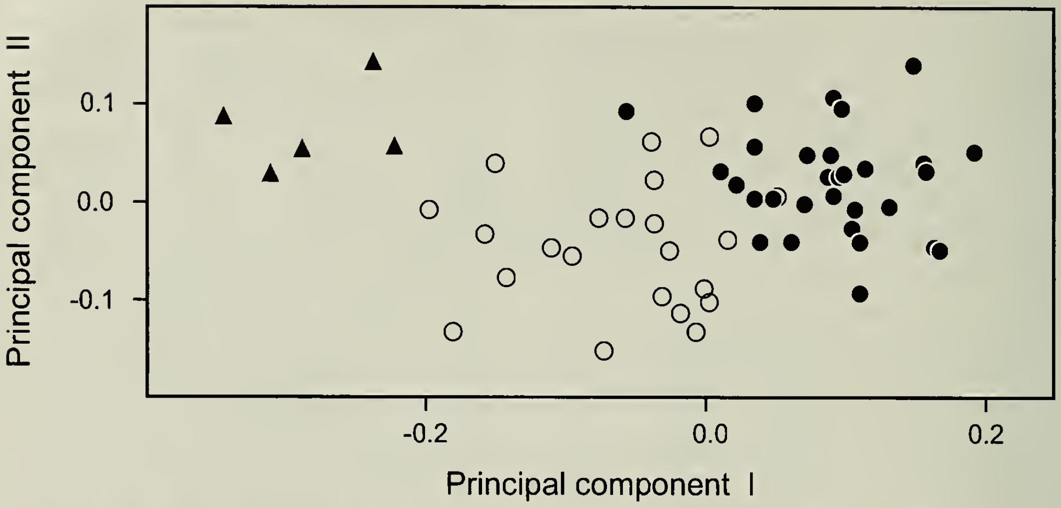

Fig. 4. Plot of specimen scores on the first two axes of a principal components analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, showing dwarfing of sloths on Isla Escudo and four other islands. Specimens from Isla Escudo are marked with solid triangles; specimens from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. The first principal component represents general size.

meaning dwarf or pygmy. Suitable vernacular name is pygmy three-toed sloth.

Distribution.—Known only from Isla Escudo de Veraguas, Province of Bocas del Toro, Republic of Panamá, where it is found exclusively in red mangroves at sea level (Fig. 6).

Diagnosis.—A species of *Bradypus* characterized by the following combination of characters: size small (Table 2); orange speculum on dorsum of adult males; nape without black mane; face tan with distinctive dark band across forehead; long hair of forehead hanging over face, giving the impression of a hood; pterygoids not inflated; no foramina in anterodorsal nasopharynx; frontal sinuses swollen; stylomastoid foramen miniscule, external carotid foramen usually absent or minuscule; external auditory meatus large; ventral surface of hyoid (stylohyal) smoothly concave; descending process of jugal long and thin; coronoid process of mandible thin and strongly falcate.

Description.—Size small (n = 7 adults: total length, $\bar{X}$ = 505.4 mm, range 485–530 mm; tail, $\bar{X}$ = 49.7 mm, range 45–60 mm; hind foot, $\bar{X}$ = 102.4 mm, range 94–110 mm; mass, $\bar{X}$ = 2.9 kg, range 2.5–3.5 kg); dorsal coloration usually blotchy and always with a midsagittal stripe; adult males with orange speculum, woolly around anterior margin; fur of crown long and shaggy, hanging over short hair of face to give a hooded appearance; brow very dark with abrupt posterior termination (line on brow present); face buff with orange wash around dark eye stripe; throat grizzled gray-brown.

Skull small (n = 6 adults: greatest length, $\bar{X}$ = 69.1 mm, range 67.5–72.2 mm; anterior zygomatic breadth, $\bar{X}$ = 41.5 mm, range 38.3–45.7 mm; maxillary toothrow length, $\bar{X}$ = 23.3 mm, range 22.3–24.7 mm; see also Table 2) and gracile (Fig. 5); parietal ridges weak and usually convex (hourglass-shaped when viewed dorsally); masseter-temporal fossa rather smooth; pterygoids thin, not inflated; no foramina present in anterodorsal nasopharynx; premaxillae minute, barely if at all articulated with maxillary; zygomatic arch incomplete, anterior and posterior roots slender; descending process of jugal long and thin; lambdoidal crest continuous across posterior margin of occiput, lateral margins of crest straight in lateral view; occipital region barely projecting posterior to lambdoidal crest; hyoid (stylohyal) smoothly arched on ventral surface to point of articulation with epihyal on anterior limb; posterior limb of hyoid usually wider than anterior limb; external auditory meatus large; stylomastoid foramen minute; external carotid foramen usually closed or miniscule; ventral mandibular surface strongly concave; coronoid process of mandible thin and strongly falcate.

Tooth formula: (anterior chisel-shaped teeth 1/1, molariform teeth 4/3) × 2 = 18 (terminology of Naples 1982). Upper anterior chisel-shaped tooth tiny or absent; lower anterior chisel-shaped tooth anteroposteriorly compressed.

Measurements of the holotype.—Total length, 510 mm; tail length, 54 mm; hind foot length, 94 mm; mass, 3.5 kg. Cranial measurements (in mm): GLS, 68.8; AZB, 43.6; PZB, 40.7; POB, 20.5; SPL, 21.3; MTRL, 22.8; PPL, 33.3; PB, 16.3; BD, 24.7; ABAR, 3.2; DJPL, 16.2; EAM, 6.7; SPB, 5.0; ARB, 12.8.

Table 5.—Loadings, eigenvalues, and cumulative percent of variance explained for the first three axes of a principal components analysis undertaken on three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, using the covariance matrix of $\log_{10}$-transformed values of 14 cranial measurements and three external measurements for each of 57 individuals. See Materials and Methods for abbreviations. The first principal component represents general size, which is uncorrelated with external auditory meatus diameter (EAM).

	PC I	PC II	PC III
TOTAL	0.786	0.302	0.103
TAIL	0.331	0.788	0.456
HF	0.801	0.141	−0.057
GLS	0.878	0.221	0.075
AZB	0.905	0.049	−0.218
PZB	0.895	−0.010	−0.214
POB	0.682	0.129	0.044
SPL	0.874	−0.062	0.073
MTRL	0.610	0.164	0.214
PPL	0.839	0.269	0.017
PB	0.712	0.236	−0.042
BD	0.794	0.054	−0.187
ABAR	0.866	−0.092	−0.419
DJPL	0.354	0.348	−0.251
EAM	−0.044	0.481	−0.252
SPB	0.689	−0.477	0.455
ARB	0.842	−0.191	0.200
Eigenvalue & (cumulative % variance explained)	0.0164 (51.2%)	0.0046 (65.5%)	0.0033 (75.9%)

Table 6.—Results of ANOVA of greatest length of skull (GLS) measurements. All possible pairwise comparisons were made among samples of *Bradypus* from the five outer islands of Bocas del Toro, Panamá and six samples of *B. variegatus* from mainland localities outside Bocas del Toro using Tukey's procedure with a family-wide error rate of $\alpha = 0.05$. Results for comparisons of island populations vs. mainland populations outside Bocas del Toro are presented here. Significant comparisons are marked with an asterisk (*), whereas nonsignificant ones are denoted "*n.s.*" Bonanza, El Recreo, and Tepeyak are localities in Nicaragua; Bajo Calima-Río Raposo and Tumaco lie along the southern Pacific coast of Colombia; and Mojui dos Campos is located in the lower Amazon of Brazil. Note that sloths from Isla Escudo are significantly smaller than those of all mainland localities outside Bocas del Toro, whereas the *Bradypus* from the four other outer islands of Bocas del Toro fall within the range of variation of *B. variegatus* in South America. Descriptive statistics (mean ± 2 standard errors, minimum–maximum, and sample size) are given here in mm for mainland localities outside Bocas del Toro; see Table 2 for descriptive statistics of localities in Bocas del Toro.

	Bonanza 78.9 ± 1.12 75.3–82.3 (12)	El Recreo 78.5 ± 1.15 76.1–80.7 (7)	Tepeyak 83.2 ± 3.08 80.0–86.5 (4)	Bajo Calima-Río Raposo 73.7 ± 2.18 68.9–76.8 (6)	Tumaco 76.9 ± 4.18 70.6–79.3 (4)	Mojui dos Campos 72.8 ± 1.15 67.0–78.3 (21)
Isla Colón	*	*	*	*n.s.*	*n.s.*	*n.s.*
Isla Bastimentos	*	*	*	*n.s.*	*	*n.s.*
Cayo Nancy	*n.s.*	*n.s.*	*	*n.s.*	*n.s.*	*n.s.*
Cayo Agua	*	*	*	*n.s.*	*n.s.*	*n.s.*
Isla Escudo	*	*	*	*	*	*

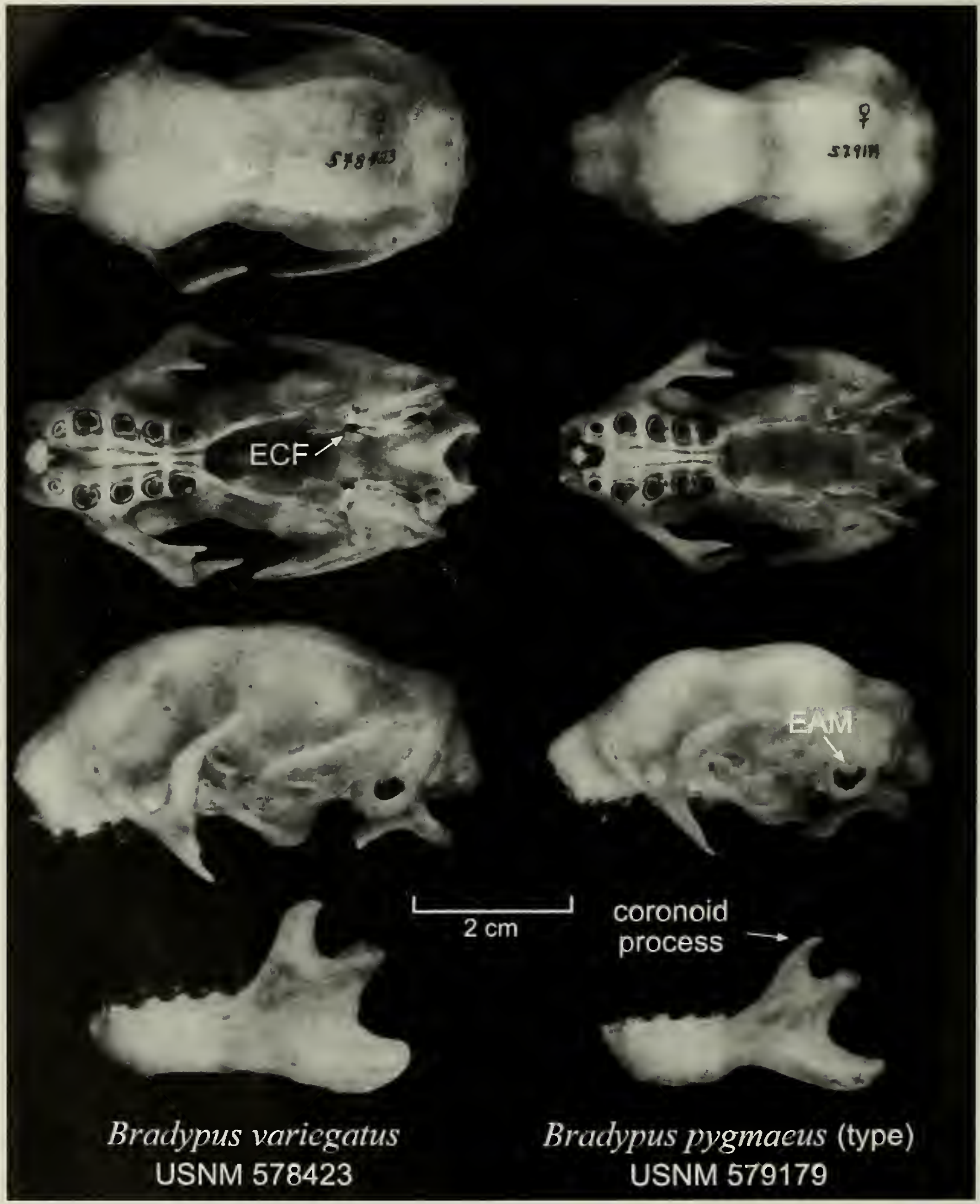

Fig. 5. Dorsal, ventral, and lateral views of the crania and lateral view of the mandibles of the holotype of *Bradypus pygmaeus* (USNM 579179, right) from Isla Escudo and a specimen of *B. variegatus* from the adjacent mainland on the Península Valiente (USNM 578423, left). Note the diminutive size and gracile qualities of *B. pygmaeus* and the open external carotid foramen (ECF) of USNM 578423, which is closed in USNM 579179. Also note the strongly falcate coronoid process on the mandible of *B. pygmaeus* and the large external auditory meatus (EAM) characteristic of that species, despite its overall small size.

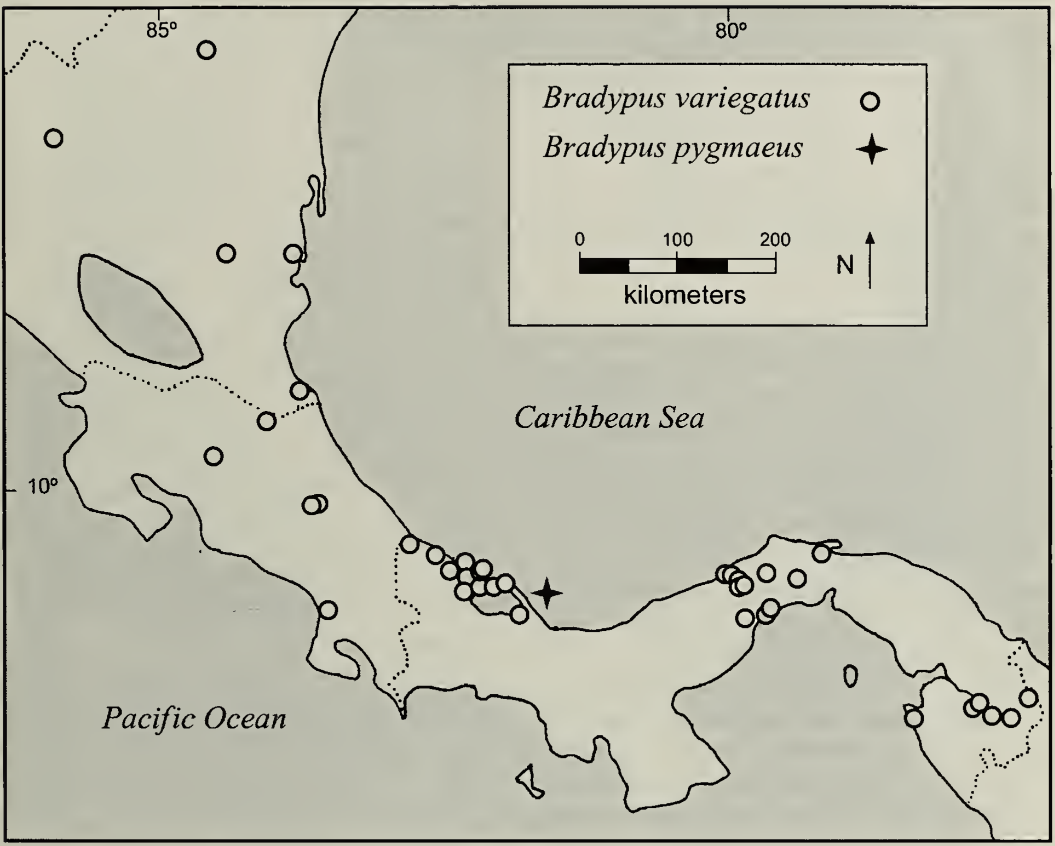

Fig. 6. Verified Central American distribution of *Bradypus*. Georeferenced collection localities reported here are plotted for *B. variegatus* (open circles) and *B. pygmaeus* (star). The distribution of *Bradypus variegatus* continues northward into Honduras (voucher specimens from the Río Patuca region [see Specimens examined] and additional sight records reported in Marineros & Martínez-Gallegos 1998) and south into South America (see Fig. 7). *Bradypus pygmaeus* is endemic to Isla Escudo de Veraguas in western Panamá. See Specimens examined sections for full provenience and museum catalogue numbers.

Comparisons.—Compared with populations of *Bradypus variegatus* on the adjacent mainland, *B. pygmaeus* averages approximately 40% smaller in mass, 15% smaller in total length, and 12–16% smaller in most cranial dimensions. It is smaller than any studied population of *Bradypus variegatus* in Central or South America (Tables 2, 3, and 6). Additionally, its external auditory meatus is conspicuously large for a sloth of overall small size. The diameter of the EAM decreases as the bulla ossifies; the development of this region of the skull is especially truncated in *B. pygmaeus* (Fig. 5).

Discrete cranial characters separate *Bradypus pygmaeus* from all other species of the genus. It lacks the distinctly inflated pterygoid sinuses and the two or three roughly circular foramina in each side of the anterodorsal nasopharynx of *B. torquatus* (Wetzel & Avila-Pires 1980, Wetzel 1985). It lacks the pair of oblong foramina present in the medial roof of the anterodorsal nasopharynx of *B. tridactylus* (Wetzel 1985). From populations of the closely related *B. variegatus*—including both mainland sloths and the moderately dwarfed sloths of other islands in Bocas del Toro—the pygmy sloth differs in having (Fig. 5):

external carotid foramen, through which the carotid artery normally passes, absent or minute in most specimens (the homologous foramen is markedly larger in *B. variegatus,* suggesting a different pattern of cranial circulation); stylomastoid foramen at the posterior external base of the auditory bulla tiny (the facial nerve exits this foramen in *B. variegatus,* in which the foramen is markedly larger and almost always visible to the naked eye); external auditory meatus large (usually smaller in *B. variegatus* and all other three-toed sloths); ventral edge of stylohyoid usually smoothly concave (angular or undulating in *B. variegatus*); coronoid process of the mandible slender and strongly falcate (usually thick and straight-edged or only moderately curved in *B. variegatus*). No other insular population of three-toed sloth in Bocas del Toro shows autapomorphic cranial characters.

Externally, *Bradypus pygmaeus* may be separated from *B. torquatus* of both sexes by the lack of a black dorsal mane originating at the nape and by the presence of short, tan facial pelage with a black stripe lateral to the eye; and in adult males by possessing a dorsal speculum. From *B. tridactylus,* the pygmy sloth is distinguished by its tan facial and gular pelage and dark stripe lateral to the eye. In contrast, *B. tridactylus* has brilliant golden hair on the brow, face, and throat. The pygmy sloth differs externally from *B. variegatus* by long hair projecting over the brow, creating the aspect of a hood (Table 1). This character provoked Handley to refer to this sloth in the field as the "monk sloth." No other sloth of the Bocas islands is hooded, and the "ruff" on the brow (hair projecting over the forehead) mentioned for other Central American *Bradypus* by Goldman (1920:57), Goodwin (1946:352), Hall (1981:279), and others is not so long and distinctive.

Specimens examined.—Bradypus pygmaeus, total 10. Panamá (10). Bocas del Toro: Isla Escudo de Veraguas (9°06′N, 81°33′W), 1 (USNM 578413); Isla Escudo de Veraguas (9°06′N, 81°33′W), West Point, 9 (USNM 579171–579175, 579176*, 579177–579179).

Bradypus torquatus Illiger, 1811

Distribution.—Restricted to the Atlantic forests of southeastern Brazil (Fig. 7; Wetzel & Avila-Pires 1980).

Diagnosis.—Size large; no speculum on dorsum (contra Eisenberg & Redford 1999: 94); nape with distinct black plume or mane; facial and body pelage grizzled; hair of forehead short; pterygoids distinctly inflated; two or three small, circular foramina present on each side of anterodorsal nasopharynx.

Comparisons.—This species is easily separated from all other species of the genus by its black dorsal mane and inflated pterygoids.

Comments.—Extremely rare in museum collections. Endangered due to deforestation in its restricted range (Emmons & Feer 1997). Considered the most basal species of *Bradypus* (Wetzel & Avila-Pires 1980) and placed in its own subgenus, *Scaeopus.*

Specimens examined.—Bradypus torquatus, total 4. Brazil (4). Bahia. Itabuna, near Ilhéus [14°48′S, 39°16′W], 1 (USNM 259473); Tres Bracos, Fazenda Piabanha (13°32′S, 39°45′W), 37 km N, 34 km E Jequie, 2 (USNM uncatalogued, field numbers MTB 1706–1707). State unknown: no specific locality, 1 (MCZ 1024).

Bradypus tridactylus Linnaeus, 1758

Distribution.—The Guianas and adjacent regions of eastcentral Venezuela (Estado Bolívar) and northcentral Brazil, principally north of the Amazon (Fig. 7). Distribution probably does not extend southwest of the Rio Negro or as far south of the Amazon as indicated in Eisenberg & Redford (1999), where it is replaced by *Bradypus variegatus.*

Diagnosis.—Size average for genus; orange speculum present on dorsum of adult males; nape without black mane; face and

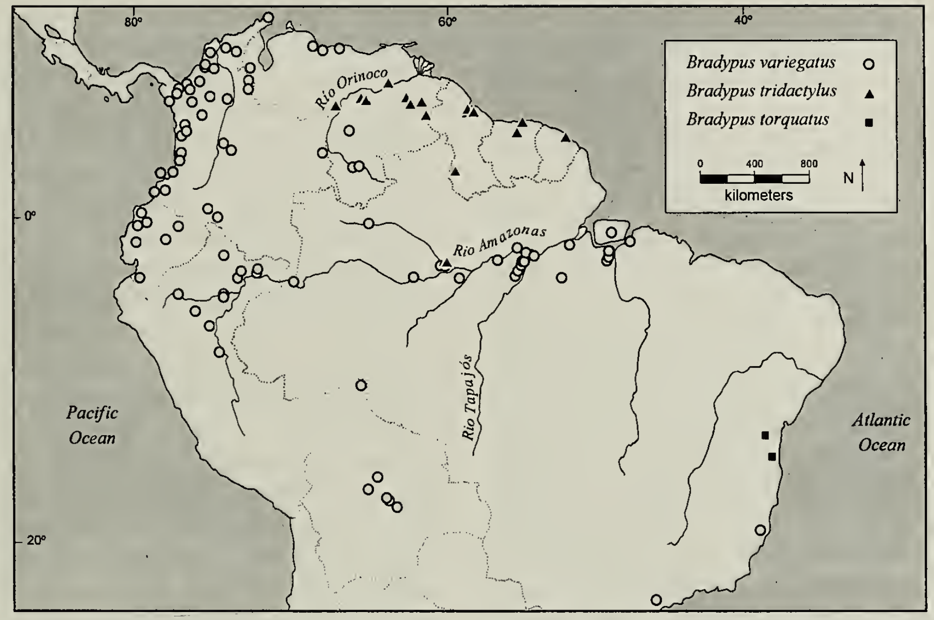

Fig. 7. Verified South American distribution of *Bradypus*. Georeferenced collection localities are mapped for *B. variegatus* (open circles), *B. tridactylus* (solid triangles), and *B. torquatus* (solid squares). The distribution of *Bradypus variegatus* continues northwest into Central America (see Fig. 6) and south to Argentina (voucher specimen from Jujuy province, see Specimens examined). Wetzel and Avila-Pires (1980) reported additional distributional records for *B. torquatus*, which ranges southward from the localities of that species confirmed and plotted here. See Specimens examined sections for full provenience and museum catalogue numbers.

forehead golden with no dark stripe at level of eyes (contra Emmons & Feer 1997:43); throat golden to the base of the hairs, or predominantly golden with bases of hairs smoky gray; hair of forehead short and stiff; pterygoids not inflated; a single pair of oblong foramina present in the anterodorsal nasopharynx; frontal sinuses seldom swollen.

Comparisons.—Bradypus tridactylus may be easily separated from *B. torquatus* by the lack of a black dorsal mane or inflated pterygoid sinuses. It is most similar to *B. variegatus,* whose range it probably contacts in Venezuela and Brazil. It differs from that species by possessing a pair of oblong foramina in the anterodorsal nasopharynx, and by its golden throat. All *B. tridactylus* have golden faces and throats, either golden to the base of the hair or with a slight smoky gray color at the base of the hairs. In contrast, most *B. variegatus* have tan faces. Many specimens of *B. variegatus* in South America possess golden faces, however, and a few Brazilian populations even have throats frosted with golden-tipped fur (e.g., localities on the lower Rio Tapajós), but the base of the gular hairs is characteristically brown for most of the length of the hair in those populations. The golden facial and gular hair of *B. tridactylus* is generally shorter and stiffer than in *B. variegatus.* See Comments in *B. variegatus.* No *B. pygmaeus* have golden throats or faces. The dorsum of *B. tridactylus* is often speckled or blotchy, but this character does not serve to distinguish it from *B. variegatus* (contra Eisenberg 1989, Eisenberg & Redford 1999), which often displays this trait as well.

Comments.—In the older literature, individuals of *Bradypus variegatus* were often incorrectly reported as *B. tridactylus.*

Specimens examined.—Bradypus tridactylus, total 50. Brazil (6). Amazonas: Manaus [3°08′S, 60°01′W], 1 (AMNH 143012);

Rio Amazonas, bought in Manaus [3°08′S, 60°01′W], 4 (FMNH 165441–165444); Rio Amazonas, Manaus [3°08′S, 60°01′W], Hacienda Rio Negro, 1 (AMNH 78968). French Guiana (1). Cayenne [4°56′N, 52°20′W], 1 (AMNH 77891). Guyana (20). Cuyuni-Mazaruni: Essequibo, Kartabo Point [6°23′N, 58°41′W], 12 (AMNH 42454, 42871–42872, 42888, 48369, 74134–74137, 142932, 142934, 142992); Kalacoon [= Kalakun, 6°24′N, 58°39′W], 2 (AMNH 48103, 269846); Kartabo [6°23′N, 58°41′W], 1 (AMNH 48180); Kartabo River, 1 (AMNH 74131); Kyk-over-al [island in Mazaruni River facing Karatabu Point (= Kartabo Point), AMS 1944], 1 (AMNH 48104). Demerara-Mahaica: Dunoon [6°25′N, 58°18′W, Hershkovitz 1977], 1 (UMMZ 46410). Upper Takutu-Upper Essequibo: Dadanawa [2°50′N, 59°30′W], 20 mi E, 1 (USNM 362241); no specific locality [in former Rupununi], 1 (USNM 395070). Suriname (7). Brokopondo: Saramacca Rivier, Loksie Hattie [5°10′N, 55°28′W, Hershkovitz 1977], 1 (FMNH 95443). Paramaribo: near Paramaribo [5°50′N, 55°10′W], 1 (MCZ 19570); Paramaribo [5°50′N, 55°10′W], 900 ft, 2 (FMNH 93297, 95446); Paramaribo [5°50′N, 55°10′W], brush land, 900 ft, 1 (FMNH 93296). Saramacca: La Poule, 2 (FMNH 95444–95455). Venezuela (16). Bolívar: Camarata Valley, 450 m, 1 (AMNH 135474); Ciudad Bolívar [8°08′N, 63°33′W], 3 (AMNH 16134–16136); El Manaco (6°17′N, 61°19′W), 59 km SE El Dorado, 150 m, 1 (USNM 374821); La Bomba [7°02′N, 61°33′W], 1 (AMNH 30738); Los Patos (7°11′N, 62°22′W), 25 km SE El Manteco, 350 m, 2 (USNM 374822, 387803); Maripa [7°26′N, 65°09′W], 2 (AMNH 21305–21306); Río Suapure [6°48′N, 67°01′W], 4 (AMNH 16932–16934, 17560); Río Supamo (7°00′N, 62°15′W), 50 km SE El Manteco, 150 m, 1 (USNM 374818); Ríos Mato [7°09′N, 65°07′W] and Caura, 1 (AMNH 30201).

Bradypus variegatus Schinz, 1825

Distribution.—From eastern Honduras to northern Argentina (Wetzel & Avila-Pires 1980, McCarthy et al. 1999). Widespread in forested areas at low-to-middle elevations of eastern Central America (Fig. 6); South America west of the Andes to southern Ecuador; east of the Andes in South America throughout Amazonian forests (but not in the Guianan region, where replaced by *B. tridactylus*); and in some areas of southeastern Brazil and northern Argentina (Fig. 7). Absent from the open *llanos* of Colombia and Venezuela, the Brazilian *cerrado,* and other savanna habitats—contrary to distributional maps provided by Emmons & Feer (1997) and Eisenberg & Redford (1999).

Diagnosis.—Size variable but most populations averaging at least 72 mm in GLS; orange speculum present on dorsum of adult males; nape without black mane; face tan or golden—if golden, hairs usually with dark brown bases; face usually with dark band lateral to eye; throat brown or occasionally brown frosted with golden; hair of forehead variable in length but never hanging over face giving the appearance of a hood; pterygoids not inflated; no foramina present in anterodorsal nasopharynx; frontal sinuses often but not always well-swollen; stylomastoid foramen large; external carotid foramen large; external auditory meatus medium in size; ventral surface of hyoid (stylohyal) distinctly bent or undulating, not smoothly concave; descending process of jugal variable, but usually relatively short and robust; coronoid process of mandible thick.

Comparisons.—This species lacks the black dorsal mane and inflated pterygoid sinuses characteristic of *B. torquatus. Bradypus tridactylus* has a pair of oblong foramina in the anterodorsal nasopharynx lacking in *B. variegatus* (although in young of Age class 1, the roof of the nasopharynx is poorly ossified, complicating the identification of newborn and juvenal individuals of *B. variegatus* and *B. tridactylus*). Also, *B. variegatus* has a brown throat (rarely frosted with golden), in contrast to *B. tridactylus,* which has a brilliant golden throat with hairs golden to the base of the hairs, or with only a slight smoky gray tint to the bases. See account of *B. pygmaeus* for comparisons with that closely related species.

Comments.—Bradypus variegatus is the only species of the genus that displays notable geographic variation. In Central America, it almost always has a tan face. Many specimens from South America—especially from southwestern Colombia, western Ecuador, and northcentral Brazil—possess strikingly golden faces, although the bases of the facial hairs are usually dark brown. A few populations in northern Brazil (e.g., on the lower Rio Tapajós) also show a strong golden frosting on the throat. This species also varies widely in the blotchiness of its dorsal coloration. Cranially, specimens from west of the Andes tend to have more elongated, strongly hourglass-shaped skulls, whereas many populations east of the Andes possess proportionately shorter, wider skulls. All populations agree with the diagnoses of Wetzel (1985) in lacking foramina in the anterodorsal nasopharynx.

Some populations show moderate dwarfing in size. The series from Mojui dos Campos represents one of the few such South American populations. In Central America, populations of *Bradypus variegatus* on several islands of the Laguna de Chiriquí in Bocas del Toro, Panamá average smaller than most but not all populations of the species that we examined from the mainland (Tables 2 and 6). If similar series were available from throughout the species' range, a detailed study of geographic variation might show that these populations deserve subspecific status. Given the present state of understanding of geographic variation within *B. variegatus,* however, it is premature to recognize subspecies of this wide-ranging and highly variable species.

Bradypus gorgon Thomas, 1926 (the only named insular form of the genus prior to this study) does not show dwarfing similar to that of *B. pygmaeus,* and it is conspecific with *B. variegatus. Bradypus gorgon* is from Isla Gorgona, an island with an area of 15.6 km^2 (Aguirre-C. & Rangel-Ch. 1990) approximately 30 km off the southwestern coast of Colombia. Isla Gorgona is located on the continental shelf of South America (von Prahl 1986) and has strong biological affinities with the lowlands of western Colombia and Ecuador (Alberico 1986, Rangel-Ch. 1990b). Although its geological history remains controversial (Aguirre-C. & Rangel-Ch. 1990), it may represent the tip of a sunken volcanic peak belonging to a fourth (coastal) Colombian cordillera (Haffer 1970, Alberico 1986). This coastal cordillera, or at least an arc of volcanic islands, was formed at the end of the middle Eocene, including the Serranía del Baudó, Serranía de los Saltos, and Alto de Nique, in western Colombia and extreme eastern Panamá (Haffer 1970, see also Hershkovitz 1969, Coates & Obando 1996). In the late Pliocene, the Atrato-San Juan sea corridor (= Bolívar Geosyncline) closed, uniting these volcanic blocks with the main body of South America (Alberico 1990, Coates & Obando 1996). Subsequently, glacial cycles alternately raised and lowered sea level; during one or more of these episodes, Isla Gorgona presumably became isolated from the adjacent Chocoan lowlands.

Thomas justified naming *Bradypus gorgon* partly on the basis of size: "Size small, about as in *tridactylus, infuscatus,* and *ephippiger,* the skull markedly smaller than in the Ecuadorean *macrodon*" (Thomas 1926:309–310). *Bradypus infuscatus, B. ephippiger,* and *B. macrodon* are currently considered junior synonyms of *B. variegatus* (see Gardner 1993). Three of the four taxa that Thomas compared with the sloth from Isla Gorgona occur only east of the Andes, making them poor comparisons. Thomas (1917) restricted the fourth one, *B. ephippiger,* to NW Colombia, and Cabrera

(1957) further restricted it to the Río Atrato region. Thus, a better comparison for the *Bradypus* from Isla Gorgona would have been with *B. epipphiger* rather than with *B. macrodon,* as the occurrence of *B. ephippiger* west of the Andes in Colombia places it in the biogeographic region from which the sloth on Isla Gorgona almost certainly was derived.

Contrary to Thomas' conclusions, in the two specimens from Isla Gorgona for which we have measurements (both adults), the greatest length of the skull averages near that of adults from the closest available mainland populations in southwestern Colombia (Isla Gorgona: GLS, $\bar{X}$ = 76.7, standard error of the mean (SEM) = 1.20, n = 2; Río Raposo & Bajo Calima: GLS, $\bar{X}$ = 73.7, SEM = 1.09, n = 6; Tumaco: GLS, $\bar{X}$ = 76.3, SEM = 2.85, n = 3). We agree with Wetzel & Avila-Pires (1980) and Gardner (1993) in considering *Bradypus gorgon* to be conspecific with *B. variegatus.*

Isla Gorgona is twice as far from the mainland as any of the islands of Bocas del Toro, falls within the size range of those islands, and surely has been isolated longer, since it is separated from the mainland by water about 70 m deep (Alberico 1986), whereas the greatest depth of water separating Isla Escudo from the adjacent mainland is ca. 29 m (Kalko & Handley 1994). This raises the question of why the three-toed sloth on Isla Gorgona has not undergone a decrease in size similar to that of *Bradypus pygmaeus* on Isla Escudo. We speculate that dwarfism in *B. pygmaeus* may be related to foraging in mangroves, which are absent from Isla Gorgona (Rangel-Ch. 1990a). Another scenario that should not be dismissed is the possibility that three-toed sloths could have been recently introduced to Isla Gorgona from the mainland by humans (Alberico 1986).

Specimens examined.—Bradypus variegatus, total 467. Argentina (1). Jujuy: no specific locality, 1 (FMNH 21672). Bolivia (13). Beni: Beni River [10°23′S, 65°24′W], 1 (USNM 238668); Río Mamoré [10°23′S, 65°23′W], 5 km S Guayaramerin, 1 (AMNH 209940); Río Mamoré [10°23′S, 65°23′W], 8 km N Exaltación, 1 (AMNH 211663). Cochabamba: Todos Santos [16°48′S, 65°08′W], 1 (AMNH 38784). Santa Cruz: Buena Vista [17°27′S, 63°40′W], 4 (AMNH 61792; FMNH 21393–21394, 21430); Buena Vista [17°27′S, 63°40′W], 450 m, 1 (FMNH 51871); Río Surutú [17°24′S, 63°51′W], 400 m, 1 (AMNH 61791); Río Yapacaní [16°00′S, 64°25′W], 1 (FMNH 51870); Santa Cruz de la Sierra [17°48′S, 63°10′W], 1 (AMNH 133435); 5 km E Río Palometillas, 300 m, 1 (AMNH 261304). Brazil (130). Amazonas: Rio Amazonas, Santo Antonio de Amatary, 1 (AMNH 93103); Rio Amazonas, south bank, Villa Bella Imperatriz [= Parintins, 2°36′S, 56°44′W], 12 (AMNH 93104–93115); Rio Madeira, Rosarinho [3°42′S, 59°08′W], 4 (AMNH 92335, 92828–92829, 92845); Rio Madeira, Rosarinho, Santo Antonio de Uayará, 3 (AMNH 92332–92334); Rio Negro, Cacao Pereira [3°08′S, 60°05′W], Igarapé, 2 (AMNH 80447–80448); Rio Negro, Iaunari [0°31′S, 64°50′W], 1 (AMNH 79396); Rio Negro, Manaus [3°08′S, 60°01′W], 1 (AMNH 91353); Rio Solimões, Codajás [3°50′S, 62°05′W], 1 (FMNH 50906); Solimões, 1 (AMNH 37155). Espíritu Santo: Lagoa Juparana [19°20′S, 40°04′W, Hershkovitz 1977], 4000 ft, 1 (AMNH 78844). Pará: Altamira, 85 km SW, east bank Rio Iriri (3°50′S, 52°40′W), 1 (USNM 549523); Belém [1°27′S, 48°29′W], 2 (MCZ 31001; USNM 393816); Belém [1°27′S, 48°29′W], Utinga, 2 (USNM 339631–339632); Curralinho, 2 (AMNH 133438, 133457); Curralinho, Ilha de Marajó [1°00′S, 49°30′W], 8 (AMNH 133406, 133415, 133419, 133421, 133426, 133432–133433, 133455); Ilha de Marajó [1°00′S, 49°30′W], 4 (FMNH 34401, 34712–34714); Patagonia, 12 mi, 2 (AMNH 75140–75141); Rio Amazonas, Igarapé Piaba [1°55′S, 55°33′W], 3 (MCZ 30993, 30995, 31002); Rio Majary, Recreio [1°42′S, 52°12′W], 1 (AMNH 95841); Rio Tapajós, Aramanay [2°45′S, 54°59′W, Hershkovitz 1977], 3

Observations on the Endemic Pygmy Three-Toed Sloth, *Bradypus pygmaeus* of Isla Escudo de Veraguas, Panamá

Sam Kaviar, **Jakob Shockey***, **Peter Sundberg**

The Evergreen State College, Olympia, Washington, United States of America

Abstract

Our objective was to ascertain the population status of the Pygmy Three-toed Sloth, *Bradypus pygmaeus*, an IUCN Critically Endangered species, on Isla Escudo de Veraguas, Panama. *Bradypus pygmaeus* are thought to be folivorous mangrove specialists; therefore we conducted a visual systematic survey of all 10 mangrove thickets on the island. The total mangrove habitat area was measured to be 1.67 ha, comprising 0.024% of the total island area. The population survey found low numbers of *B. pygmaeus* in the mangrove thickets and far lower numbers outside of them. The connectivity of subpopulations between these thickets on the island is not established, as *B. pygmaeus* movement data is still lacking. We found 79 individuals of *B. pygmaeus*; 70 were found in mangroves and 9 were observed just beyond the periphery of the mangroves in non-mangrove tree species. Low population number, habitat fragmentation and habitat loss could lead to inbreeding, a loss of genetic diversity, and extinction of *B. pygmaeus*.

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* E-mail: jakob.shockey@me.com

These authors contributed equally to this work.

Introduction

The Pygmy Three-toed Sloth, *Bradypus pygmaeus*, was first described as a species in 2001 [1]. *Bradypus pygmaeus* is morphologically distinct from *Bradypus variegatus*, most obviously in their reduced body size, although genetic differentiation has not been shown [2]. *Bradypus pygmaeus* are found only on the 4.3 km^2 island of Isla Escudo de Veraguas (=Isla Escudo), 17.6 km off the Caribbean coast of Panama [1]. To date, researchers have only observed pygmy sloths in the red mangroves (*Rhizophora mangle*) of Isla Escudo's tidal areas, leading to the working hypothesis of obligate red mangrove dietary specialization within the species [1].

Little research has been conducted on *B. pygmaeus* [3]. The dwarfism of *B.pygmaeus* may be due to their folivorous dietary specialization [4], although this hypothesis is not entirely supported [2]. Alternatively, dwarfism may be the result of the inability of sloths to defend food territories [5]. *Bradypus pygmaeus* is an IUCN Critically Endangered species, and understanding the dietary needs of *B. pygmaeus* is critical to developing any conservation plan. Initially, we attempted to falsify the hypothesis that *B. pygmaeus* are obligate mangrove specialists by attempting to track individuals that were outside the mangroves and observe one eating from a non-mangrove tree. We spotted three sloths outside the mangroves within a few hours of arrival on the island but did not see them eat. For the next three weeks we searched for more *B. pygmaeus* outside the mangrove thickets but did not find any. The scarcity of individuals outside of mangrove thickets and the paucity of individuals within them spawned the current study ascertaining the population number of *B. pygmaeus*. Our research focused on assessing the total population size of *B. pygmaeus* and delineating the distribution of this population on Isla Escudo. We assessed mangrove habitat size and quality as well as geographic distribution of habitats on Isla Escudo.

Methods

We initially determined the location of all mangrove thickets and then surveyed them for sloths. First, we mapped the boundary of every mangrove thicket on Isla Escudo with Global Positioning System receiver (Garmin60CSx) waypoint tracks. We used ecological boundaries between mangrove species and other tree types as well as breaks in the canopy layer to define mangrove thickets, which we assigned ID numbers 1–10 (Fig. 1). After delineating each mangrove thicket, we conducted a line transect survey, with each of three observers spaced 3 m apart and walking a fixed compass bearing across the thicket. Each observer observed a strip width 4 m wide (2 m to each side). We did not control for canopy density in strip survey lines. When we reached far edge of the mangrove thicket the transect lines were shifted and the survey conducted along the opposite compass bearing. There was no overlap between transect lines (Fig. 2). This systematic visual survey was conducted throughout all mangrove thickets. When we encountered a sloth an identity number was assigned, and the sloth's location recorded with a GPS. Date, time, and notes on the physical appearance and dorsal coloration of each sloth were recorded. This strictly observational study was conducted under permit #SEA4311, titled "Status de *Bradypus pygmaeus* en Escudo de Veraguas, Panamá", from La Autoridad Nacional del Ambiente (ANAM). No animals were handled in this research.

This method was robust because the canopy density of mangroves is relatively thin, making for easy spotting of sloths. We also controlled for double counting by beginning and finishing

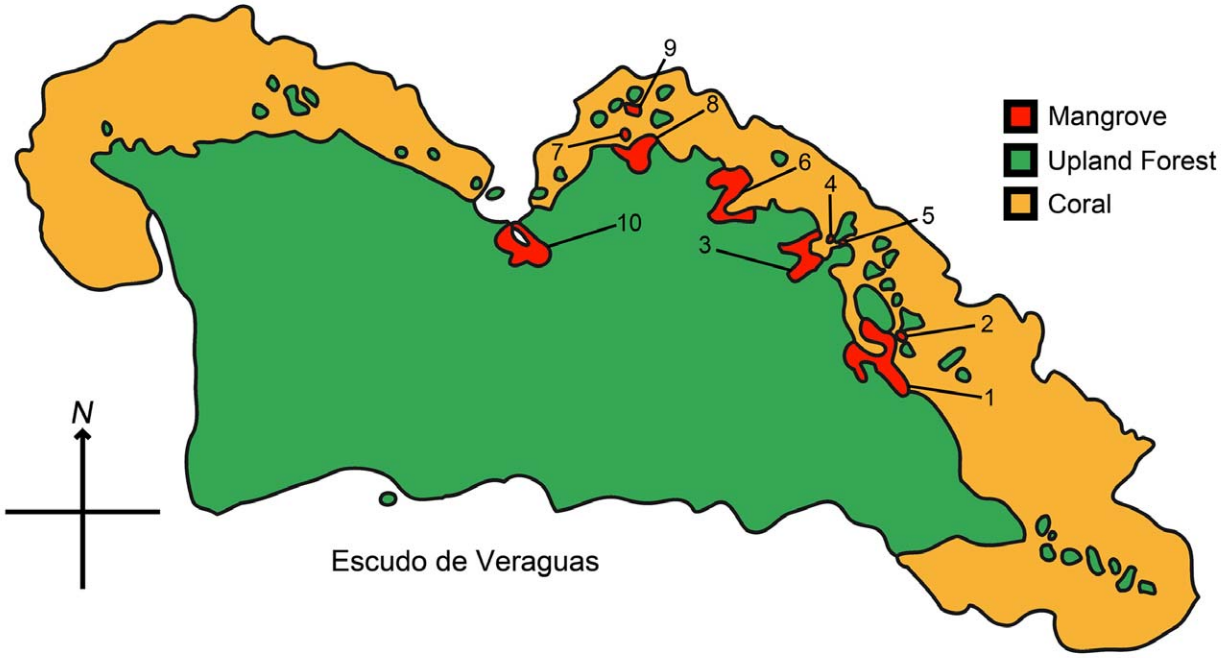

Figure 1. Map of all mangrove thicket locations found on Isla Escudo de Veraguas based on GPS data, showing thicket ID numbers.
doi:10.1371/journal.pone.0049854.g001

the census for a thicket within the same day. Our census took place over a three-day time span. Mangrove thickets 1 and 2 were surveyed on May 8th, thickets 3–6 were surveyed on May 9th, and thickets 7–10 were surveyed on May 11th 2011. We may have missed both sloths hidden in bromeliads on mangroves and babies that blended into their mother. Values are provided ±1 standard deviation.

Results

We located 70 *B. pygmaeus* individuals within the mangrove habitat of Isla Escudo. This represents a minimum estimate, since we observed nine sloths outside of the survey areas. All of the sloths we observed in non-mangrove trees were within 20 meters of a mangrove thicket.

We mapped all mangrove stands upon Isla Escudo by GPS, from which data we generated a visual representation (Fig. 1). We calculate that the total mangrove habitat to be 106,699 m^2, which

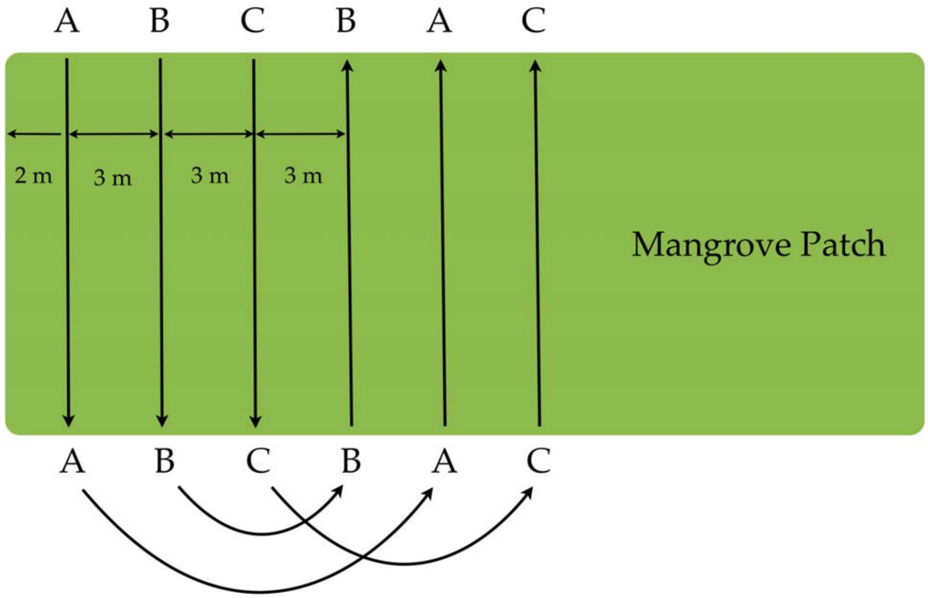

Figure 2. Schematic of strip census method used to survey mangrove thickets for *Bradypus pygmaeus*. Surveyors A, B, and C alternated positions for every survey strip.
doi:10.1371/journal.pone.0049854.g002

Table 1. Results from census of *Rhizophora mangle* for *Bradypus pygmaeus*, Isla Escudo, 9° 5′58′′N 81°33′22"W, May 2011.

Thicket	Area (m^2)	Population (individual)	Density (ind./100 m^2)
Thicket 1	35094	16	0.046
Thicket 10	23095	11	0.048
Thicket 3	18533	15	0.081
Thicket 6	14224	14	0.098
Thicket 8	13579	13	0.096
Thicket 4	606	0	0
Thicket 9	569	0	0
Thicket 7	483	1	0.21
Thicket 2	445	0	0
Thicket 5	71	0	0
Total	106699	70	0.067
Average ± Standard deviation.	10670±12282	7±7.3	0.058±0.066

doi:10.1371/journal.pone.0049854.t001

is 0.024% of the total island area. Average mangrove thicket size was 10,670±12,282 m^2 and the average presence of *B. pygmaeus* within a thicket was 7±7.3 individuals (Table 1). Densities of *B. pygmaeus* individuals were highest in the medium sized mangrove thickets (thickets 3, 6 and 8 at 0.081, 0.098 and 0.096 ind./100 m^2 respectively), while the larger thickets (1 and 10) had lower densities (at 0.046 and 0.048 ind./100 m^2 respectively). Nevertheless, in a simple linear regression (Fig. 3), these data suggest that overall population levels are dependent on mangrove thicket area, with $y = 0.0005 \times +1.3202$, and $R^2 = 0.80493$.

Discussion

It is critical for the survival of *B. pygmaeus* to ascertain whether or not they are obligate mangrove specialists and how able are they to disperse through the non-mangrove mixed lowland tropical forest, or utilize these forests for food. Our early fieldwork investigated whether any sloths found outside mangrove habitats consumed leaves. Although we spotted sloths in this non-mangrove forest at varies points in our fieldwork, we never saw one eat in this lowland forest. We saw sloths eating mangrove foliage on many occasions.

The mangroves on Isla Escudo are fragmented into five clumps separated by either non-mangrove, mixed forest or sea water. Within these thickets, we noted many instances of anthropogenic cutting of mangroves that interrupted the canopy layer between previously continuous mangrove habitat. The genus *Bradypus* is noted for its lack of ability to move on the ground [6]. Although we did not take data on the size or distribution of these cuts, we estimate them to occur over roughly 30% of the total mangrove

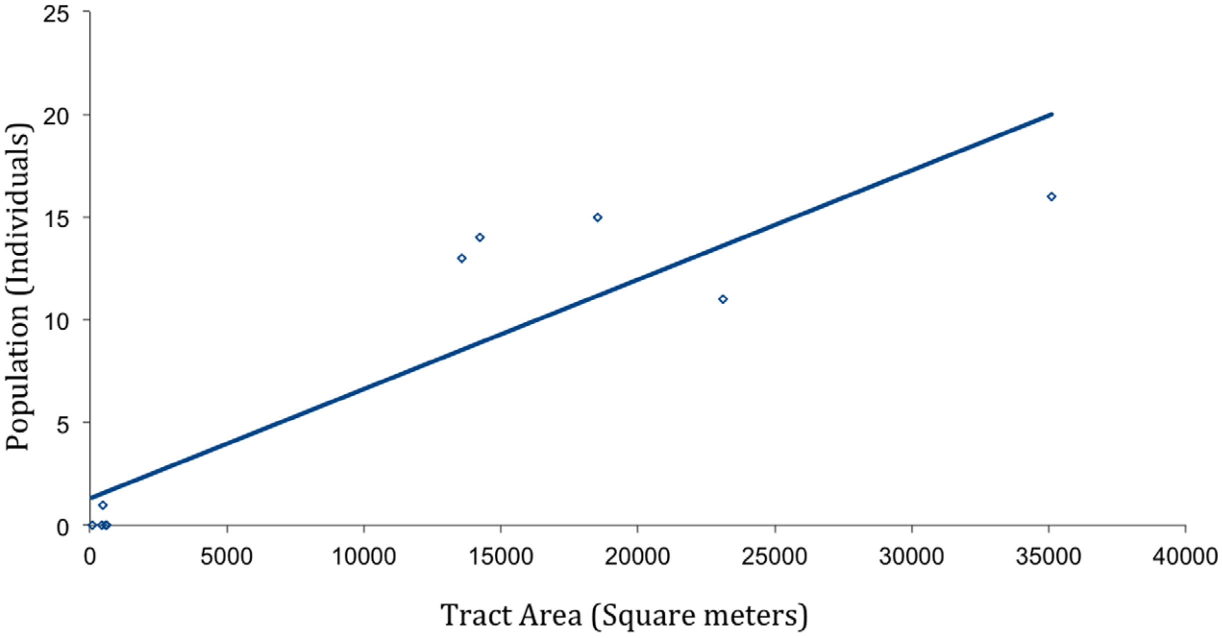

Figure 3. Regression analysis of population as dependent on (mangrove) area, where $y = 0.0005 \times +1.3202$ and $R^2 = 0.80493$. The symbols for thickets 2,4 and 9 overlap.
doi:10.1371/journal.pone.0049854.g003

habitat we surveyed. The distribution of this cutting between the ten identified mangrove thickets was not consistent, and may be a factor in *B. pygmaeus* density. We do not know the effects of these cuts on *B. pygmaeus*, yet we assume that this habitat disturbance and fragmentation could contribute to a decline of their population.

These deforested areas appear to be the result of logging by local people with hand tools. We observed numerous felled trees with machete and saw marks. It appears that the largest mangrove trees were selectively felled and in numerous thickets the largest mangroves trees we observed had been cut, but remained decomposing on the ground. Often the roots and branches of these trees were stripped away and the mangrove trunks were left behind. This observation supports the idea that mangrove logging takes place to support cooking fires using small diameter hardwood (Lenin Riquelme, Conservación, Naturaleza y Vida Panama (CONAVI), personal communication, October 21, 2010). In other thickets, the tallest standing mangrove trees were at the end of the thicket, farthest away from sea access.

We observed two dead *B. pygmaeus* bodies. The first carcass we found was decayed to bones and hair. We assume that these bodies were relatively fresh since decomposition happens quickly in the tropics; however, quantification of the time since death is not possible given our limited data on affecting environmental conditions. The second carcass was in a lesser state of decay, with some epidermal degradation, but overall recognizable features. These carcasses were still fully intact, suggesting that they were not killed by predation. If so, these observations lead us to suspect a high rate of death through disease, habitat loss, or natural causes in the population of *B. pygmaeus*. As an insular endemic species, *B. pygmaeus* may be adapted to a relatively high rate of inbreeding and have diminished risk of deadly recessive allele expression [7]. However, loss of allele variations could negatively affect the ability of *B. pygmaeus* to adapt to changes in its environment such as novel pathogens and climate change.

For *B. pygmaeus* to survive, protection of mangroves is needed. We also observed feral domestic cats on Isla Escudo, which is of concern to such a small *B. pygmaeus* population. Isla Escudo had four camps built of locally found materials in small deforested coastal areas. These camps house local Ngöbe fisherfolk who live in nearby mainland coastal communities but camp on Isla Escudo in order to have fishing trips at sea and around the island's coral reefs. There is a camp on the eastern end of the island where fish was sold to fish buyers from Chiriquí Grande and elsewhere in Bocas Del Toro province for the local and international tourist market. The largest market was for lobster, however we observed many species of fish taken and one instance of shark finning in which the dorsal fins of five sharks were removed, and the sharks were left and died in the shallow breakwater of Isla Escudo. During our study we met with leaders of the Ngöbe community. It was brought to our attention that scientific research on Isla Escudo has been conducted without any discussion with the Ngöbe people. Conservation will fail if it does not include the local people [8].

Acknowledgments

We would like to thank our professors Heather Heying and Bret Weinstein, the people of the Asunto Indigena office in Panama City, Esteban Poncé and his family, Anel Hooker, the mayor of Kusapin, the workers at the school of Kusapin, the congress of the Ngöbe-Bugle Comarca, and all the other people that welcomed us into the community. We would also like to thank the Institute for Tropical Ecology and Conservation, specifically Pete Lahanas and Joe Maher. We would also like to thank Lenin Riquelme for orienting us to the project and Bryson Voirin for his cautionary advice. We relied greatly on the expertise of Julian Sammons in GIS mapping, and Scott Eckert for editorial assistance. We thank John Calambokidis, Erik Thuesen and Ross Matteson for their support in the final stages of our project. We are very grateful to Stephen Bartlett for translating our paper into Spanish so that we could share it with the people of Kusapin. We also feel immense gratitude for our classmates, specifically Miranda Ciotti and Nick Mobus.

Author Contributions

Conceived and designed the experiments: JS SK PS. Performed the experiments: JS SK PS. Analyzed the data: JS SK PS. Wrote the paper: JS SK PS. Final manuscript revision: JS.

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Conservation Actions

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Taxonomy [top]

Kingdom	Phylum	Class	Order	Family
ANIMALIA	CHORDATA	MAMMALIA	PILOSA	BRADYPODIDAE

Scientific Name:	*Bradypus pygmaeus*
Species Authority:	Anderson & Handley, 2001
Common Name/s: English – Pygmy Three-toed Sloth Spanish – Perezoso Pigmeo	
Taxonomic Notes:	*Bradypus pygmaeus* has only recently been described by Anderson and Handley (2001) as a separate species.

Assessment Information [top]

Red List Category & Criteria:	Critically Endangered B1ab(ii,iii)+2ab(ii,iii) ver 3.1
Year Published:	2011
Date Assessed:	2010-06-27
Assessor/s:	Anderson, R. & Moraes-Barros, N. and Voirin, B.
Reviewer/s:	Superina, M. & Abba, A.M.
Contributor/s:	
Justification: *Bradypus pygmaeus* is listed as Critically Endangered as this species has a very restricted range, being found only on one very small island less than 5 km² in size, and there is likely a continuing decline in the quality of habitat and area of occupancy due to habitat degradation.	
History:	2006 – Critically Endangered (IUCN 2006) 2006 – Critically Endangered

Geographic Range [top]

Range Description:	*Bradypus pygmaeus* is known only from Isla Escudo de Veraguas, in the islands of Bocas del Toro, Panama. Sloths on the younger islands of the Bocas del Toro archipelago are conspecific with *Bradypus variegatus*. Isla Escudo de Veraguas has an area of approximately 4.3 km² and is about 17.6 km from the mainland of Panama.
Countries:	**ve:** ma
Range Map:	Click here to open the map viewer and explore range.

Population [top]

Population:	There is no information available on the population status of *B. pygmaeus*. The population is likely to be relatively small and presumably consists of less than 500 individuals.
Population Trend:	⬇ Decreasing

Habitat and Ecology [top]

Habitat and Ecology:	This smallest of all sloths, this species has only been recorded in the red mangrove forests surrounding the island, currently estimated at just 1.3–1.5 km² in area. It has not been recorded from forest patches within the island. As far as is known, it primarily, if not exclusively, feeds on mangrove leaves.
Systems:	Terrestrial

Threats [top]

Major Threat(s):	Although the island is uninhabited, there are seasonal visitors (fishermen, campesinos, lobster divers and local people) who are known to hunt the sloths opportunistically (B. Voirin pers. comm. 2010). Preliminary studies suggest a low level of genetic diversity among pygmy sloths (Silva *et al*. 2010, N. Moraes-Barros pers. comm. 2010), which could lead to endogamic depression if the (already low) population size decreases any further. Previously, it was thought that there were potential threats from the development of the island for tourism; it has now been confirmed that this is not likely as the whole island is now a marine reserve and very few tourists visit the island (B. Voirin pers. comm., 18 July 2010). However, cutting of the mangroves by indigenous people continues to reduce the area of available habitat for this species. Over the past five years mangrove coverage has been greatly reduced.

Conservation Actions [top]

Conservation Actions:	*B. pygmaeus* is endemic to a single island of Panama, which is protected as a wildlife refuge and is contained within the Comarca Indigenous Reserve. There is a need to improve the enforcement of this protected area, which currently receives little attention from wildlife protection authorities. Conservation of the species could be improved through local awareness programmes, specifically those promoting sloths as conservation flagship species.

Citation:	Anderson, R. & Moraes-Barros, N. and Voirin, B. 2011. *Bradypus pygmaeus*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on **12 November 2013**.
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The 2010 Sloth Red List Assessment

Author(s): Mariella Superina, Tinka Plese, Nadia Moraes-Barros and Agustín Manuel Abba
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URL: http://www.bioone.org/doi/full/10.5537/020.011.0202

The 2010 Sloth Red List Assessment

Mariella Superina
Tinka Plese
Nadia Moraes-Barros
Agustín Manuel Abba

Abstract

The conservation status of all sloth species was re-assessed in May and June 2010 by the IUCN/SSC Anteater, Sloth and Armadillo Specialist Group. Four out of six species were categorized as Least Concern. Two sloths were classified in a threatened category according to the IUCN Red List of Threatened Species; *Bradypus torquatus* was listed as Vulnerable, and *Bradypus pygmaeus* as Critically Endangered. Sloths are mainly threatened by hunting, illegal pet trade, and by habitat degradation and fragmentation. According to the 2010 assessment, the taxonomy of all six species requires further research. Data on their population size, range, and dynamics, as well as their life history, is still insufficient.

Keywords: Conservation status, threats, *Bradypus*, *Choloepus*, Pilosa, Xenarthra

Introduction

Six years after the last assessment (Fonseca and Aguiar, 2004), the IUCN/SSC Anteater, Sloth and Armadillo Specialist Group re-evaluated the conservation status of the four *Bradypus* and two *Choloepus* species in May and June 2010. The IUCN Red List Categories and Criteria, version 3.1 (IUCN, 2001) were used. Eight researchers provided data on the geographic range, population size and status, habitat and ecology, threats, and existing conservation measures of sloths. All assessments were checked for consistency by at least two specialists.

Five sloths maintained their Red List category, while *Bradypus torquatus* was downgraded from Endangered to Vulnerable due to new and more accurate data on its extent of occurrence (Table 1). As in 2004, four out of six species were categorized as Least Concern. The population trend of these sloths is, however, unknown (Table 1). Two sloths were classified in a threatened category: *Bradypus pygmaeus* was listed as Critically Endangered, and, as mentioned before, *Bradypus torquatus* was re-categorized as Vulnerable (Table 1). Both species have negative population trends and thus require close monitoring.

Sloths are mainly threatened by hunting, either to be used as a protein source or to be (illegally) sold as pets (at least four out of six species), and by habitat degradation and fragmentation (*B. torquatus* and *C. hoffmanni*). Several research gaps have been identified; according to the 2010 assessment, the taxonomy of all six species requires further research (Fig. 1). Furthermore, data on their population size, range, and dynamics, as well as their life history, is still insufficient.

All sloths occur in at least one protected area, and education programs are in place in part of the range of five species (Fig. 2). *Bradypus torquatus* is the only xenarthran for which an action recovery plan exists. *Bradypus variegatus* is listed in CITES Appendix II, and the Costa Rican populations of *C. hoffmanni* are included in Appendix III (CITES, 2009). No harvest management or area-based management plans exist for any sloth species.

We thank all researchers, graduate students, rangers, and enthusiasts who participated in the 2010 Sloth Red List Assessment. Detailed species descriptions and updated range maps can be found on the following pages.

Table 1. Historical overview of the Red List categories and current population trends of the six sloth species. See glossary for definitions of the categories.

Species	1996	2004	2010	Population trend
Bradypus pygmaeus	--	**CR** B1ab(i,ii,iii)	**CR** B1ab(ii,iii)	↓
Bradypus torquatus	**EN**	**EN** B1ab(i,ii,iii)	**VU** B2ab(i,ii,iii)	↓
Bradypus tridactylus	**LR/lc**	**LC**	**LC**	**?**
Bradypus variegatus	**LR/lc**	**LC**	**LC**	**?**
Choloepus didactylus	**DD**	**LC**	**LC**	**?**
Choloepus hoffmanni	**DD**	**LC**	**LC**	**?**

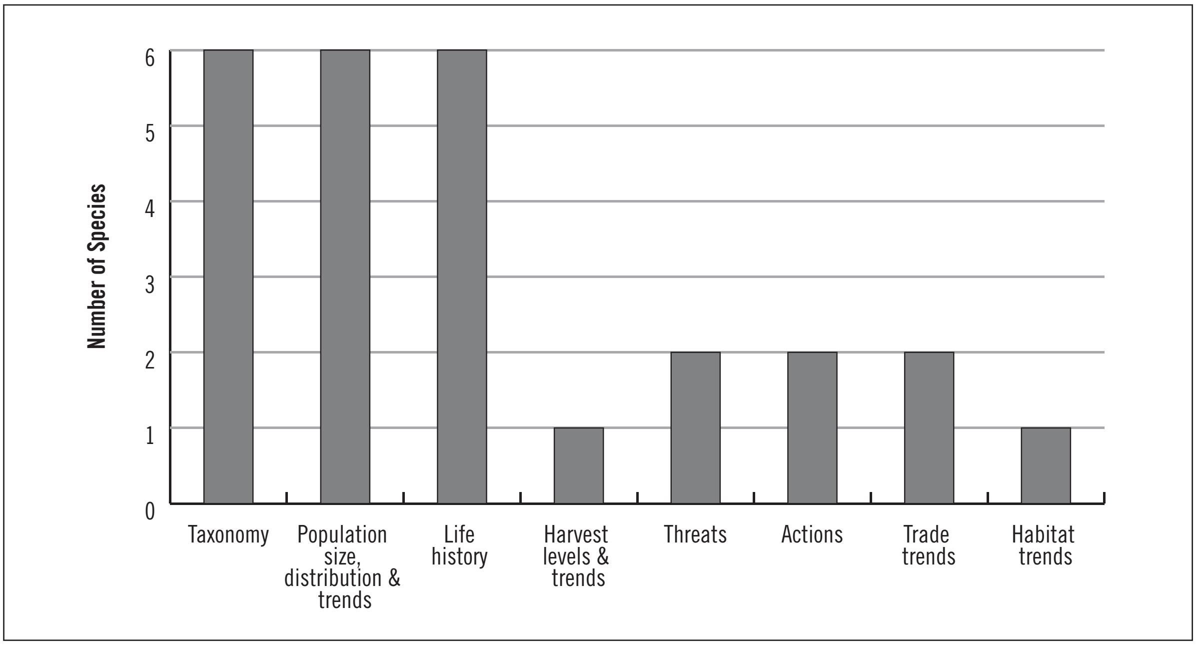

Figure 1. Research priorities for sloths

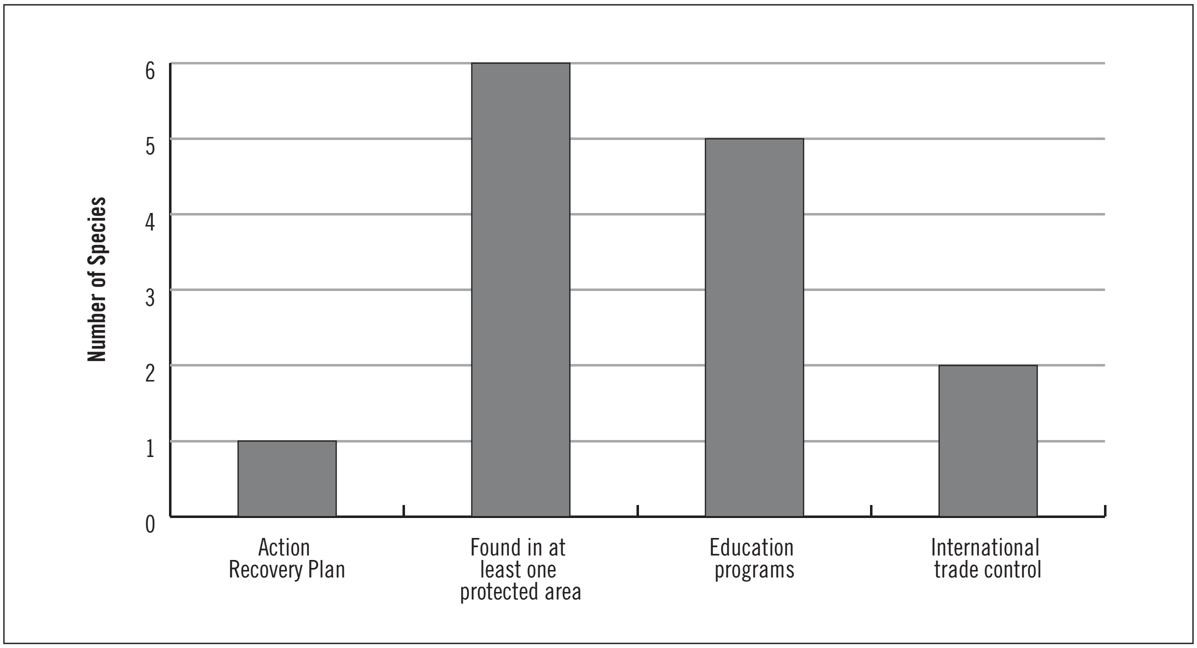

Figure 2. Existing conservation measures for sloths

Bradypus pygmaeus

Critically Endangered (CR B1ab(ii,iii))

Photograph: Bryson Voirin

Common Names: Pygmy three-toed sloth (English), perezoso pigmeo (Spanish), preguiça anã (Portuguese).

Assessment Rationale: *B. pygmaeus* is listed as Critically Endangered as this species has a very restricted range, being found only on one very small island less than 5 km² in size, and there is likely a continuing decline in the quality of habitat and area of occupancy due to habitat degradation.

Taxonomic Note: *B. pygmaeus* has only recently been described as a separate species (Anderson and Handley, 2001).

Geographic Range: *B. pygmaeus* is known only from Isla Escudo de Veraguas, in the islands of Bocas del Toro, Panama (Fig. 3). Sloths on the younger islands of the Bocas del Toro archipelago are conspecific with *Bradypus variegatus* (Anderson and Handley, 2001, 2002). Isla Escudo de Veraguas has an area of approximately 4.3 km² and is about 17.6 km from the mainland of Panama. Based on the area of red mangrove forest on Isla Escudo de Veraguas, the area of occupancy is estimated at 1.3 to 1.5 km².

Population: There is no information available on the population status of *B. pygmaeus*. The population is likely to be relatively small and presumably consists of less than 500 individuals.

Habitats and Ecology: This smallest of all sloths has only been recorded in the red mangrove forests surrounding the island, currently estimated at 1.3 to 1.5 km². It has not been recorded from forest patches within the island. As far as is known, it primarily, if not exclusively, feeds on mangrove leaves.

Threats: Although the island is uninhabited, there are seasonal visitors (fishermen, lobster divers and local people) who are known to opportunistically hunt the sloths (B. Voirin, pers. comm., 2010). Preliminary studies suggest a low level of genetic diversity among pygmy sloths (Silva *et al.*, 2010; N. Moraes-Barros, pers. comm., 2010), which could lead to endogamic depression if the (already low) population size decreases any further.

Conservation: *B. pygmaeus* is endemic to a single island of Panama, which is protected as a wildlife refuge and is contained within the Comarca Indigenous Reserve. There is a need to improve the enforcement of this protected area, which currently receives little attention from wildlife protection authorities. Conservation of the species could be improved through local awareness programs, specifically those promoting sloths as conservation flagship species.

Assessors: Anderson, R., Moraes-Barros, N. and Voirin, B.

Evaluators: Superina, M. and Abba, A.M.

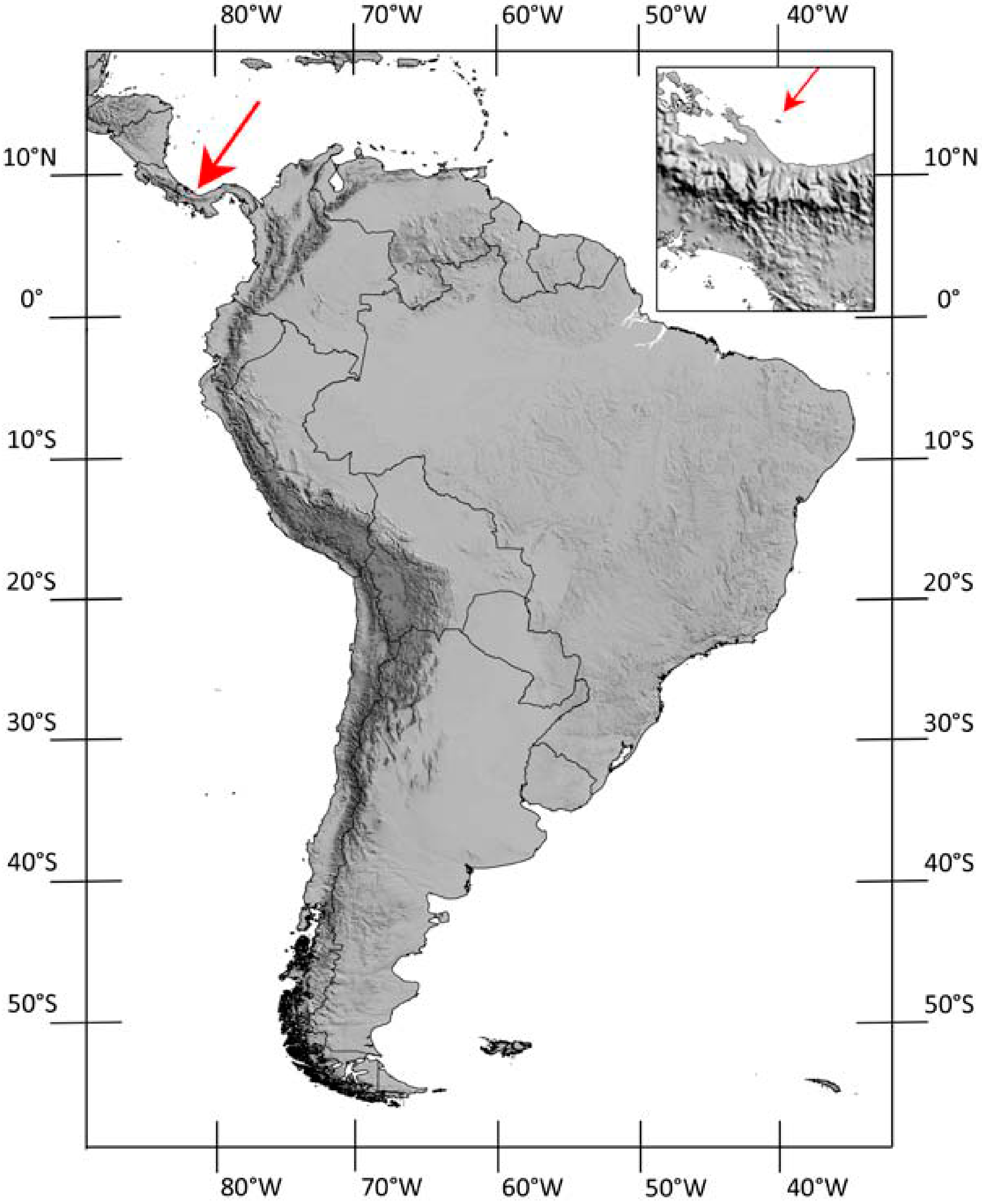

Figure 3. *Bradypus pygmaeus*. Based on Anderson and Handley (2001); Gardner (2007); Aguiar and Fonseca (2008).

Bradypus torquatus

Vulnerable (VU B2ab(i,ii,iii))

Photograph: Kevin Schafer, www.kevinschafer.com

Common Names: Maned three-toed sloth (English), maned sloth (English), preguiça (Portuguese), preguiça-de-coleira (Portuguese), bicho-preguiça (Portuguese).

Assessment Rationale: *B. torquatus* was previously listed as Endangered based on its very restricted extent of occurrence. However, new data and a detailed range analysis based on all confirmed locations and habitat preferences revealed that the extent of occurrence is larger than previously thought. Recent analyses of the available habitat left for *B. torquatus* suggest that this species has an area of occupancy less than 1,000 km² (based on remaining forest within its highly fragmented range). Nevertheless, its range, area of occupancy, and habitat are in continuing decline due to ongoing habitat loss and degradation in the Brazilian Atlantic forest. Furthermore, it is threatened by hunting. *B. torquatus* is therefore listed as Vulnerable, with the caveat that a re-assessment should be performed as soon as more data on the wild populations become available.

Taxonomic Note: There are three genetically distinct populations of this species in the states of Bahia, Espírito Santo and Rio de Janeiro (Moraes-Barros *et al.*, 2002, 2006; Lara-Ruiz *et al.*, 2008). The northern population (in southern Bahia) might be considered a separate subspecies (Lara-Ruiz *et al.*, 2008), although indistinguishable from the others in external morphology (A. Chiarello, pers. comm., 2010). For information on the genetic diversity of maned sloths, see also Lara-Ruiz (2004).

Geographic Range: *B. torquatus* is restricted to the coastal Atlantic forests of eastern Brazil (Fig. 4). Historically, it possibly occurred throughout the coastal forest of Bahia through to the state of Pernambuco (footnote by O. Pinto in Wied's 19th century account; Coimbra-Filho, 1972). At present, the southern part of the state of Bahia is the primary stronghold for the species. Maned sloths were recently reported from the state of Sergipe (Chagas *et al.*, 2009) but thus far no records have been collected in the adjacent state of Alagoas. The extensive deforestation of suitable habitat in this state suggests that it is unlikely to survive there. A natural biogeographic gap occurs in northern Espírito Santo, perhaps due to a higher degree of deciduity in the forests of this region (Hirsch and Chiarello, in press). The species does not occur from the left bank of Doce River to the vicinity of Mucuri River. It has been reported from extreme northern Minas Gerais on the left bank of Jequitinhonha River. *Bradypus torquatus* has been introduced to some National Parks in Espírito Santo (Caparaó National Park) and Rio de Janeiro (Tijuca National

Park), among other areas, although it is not known if the species is still present at these sites. It ranges from sea level to 1,290 m asl. Its extent of occurrence is estimated at 90,000 km^2 (Hirsch and Chiarello, in press) and its area of occupancy at 1,000 km^2 (Hirsch and Chiarello, unpublished data).

Population: In some parts of Bahia and Espírito Santo, the animals are locally abundant in forest fragments (Chiarello, pers. comm., 2010) although the population density is not well known. Genetic studies indicate no gene flow between the populations of southern Bahia (Ilhéus) and Espirito Santo (Santa Teresa), and those of Poço das Antas (Rio de Janeiro). It appears that these populations have been isolated before the anthropogenic fragmentation of habitat, possibly beginning in the Pleistocene (Moraes-Barros *et al.*, 2006; Lara-Ruiz *et al.*, 2008). In general, little genetic diversity is exhibited within individual populations, but the northernmost population (Bahia) is the genetically more diverse (Moraes-Barros *et al.*, 2006; Lara-Ruiz *et al.*, 2008). Overall, the global population of *B. torquatus* is assumed to be decreasing in response to the continuing loss and fragmentation of suitable habitat, the Atlantic forest (Ribeiro *et al.*, 2009).

Habitats and Ecology: This largely arboreal species is found in wet tropical forest, most typically in areas with an annual precipitation of 1,200 mm or higher and lacking a dry season. Most records are from evergreen forests, and just a handful of sightings are from semi-deciduous forests (Hirsch and Chiarello, in press). It can be found in secondary forest habitats, including "cabrucas" (cocoa plantations under native forests in southern Bahia; Cassano *et al.*, in press). Some animals have been sighted in forest fragments as small as 20 ha, although the long-term persistence of populations at these sites is unknown. It is a strict folivore that feeds on a relatively small number of food plants (Chiarello, 2008). Chiarello (1998) found that leaves from 21 species formed 99% of the diet of three animals. Like other congeneric sloths, animals descend from trees periodically to urinate and defecate. The females give birth to one young per year, predominantly at the end of the wet season and beginning of the dry season (February-April), and copulation concentrates in the late dry and early wet seasons (August-October; Dias *et al.*, 2009). Sexual maturity is probably reached between the second and third year and longevity in the wild is over 12 years (Lara-Ruiz and Chiarello, 2005).

Threats: The rate of deforestation in the Atlantic forest of eastern Brazil has decreased dramatically in the last three decades but has not stopped (Ribeiro *et al.*, 2009), so the pressure on habitat continues. In southern Bahia the economic crisis of the cocoa plantation (*Theobroma cacao*) puts a pressure on farmers of this product to clear their forest to make room for other economic alternatives, mainly pastures. In other areas, native forests are cleared for other reasons, including coal production, agriculture and city sprawl. The genetic integrity of distinct populations is threatened by the release of confiscated animals at different sites without knowledge or understanding of their origins. Additional threats include subsistence hunting and accidental mortality of *B. torquatus* on roads. Sloths attract the attention when spotted and might be killed just for the sake of curiosity. Although the species is not actively pursued by hunters, individuals might sometimes fall victims of subsistence hunting when spotted by local people. Although hunting is legally forbidden in Brazil, enforcement is ineffective and practically inexistent.

Conservation: *B. torquatus* is present in a number of protected areas, such as the Biological Reserves of Una (Bahia), Augusto Ruschi (Espírito Santo) and Poço das Antas (Rio de Janeiro), among others. The low genetic diversity within fragmented populations indicates a need to develop corridors of suitable habitat between these populations. Confiscated animals should be genetically characterized to determine the most appropriate release site. Data on dispersal ability, sex ratio, mating system, and population density are virtually unknown but important for conservation planning and monitoring. The species has been successfully translocated (Chiarello *et al.*, 2004). Awareness programs are in place in Espírito Santo, Brazil.

Assessors: Chiarello, A. and Moraes-Barros, N.

Evaluators: Hayssen, V. and Abba, A.M.

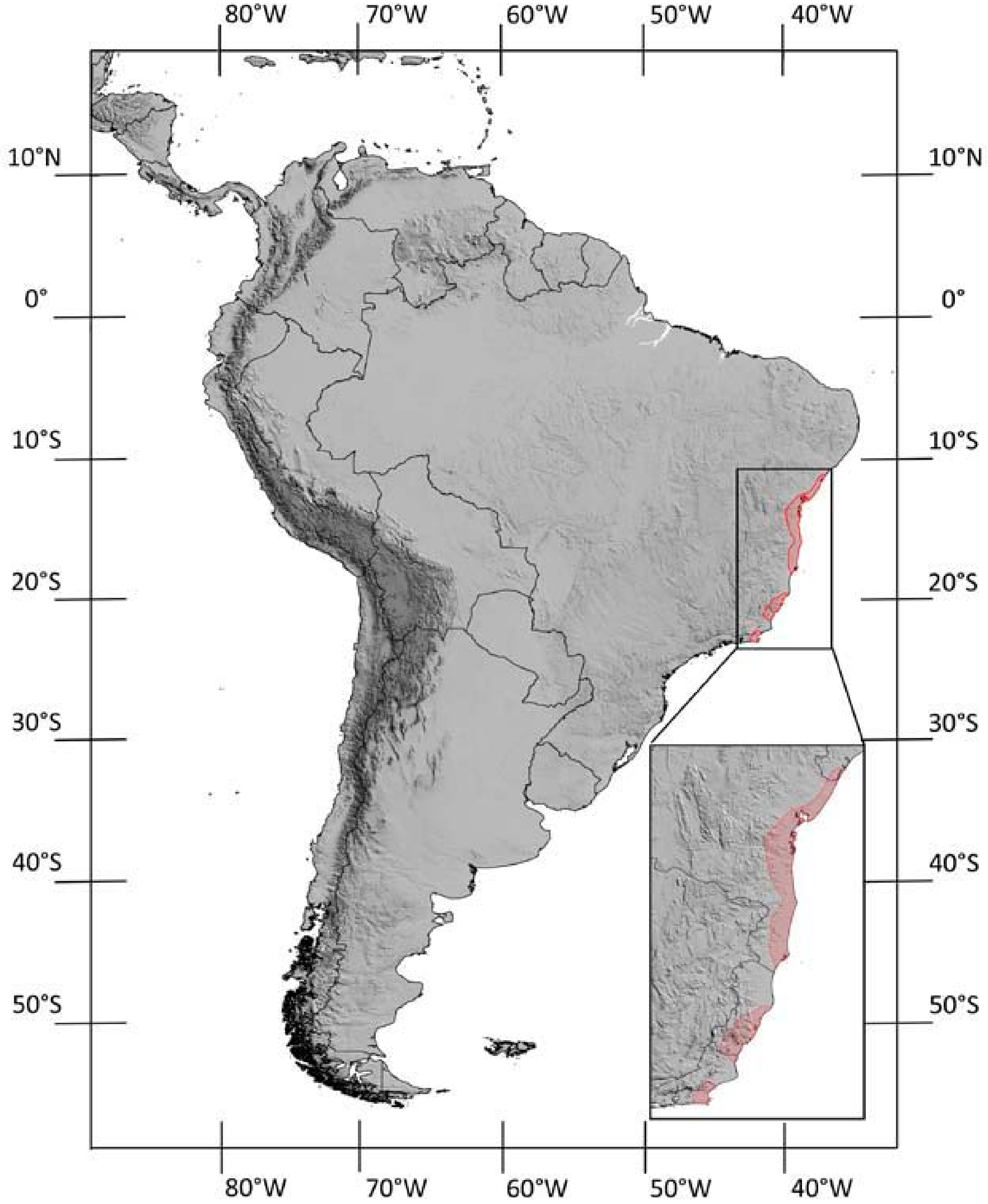

Figure 4. *Bradypus torquatus.* Based on Wetzel (1982); Emmons and Feer (1997); Eisenberg and Redford (1999); Gardner (2007); Aguiar and Fonseca (2008); Chagas *et al.* (2009); Hayssen (2009a); Boffy *et al.* (2010); Hirsch and Chiarello (in press); A. Chiarello, pers. comm. (2010).

Bradypus tridactylus

Least Concern (LC)

Photograph: Monique Pool

Common Names: Pale-throated three-toed sloth (English), pale-throated sloth (English), perezoso de tres dedos (Spanish), preguiça (Portuguese), preguiça-de-bentinho (Portuguese), preguiça-do-norte (Portuguese), ai (Portuguese).

Assessment Rationale: *B. tridactylus* is listed as Least Concern in view of its wide distribution in one of the most pristine areas of the Amazon basin, and its having been recorded as locally relatively abundant.

Geographic Range: *B. tridactylus* occurs in the Guyana Shield region, from Venezuela south of the Orinoco (although its distribution crosses at the delta region) into northern Brazil (south to the Amazonas/Solimões), through to Guyana, Suriname and French Guiana (Fig. 5). It does not occur south of the Amazon River. Its extent of occurrence is estimated at 1,000,000 km^2.

Population: Population density estimates vary from 1.7 animals per km^2 in French Guiana (Taube *et al.,* 1999) to 2.21 animals per hectare (or 221 animals per km^2) in Manaus, Brazil (Chiarello, 2008).

Habitats and Ecology: *B. tridactylus* is found in lowland and montane tropical moist forest. It has been recorded on "tepuis" (table-top mountains). The head and throat of adult sloths are yellowish to white and contrast with the grayish body that bears white spots. Males can be distinguished from females by their dorsal orange-yellow patch with a broad black central line (Hayssen, 2009b). Both males and females reach reproductive age at three to six years. A single young is born after a gestation of six months (Taube *et al.*, 2001; Gilmore *et al.*, 2008).

Threats: There are no major threats to this sloth species.

Conservation: *B. tridactylus* has been recorded from many protected areas.

Assessors: Chiarello, A. and Moraes-Barros, N.

Evaluators: Superina, M. and Abba, A.M.

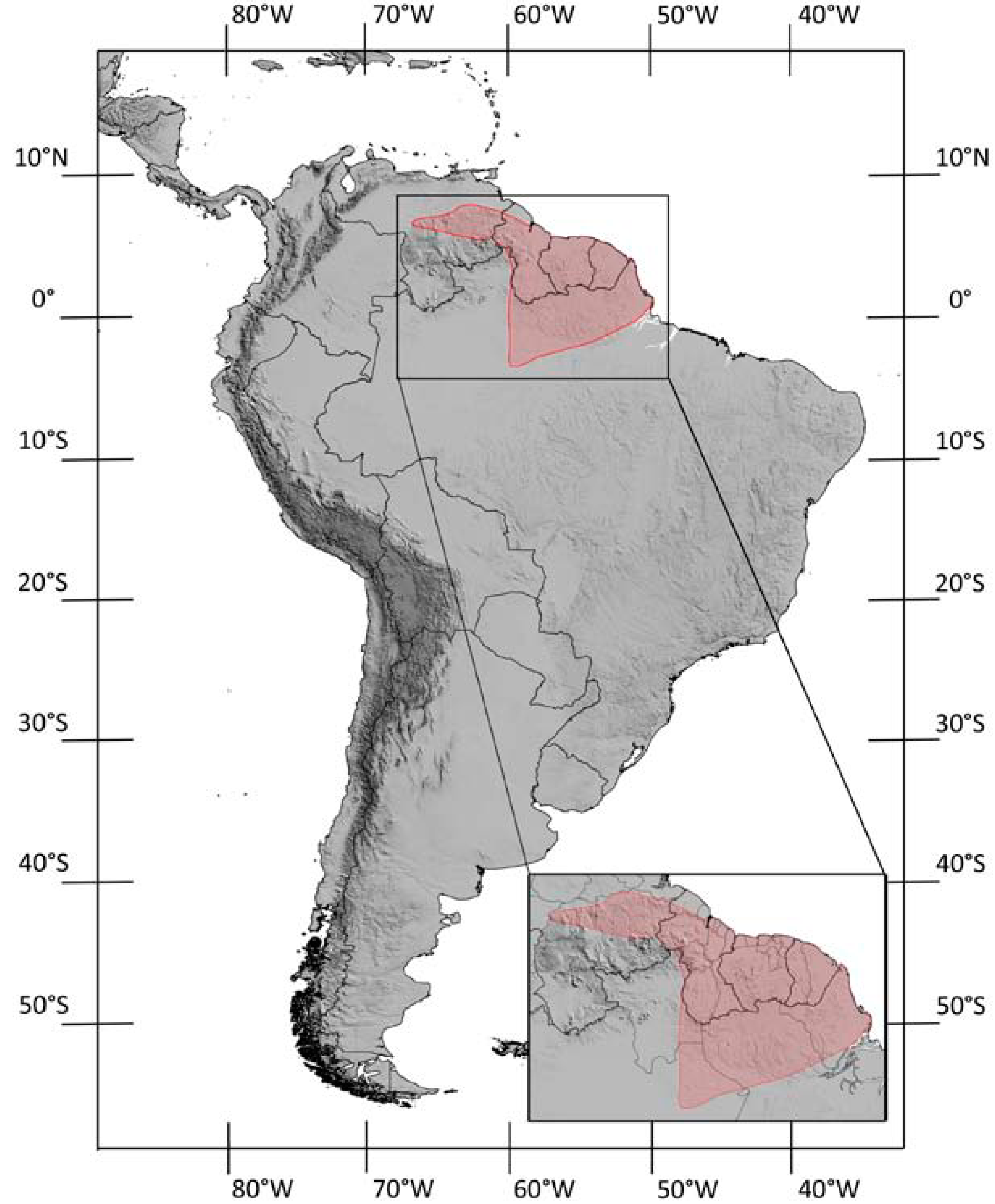

Figure 5. *Bradypus tridactylus.* Based on Wetzel (1982); Emmons and Feer (1997); Eisenberg and Redford (1999); Taube *et al.* (1999); Engstrom and Lim (2000); Gardner (2007); Aguiar and Fonseca (2008); Hayssen (2009b); Moraes-Barros *et al.* (2010); N. Moraes-Barros, pers. comm. (2009).

Bradypus variegatus

Least Concern (LC)

Photograph: Simonne Schinem

Common Names: Brown-throated three-toed sloth (English), brown-throated sloth (English), Bolivian three-toed sloth (English), perezoso tridáctilo (Spanish), perezoso bayo (Spanish), perezoso grisáceo (Spanish), guasa (Spanish), preguiça (Portuguese), preguiça-comum (Portuguese), bicho-preguiça (Portuguese), preguiça de óculos (Portuguese), ai (Portuguese), paresseux tridactyle (French), bradype (French), aï de Bolivie (French), paresseux tridactyle de Bolivie (French).

Assessment Rationale: *B. variegatus* is listed as Least Concern in view of its wide distribution including a large part of the Amazon forest, presumed large population, its occurrence in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a threatened category.

Taxonomic Note: Seven subspecies are recognized according to Gardner (2007). Recent phylogeographic studies revealed that *B. variegatus* from the Central American, western Amazon and Atlantic forests constitute distinct and unique evolutionary units that are distinguishable by molecular and morphological traits (Moraes-Barros *et al.*, 2002, 2006, 2007).

Geographic Range: *B. variegatus* ranges from Honduras in the north, through southern Central America. In South America, it ranges from Colombia into western and southern Venezuela, and south into Ecuador, eastern Peru and Bolivia, into Brazil and northern Argentina (where it is probably extinct; Fig. 6). Its distribution overlaps with *B. torquatus* in the central part of the Atlantic forest (Hirsch and Chiarello, unpublished data). In Brazil, the species currently occurs in forested areas of the Amazon, Atlantic forest, and Cerrado biomes. There are historical records of *B. variegatus* in the Caatinga biome (Moraes-Barros, unpublished data). Its presence in the Pantanal biome of Brazil remains unconfirmed, but the species might occur in the contact zones between this biome and the Amazon forest to the north. Additional field studies are thus necessary in order to properly define the current species distribution in the Cerrado, Caatinga and Pantanal. The southernmost distribution of this sloth in Brazil was reported by Cabrera (1957) as the state of Rio Grande do Sul, which could, however, not be confirmed (Gardner, 2007). It is historically absent from the state of Santa Catarina (Brazil) and northeastern Argentina; the southernmost confirmed record of the species is near Londrina, in the state of Paraná, Brazil, but today it is considered extinct in this state (Mikich and Bernils, 2004). The last record from Argentina was collected in Jujuy province and dates back to 1916 (Vizcaíno *et al.*, 2006), but field studies specifically aiming at this species are lacking from this country. *B. variegatus* is found from sea level to at least 2,400 m asl (Ureña *et al.*, 1986). The extent of occurrence of this species amounts to approximately 10,000,000 km^2. Its area of occupancy is declining; this is particularly true for the Brazilian Atlantic forest and the Colombian populations.

Population: Population densities of *B. variegatus* have been estimated at 2.2 to 6.7 animals per hectare in the Brazilian Amazon (Queiroz, 1995), 8.5 animals per hectare in Panama (Montgomery and Sunquist, 1975), and 0.6 to 4.5 animals per hectare in the tropical dry forest of Colombia (Acevedo and Sanchez, 2007). No demographic information is available from the remaining area of distribution. *B. variegatus* is commonly found in public squares, where densities can reach 12.5 animals per hectare (Manchester and Jorge, 2009). Severe fragmentation has been reported from the populations in Colombia and from the eastern Brazilian subspecies *B. v. brasiliensis*, which presents the lowest levels of genetic diversity among all *B. variegatus*. The genetic diversity is only comparable to that observed in the Critically Endangered pygmy sloth (*B. pygmaeus*). Molecular studies also indicate that genetic diversity in the northern Atlantic forest subspecies *B. v. variegatus* is lower than values observed for sympatric populations of *B. torquatus* (Moraes-Barros *et al.,* 2006).

Habitats and Ecology: The brown-throated three-toed sloth has been recorded from a number of forest types, including seasonal mesic tropical forest, semi-deciduous forest (inland Atlantic forest), cloud forest, and lowland tropical forest. It inhabits cacao plantations in Costa Rica (Vaughan *et al.*, 2007). This sloth species produces one litter of one infant at intervals of at least 19 months (Bezerra *et al.*, 2008; T. Plese, pers. comm., 2010). Mating period varies depending on the year and geographical region, but occurs mainly in spring (*i.e.*, from July to November in South America and from February to May in Central America).

Threats: It appears that there are no major threats to *B. variegatus* at the global level. Nevertheless, some populations, especially in Colombia and Brazil, are declining due to deforestation leading to severe habitat degradation and fragmentation. Furthermore, they are hunted by local indigenous communities. In Brazil, especially in the northeastern region and in the Amazon, and in Colombia the common sloth is hunted and sold in public markets as food, medicine, and as a pet species. In several touristic sites, *B. variegatus* is used by locals to entertain visitors. Wild-caught individuals, especially offspring, are sold as pets to tourists in Colombia (Moreno and Plese, 2006). This illegal trade is increasing and represents a cause of concern due to its impact on the wild populations.

Conservation: *B. variegatus* is present in many protected areas. It is included in CITES Appendix II. Education and awareness programs are being carried out by Fundación Unau in Colombia.

Assessors: Chiarello, A., Plese, T. and Moraes-Barros, N.

Evaluators: Superina, M. and Abba, A.M.

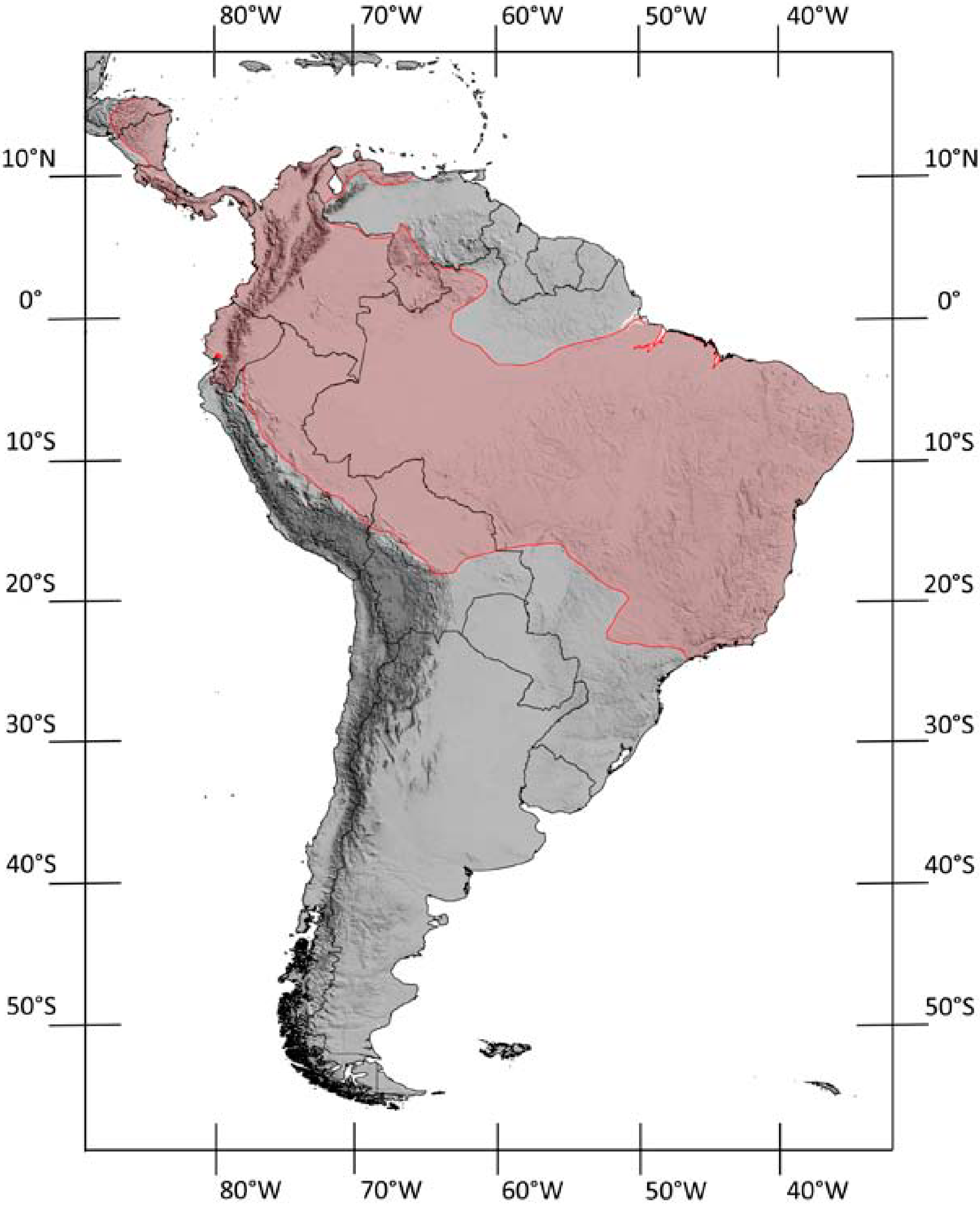

Figure 6. *Bradypus variegatus.* Based on Hall (1981); Ureña *et al.* (1986); Eisenberg (1989); Redford and Eisenberg (1992); Pacheco *et al.* (1995); Emmons and Feer (1997); Reid (1997); Eisenberg and Redford (1999); Lord (2000); Cáceres (2004); Mikich and Bernils (2004); Moreno and Plese (2005); Medri *et al.* (2006); Gardner (2007); Tirira (2007); Aguiar and Fonseca (2008); Romero *et al.* (2008); Hayssen (2010); Moraes-Barros *et al.* (2010); Í. M. Medri, pers. comm. (2009); N. Moraes-Barros, pers. comm. (2009); T. Plese, pers. comm. (2009).

Choloepus didactylus

Least Concern (LC)

Photograph: John A. Nyakatura

Common Names: Southern two-toed Sloth (English), Linné's two-toed sloth (English), perezoso de dos dedos (Spanish), perico ligero (Spanish), preguiça-real (Portuguese), unau (Portuguese).

Assessment Rationale: *C. didactylus* is listed as Least Concern in view of its wide distribution, presumed large population, its occurrence in a number of protected areas, and because it is unlikely to be declining fast enough to qualify for listing in a threatened category.

Geographic Range: The southern two-toed sloth ranges through Venezuela (the delta and south of the Río Orinoco) and the Guianas (French Guiana, Guyana, and Suriname) south into Brazil (Maranhão state west along the Rio Amazonas/Solimões) and west into the upper Amazon Basin of Ecuador and Peru (Fig. 7). Its southern limit in the western Amazon of Brazil is unclear. It occurs in the southern departments of Colombia, with its northern limit being the departments of Meta and Guainía. It ranges from sea level up to 2,438 m asl (Britton, 1941). The extent of occurrence of this sloth is approximately 4,200,000 km^2.

Population: In Suriname, *C. didactylus* has been found at densities of 0.9 animals per hectare (Taube *et al.,* 1999). In the Brazilian Amazon, estimated densities range from 0.13 individuals per hectare (Manaus region) to 0.88 animals per hectare in the flooded forests (Mamirauá Reserve; Queiroz, 1995; Chiarello, 2008).

Habitats and Ecology: This sloth species is found in tropical moist lowland and montane forest. Two-toed sloths have nocturnal and solitary habits. Gestation length seems to be approximately ten months (Eisenberg and Maliniak, 1985) but estimates are quite variable. Males and females reach sexual maturity at approximately two years of age. Longevity in captive conditions is at least 18 years.

Threats: There are no major threats to *C. didactylus*. Because they are usually found high in the canopy, motionless and virtually invisible, they are not as commonly hunted as armadillos or tamanduas, and there are taboos against their consumption by some native groups. They are probably hunted opportunistically, but there is no serious bushmeat trade.

Conservation: *C. didactylus* is present in many protected areas.

Assessors: Plese, T. and Chiarello, A.

Evaluators: Abba, A.M. and Superina, M.

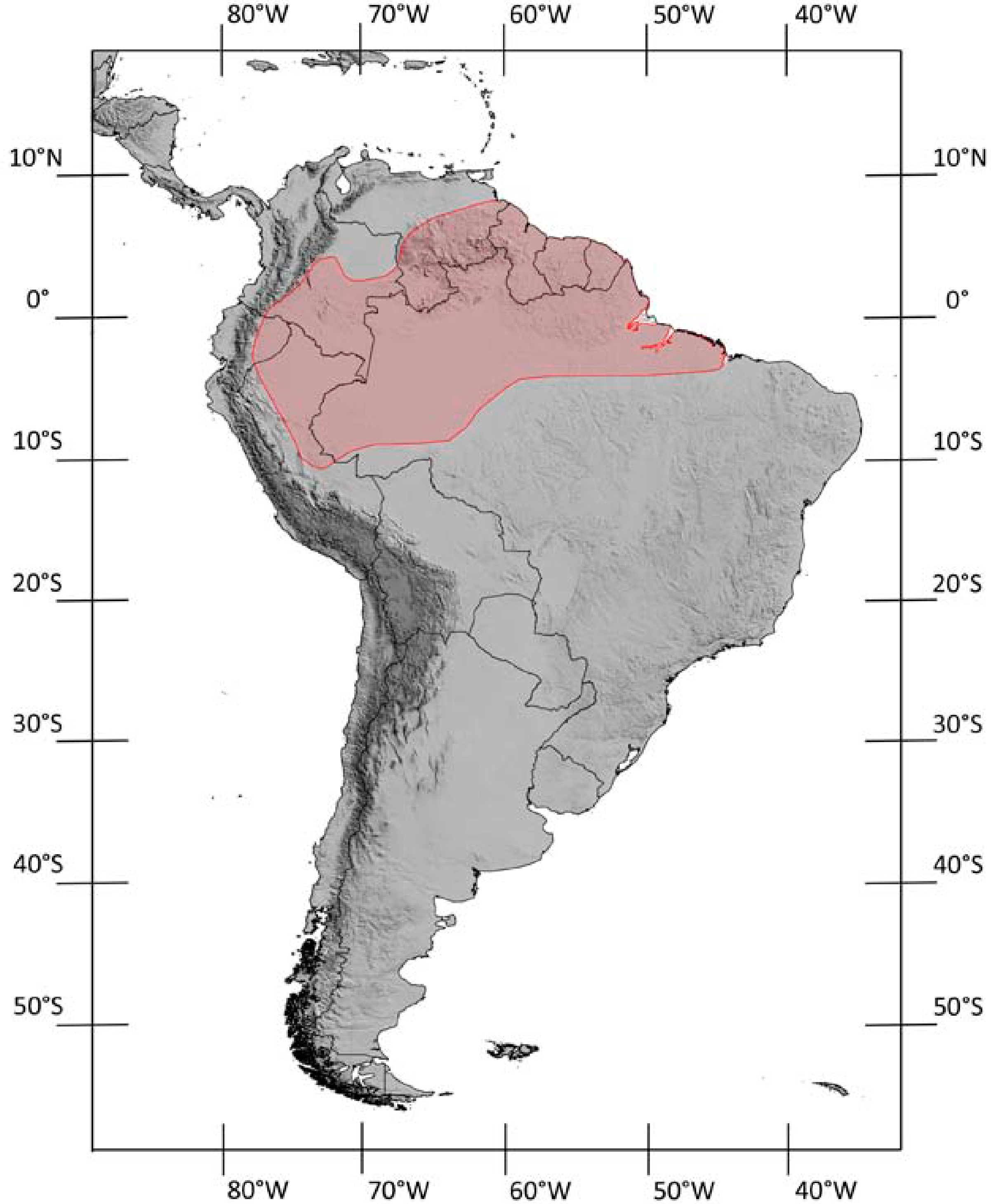

Figure 7. *Choloepus didactylus.* Based on Hall (1981); Pacheco *et al.* (1995); Emmons and Feer (1997); Adam (1999); Engstrom and Lim (2000); Gardner (2007); Tirira (2007); Aguiar and Fonseca (2008).

Choloepus hoffmanni

Least Concern (LC)

Photograph: Fundación Unau

Common Names: Hoffmann's two-toed sloth (English), perezoso (Spanish), perico ligero (Spanish), unau (Spanish), unau d'Hoffmann (French).

Assessment Rationale: *C. hoffmanni* is listed as Least Concern in view of its wide distribution, presumed large population, its occurrence in a number of protected areas, its tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a threatened category. However, because of ongoing deforestation, the northern population (nominate subspecies) of this species could potentially be assessed as Near Threatened.

Taxonomic Note: Five subspecies are recognized by Gardner (2007).

Geographic Range: *C. hoffmanni* has two disjunct populations. The northernmost population ranges from Nicaragua south into western Venezuela. The southern population is found from north-central Peru through extreme western Brazil (south-western Amazonas and probably Acre states) to central Bolivia (Fig. 8). There is a doubtful, outlying record for this species from the Rio Aripuanã, Mato Grosso state, Brazil (Fonseca and Aguiar, 2004). Its range within Brazil is unclear, and further surveys are needed. This species ranges from sea level to 3,300 m asl in Costa Rica; up to 1,925 m asl in Panama; and up to 1,150 m asl in the southern Andes of Venezuela. In Colombia, the species is found in the biogeographical regions of the Andean zone, Caribbean and Chocó, more specifically in the departments of Cauca, Chocó, Cundinamarca, Nariño, Quindío, Sucre, Valle del Cauca, and Santanderes from sea level up to 3,000 m asl (Alberico *et al.*, 2000; Moreno, 2003; Acevedo and Sanchez, 2007). Its extent of occurrence is approximately 1,600,000 km^2.

Population: This two-toed sloth occurs at densities of 1.05 animals per hectare on Barro Colorado Island, Panama (Montgomery and Sunquist, 1975). It has been found at densities of 0.3 to 1.5 animals per hectare in the Andean region of Colombia, while densities in the lowlands of northern Colombia were 0.2 to 0.83 individuals per hectare (Alvarez, 2004; Acevedo and Sanchez, 2007) and only 0.079 sloths per hectare in the natural reserve "La Montaña del Ocaso", Quindío, Colombia (Aguilar-Isaza and López-Obando, 2009).

Habitats and Ecology: *C. hoffmanni* is found in lowland and montane tropical forest, both deciduous and mixed-deciduous. In Central America, it occurs in evergreen and semi-deciduous tropical moist forest as well as in secondary forest, but it is rare or absent in lowland dry forest. In Costa Rica, it is able to use cocoa plantations as habitat and frequently ventures into relatively open pastures in search of isolated feeding trees (Vaughan *et al.*, 2007). It can also occur in dry grassland with thorny shrubs and trees (Nicaragua; Genoways and Timm, 2003). These sloths are rather solitary. Their herbivore-omnivore diet consists mainly of leaves, fruits and sap of some trees. Both genders reach reproductive maturity at three years of age. Gestation length is approximately 11 months.

Threats: It appears that there are no major threats to *C. hoffmanni* at the global level. Nevertheless, populations in the northwestern part of its range, especially in Colombia and Central America, are declining due to severe habitat degradation and fragmentation. Furthermore, they are hunted by indigenous communities. Wild-caught individuals, especially offspring, are sold as pets to tourists in Colombia (Moreno and Plese, 2006). This illegal trade is increasing and represents a cause of concern due to its impact on the wild populations.

Conservation: *C. hoffmanni* is present in many protected areas. It is included in CITES Appendix III for Costa Rica (CITES, 2009). Further research is needed to establish whether there are taxonomic differences between the two disjunct populations. Ongoing education and awareness programs are carried out by Fundación Unau in Colombia.

Assessors: Plese, T. and Chiarello, A.

Evaluators: Abba, A.M. and Superina, M.

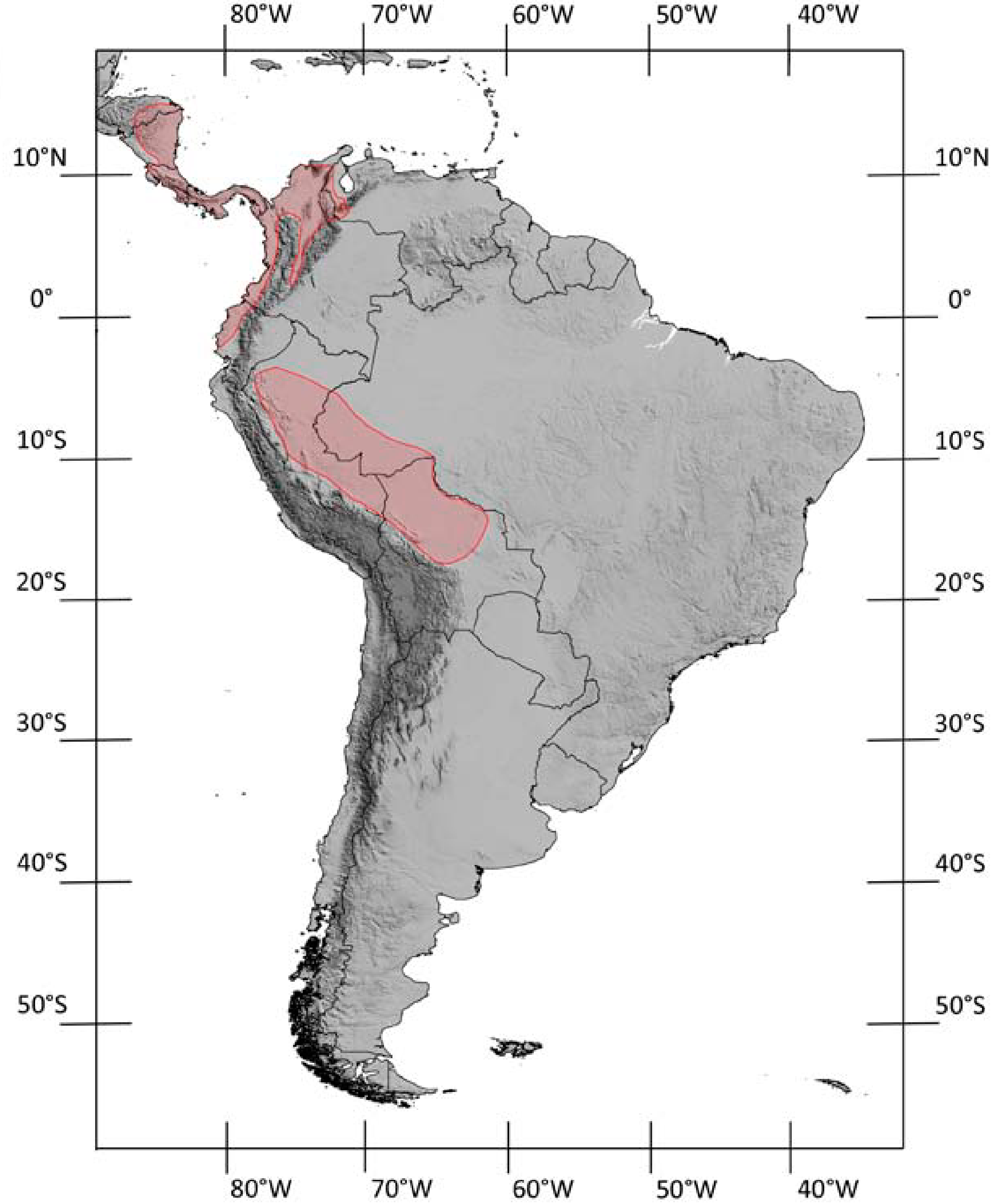

Figure 8. *Choloepus hoffmanni*. Based on Wetzel (1982); Eisenberg (1989); Salazar Bravo *et al.* (1990); Pacheco *et al.* (1995); Anderson (1997); Emmons and Feer (1997); Reid (1997); Eisenberg and Redford (1999); Alberico *et al.* (2000); Genoways and Timm (2003); Moreno (2003); Acevedo and Sanchez (2007); Gardner (2007); Tirira (2007); Aguiar and Fonseca (2008).

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Mariella Superina, IMBECU, CCT CONICET Mendoza, Parque General San Martín s/n, Casilla de Correos 855, Mendoza (5500), Argentina, e-mail: <mariella@superina.ch>; **Tinka Plese**, Fundación Unau, Circular 1ª, #73-24, Medellín, Colombia, e-mail: <unau@une.net.co>; **Nadia Moraes-Barros**, Labec, Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo-USP, Rua do Matão 277, São Paulo, CEP 05508-090, Brasil; and **Agustín M. Abba**, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina, e-mail: <abbaam@yahoo.com.ar>.

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MAMMALIAN SPECIES 812:1–4

Bradypus pygmaeus (Pilosa: Bradypodidae)

VIRGINIA HAYSSEN

Department of Biology, Smith College, Northampton, MA 01063, USA; vhayssen@email.smith.edu

Abstract: *Bradypus pygmaeus* Anderson and Handley, 2001, the pygmy three-toed sloth, is a dwarf bradypodid that is 1 of 4 species of *Bradypus*. It is easily distinguished from its conspecifics by its small size and restricted distribution (endemic to Isla Escudo de Veraguas of Bocas del Toro, off the Caribbean coast of Panama). *B. pygmaeus* is found exclusively in red mangroves at sea level, and it is listed as critically endangered by the International Union for the Conservation of Nature and Natural Resources because of its restricted range and declining population size that is due to hunting and tourism. DOI: 10.1644/812.1.

Key words: dwarf sloth, endangered species, folivore, monk sloth, Panama endemic, sloth, three-toed sloth

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Bradypus Linnaeus, 1758

Bradypus Linnaeus, 1758:34. Type species *Bradypus tridactylus* Linnaeus, 1758, by subsequent designation (Miller and Rehn 1901).

Tardigradus Brisson, 1762:21. Unavailable name.

Ignavus Blumenbach, 1779:70. Type species *Ignavus tridactylus*: Blumenbach, 1779 (= *Bradypus tridactylus* Linnaeus), by monotypy.

Pradypus Ledru, 1810:257, footnote. Incorrect subsequent spelling of *Bradypus* Linnaeus.

Choloepus: Desmarest, 1816:327. Part; not *Choloepus* Illiger, 1811.

Acheus F. Cuvier, 1825:194. Type species *Bradypus tridactylus* Linnaeus, by monotypy.

Achaeus Erman, 1835:22. Incorrect subsequent spelling of *Acheus* F. Cuvier.

Achaeus Gray, 1843:xxviii. Incorrect subsequent spelling of *Acheus* F. Cuvier.

Arctopithecus Gray, 1843:xxviii. Nomen nudum.

Arctopithecus Gray, 1850:65. Preoccupied by *Arctopithecus* Virey, 1819 (Primates).

Scaeopus Peters, 1864:678. Type species *Bradypus torquatus* Illiger, 1811, by monotypy.

Hemibradypus Anthony, 1906:292. Type species *Hemibradypus mareyi* R. Anthony, 1907, by subsequent designation (R. Anthony 1907:220).

Eubradypus Lönnberg, 1942:5. Type species *Bradypus tridactylus* Linnaeus, 1758, by original designation.

Neobradypus Lönnberg, 1942:10. Unavailable name.

CONTEXT AND CONTENT. Order Pilosa, suborder Folivora, family Bradypodidae. *Bradypus* is the sister-taxon to all other sloths including several groups of extinct ground sloths as well as extant two-toed sloths (*Choloepus*) based on craniodental characters (Gaudin 2004). This generic synonymy is modified from Gardner (2007). The following key to the 4 species of *Bradypus* is from Wetzel (1985) with modifications from Anderson and Handley (2001):

Fig. 1.—An adult *Bradypus pygmaeus* from Isla Escudo de Veraguas. Used with permission of the photographer Bill Hatcher.

Fig. 2.—Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult female *Bradypus pygmaeus* (United States National Museum 579177; age class 2 of Anderson and Handley [2001]). Greatest length of cranium is 68.7 mm.

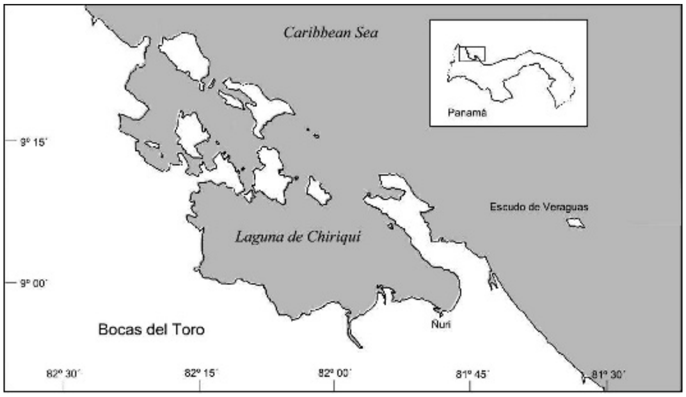

Fig. 3.—*Bradypus pygmaeus* is endemic to Isla Escudo de Veraguas east of Laguna de Chiriquí (modified with permission from Anderson and Handley [2002]).

1. Long, black hair beginning at nape of neck projects over shoulders as 2 plumes that unite on upper back; no speculum in males; skull with pterygoid sinuses distinctly inflated .... *B. torquatus*

   No black plume on dorsum; facial hair shorter than dorsal hair and of a different color; males with middorsal yellow-to-orange speculum; pterygoids not inflated 2 2

2. Throat yellowish golden, continuous with pale color of forehead, lacking dark markings on face; foramina present in anterodorsal nasopharynx .... *B. tridactylus*

   Throat and sides of face brown or hairs on throat only slightly frosted with golden-yellow tips, prominent dark brown forehead and orbital stripe typically present, outlining paler color of ocular area on face; no foramina present in anterodorsal nasopharynx 3

   Size small (total length, 485–530 mm); skull small (greatest length, 67–72 mm) and gracile; large external auditory meatus; known only from Bocas del Toro, Panamá .... *B. pygmaeus*

   Size variable (total length, 485–750 mm); skull variable (greatest length, 68–86 mm) and robust; medium external auditory meatus; known from eastern Honduras to northern Argentina .... *B. variegatus*

Bradypus pygmaeus Anderson and Handley, 2001
Pygmy Three-toed Sloth

Bradypus pygmaeus Anderson and Handley, 2001:17. Type locality "Panamá: Bocas del Toro: Isla Escudo de Veraguas, West Point."

Context and Content. Context as for genus. *Bradypus pygmaeus* is monotypic.

DIAGNOSIS

Bradypus pygmaeus is a dwarf, 3-toed sloth with a gracile skull and an auditory meatus that is large for the size of the skull (Anderson and Handley 2001). *B. variegatus* is generally larger in size than *B. pygmaeus*, with a more robust skull. The coronoid process of the mandible for *B. pygmaeus* is thin and falcate, whereas that of *B. variegatus* is thick (Anderson and Handley 2001).

GENERAL CHARACTERS

Pygmy three-toed sloths resemble *B. variegatus* except for their smaller size (Anderson and Handley 2002). The face of *B. pygmaeus* is buff to tan with a dark band across the brow and an orange wash around the dark eye stripe. Hair on the crown and shoulders is long, shaggy, and forms an obvious hood around short facial hair. The throat is agouti gray-brown and the dorsum is blotchy in color with a dark midsagittal stripe. Males have a dorsal, orange speculum with woolly hair along the margin (Anderson and Handley 2001). Average external measurements (in mm or kg) with parenthetical *SE*, range, and sample size for adults of mixed sex are: total length, 505.4 (5.71, 485–530, 7); length of tail, 49.7 (2.13, 45–60, 7); length of hind foot, 102.4 (1.96, 94–110, 7); length of ear, 10 (–, 10–10, 1), body mass, 2.9 (0.185, 2.5–3.5, 7—Anderson and Handley 2001).

The skull of *B. pygmaeus* is small and gracile with weak and often convex parietal ridges, thin pterygoids, no foramina in the anterodorsal nasopharynx, minute premaxillae barely articulating with the maxillary, an incomplete zygomatic arch with slender roots, a long, thin descending process of the jugal, and a lambdoidal crest that is continuous across the posterior edge of the occiput. Average cranial measurements (in mm) with parenthetical *SE*, range, and sample size for adults of mixed sex are: greatest length of skull, 69.0 (0.67, 67.5–72.2, 6); anterior zygomatic breadth, 41.5 (1.15, 38.3–45.7, 6); posterior zygomatic breadth, 39.5 (1.02, 36.5–42.9, 6); postorbital breadth, 21.2 (0.395, 20.2–22.4, 6); length of squamosal process, 21.5 (0.405, 20.3–22.9, 7); breadth of squamosal process, 4.3 (0.235, 3.5–5.0, 7); length of maxillary toothrow, 23.3 (0.38, 22.3–24.7, 6); postpalatal length, 34.8 (0.60, 33.3–37.0, 6); palatal breadth, 16.3 (0.245, 15.5–17.2, 7); depth of braincase, 24.5 (0.195, 23.7–25.0, 6); breadth of antorbital bar, 3.2 (0.135, 2.8–3.7, 7); length of descending jugal process, 16.2 (0.46, 14.7–18.0, 7); diameter of external auditory meatus, 5.9 (0.225, 5.3–6.7, 7); breadth of ascending mandibular ramus, 13.2 (0.46, 11.9–14.9, 7—Anderson and Handley 2001).

DISTRIBUTION

Bradypus pygmaeus is endemic to Isla Escudo de Veraguas of Bocas del Toro, off the Caribbean coast of Panama (Anderson and Handley 2001). This 4.3-km^2 island separated from the mainland about 8,900 years ago and is currently 17.6 km distant (Anderson and Handley 2001). No fossils are known.

FORM AND FUNCTION

Bradypus pygmaeus has 18 teeth, 10 on the upper jaw (2 anterior chisel-shaped teeth and 8 molariform teeth) and 8 on the lower jaw (2 anterior chisel-shaped teeth and 6 molariform teeth—Anderson and Handley 2001; Naples 1982). The upper, anterior, chisel-shaped teeth are tiny or absent and the lower ones are compressed anteroposteriorly (Anderson and Handley 2001). The morphology of *B. pygmaeus* represents rapid speciation in an insular setting (Anderson and Handley 2002).

ONTOGENY AND REPRODUCTION

Cranial characteristics define 4 age classes. Newborns and juveniles have small skulls with open sutures, small and poorly developed anterior skull elements, smooth masseter–temporal fossa, no postmastoid fossa, frontal sinuses with little swelling, and lambdoidal crest not yet formed. Immatures also have open sutures and a smooth masseter–temporal fossa, but are intermediate in size with somewhat swollen frontal sinuses, a lambdoidal crest, anterior frontal elements nearing adult proportions, and sometimes postmastoid fossae. Young adults have large skulls with open sutures; the anterior frontal elements have adult proportions and the rest of the skull has some of the following: prominent postmastoid fossae, swollen frontal sinuses, rugose masseter–temporal fossae, and a sharply edged lambdoidal crest. The large skulls of full adults have some or all sutures that are closed, fully developed anterior skull elements, rugose masseter–temporal fossae, prominent postmastoid fossae, swollen frontal sinuses, and a sharply edged lambdoidal crest (Anderson and Handley 2001).

ECOLOGY AND BEHAVIOR

Bradypus pygmaeus occurs exclusively in red mangroves at sea level (Anderson and Handley 2001). The film *Hanging with the Sloth* documents pygmy three-toed sloth behavior including terrestrial and arboreal locomotion and swimming (Ledbetter 2005). A genus-level review of captive husbandry is available (Raines 2005).

CONSERVATION

Bradypus pygmaeus is listed as Critically Endangered by the International Union for the Conservation of Nature and Natural Resources because of its restricted range and population decline as a result of hunting and tourism (Samudio et al. 2006).

REMARKS

Bradypus is from the Greek for slow-footed. The specific epithet is from the Latin *pygmaeus* meaning dwarf or pygmy (Anderson and Handley 2001). Common names are monk sloth and dwarf sloth.

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R. P. Anderson provided astute and helpful comments as well as modifications to the distribution map. A. Keller provided bibliographic support for this account. Funding was from the Blakeslee Grant for Genetics Research at Smith College.

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Morphology, molecular phylogeny, and taxonomic inconsistencies in the study of *Bradypus* sloths (Pilosa: Bradypodidae)

NADIA DE MORAES-BARROS,* JULIANA A. B. SILVA, AND JOÃO STENGHEL MORGANTE

Laboratorio de Biologia Evolutiva e Conservação de Vertebrados (LABEC), Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 277, Cidade Universitária, São Paulo, São Paulo, Brazil, 05508-090

** Correspondent: namoraes@ib.usp.br*

This study focuses on morphological and molecular data analyses, misidentifications, and phylogenetic inconsistencies regarding *Bradypus variegatus* (the brown-throated sloth) and *B. tridactylus* (the pale-throated sloth). Misidentifications were recorded on 75 of 313 museum specimens of *Bradypus*. Almost 90% of the misidentified specimens were *B. variegatus* from north-central Brazil, erroneously attributed to *B. tridactylus*. These misidentified specimens are reported in taxonomic reviews as the southernmost records of *B. tridactylus*. A history of confusing nomenclature regarding sloth species exists, and these particular misidentifications could be attributable to the similarity in face and throat color between *B. variegatus* from north-central Brazil and *B. tridactylus*. The molecular phylogeny of morphologically confirmed sloth specimens exhibits 2 monophyletic lineages representing *B. variegatus* and *B. tridactylus*. The split time between these 2 lineages was estimated at 6 million years ago (mya), contradicting previous studies that estimated this divergence to be 0.4 mya. Taxonomic inconsistencies were detected when comparing the molecular phylogeny to previously published DNA sequences ascribed to *B. tridactylus*. Misidentification or introgression could underlie such phylogenetic incongruities. Regardless of their causes, these discrepancies lead to misstatements regarding geographic distribution, phylogeny, and taxonomy of *B. variegatus* and *B. tridactylus*.

Key words: misidentification, molecular data, phylogenetic incongruity, three-toed sloth

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The development of molecular markers and increasing knowledge about the processes and rates of molecular change have provided remarkable tools to detect, describe, and explain biological diversity. Therefore, an ever-growing resource of DNA sequences has become available, mostly over the Internet as public databases (such as GenBank). These databases represent an important resource for studies of phylogeny, biogeography, phylogeography, conservation genetics, molecular taxonomy, genetic diversity, and intraspecific units as targets for conservation (Nikolaev et al. 2007; Ranwez et al. 2007; Thomas 2008).

Beyond the basic utility and value of such databases, several issues regarding the use of these DNA data in making evolutionary, phylogenetic, or biodiversity inferences are important. Usually, molecular phylogenetic studies are concerned with the characteristics of genes and the methods used to construct trees. These aspects include homoplasy, introgression, deviation from neutrality, rate heterogeneity among taxa, confidence in estimated molecular trees, and artifacts such as long-branch attraction. However, elementary attributes such as the correct identification of specimens also warrant careful consideration (Hawksworth 2004; Vilgalys 2003). The most frequent taxonomic errors occur in those groups of organisms where identification is particularly challenging, because of the small size of the species involved, morphological similarity among them, or lack of adequate tools for identification. These issues are common for species of fungi, insects, nematodes, and protists. However, the problem applies across a wide spectrum, from cell lines to large mammals (Hawksworth 2004).

A case of taxonomic misidentification cited in the literature relates to 2 Neotropical mammals, the brown-throated sloth (*Bradypus variegatus*) and the pale-throated sloth (*B. tridactylus*). *B. variegatus* is a widely distributed species occurring throughout most of Central and South America. It is sympatric with *B. tridactylus* in northern Brazil along the

Negro and Amazon rivers. *B. tridactylus* also is found in Guyana and adjacent regions of east-central Venezuela and north-central Brazil (Gardner 2007; Wetzel and Ávila-Pires 1980). *B. variegatus* and *B. tridactylus* are distinguishable by color differences in the hairs of the face and throat and by a pair of foramina at the anterodorsal nasopharynx present only in *B. tridactylus* (Wetzel and Ávila-Pires 1980). Although morphological differences occur between these sloths, in the older literature most *B. variegatus* were referred erroneously to *B. tridactylus* (Anderson and Handley 2001; Gilmore et al. 2000). In the review of *Bradypus* by Anderson and Handley (2001) the authors presented a list of analyzed museum specimens but did not indicate which specimens were misidentified.

Correct taxon assignment is of paramount importance to conservation of biodiversity because inappropriate decisions can be made if taxonomic assignments are incorrect. Within *Bradypus*, the maned sloth (*B. torquatus*) and the pygmy sloth (*B. pygmaeus*) are threatened with extinction because of their restricted geographical distributions and loss of habitat. *B. variegatus* and *B. tridactylus* are considered of least concern (International Union for the Conservation of Nature and Natural Resources 2009). However, few studies exist on natural populations, especially regarding demography, and such investigations could improve understanding of the endangerment status of species. Analyses of population genetics data have been reported for only 2 sloth species, *B. torquatus* and *B. variegatus* (Lara-Ruiz et al. 2008; Moraes-Barros et al. 2006, 2007). The remaining molecular data generated for three-toed sloths are mostly from studies describing the placement of Xenarthra in eutherian phylogeny (Arnason et al. 1997; Eizirik et al. 2001; Murphy et al. 2007; Prasad et al. 2008) or on sloth phylogeny (Barros et al. 2003, 2008; Greenwood et al. 2001; Poinar et al. 2003). In GenBank ~11% of the total nonprimate eutherian DNA data available (until February 2010) are from xenarthrans. Although the proportion of xenarthran DNA data is high and similar to that allotted to other mammalian groups such as carnivores (11%) and insectivores (7%), only 0.008% of the xenarthran DNA sequences are from *Bradypus*.

A better characterization of sloth diversity is needed, given the few molecular studies published to date and the possibility of misidentification between *B. variegatus* and *B. tridactylus*. Discussions on molecular systematics, evolution, and genetic diversity can result in incorrect conclusions when taxonomic identification is inaccurate. Here we describe the occurrence of misidentification related to the brown and pale-throated sloths, investigate incongruities in molecular phylogenies, and discuss the implications of these problems for current knowledge of three-toed sloths. We used comparative analysis of morphological and molecular data obtained from specimens sampled in nature, museum collections, and online DNA databases.

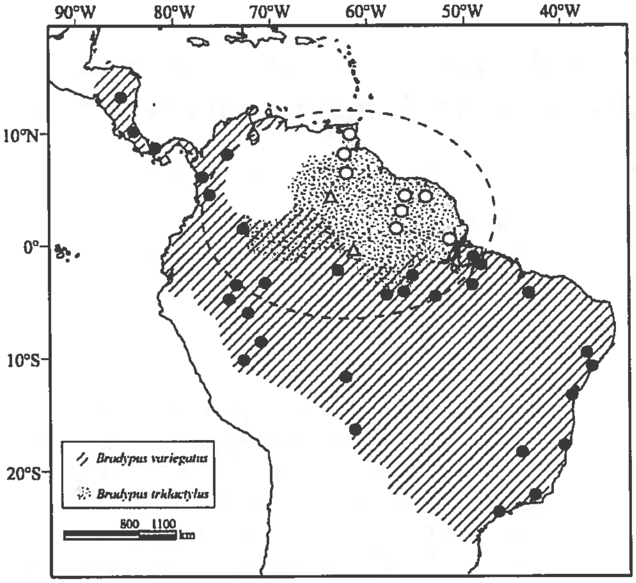

Fig. 1.—Geographic distributions of *Bradypus variegatus* and *B. tridactylus* according to the International Union for the Conservation of Nature and Natural Resources Global Mammal Assessment and Edentate Specialist Group (Aguiar 2004). The dashed line delimits the inferred region of sympatry. Symbols indicate localities of analyzed specimens for the 2 species (black circles = *B. variegatus*; open circles = *B. tridactylus*; open triangles = both species), identified according to morphological criteria.

MATERIALS AND METHODS

Specimens and DNA sequences.—To review the taxonomic identity of three-toed sloths we examined the morphology of skulls from the following natural history museums: AMNH—American Museum of Natural History, New York; FMNH—Field Museum of Natural History, Chicago, Illinois; IEPA—Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Amapá, Brazil; MN—Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil; MPEG—Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; MZUSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil; and USNM—United States Natural History Museum, Washington, D.C. We performed molecular analysis, comparing DNA sequences obtained from taxonomically reviewed specimens to sequences available from GenBank. All information regarding specimens is described in Appendix I.

Taxonomic identification based on morphology.—Three-toed sloth museum specimens (Appendix I) had their species identity established by the presence or absence of the paired foramina in the anterodorsal nasopharynx (Anderson and Handley 2001; Wetzel and Ávila-Pires 1980). Because cranial morphology was used for taxonomic identification, specimens lacking skulls or with crania broken at the nasopharynx region were not included. Specimen identity was compared with the previously attributed taxon name and corrected as needed. For some museum specimens molecular data also were obtained (Moraes-Barros and Morgante 2007) and used in phylogenetic analysis. The main localities of analyzed specimens and the currently inferred geographic distributions of *B. variegatus* and *B. tridactylus* are shown in Fig. 1.

Molecular phylogeny and taxonomic inconsistencies.—We estimated molecular phylogenetic trees using segments of mitochondrial cytochrome-*b* (*Cytb*; 471 base pairs [bp]) and 16S rRNA (16S; 498 bp) genes obtained only from *Bradypus* sloths for which taxonomic identification could be confirmed by morphological analysis (DNA control data sets). The analyzed specimens encompassed *B. tridactylus*, *B. variegatus*, and *B. torquatus*. For *B. tridactylus* only 2 individuals from the same locality were analyzed. Specimens of *B. variegatus* included representatives of the *B. variegatus* Management Units described by Moraes-Barros et al. (2007). A total of 8 individuals representing the 6 distinct *B. variegatus* Management Units and 2 *B. torquatus* were analyzed (Appendix I). DNA samples were obtained from museum specimens (ethanol-preserved, frozen tissues, or study skins) and from living animals (blood samples). Living specimens were captured in nature (Appendix I) and identified from external morphology (Anderson and Handley 2001). Blood samples were collected for DNA analysis according to specific permits (Ibama 02001.000877/2003; Ibama/ICMBio 19267-1) and animal handling and care were consistent with guidelines of the American Society of Mammalogists (Gannon et al. 2007). After sampling, animals were released. Blood samples were transferred to tubes containing ethanol or heparin and stored at −20°C. These samples were deposited in our DNA and tissue collection (Laboratorio de Biologia Evolutiva e Conservação de Vertebrados [LABEC]; Appendix I). Methods used to extract, amplify, and sequence DNA varied according to the level of degradation and source of DNA (ethanol-preserved, frozen tissue, blood, or museum study skins) and were performed according to the protocol and primers in Moraes-Barros and Morgante (2007).

Phylogenetic relationships were reconstructed in PAUP* version 4.0b10 (Swofford 2002) through maximum-likelihood and neighbor-joining methods, depending on the analysis as discussed below. The maned sloth (*B. torquatus*), two-toed sloth (*Choloepus didactylus*), and the southern tamandua (*Tamandua tetradactyla*) were used as outgroups. The Akaike information criterion (AIC) implemented in the computer program Modeltest version 3.06 (Posada and Crandall 1998) was used to identify the most appropriate model of DNA substitution for each data set (sets of concatenated *Cytb* and 16S genes and independent data sets for each gene). The best model found for the data set of concatenated *Cytb* and 16S genes was the general time reversible (GTR) model (Rodríguez et al. 1990) including gamma distribution with shape parameter (α). The Tamura–Nei (TrN) model (Tamura and Nei 1993) including proportion of invariant sites (I) was identified as the best model for the independent data sets of *Cytb* and 16S. The analyses were carried out with a heuristic search using the tree-bisection-reconnection branch swapping algorithm and ''as is'' addition. The robustness of trees was determined by 1,000 (neighbor-joining) and 100 (maximum-likelihood) bootstrap replications.

Control data sets (each gene as an independent data set and a set of concatenated gene sequences) were 1st used to infer maximum-likelihood and neighbor-joining trees. We estimated divergence times for the main *Bradypus* lineages to compare our data with published studies on split times between *B. variegatus* and *B. tridactylus*. Barros et al. (2003, 2008) used mitochondrial 16S and 12S genes to estimate a split between *B. variegatus* and *B. tridactylus* of about 400,000 years ago. We used the maximum-likelihood phylogeny based on control data set of concatenated *Cytb* (471 bp) and 16S (498 bp) gene segments. Estimates of divergence times were obtained using the penalized likelihood method (Sanderson 2002) implemented with program R8s 1.7.1 (Sanderson 2003). Not having fossil records of arboreal sloths or the mitochondrial DNA (mtDNA) substitution rate for *Bradypus*, we used the same criteria of Barros et al. (2003, 2008) to calibrate the tree and estimate divergence times. Our calibration point was the split between *Choloepus* and *Bradypus*, which occurred 21–18 million years ago (mya—Delsuc et al. 2001, 2004).

We expected that molecular trees, obtained with the control data sets, would show distinct monophyletic groups corresponding to each sloth species. This phylogenetic pattern would indicate congruence between molecular phylogeny and taxonomy. Conversely, any observed incongruence would be evidence of incomplete lineage sorting or introgression. After this 1st analysis new phylogenies were obtained using the control data sets plus homologous DNA sequences identified as *B. variegatus* and *B. tridactylus* available in GenBank. Each gene was considered an independent data set so the distinct sequences available in GenBank could be evaluated. Phylogenies were estimated with the neighbor-joining method because of its computational speed and high accuracy, especially when the evolutionary dynamics among the sequences have remained the same over time. Therefore, in these analyses we considered only sequences of *B. variegatus* and *B. tridactylus*, using *B. torquatus* as outgroup. We assume that if the molecular phylogeny of morphologically reviewed specimens is congruent with taxonomy, phylogenetic inconsistencies involving DNA sequences from GenBank could be explained by misidentification. We could not analyze all DNA sequences of *B. variegatus* and *B. tridactylus* available in GenBank because our control data set was limited to only 2 genes. Therefore, we investigated only *Cytb* and 16S sequences. DNA sequences generated in this study are available in GenBank under accession numbers HM352889–HM352908.

RESULTS

Taxonomic attribution based on cranial morphology.—We identified 313 sloth museum specimens based on cranial morphology without difficulty, except when crania were broken at the anterodorsal nasopharynx, as for specimen MZUSP 23159. For this particular specimen analysis of hairs on the face and throat on the preserved skin was possible, and we obtained DNA for molecular analysis. We found misidentification events in almost all collections except the

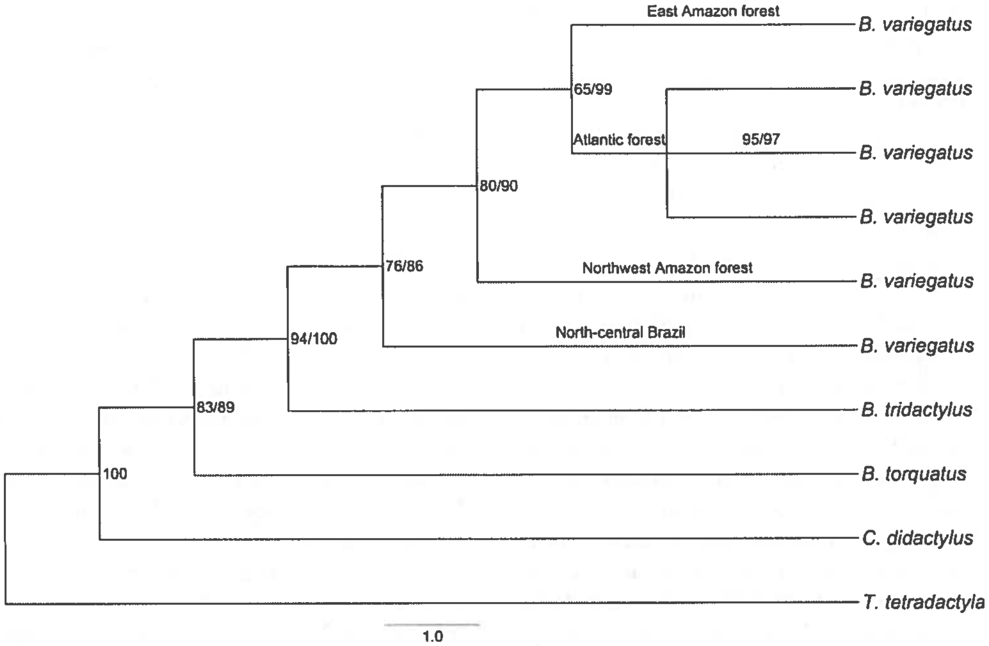

FIG. 2.—Bootstrap maximum-likelihood (ML) consensus tree obtained using concatenated cytochrome-*b* (*Cytb*) and 16S sequences from morphologically validated specimens of *Bradypus*. Tree was estimated using the general time reversible model (Rodríguez et al. 1990) and gamma distribution with shape parameter $\alpha = 0.3089$. Similar topologies were obtained in neighbor-joining (NJ) trees. Numbers at the nodes indicate maximum-likelihood–neighbor-joining bootstraps. Terminals for *B. variegatus* are identified according to the geographic location of sampled individuals and reflect exclusive mitochondrial DNA lineages previously described in Moraes-Barros et al. (2007). Genbank DNA sequences from *Choloepus didactylus* (accession number Z48942) and *Tamandua tetradactyla* (accession number NC004032) were used as outgroups. Scale at the bottom represents number of substitutions per site.

USNM collection. About 24% of all specimens (75/313) were misidentified, and 96% of the misidentifications were individuals of *B. variegatus* erroneously assigned to *B. tridactylus*. Also, 65 of the 75 misidentified specimens were from north-central Brazil (Appendix I).

Molecular phylogeny, taxonomic incongruity, and divergence times.—Using only DNA sequences from specimens whose taxonomic identification was confirmed, the *Cytb* and 16S data sets revealed similar topologies. Thus, we used the concatenated sequences for analysis considering the GTR model and $\alpha = 0.3089$. The resultant data set was 969 bp and recovered 2 main clades corresponding to *Bradypus* species. Within *B. variegatus* distinct clades corresponding to Management Units previously described by Moraes-Barros et al. (2007; Fig. 2) were observed.

We obtained a *Cytb* sequence from 1 specimen (MZUSP 23159) for which taxonomic identification could only be inferred based on the hair colors of the face and throat. The color pattern was characteristic of *B. tridactylus*, and the DNA sequence was similar to sequences obtained from 2 morphologically identified members of the same species (Fig. 3).

Phylogenies of *Cytb* and the 16S mtDNA sequences available in GenBank were estimated using the TrN model including $I = 0.6928$ (*Cytb*) and $I = 0.6363$ (16S). We observed inconsistencies in DNA sequences between the attributed name and the molecular phylogeny. GenBank sequences, putatively derived from either *B. variegatus* or *B tridactylus*, grouped together in a clade representative of *B. variegatus* (Figs. 3 and 4).

According to our results, the time of split between *B. tridactylus* and *B. variegatus* occurred between 6.0 and 4.8 mya, depending on the maximum and minimum values of the calibration point (21–18 mya). We also calculated divergence times for the split between *B. torquatus* and the *B. variegatus–B. tridactylus* lineages (14–11 mya) and the base of diversification of all *B. variegatus* lineages (5.0–3.8 mya).

DISCUSSION

Despite having no difficulty identifying sloth specimens based on cranial morphology, we observed numerous taxonomic misidentifications, as previously reported in the literature. These misidentified specimens were detected in all museum collections (AMNH, FMNH, MN, MPEG, and MZUSP) except USNM. Although misidentifications occurred in the official collection lists from most museums, corrections to the original identification were attached to the specimens from AMNH, FMNH, and MPEG. Therefore, the use of sloth museum collection lists, without careful examination of specimens, can be problematic.

Bradypus variegatus and *B. tridactylus* have a confusing nomenclatural history. A complete and recent description of this topic is presented in Hayssen (2009, 2010). In short, after Schinz (1825) described *B. variegatus*, more than 50 names were applied to the species, including "*B. tridactylus*" (De Blainville 1840; Trouessart 1898; Vieira 1955). Throughout this period "*B. tridactylus*" was what is now *B. variegatus*,

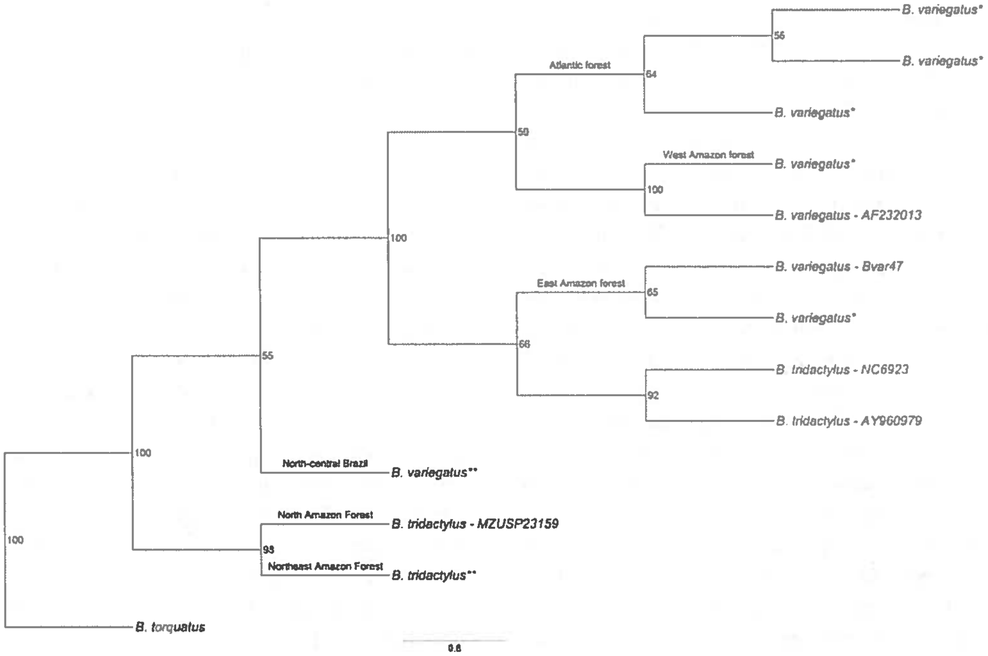

FIG. 3.—Neighbor-joining (NJ) phylogeny of cytochrome-*b* sequences of *Bradypus* from GenBank (identified by accession numbers) and from specimens identified based on external (*) and cranial (**) morphology. Tree was inferred using the Tamura–Nei model (Tamura and Nei 1993) with a proportion of invariant sites I = 0.6928. Numbers at the nodes indicate bootstrap values from 1,000 replications. Terminals in light gray indicate phylogenetic incongruities. Scale at the bottom represents number of substitutions per site.

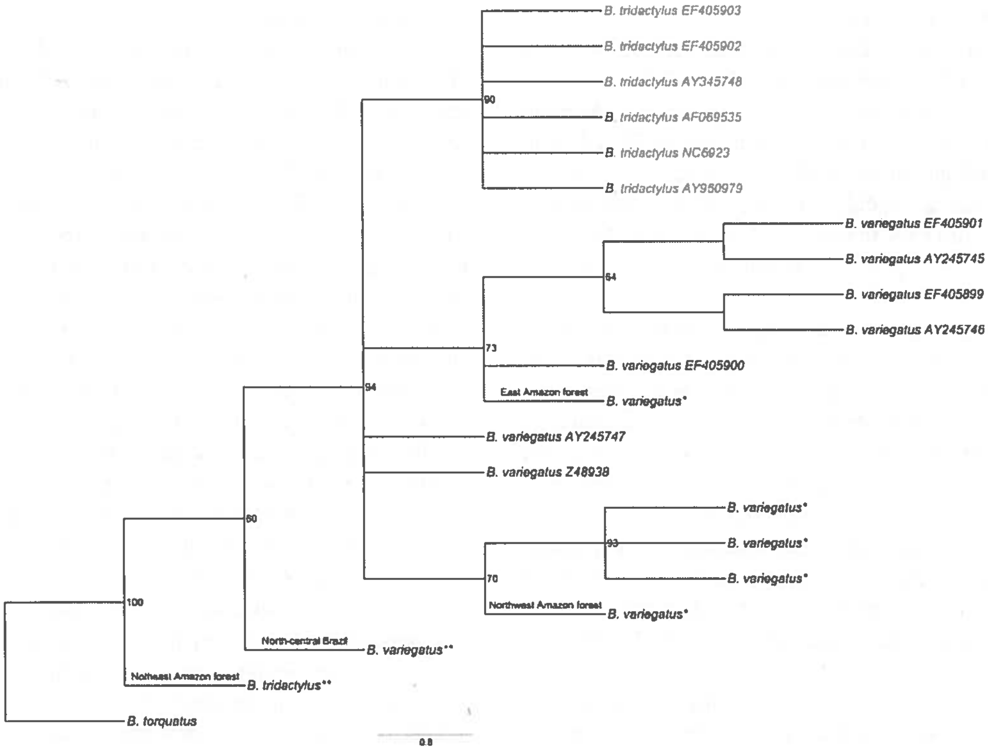

FIG. 4.—Neighbor-joining (NJ) phylogeny of 16S sequences of *Bradypus* from GenBank (identified by accession numbers) and from specimens identified based on external (*) and cranial (**) morphology. Tree was inferred using the Tamura–Nei model (Tamura and Nei 1993) with a proportion of invariant sites I = 0.6363. Numbers at the nodes indicate bootstrap values from 1,000 replications. Terminals in light gray indicate phylogenetic incongruities. Scale at the bottom represents number of substitutions per site.

not as a result of misidentification but in agreement with the accepted nomenclature. For instance, Ávila-Pires and Gouveia (1977) described a brown-throated sloth from an Atlantic forest nature reserve as "*B. tridactylus*." Wetzel (1982) clarified the nomenclature of the 2 species, but problems persist in correctly assigning species names to individual specimens. The morphology of some *B. variegatus* populations, as we discuss below, contributes to this difficulty.

We observed that 96% of the misidentified specimens were *B. variegatus* erroneously attributed to *B. tridactylus*. Also, the majority of misidentified *B. variegatus* were from north-central Brazil where the 2 species might be sympatric. A history of confusing nomenclature exists, and these particular misidentifications could be attributable to the similarity in face and throat color between the north-central Brazil *B. variegatus* and *B. tridactylus*. Most specimens of the two species show pronounced differences in hair colors of the face and throat. *B. tridactylus* has bright golden-yellow hairs, whereas *B. variegatus* has a brownish face and throat, at least at the base of the hairs. In addition, most individuals of *B. variegatus* have a dark facial stripe not present in *B. tridactylus*. However, a few populations of *B. variegatus* from north-central Brazil (e.g., on the lower Tapajós River) exhibit a strong golden frosting on the throat. Unlike *B. tridactylus*, which has golden color to the base of the hairs, the hairs on *B. variegatus* are usually dark brown at the base (Anderson and Handley 2001). Therefore, misidentification of *Bradypus* sloths in museum collections also can arise from incomplete analysis of morphological traits.

Despite the apparent similarities of facial hair color among some populations of *B. variegatus* and *B. tridactylus*, cranial morphology and molecular data are diagnostic. Museum specimens of *B. variegatus* from north-central Brazil, with face and throat pelage similar to that of *B. tridactylus*, did not have a pair of nasopharyngeal foramina, a trait exclusive to *B. tridactylus*. Also, mtDNA sequences obtained from 1 of these specimens did not group with homologous sequences of *B. tridactylus*.

The molecular phylogeny based only on DNA sequences of morphologically reviewed specimens showed no incongruity. We then added to the analysis DNA sequences from specimens whose identification could not be confirmed by morphological analysis. One of these was museum specimen MZUSP 23159. This sloth was originally attributed to *B. tridactylus*, and its identification was confirmed based only on analysis of face and throat hairs. The obtained DNA sequence revealed a haplotype similar to that observed in 2 specimens of *B. tridactylus* identified based on cranial and pelage traits. Therefore, we assume that specimen MZUSP 23159 is *B. tridactylus*.

The mtDNA sequences from GenBank had inconsistencies between attributed species names and the molecular phylogeny. All GenBank sequences putatively derived from either *B. variegatus* or *B. tridactylus* grouped with *B. variegatus*. Therefore, the inconsistencies recorded were from GenBank DNA sequences erroneously attributed to *B. tridactylus*.

Incongruity in the topology of molecular phylogenies can be caused by incomplete lineage sorting, introgression, or taxonomic misidentification (Avise 2004). The process of incomplete lineage sorting is more likely to occur in sister species shortly after their separation or at intermediate times since speciation (Avise 2004). Our molecular dating indicates the split between *B. variegatus* and *B. tridactylus* to be 6.0–4.8 mya. With a 6-year generation time and a life span of 30–40 years for three-toed sloths (Anderson and Handley 2001), *B. variegatus* and *B. tridactylus* sharing ancient mtDNA haplotypes would be unlikely.

The occurrence of ancient hybridization and backcrosses between these 2 species could have led to introgression of mtDNA, resulting in individuals morphologically matching 1 species but carrying mtDNA of the other. Mitochondrial DNA introgression is only detectable using multiple markers, including morphology and molecular data or distinct genes from mitochondrial and nuclear genomes (Good et al. 2008). We did not observe incongruity comparing morphological and molecular data, which could have been evidence of introgression. Our molecular phylogeny included sloths from Atlantic and Amazon forests and encompassed most of the region where *B. variegatus* and *B. tridactylus* might be sympatric. All DNA sequences were obtained from individuals identified based on external or skull morphology. The corresponding DNA sequences presented a phylogenetic pattern consistent with the taxonomic identifications, and all mtDNA lineages of *B. variegatus* coalesce after the split between the brown-throated and pale-throated three-toed sloths. However, although our control data sets are constituted from DNA sequences obtained from sloths from different geographical regions, we did not sample most of the geographical distribution of *B. tridactylus*. We have sampled only 2 individuals of *B. tridactylus* that share the same haplotype. Thus, we can discard introgression from *B. tridactylus* into *B. variegatus* only for our control data sets. Nevertheless, phylogenetic discrepancies in GenBank DNA sequences of *Bradypus* also could have occurred due to misidentifications. However, no information exists as to the source of those DNA sequences in the Genbank files, so we cannot confirm incorrect identification or discard introgression as the cause of this phylogenetic mismatch. In molecular phylogenetic studies in cuckoos and Old World finches, Sorenson and Payne (2001, 2002) and Payne and Sorenson (2003) were able to confirm the identification of 120 specimens and correct it for another 8. However, this was possible only by comparing the genetic data to specimen vouchers.

Correctness in taxonomy is important when analyzing DNA samples. When inconsistencies in molecular phylogeny are detected, it is impossible to investigate the cause of incongruity when no associated preserved specimen is available. However, for some species (such as those threatened with extinction), preserving each specimen from which DNA was obtained is not realistic. In these cases, DNA vouchers associated with published sequences would be recommended.

If phylogenetic inconsistencies are detected in a published molecular data, posterior analysis of different and independent molecular markers can made with the associated DNA.

Whatever the causes of inconsistencies in molecular phylogenies, the Genbank DNA sequences of *Bradypus* clearly are mismatched. Our aim is not to denigrate previous studies or public DNA databases but rather to raise awareness among investigators who use these data in molecular biology studies. The dissimilar DNA sequences of *B. tridactylus* encompass a complete mitochondrial genome analysis (*Cytb* and 16S—McLenachan and Penny 2005), sequences used in a phylogenetic study of the relationships among the main mammalian orders (16S—Stanhope et al. 1998), and DNA segments used to study the phylogeny of sloth species (16S—Barros et al. 2003). The observed divergences do not impose errors in the phylogenetic discussion of Stanhope et al. (1998), because the DNA sequence was used only to represent a three-toed sloth, which is correct. However, the assumption that any of these DNA sequences represent an mtDNA lineage of *B. tridactylus* is mistaken.

According to our analysis of the control data set of concatenated *Cytb* and 16S, the split between mtDNA lineages of *B. torquatus* and those of the remaining *Bradypus* occurred about 12 mya, a date corresponding to that obtained by Barros et al. (2003, 2008). The inferred split time between *B. tridactylus* and *B. variegatus* was between 6.6 and 4.8 mya, depending on the calibration point (21–18 mya). This date differs from the 0.4 mya estimated by Barros et al. (2003, 2008) using 16S and 12S mtDNA sequences. Considering the results presented here, we assume that the date obtained by Barros et al. (2003, 2008) applies to the divergence between 2 mitochondrial lineages of *B. variegatus*. The split between *B. variegatus* and *B. tridactylus*, estimated in our analysis at about 6 mya, could have been missed if a wide sampling of taxonomically reviewed specimens had not been included in the analysis. This inferred date agrees with Delsuc et al. (2002), who argued that most xenarthran diversification occurred in the Miocene or early Pliocene.

In the case of three-toed sloths, phylogenetic inconsistencies and missing data seem to have influenced previous studies on sloth evolutionary history. Although we cannot state that misidentifications underlie the taxonomic incompatibility observed for available GenBank DNA sequences, our morphological analyses of museum specimens of *Bradypus* prove that taxonomic misidentifications do occur, as previously suggested by Anderson and Handley (2001). A critical outcome of the misidentifications is the inferred geographical distribution of *B. variegatus* and *B. tridactylus*. The actual distribution of *B. tridactylus* is narrower than previously inferred (Gardner 2007; International Union for the Conservation of Nature and Natural Resources 2009). Some misidentified *B. variegatus* were reported in taxonomic reviews as records of *B. tridactylus*. These specimens are *B. variegatus* from Colombia and north-central Brazil, southward to the Amazon River (Fig. 1). We agree with Anderson and Handley (2001), who pointed out that the distribution of *B. tridactylus* probably does not extend southwest of the Rio Negro or as far south of the Amazonas River. We do not agree with Hayssen (2010), who suggested that *B. variegatus* does not occur north of the Amazon. There are morphologically confirmed *B. variegatus* from north of the Amazon in the MUZUSP and MPEG collections (Appendix I). Therefore, the geographic distributions of *B. variegatus* and *B. tridactylus* need further clarification.

A better understanding of three-toed sloth genetic diversity also is needed. This is particularly important if we consider the genetically divergent populations within the species, as described in recent phylogeography studies (Moraes-Barros et al. 2006, 2007). These authors identified genetically distinct populations of *B. variegatus* distributed throughout the Amazon and Atlantic forest. These populations were classified as Management Units and indicated as intraspecific targets for conservation purposes. The mtDNA lineages that constitute these Management Units were inferred from segments of the control region, a highly polymorphic DNA segment. Our phylogenetic analysis corroborates the divergence among these lineages. Moreover, additional mtDNA lineages of *B. variegatus* were revealed by adding GenBank sequences to the phylogenies. Most of the GenBank DNA sequences that group with *B. variegatus* are identified as *B. tridactylus*. These divergent sequences represent about 20% of the observed mtDNA diversity of *B. variegatus*. This indicates that genetic diversity within *B. variegatus* is higher than previously reported. Also, marked divergences occur among haplogroups of *B. variegatus*, suggesting the existence of different and independent evolutionary lineages. For example, the mtDNA lineage representing sloths from north-central Brazil is divergent and basal within the *B. variegatus* group. In our study only the South American *B. variegatus* and 3 *B. tridactylus* from northern Brazil were analyzed. *B. variegatus* also is distributed throughout Central America, and no study has been performed on the molecular diversity of *B. tridactylus* from the Guiana Shield. Therefore, to investigate potential speciation events properly and confirm the reciprocal monophyly of *B. variegatus* and *B. tridactylus*, wider geographic sampling and the use of independent molecular markers will be needed. Nevertheless, our results show the importance of accurate specimen identification in molecular systematics.

RESUMO

Este trabalho tem como foco a análise de dados morfológicos e moleculares, o estudo de erros de identificação e de inconsistências filogenéticas, referentes às espécies *Bradypus variegatus* (preguiça de garganta marrom) e *B. tridactylus* (preguiça de garganta clara). Foram registrados erros de identificação em 75 dos 313 espécimes analisados em diferentes coleções científicas. Cerca de 90% dos erros de identificação foram observados em *B. variegatus*, provenientes da região centro norte do Brasil, erroneamente identificados como *B. tridactylus*. Esses espécimes são citados

na literatura como registros do limite sul da distribuição de *B. tridactylus*. A história da nomenclatura destas espécies de preguiça denota certa confusão. Ainda assim, os erros de identificação destes espécimes em particular pode ser atribuído às semelhanças na coloração dos pelos da face e garganta, observadas entre *B. variegatus* da região centro norte do Brasil e *B. tridactylus*. A filogenia molecular de espécimes de preguiça, cuja identificação foi confirmada através de dados morfológicos, denota 2 grupos monofiléticos representantes das espécies *B. variegatus* e *B. tridactylus*. A divergência entre estes 2 grupos foi datada em 6,0 ma. Este resultado contradiz estudos anteriores os quais estimaram esta divergência em 0,4 ma. Ademais, foram observadas inconsistências taxonômicas ao incluir sequências de DNA, publicadas anteriormente e atribuídas à espécie *B. tridactylus*, à filogenia molecular. Erros de identificação ou processos como introgressão poderiam ser a causa de tal incongruência. Independente da origem, as divergências observadas levaram a proposições falsas em relação à distribuição geográfica, filogenia e taxonomia de *B. variegatus* e *B. tridactylus*.

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APPENDIX I

Detailed description of analyzed specimens presented by geographic locality. Taxonomic identification, as listed in museum collections, is presented along with the identification reviewed by morphological analysis of the skull (M). Species names in boldface type denote corrected taxonomic identification. DNA samples were obtained from some museum specimens and from specimens captured and sampled in the wild. Museum and DNA collection acronyms are defined in "Materials and Methods."

		Specimen locality	Specimen	Initial identification	Reviewed identification	Analysis (M, DNA)
Bolivia	Beni	Rio Mamoré—10°23′S, 65°23′W	AMNH209940	*B. variegatus*	*B. variegatus*	M
	Santa Cruz	Buena Vista—17°27′S, 63°40′W	AMNH61792	*B. variegatus*	*B. variegatus*	M
			FMNH51871	*B. variegatus*	*B. variegatus*	M
			FMNH21393	*B. variegatus*	*B. variegatus*	M
			FMNH21394	*B. variegatus*	*B. variegatus*	M
		Rio Suruto—17°24′S, 63°51′W	AMNH61791	*B. variegatus*	*B. variegatus*	M
		Santa Cruz de La Sierra—17°48′S, 63°10′W	AMNH133435	*B. variegatus*	*B. variegatus*	M
		Santa Cruz da La Sierra, 5 km E Rio Palometillas	AMNH 261304	*B. variegatus*	*B. variegatus*	M
Brazil	Alagoas	Manimbu—10°10′S, 36°22′W	MZUSP7528	*B. variegatus*	*B. variegatus*	M
		São Miguel dos Campos—09°46′S, 36°05′W	MZUSP7370	*B. variegatus*	*B. variegatus*	M
	Amapá	Estrada Campo Verde km 7, Porto Platou	MN20578	*B. tridactylus*	*B. tridactylus*	M
		RDS Rio Iratapuru, Lago Baliza	IEPA626	*B. tridactylus*	*B. tridactylus*	M, DNA
			IEPA627	*B. tridactylus*	*B. tridactylus*	M, DNA
		Cachoeira de Santo Antônio, Rio Jari, Ilha do Cemitério	MPEG21809	*B. tridactylus*	*B. tridactylus*	M
	Amazonas	Balbina—01°50′S, 59°30′W	MZUSP23159[a]	*B. tridactylus*	*B. tridactylus*	DNA
		Estirão do Equador, Rio Javari	MPEG1840	*B. variegatus*	*B. variegatus*	M
		Lago do Batista—03°18′S, 58°15′W	MZUSP5303	***B. tridactylus***	***B. variegatus***	M
			MN6064	*B. variegatus*	*B. variegatus*	M
			MN6065	*B. variegatus*	*B. variegatus*	M
		Maraã—1°48′S, 65°22′W	MZUSP13506	*B. variegatus*	*B. variegatus*	M
		Maraã—Setor Coraci, Rio Coracizinho, RDS Amanã	MPEG36645	*B. variegatus*	*B. variegatus*	M
		Rio Amazonas, south bank, Vila Bela Imperatriz, Santa Clara—2°36′S, 56°44′W	AMNH93108	***B. tridactylus***	***B. variegatus***	M
			AMNH93109	***B. tridactylus***	***B. variegatus***	M
			AMNH93110	***B. tridactylus***	***B. variegatus***	M
			AMNH93111	***B. tridactylus***	***B. variegatus***	M
			AMNH93112	***B. tridactylus***	***B. variegatus***	M
			AMNH93113	***B. tridactylus***	***B. variegatus***	M
			AMNH93114	***B. tridactylus***	***B. variegatus***	M
			AMNH93115	***B. tridactylus***	***B. variegatus***	M
			AMNH93104	***B. tridactylus***	***B. variegatus***	M
			AMNH93105	***B. tridactylus***	***B. variegatus***	M
			AMNH93106	***B. tridactylus***	***B. variegatus***	M
		Rio Amazonas, Santo Antonio do Amatary—03°00′S, 58°00′W	AMNHA93103	***B. tridactylus***	***B. variegatus***	M
		Rio Madeira, Rosarinho—34°02′S, 59°08′W	AMNH92845	*Bradypus sp.*	*B. variegatus*	M
			AMNH92829	***B. tridactylus***	***B. variegatus***	M
			AMNH92335	***B. tridactylus***	***B. variegatus***	M
		Rio Madeira, Rosarinho, Santo Antonio do Uayara	AMNH92333	***B. tridactylus***	***B. variegatus***	M
			AMNH92334	***B. tridactylus***	***B. variegatus***	M
			AMNH92332	***B. tridactylus***	***B. variegatus***	M
		Rio Negro—no specific locality	MN30471	***B. variegatus***	***B. tridactylus***	M
			MN30472	*B. variegatus*	*B. variegatus*	M
			MN30480	***B. variegatus***	***B. tridactylus***	M
			MN30482	*B. variegatus*	*B. variegatus*	M
		Rio Negro, Cacao Pereira—3°08′S, 60°05′W	AMNH80447	***B. tridactylus***	***B. variegatus***	M
			AMNH80448	***B. tridactylus***	***B. variegatus***	M
		Rio Negro, Manaus—3°08′S, 60°01′W	AMNH91353	***B. tridactylus***	***B. variegatus***	M
		Rio Negro, Manaus, Hacienda Rio Negro	AMNH78968	*B. tridactylus*	*B. tridactylus*	M
		Rio Solimoes, no specific locality	AMNH37155	***B. tridactylus***	***B. variegatus***	M
	Bahia	Bahia, Ilhéus—Atlantic Forest—14°47′S, 39°03′W	LABECBA1001[a]	*B. torquatus*	*B. torquatus*	DNA
			LABEC01014[a]	*B. torquatus*	*B. torquatus*	DNA
			LABECBA2006[a]	*B. variegatus*	*B. variegatus*	DNA
	Espírito Santo	Lagoa Juparana—19°20′S, 40°04′W	AMNH78844	***B. tridactylus***	***B. variegatus***	M
		no specific locality	MN23889	*B. variegatus*	*B. variegatus*	M
	Maranhão	Imperatriz	MPEG2440	*B. variegatus*	*B. variegatus*	M

Appendix I.—Continued.

	Specimen locality	Specimen	Initial identification	Reviewed identification	Analysis (M, DNA)
	Miritiba—2°36′S, 50°43′W	MZUSP2897	*B. variegatus*	*B. variegatus*	M
		MZUSP2898	*B. variegatus*	*B. variegatus*	M
		MZUSP2597	*B. variegatus*	*B. variegatus*	M
Minas Gerais	Passos—20°43′S, 46°37′W	MN23905	*B. variegatus*	*B. variegatus*	M
		MN23906	*B. variegatus*	*B. variegatus*	M
		MN23904	*B. variegatus*	*B. variegatus*	M
	Rio Novo	MN23888	*B. variegatus*	*B. variegatus*	M
	Teófilo Otoni—Atlantic Forest	LABEC02079[a]	*B. variegatus*	*B. variegatus*	DNA
Pará	Abaeté	MN2379	*B. variegatus*	*B. variegatus*	M
	Altamira	LABEC-Bvar47[a]	*B. variegatus*	*B. variegatus*	DNA
	Altamira, 85 km SW, E bank Rio Iriri—3°50′S, 52°40′W	USNM549523	*B. variegatus*	*B. variegatus*	M
	Belém, Utinga—1°27′S, 48°29′W	USNM339632	*B. variegatus*	*B. variegatus*	M
		MPEG2357	*B. variegatus*	*B. variegatus*	M
	Belém, Castanhosinho, Igarapé	MPEG1514	*B. variegatus*	*B. variegatus*	M
	Belém, Instituto Agronômico do Norte	MPEG2666	*B. variegatus*	*B. variegatus*	M
	Belém	MPEG946	***B. tridactylus***	***B. variegatus***	M
		MPEG969	***B. tridactylus***	***B. variegatus***	M
	Belterra—02°38′S, 54°57′W	MN5636	*B. variegatus*	*B. variegatus*	M
		MN5693	*B. variegatus*	*B. variegatus*	M
		MN5695	*B. variegatus*	*B. variegatus*	M
		MN5752	*B. variegatus*	*B. variegatus*	M
		MN5755	*B. variegatus*	*B. variegatus*	M
		MN5779	*B. variegatus*	*B. variegatus*	M
		MN5787	*B. variegatus*	*B. variegatus*	M
		MN5630	*B. variegatus*	*B. variegatus*	M
		MPEG22512	*B. variegatus*	*B. variegatus*	M
		MPEG20174	*B. variegatus*	*B. variegatus*	M
		MPEG20194	*B. variegatus*	*B. variegatus*	M
		MPEG20171	*B. variegatus*	*B. variegatus*	M
		MPEG20170	*B. variegatus*	*B. variegatus*	M
		MPEG20173	*B. variegatus*	*B. variegatus*	M
		MPEG20169	*B. variegatus*	*B. variegatus*	M
	Benevides, Retiro de Nazaré, Estância	MPEG2693	*B. variegatus*	*B. variegatus*	M
	Bravo	MZUSP5302	***B. tridactylus***	***B. variegatus***	M
	Cacoal	MPEG4649	*B. variegatus*	*B. variegatus*	M
	Cametá—02°15′S, 49°30′W	MZUSP5429	*B. variegatus*	*B. variegatus*	M
	Castanhal	MPEG2352	*B. variegatus*	*B. variegatus*	M
		MPEG2356	*B. variegatus*	*B. variegatus*	M
	Faro—02°11′S, 56°44′W	MN2383	*B. tridactylus*	*B. tridactylus*	M
	Fordlandia—3°40′S, 55°30′W	MZUSP13498	*B. variegatus*	*B. variegatus*	M
		MZUSP13501	*B. variegatus*	*B. variegatus*	M
		FMNH94551	*B. variegatus*	*B. variegatus*	M
		MZUSP13502	*B. variegatus*	*B. variegatus*	M
		MZUSP13497	*B. variegatus*	*B. variegatus*	M
	Igarapé Açu	MPEG2354	*B. variegatus*	*B. variegatus*	M
	Igarapé Açu, Lazarópolis do Prata	MPEG2353	***B. tridactylus***	***B. variegatus***	M
	Ilha de Marajó	FMNH34401	*B. variegatus*	*B. variegatus*	M
	Ilha de Marajó, Curralinho—10°00′S, 49°30′W	AMNH133438	***B. tridactylus***	***B. variegatus***	M
		MN23897	*B. variegatus*	*B. variegatus*	M
		MN5033	*B. variegatus*	*B. variegatus*	M
		MN5014	*B. variegatus*	*B. variegatus*	M
		AMNH133406	***B. tridactylus***	***B. variegatus***	M
		AMNH133419	***B. tridactylus***	***B. variegatus***	M
		AMNH133426	***B. tridactylus***	***B. variegatus***	M
		AMNH133432	***B. tridactylus***	***B. variegatus***	M
		AMNH133433	***B. tridactylus***	***B. variegatus***	M
		AMNH133455	***B. tridactylus***	***B. variegatus***	M
		MN5015	*B. variegatus*	*B. variegatus*	M
		MN5017	*B. variegatus*	*B. variegatus*	M
		MN5019	*B. variegatus*	*B. variegatus*	M
		MN5033	*B. variegatus*	*B. variegatus*	M
		MN5034	*B. variegatus*	*B. variegatus*	M

APPENDIX I.—Continued.

Specimen locality	Specimen	Initial identification	Reviewed identification	Analysis (M, DNA)
	MN5037	*B. variegatus*	*B. variegatus*	M
	MN5038	*B. variegatus*	*B. variegatus*	M
	MN5040	*B. variegatus*	*B. variegatus*	M
	MN5045	*B. variegatus*	*B. variegatus*	M
Ipixuna, Rio Capim Grande	MPEG23920	*B. variegatus*	*B. variegatus*	M
Juruti	MPEG38375	***B. tridactylus***	***B. variegatus***	M
No specific locality	FMNH25316	*B. variegatus*	*B. variegatus*	M
	FMNH25317	*B. variegatus*	*B. variegatus*	M
	FMNH25318	*B. variegatus*	*B. variegatus*	M
	FMNH25319	*B. variegatus*	*B. variegatus*	M
	MPEG6751	*B. variegatus*	*B. variegatus*	M
	MPEG6752	*B. variegatus*	*B. variegatus*	M
	MPEG6750	***B. tridactylus***	***B. variegatus***	M
	MPEG945	***B. tridactylus***	***B. variegatus***	M
	MPEG1475	*B. variegatus*	*B. variegatus*	M
	MPEG929	***B. tridactylus***	***B. variegatus***	M
	MPEG6749	*B. variegatus*	*B. variegatus*	M
Óbidos—01°55′S, 55°31′W	MN5962	*B. variegatus*	*B. variegatus*	M
Paragominas, Faz. Cauxi	MPEG26312	*B. variegatus*	*B. variegatus*	M
Parauapebas—East Amazon Forest	LABEC-AC109[a]	*B. variegatus*	*B. variegatus*	DNA
Patagonia, km 27	AMNH75140	***B. tridactylus***	***B. variegatus***	M
Porto Santarém	FMNH21551	*B. variegatus*	*B. variegatus*	M
Rio Majary, Recreio—01°42′S, 52°12′W	AMNH95841	***B. tridactylus***	***B. variegatus***	M
Rio Tapajós, Aramanay—02°45′S, 54°59′W	AMNH95102	***B. tridactylus***	***B. variegatus***	M
	AMNH95101	***B. tridactylus***	***B. variegatus***	M
Rio Tapajós, Igarape Amorin—02°26′S, 55°00′W	AMNH95329	***B. tridactylus***	***B. variegatus***	M
	AMNH95329	***B. tridactylus***	***B. variegatus***	M
Rio Tapajós, Inajatuba	AMNH95326	***B. tridactylus***	***B. variegatus***	M
	AMNH95327	***B. tridactylus***	***B. variegatus***	M
	AMNH95328	***B. tridactylus***	***B. variegatus***	M
	AMNH95325	***B. tridactylus***	***B. variegatus***	M
	AMNH95103	***B. tridactylus***	***B. variegatus***	M
Rio Tapajós, Caxiricatuba—02°50′S, 55°08′W	AMNH95104	***B. tridactylus***	***B. variegatus***	M
Rio Tapajós, Igarape Bravo—02°26′S, 55°00′W	AMNH95106	***B. tridactylus***	***B. variegatus***	M
	AMNH95105	***B. tridactylus***	***B. variegatus***	M
Rio Tocantins, Baiao—02°41′S, 49°41′W	AMNH96255	***B. tridactylus***	***B. variegatus***	M
Rio Tocantins, Ilha do Taiuna—02°15′S, 49°30′W	AMNH97315	***B. tridactylus***	***B. variegatus***	M
	AMNH96245	***B. tridactylus***	***B. variegatus***	M
	AMNH96246	***B. tridactylus***	***B. variegatus***	M
	AMNH96249	***B. tridactylus***	***B. variegatus***	M
	AMNH96250	***B. tridactylus***	***B. variegatus***	M
	AMNH96252	***B. tridactylus***	***B. variegatus***	M
	AMNH96242	***B. tridactylus***	***B. variegatus***	M
	AMNH97315	***B. tridactylus***	***B. variegatus***	M
	AMNH96244	***B. tridactylus***	***B. variegatus***	M
Rio Tocantins, Mocajuba—02°35′S, 49°30′W	AMNH96254	***B. tridactylus***	***B. variegatus***	M
	AMNH96253	***B. tridactylus***	***B. variegatus***	M
Rio Tocantins, Tucuruí, Ilha Tocantins	MPEG12479	*B. variegatus*	*B. variegatus*	M
Rio Tocantins, Tucuruí, Vila Brabo	MPEG12480	*B. variegatus*	*B. variegatus*	M
Rod. Belém–Brasilia km 307	MPEG1742	*B. variegatus*	*B. variegatus*	M
Santarém—north-central Brazil—02°26′S, 54°42′W	AMNH40830	***B. tridactylus***	***B. variegatus***	M
	MN23899	*B. variegatus*	*B. variegatus*	M
	MN23900	*B. variegatus*	*B. variegatus*	M
	MN23901	*B. variegatus*	*B. variegatus*	M
	MN23902	*B. variegatus*	*B. variegatus*	M
	USNM111636	*B. variegatus*	*B. variegatus*	M
	USNM239454	*B. variegatus*	*B. variegatus*	M
	MN23902	*B. variegatus*	*B. variegatus*	M
	AMNH40829	***B. tridactylus***	***B. variegatus***	M
	MPEG10232	*B. variegatus*	*B. variegatus*	M
	MPEG10233	*B. variegatus*	*B. variegatus*	M
	MPEG10235	*B. variegatus*	*B. variegatus*	M
	MPEG10236	*B. variegatus*	*B. variegatus*	M, DNA

APPENDIX I.—Continued.

	Specimen locality	Specimen	Initial identification	Reviewed identification	Analysis (M, DNA)
		MPEG10239	*B. variegatus*	*B. variegatus*	M
		MPEG20199	*B. variegatus*	*B. variegatus*	M
		MPEG20203	*B. variegatus*	*B. variegatus*	M
	Santarém, Ipanema	MN11596	*B. variegatus*	*B. variegatus*	M
		MN11597	*B. variegatus*	*B. variegatus*	M
	Santarém, Mojuí dos Campos—2°26′S, 54°42′W	USNM545912	*B. variegatus*	*B. variegatus*	M
		USNM545913	*B. variegatus*	*B. variegatus*	M
		USNM545914	*B. variegatus*	*B. variegatus*	M
		USNM545915	*B. variegatus*	*B. variegatus*	M
		USNM545916	*B. variegatus*	*B. variegatus*	M
		USNM545918	*B. variegatus*	*B. variegatus*	M
		USNM545919	*B. variegatus*	*B. variegatus*	M
		USNM545920	*B. variegatus*	*B. variegatus*	M
		USNM545921	*B. variegatus*	*B. variegatus*	M
		USNM545922	*B. variegatus*	*B. variegatus*	M
		USNM545924	*B. variegatus*	*B. variegatus*	M
		USNM545925	*B. variegatus*	*B. variegatus*	M
		USNM545926	*B. variegatus*	*B. variegatus*	M
		USNM545930	*B. variegatus*	*B. variegatus*	M
		USNM545931	*B. variegatus*	*B. variegatus*	M
		USNM545932	*B. variegatus*	*B. variegatus*	M
		USNM546934	*B. variegatus*	*B. variegatus*	M
		USNM545935	*B. variegatus*	*B. variegatus*	M
		USNM545936	*B. variegatus*	*B. variegatus*	M
		USNM545937	*B. variegatus*	*B. variegatus*	M
		USNM545911	*B. variegatus*	*B. variegatus*	M
		MPEG13282	*B. variegatus*	*B. variegatus*	M
		MPEG13269	*B. variegatus*	*B. variegatus*	M
		MPEG13283	*B. variegatus*	*B. variegatus*	M
		MPEG13285	*B. variegatus*	*B. variegatus*	M
		MPEG13287	*B. variegatus*	*B. variegatus*	M
		MPEG13263	*B. variegatus*	*B. variegatus*	M
		MPEG13265	*B. variegatus*	*B. variegatus*	M
		MPEG13274	*B. variegatus*	*B. variegatus*	M
		MPEG20192	*B. variegatus*	*B. variegatus*	M
		MPEG13271	*B. variegatus*	*B. variegatus*	M
		MPEG13272	*B. variegatus*	*B. variegatus*	M
		MPEG13278	*B. variegatus*	*B. variegatus*	M
		MPEG13270	*B. variegatus*	*B. variegatus*	M
		MPEG13277	*B. variegatus*	*B. variegatus*	M
		MPEG20193	*B. variegatus*	*B. variegatus*	M
		MPEG13275	*B. variegatus*	*B. variegatus*	M
		MPEG13273	*B. variegatus*	*B. variegatus*	M
		MPEG13262	*B. variegatus*	*B. variegatus*	M
		MPEG13264	*B. variegatus*	*B. variegatus*	M
		MPEG13281	*B. variegatus*	*B. variegatus*	M
		MPEG13268	*B. variegatus*	*B. variegatus*	M
		MPEG13276	*B. variegatus*	*B. variegatus*	M
	Santarém, Santarém–Cuiabá km 35	USNM461731	*B. variegatus*	*B. variegatus*	M
	Santarém, Santarém–Cuiabá km 16	MPEG8533	*B. variegatus*	*B. variegatus*	M
	Taperinha	MPEG4648	***B. tridactylus***	***B. variegatus***	M
		MPEG4650	*B. variegatus*	*B. variegatus*	M
	Vigia, São Francisco	MPEG2358	*B. variegatus*	*B. variegatus*	M
Rio de Janeiro	Barreiros	MN1162	*B. variegatus*	*B. variegatus*	M
	Rio de Janeiro, Jacarepaguá	AMNH133437	***B. tridactylus***	***B. variegatus***	M
	Parati, Pedra Branca—23°13′S, 44°43′W	MN6103	*B. variegatus*	*B. variegatus*	M
		MN6702	*B. variegatus*	*B. variegatus*	M
		MN7608	*B. variegatus*	*B. variegatus*	M
		MN7609	*B. variegatus*	*B. variegatus*	M
		MN8450	*B. variegatus*	*B. variegatus*	M
		MN5650	*B. variegatus*	*B. variegatus*	M
	Teresópolis—02°26′S, 45°09′W	MN2387	*B. variegatus*	*B. variegatus*	M
	Teresópolis, Fazenda Boa Fé	MN7615	*B. variegatus*	*B. variegatus*	M

APPENDIX I.—Continued.

		Specimen locality	Specimen	Initial identification	Reviewed identification	Analysis (M, DNA)
			MN23892	*B. variegatus*	*B. variegatus*	M
			MN7262	*B. variegatus*	*B. variegatus*	M
	Roraima	Rio Mucajai, Rio Branco—Northwest Amazon Forest—2°22′N 60°58′W	MZUSP13500	*B. variegatus*	*B. variegatus*	M, DNA
	São Paulo	Santos	USNM63004	*B. variegatus*	*B. variegatus*	M
		São Paulo, Jaraguá—23°27′S, 46°44′W	FMNH94296	*B. variegatus*	*B. variegatus*	M
		São Paulo—Atlantic Forest	LABECDpv13431[a]	*B. variegatus*	*B. variegatus*	DNA
			LABEC02050[a]	*B. variegatus*	*B. variegatus*	DNA
Colombia		No specific locality	FMNH88489	*B. variegatus*	*B. variegatus*	M
	Bolívar	San Juan Nepomuceno—09°58′N, 75°04′W	FMNH68916	*B. variegatus*	*B. variegatus*	M
	Caquetá	No specific locality	FMNH140254	***B. tridactylus***	***B. variegatus***	M
	Cauca	Rio Saija—02°52′N, 77°41′W	FMNH90060	*B. variegatus*	*B. variegatus*	M
	Cesar	Colombia: Colonia Agrícola de Caracolicito—10°18′N, 74°00′W	USNM281352	*B. variegatus*	*B. variegatus*	M
			USNM281353	*B. variegatus*	*B. variegatus*	M
	Choco	Golfo de Uraba, Unguia—08°01′N, 77°97′W	FMNH69587	*B. variegatus*	*B. variegatus*	M
			FMNH69588	*B. variegatus*	*B. variegatus*	M
			FMNH69589	*B. variegatus*	*B. variegatus*	M
			FMNH69590	*B. variegatus*	*B. variegatus*	M
	Córdoba	Catival, upper Rio San Jorge—08°17′N, 75°41′W	FMNH68921	*B. variegatus*	*B. variegatus*	M
			FMNH68919	*B. variegatus*	*B. variegatus*	M
			FMNH68920	*B. variegatus*	*B. variegatus*	M
		Rio Baudo, Rio Sando—05°03′N, 76°57′W	FMNH90061	*B. variegatus*	*B. variegatus*	M
	Putumayo	Rio Mecaya—02°8′N, 75°20′W	FMNH70812	*B. variegatus*	*B. variegatus*	M
			FMNH70813	*B. variegatus*	*B. variegatus*	M
	Sucre	Coloso, Las Campanas—09°30′N, 75°21′W	FMNH68918	*B. variegatus*	*B. variegatus*	M
	Valle del Cauca	Zabaletas, 500 m	FMNH86762	*B. variegatus*	*B. variegatus*	M
			FMNH86879	*B. variegatus*	*B. variegatus*	M
Costa Rica	Cartago	Angostura—09°53′N, 83°38′W	USNM12871	*B. variegatus*	*B. variegatus*	M
	Limón	Talamanca	USNM12103	*B. variegatus*	*B. variegatus*	M
Ecuador	Napo	Rio Suno—04°2′S, 77°08′W	FMNH31119	*B. variegatus*	*B. variegatus*	M
Guyana		No specific locality	AMNH130106	*B. tridactylus*	*B. tridactylus*	M
			AMNH140498	*B. tridactylus*	*B. tridactylus*	M
			FMNH16557	*B. tridactylus*	*B. tridactylus*	M
			FMNH16556	*B. tridactylus*	*B. tridactylus*	M
	Cuyuni-Mazaruni	Essequibo, Kartabo Point—06°23′N, 58°41′W	AMNH42454	*B. tridactylus*	*B. tridactylus*	M
			AMNH48180	*B. tridactylus*	*B. tridactylus*	M
			AMNH48369	*B. tridactylus*	*B. tridactylus*	M
			AMNH74131	*B. tridactylus*	*B. tridactylus*	M
			AMNH74137	*B. tridactylus*	*B. tridactylus*	M
	Upper Takutu-Upper Essequibo	Dadanawa—02°50′N, 59°30′W	USNM362241	*B. tridactylus*	*B. tridactylus*	M
Honduras		Gracias a Dios, Patuca River	USNM21011	*B. variegatus*	*B. variegatus*	M
Nicaragua		Escondido River—12°09′N, 83°46′W	USNM51273	*B. variegatus*	*B. variegatus*	M
		El Recreo, Atlantico Sur—12°09′N, 84°26′W	USNM337714	*B. variegatus*	*B. variegatus*	M
Panama	Bocas del Toro	Isla San Cristóbal, Bocatorito—09°15′N, 82°16′W	USNM449525	*B. variegatus*	*B. variegatus*	M
	Darién	Cerro Tacarcuna—08°10′N, 77°18′W	USNM338124	*B. variegatus*	*B. variegatus*	M
		El Real—08°06′N, 77°45′W	AMNH37621	*B. variegatus*	*B. variegatus*	M
	Colón	Gatun—09°15′N, 79°56′W	AMNH36816	*B. variegatus*	*B. variegatus*	M
	Panamá	Barro Colorado Island—09°09′N, 79°51′W	FMNH30738	*B. variegatus*	*B. variegatus*	M
		La Chorrera—08°52′N, 79°48′W	AMNH31427	*B. variegatus*	*B. variegatus*	M
Peru		No specific locality	AMNH98530	*B. variegatus*	*B. variegatus*	M
	Loreto	Alto Amazonas, Rio Morona, boca Rio Amaya—04°39′S, 77°07′W	FMNH88893	*B. variegatus*	*B. variegatus*	M
		Iquitos—03°46′S, 73°15′W	AMNH98545	*B. variegatus*	*B. variegatus*	M
			AMNH98546	*B. variegatus*	*B. variegatus*	M
			AMNH98533	*B. variegatus*	*B. variegatus*	M
		Nauta, Rio Samiria, Santa Helena—04°50′S, 74°13′W	FMNH86896	*B. variegatus*	*B. variegatus*	M
		Rio Amazonas, Apayacu—03°19′S, 72°06′W	AMNH74429	*B. variegatus*	*B. variegatus*	M
		Rio Amazonas, Orosa—03°26′S, 72°08′W	AMNH73758	*B. variegatus*	*B. variegatus*	M
			AMNH73759	*B. variegatus*	*B. variegatus*	M
		Rio Amazonas, Puerto Indiana—03°28′S, 73°03′W	AMNH73757	*B. variegatus*	*B. variegatus*	M

APPENDIX I.—Continued.

		Specimen locality	Specimen	Initial identification	Reviewed identification	Analysis (M, DNA)
			AMNH73572	*B. variegatus*	*B. variegatus*	M
			AMNH73573	*B. variegatus*	*B. variegatus*	M
		Rio Samiria—04°42′S, 74°13′W	AMNH188196	*B. variegatus*	*B. variegatus*	M
			AMNH76497	*B. variegatus*	*B. variegatus*	M
			AMNH76403	*B. variegatus*	*B. variegatus*	M
		Rio Ucayali, Sarayacu—06°44′S, 75°06′W	AMNH76495	*B. variegatus*	*B. variegatus*	M
			AMNH76496	*B. variegatus*	*B. variegatus*	M
			AMNH76408	*B. variegatus*	*B. variegatus*	M
		Yurimaguas, Puerto Arturo—05°50′S, 76°03′W	FMNH20132	*B. variegatus*	*B. variegatus*	M
South America		South America—Zoo	FMNH60164	*B. variegatus*	*B. variegatus*	M
Suriname	Paramaribo	Paramaribo, 900 feet—05°50′N, 55°10′W	FMNH93297	*B. tridactylus*	*B. tridactylus*	M
	Saramacca	La Poule	FMNH95444	*B. tridactylus*	*B. tridactylus*	M
Unknown		Unknown	MN1694	***B. tridactylus***	***B. variegatus***	M
Venezuela	Amazonas	Mount Duida, Esmeralda—03°10′N, 65°33′W—left bank Rio Orinoco	AMNH76904	***B. tridactylus***	***B. variegatus***	M
		Rio Casiquiare, left bank (translated), El Merey—03°05′N, 65°05′W	AMNH78515	***B. tridactylus***	***B. variegatus***	M
	Bolívar	Camarata Valley, 450 m	AMNH135474	***B. variegatus***	***B. tridactylus***	M
		Ciudad Bolívar—08°08′N, 63°33′W	AMNH16135	*B. tridactylus*	*B. tridactylus*	M
		El Manaco—06°17′N, 61°19′W—59 km SE El Dorado	USNM374821	*B. tridactylus*	*B. tridactylus*	M
		Los Patos—07°11′N, 62°22′W—25 km SE El Manteco	USNM374822	*B. tridactylus*	*B. tridactylus*	M
		Rio Suapure—06°48′N, 67°01′W	AMNH16933	*B. tridactylus*	*B. tridactylus*	M
			AMNH17560	*B. tridactylus*	*B. tridactylus*	M
	Miranda	San Andrés—10°22′N, 65°50′W—16 km SSE Caracas	USNM372832	*B. variegatus*	*B. variegatus*	M

[a] For specimens captured and sampled in the wild from which DNA samples were obtained, taxonomic identifications were made using external morphology.

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ARTICLE

First observation on mating and reproductive seasonality in maned sloths *Bradypus torquatus* (Pilosa: Bradypodidae)

Bernardo B. Dias · Luis Alberto Dias dos Santos · Paula Lara-Ruiz · Camila Righetto Cassano · Laurenz Pinder · Adriano G. Chiarello

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Abstract Information on mating season is of paramount importance for our understanding of reproductive behavior, yet little is currently known about the breeding season of Xenarhtra as a whole and sloths in particular. A pair of maned sloths was observed copulating in September 2005 in the Atlantic Forest region of south-eastern Brazil. Our studies on mating of the manned sloth as well of other hitherto unpublished records of newborn sloths seen in the wild, together with a review of previous information, indicate that *B. torquatus* is a seasonal breeder. Infants are born predominantly at the end of the wet season and beginning of the dry season (February–April), and copulation concentrates in the late dry and early wet seasons (August–October). This strategy allows for the energy-demanding gestation and lactation to take place during the less stressful period of the year.

Keywords Atlantic forest · Copulation · Endangered species · Reproduction · Xenarthra

Introduction

Sloths are arboreal mammals that are currently classified in the order Pilosa (Magnaorder Xenarthra) and suborder Folivora (Wilson and Reeder 2005). The six extant species of sloths are divided into two families: Megalonychidae, consisting of *Choloepus didactylus* and *C. hoffmanni*, and Bradypodidae, consisting of *Bradypus torquatus*, *B. variegatus*, *B. tridactylus* and *B. pygmaeus*. Sloths are slow-moving, solitary animals that allocate a large proportion of time to resting hidden from view high up in the canopy of tropical forests (Queiroz 1995; Chiarello 1998a, 2008; Urbani and Bosque 2007). Copulation seems to occur within a very short time interval (Goffart 1971) and, therefore, it is not surprising that it has been rarely observed in nature (Richard-Hansen and Taube 1997; Bezerra et al. 2008), even during long-term studies (Chiarello et al. 2004; Lara-Ruiz and Chiarello 2005). Very little data exist on a number of aspects of reproductive behavior in most Xernarthra species, including mating season (Gilmore et al. 2008; McDonough and Loughry 2008; see also other related chapters in Vizcaino and Loughry 2008). Such information is needed, however, to understand fundamental aspects of the ethology, ecology and conservation of any species. The mating season, for example, can influence a host of attributes, including territory extent and spacing (von Hardenberg et al. 2000), the level of aggression or affiliative behaviour (Cavigelli and Pereira 2000) and the spatial and

B. B. Dias · A. G. Chiarello (✉)
Programa de Pós-graduação em Zoologia de Vertebrados,
Pontifícia Universidade Católica de Minas Gerais,
Av. Dom José Gaspar 500, Prédio 41, Belo Horizonte,
Minas Gerais 30535-610, Brazil
e-mail: bradypus@pucminas.br

L. A. Dias dos Santos
Escola Superior Educandário Seráfico São Francisco de Assis,
Santa Teresa, Espirito Santo, Brazil

P. Lara-Ruiz
Laboratório de Biodiversidade e Evolução Molecular,
Universidade Federal de Minas Gerais, Belo Horizonte,
Minas Gerais, Brazil

C. R. Cassano
Instituto de Estudos Socioambientais do Sul da Bahia,
Ilhéus, Bahia, Brazi

L. Pinder
Fundação O Boticário, Curitiba, Paraná, Brazil

temporal frequency of vocalizations (van Parijs et al 1999), among others.

The maned sloth *B. torquatus* is endemic to the Atlantic forest of Brazil and threatened with extinction (listed as "Endangered" in IUCN: Chiarello et al. 2006; IUCN 2006). Until the end of 1990s only one paper containing any information on the reproduction of this species had been published (Pinder 1993). Lara-Ruiz and Chiarello (2005) recently elucidated some important aspects related to this topic: (1) only one infant is born per parturition; (2) the inter-birth interval is 1 year; (3) breeding appears to be concentrated in February and July in the forests of Espirito Santo in south-eastern Brazil, one of the strongholds of the species. Using sighting dates of newborns and infants found in the wild and assuming a gestation length of 6 months, as is the case in other congener sloths (*B. tridactylus* and *B. variegatus*; Taube et al. 2001), Lara-Ruiz and Chiarello (2005) suggested that the mating season of *B. torquatus* takes place between September and November. This period coincides with the end of the dry season and the beginning of the wet season (Lara-Ruiz and Chiarello 2005).

We report here for the first time the direct observation of mating in *B. torquatus*. We also review information on sighting dates of newborns from a broader range of sites and regions with the aim of clarifying the reproductive seasonality of this sloth species.

Materials and methods

The observations described herein were carried out in a private forest fragment (184 ha) located in the municipality of Santa Maria de Jetibá, Espirito Santo state, which is known locally as Paulo Seike's fragment (20°02′31″S; 40°41′47″W). The forest of the region is classified as dense ombrophilous by the Brazilian Institute of Geography and Statistics (IBGE 1992) and is mostly secondary. Local topography is hilly, with average altitudes varying from 600 to 800 m a.s.l. We found no published data on climate for the study site, but meteorological data are available for the Biological Station of Santa Lúcia, which is about 18 km away and located in an area with similar topography, altitude and forest cover. Consequently, we assumed an annual average precipitation of 1868 mm and average annual temperature of 19.9°C (average of the maximum temperatures is 26.2°C; average of the minimum temperatures is 14.3°C) for the study site (Mendes and Padovan 2000). This region has a wetter and hotter season between October and March and a drier and colder season between April and September. The hottest and rainiest period is November–January and the driest and coldest is May–July (Chiarello 1998a; Mendes and Padovan 2000). The study fragment and adjoining forests have an estimated sloth population of about 100–200 individuals (A.G. Chiarello et al., unpublished data).

To calculate the approximate period during which birth takes place in the maned sloth, we used sighting dates of newborns and size or weight data of infants which, in turn, allowed us to estimate their approximate age when seen or captured. We included only observations of newborns (approx. 300 g of body weight; Lara-Ruiz and Chiarello 2005) and infants of no more than 3 months of age (approx. 600 g of body weight) in our data set in order to reduce the influence of ontogenetic variations in the estimation of mating period. Once the birth date was established, the mating date was estimated by assuming a 6-month gestation period, as is the case of other congener sloths studied to date (Taube et al. 2001).

Results

At 11:20 a.m. on September 26, 2005, during monitoring of a radio-tracked adult female *B. torquatus* ("BT8.5"), we observed this animal in an embrace with another adult sloth. The two were high in the canopy and so tightly embraced that initially we though there was only a single large sloth in the tree. For this same reason we could neither discern copulation movements nor see if their relative position was ventral–ventral or ventral–dorsal. The radio-tracked female (BT8.5) was carrying her 8-month-old infant, which weighed 500 g when first captured on April 26, 2005. The two adults stayed embraced for approximately 7 min and then separated from each other, remaining side by side on the same tree trunk. We attempted to climb the tree to capture the unidentified sloth, but heavy rainfall at the time hampered this attempt.

We returned to this tree the following morning (September 27) and observed that the radio-collared female, her infant and the unidentified sloth were still present, but that the female was now about 8 m away from the unidentified sloth. We monitored these animals for about 5 h: the female and her offspring fed on leaves and moved about in the canopy; the other sloth remained motionless throughout this period. Again, strong and constant rain hampered our attempt to climb this tree.

On the next day (September 28) we once again went to this same spot to try to capture the unidentified sloth. We arrived there at 9:30 a.m. and saw the female and her young resting and the unidentified sloth feeding. The two adult sloths were about 10 m away from each other but in the same tree. Fortunately the rain stopped for some moments enabling us to climb the tree and capture the unidentified sloth. The close inspection of its external genitals and the coloration patterns of its mane confirmed that it was a sexually mature male (see Lara-Ruiz and Chiarello 2005 for a discussion on sexual dimorphism on this species). It had a prominent penis, head-to-tail body length of 74 cm, body mass of 9 kg (heavier than all males of this species measured thus far; Lara-Ruiz and Chiarello 2005) and scars on the face. Healed scars in the face region have been observed previously in both sexes, but mostly in males. Table 1 lists this copulation event and another 21 instances of newborns observed by us in the study region and elsewhere in Brazil.

Discussion

The observations reported here, together with data collected in previous studies on sloths from this region (Lara-Ruiz and Chiarello 2005) as well as from southern Bahia (Cassano 2006) and northern Rio de Janeiro (Pinder 1993), indicate that *B. torquatus* gives birth mainly during the first half of the year, between February and April (Table 1). This period encompasses the last 2 months of the rainy season and the first month of the dry season in Espirito Santo and Rio de Janeiro States. In turn, copulation occurs predominantly during the second half of the year, centred between August and October, which encompasses the last 2 months of the dry season and the first month of the rainy season in Espirito Santo and Rio de Janeiro. This pattern was observed for the majority of cases ($n = 15$; 71.4%) listed in Table 1, suggesting that reproduction in maned sloths is seasonal. For six cases (28.6%), however, the timing of probable copulation was variable (Table 1). Interestingly, five of these six "outliers" occurred in the hotter lowland forests of southern Bahia ($n = 2$), Espirito Santo (Aracruz region; $n = 1$) and Rio de Janeiro ($n = 2$), where winter months are not so stressful as in the lower montane forests due to the lower altitudes (<100 m a.s.l.) and proximity to the sea, which buffers temperature variation. Only one "outlier" occurred in the colder lower montane of Espirito Santo.

Gilmore et al. (1994) reported that a female kept in a large, unroofed compound emitted shrill cries at regular intervals for several days, following which a male sloth somehow managed to enter the compound and copulate with her. Similarly, some local inhabitants reported that maned sloths sometimes call (a long, high pitched "eeee"), as has been reported for other congener sloths (Goffart 1971 and references therein; Montgomery and Sunquist 1974; Gilmore et al. 1994; Lara-Ruiz and Srbek-Araujo 2006). Adult and infant maned sloths routinely call in distress when captured and handled, but apart from these situations, we have only been able to record calls on one occasion—on August, 2003 in the São Lourenço Municipal Reserve (region of Santa Teresa, Espirito Santo). This date fits well into the estimated period of mating (Table 1). We suggest, however, that "mating" calls are rare events in maned sloths since these were witnessed only once during thousands of hours of direct observation. If maned sloths called routinely for "social" or reproductive reasons (see, for example, Lara-Ruiz and Srbek-Araujo 2006), we would certainly have recorded calls more often.

According to Lara-Ruiz and Chiarello (2005), the wet season, which is also the hottest season, is more favourable to both pregnant females and newborns since Xenarthrans have low metabolic rates and a relatively poor control of body temperature (McNab 1985). There is no doubt that cold weather influences sloth distribution as sloths are restricted to tropical regions from the Honduras (approx. 12°N) to southern Brazil (approx. 25°S) (Wetzel 1982). Luederwaldt (1918) reported the death of some adult sloths after cold nights in São Paulo (approx. 700 m a.s.l. and approx. 23°S). In the lower montane region of Espirito Santo environmental temperatures below 10°C are not uncommon during the coldest months of June and July. A previous study carried out in this region documented that maned sloths spend twice as much time feeding during the dry season than during in the wet season, while the distances the sloths traveled did not vary significantly between these seasons (Chiarello 1998a). These results suggest that the higher amount of time dedicated to feeding during the driest and coldest months results from an increase in demand for food and energy (Chiarello 1998a, b). Additionally, gestation would be less stressful throughout the wet season because of the greater availability of new leaves in the forest, by far the preferred food item (Chiarello 1998b).

Information on reproductive seasonality in sloths is scarce and rather contradictory. Lara-Ruiz and Srbek-Araujo (2006) observed a probable copulation attempt in *B. variegatus* in the region of Aracruz, lowland Espirito Santo, about 60 km away from the study site reported herein. Unfortunately, there is no additional data on the southern range of this sloth (southeast Brazil). In Recife, which is a region of Atlantic forest in north-eastern Brazil, Gilmore et al. (1991, 1994) reported the absence of active spermatogenesis in 11 male *B. variegatus* examined from August to February, suggesting that males are sexually inactive at this time. In contrast, Gilmore and Costa (1995) observed active spermatogenesis in two males captured in late September and early October in this same locality. Gilmore et al. (1994) suggest that in Pernambuco (also in north-eastern Brazil) copulation takes place between February and April, during the local dry season. Yet these same authors reported copulation in a semi-captive environment in November, and Bezerra et al. (2008) witnessed copulation in the wild in July in the same region. Taken together, these observations suggest that only a portion of

Table 1 Inferred period (thick underlines) of the birth and mating of *Bradypus torquatus* based on observations of wild sloths carried out at various locations in Brazil. Data sources are arranged from the northernmost (BA) to the southernmost sites (RJ)

<table>
<tr><th>Jan</th><th>Feb</th><th>Mar</th><th>Apr</th><th>May</th><th>Jun</th><th>Jul</th><th>Aug</th><th>Sep</th><th>Oct</th><th>Nov</th><th>Dec</th><th>Study site and municipality</th><th>State</th><th>Habitat</th><th>Source</th></tr>
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Table 1 continued

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Study site and municipality	State	Habitat	Source
	B						M					São Lourenço Reserve, Santa Teresa	ES	Lower-montane	Lara-Ruiz and Chiarello (2005)[l]
	B						M					São Lourenço Reserve, Santa Teresa	ES	Lower-montane	Lara-Ruiz and Chiarello (2005)[l]
	B						M					Private fragment, Santa Maria de Jetibá	ES	Lower-montane	This study[m]
	B						M					Private fragment, Santa Maria de Jetibá	ES	Lower-montane	This study[n]
								M				Private fragment, Santa Maria de Jetibá	ES	Lower-montane	This study[o]
M					B						M	Poço das Antas Reserve, Silva Jardim	RJ	Lowland	This study[p]
M					B						M	Poço das Antas Reserve, Silva Jardim	RJ	Lowland	This study[q]

B Birth, *M* mating, *BA* Bahia, *ES* Espírito Santo, *RJ* Rio de Janeiro

[a] One newborn (299 g body weight) captured along with its mother on March, 2003

[b] One newborn (300 g of body weight) captured on May, 2006 by CRC

[c] One newborn (~300 g of body weight) captured on June, 2007 by CRC

[d] One newborn (352 g of body weight) captured on January, 2007 by CRC

[e] One newborn seen on April 1996 (Putiri Fragment, owned by Aracruz Cellulose Company)

[f] One ~2 month old infant (400 g of body weight) captured on May, 2003

[g] One ~3 month old infant (500 g of body weight) captured on May, 2003

[h] One newborn (300 g of body weight) captured on July, 2003

[i] Two newborns seen on May, 1999

[j] One ~2 month old infant (420 g of body weight) captured on May, 1995

[k] One 2–3 month-old infant seen on October, 1999 by AGC

[l] Five newborns born between February and March from a radio-tracked female (BT1.5) during five consecutive years of monitoring (2000–2004) in São Lourenço Municipal Park

[m] One 2.5 month-old infant (560 g of body weight) captured on May, 2005 in the study area of the present report by BBD and LADS

[n] One ~2 month-old infant (500 g of body weight) captured on April, 2006 in the study area of the present report by BBD and LADS

[o] Present report on mating

[p] One newborn infant (365 g of body weight) captured along with its mother on July, 1984 by LP in Poço das Antas Biological Reserve

[q] One newborn infant (400 g of body weight) captured along with its mother on July, 1985 by LP in Poço das Antas Biological Reserve

B. variegatus males seem to be sexually active at any one time in the year (Gilmore et al. 1994; Gilmore and Costa 1995) or that these males exhibit an asynchronous pattern of spermatogenesis. Gilmore et al. (1994) reported an additional observation which corroborates this assertion: a female kept in semi-captivity at a location nearby Recife together with an adult male copulated with another male that entered her enclosure, while the male who lived with her did not attempt to copulate nor did he show any sort of reaction. In conclusion, this scarce and rather anecdotal information indicates that reproduction of *B. variegatus* in the Atlantic forest of north-eastern Brazil does not seem to be seasonal. Similarly, observations on *B. variegatus* carried out elsewhere indicate either the absence or only weak seasonality in reproduction (Enders 1935; Toyama et al 1990; Queiroz 1995; Taube et al. 2001). In relation to *B. tridactylus*, the little information that does exist indicates some reproductive seasonality (Beebe 1926; Richard-Hansen and Taube 1997; Taube et al. 2001).

The observation reported here and the analysis of previous data on births indicate that *B. torquatu*s reproduces seasonally, with gestation and lactation taking place during the least stressful period of the year, when temperatures are higher and preferred food items are more plentiful. Some observations indicate, however, that not all individuals from the same locality or individuals from different localities fit this pattern. Distinct phenological and climatic patterns among localities are perhaps the reason behind this variation. It is worth remembering that southern Bahia and northern Rio de Janeiro, the two most extreme locations of our sample, are separated from each other by 6° of latitude. Also, significant altitudinal variation exists between the lower montane forests of Espirito Santo (approx. 600 m a.s.l.) and all other localities (approx. 0–100 m a.s.l.). The lack of more severe low temperatures is perhaps the main reason behind those reports that did not fit the seasonal pattern presented above, as five of the six outliers are from lowland sites. We prefer, however, not to propose this hypothesis until more data from other regions of the Atlantic Forest become available. It is therefore important that further research be carried out on maned sloth populations, as reproduction remains poorly understood even for the commoner and wider-ranging sloth species. It is also essential to investigate endocrine aspects, including the control of spermatogenesis and oestrous cycles, since only with this information can we form a definite view of *B. torquatus* reproduction. In this sense, results from a recent study (Mühlbauer et al. 2006) are encouraging. These authors demonstrated that it is possible to follow the hormone cycles of male and female sloths (*Bradypus varieagatus*) through the monitoring of faecal samples by noninvasive techniques. Such methodology should be used in the future to test its applicability in *B. torquatus* as the alternative method (i.e. collection of blood samples) is more difficult and no doubt more stressful to the animals.

Acknowledgments The observation reported here took place during the project “Demography and population viability of maned sloth, *Bradypus torquatus* (Xenarthra: Bradypodidae)”, administered by Valor Natural ONG (Belo Horizonte, Brazil) and funded by the Endangered Species Program from Biodiversitas Foundation (project no. 080M/022004). Mello Leitão Museum in Santa Teresa, Instituto de Pesquisas da Mata Atlântica (IPEMA) in Vitoria, and Instituto de Estudos Socioambientais do Sul da Bahia (IESB) in Ilhéus helped with the logistics. The Brazilian Environmental Agency (IBAMA) provided authorization to capture sloths in the field (permits no. 093/2005 DIREC/CGECO and no. 085/2005 DIFAP/CGFAU). Regiane Romanini helped with the data collection. The Brazilian Science Council (CNPq) provided a research grant to AGC (no. 301100/2005-5). Two anonymous reviewers helped improve the manuscript.

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http://news.mongabay.com/2013/0920-pygmy-sloth-fiasco-dimitrova.html

Attempt to export nearly-extinct pygmy sloths sets off international incident in Panama

Tanya Dimitrova, special to mongabay.com
September 20, 2013

14 Share Share print

After this story was published, Dallas World Aquarium (DWA) complained that its side of the story had not been fairly represented, that elements of our reporting contained inaccuracies and made legal threats against Mongabay. As a result of the new input we have added a series of annotations, correcting several points and adding DWA's views. Note that the DWA provided very limited information in the original reporting despite numerous inquiries.

Baby Pygmy sloth. Photo credit: Bryson Voirin

Last Monday (9 September 2013), the police officer on morning duty at Isla Colón International Airport, Panama noticed some foreigners loading crates with what appeared to be animals on a private jet [1]. Finding this suspicious, he alerted his supervisor. Within minutes, the local police chief, the mayor of Bocas, the director of the regional office of the National Environmental Authority (ANAM), community leaders and heads of local conservation organizations were informed about the incident. Little by little, a crowd of concerned citizens from Bocas town gathered around what turned out to be eight pygmy sloths – some of the rarest mammals on Earth.

The private jet at Isla Colón International Airport, Panama which was meant to take the sloths abroad. (Photo courtesy Alianza Bocas)

The pygmy three-toed sloth (*Bradypus pygmaeus*) is one of the world's most endangered species. A recent scientific survey found fewer than 100 sloths hanging on in their island home – Isla Escudo de Veraguas, Panama. They live nowhere else in the world. For the past 15 months, Bryson Voirin, expert on pygmy sloths and member of the International Union for Conservation of Nature (IUCN) Species Survival Commission, has been tracking ten of them with radio-collars to find where on the island they spend their time. Voirin has been working on sloth conservation in Panama for the last 10 years alongside scientists from Zoological Society London, Smithsonian Tropical Research Institute (STRI) and many local organizations.

But on Monday, as the drama at the airport was developing, it became clear that the foreigners who were trying to export the pygmy sloths were Luis Sigler and Daryl Richardson of Dallas World Aquarium, Jason and Julia Heckathorn – children's books publishers and amateur naturalists based in the U.S., and Judy Arroyo and Rebecca Cliffe from a sloth rehabilitation center in Costa Rica [2].

According to the flight manifest, the charter flight was headed for Island Roatan in Honduras before its final destination: Addison airport, Dallas. None of the passengers wanted to comment about the reason for this interim destination [3].

Crates with pygmy sloths destined for Dallas World Aquarium. (Photo courtesy of Jahir Amir Torres via The Bocas Breeze)

According to Sigler, the conservation biologist on staff at the Dallas Aquarium, the rare animals were being relocated in order to establish a captive breeding population in Texas. Sigler presented to the airport officials a research permit, animal export permit and a veterinary certification – all the required paperwork for the export. The National Environmental Authority (ANAM) in Panama City has since confirmed their legitimacy.

The Dallas Aquarium local partner in Panama was Jacobo Lacs, director of Zoologico del Istmo in Colon – also a private animal center, closed to the public, where tropical birds and other animals are bred for export. According to the research permit, Lacs was supposed to take two of the eight pygmy sloths to his facility.

However, as the regional ANAM office had no knowledge of the foreign conservation project, the local authorities, aided by a crowd of 75-100 impromptu protestors, vigorously insisted that the sloths be returned to their native habitat on Isla Escudo de Veraguas.

By Monday evening, Dallas Aquarium officials had relinquished possession of the eight sloths. The animals were to be taken back to the island on Tuesday morning and released into the mangrove forest [4].

Pygmy sloth released back on Isla Escudo de Veraguas last Tuesday. Photo credit: Shannon Thomas / the Sea Turtle Conservancy.

The local protesters, however, were distrustful and so an agreement was made that two local citizens would spend the night camped out by the sloths' temporary holding enclosure in order to ensure they were not removed from the country before they could be returned to Isla Escudo de Veraguas the next morning.

Even though the eight pygmy sloths are now back in their home, all is far from over.

"We are really worried," a local resident, who asked to remain anonymous, told mongabay.com. "They said they were going to come back and this time we wouldn't be able to stop them. We think they plan to ship them out via David City, at the Pacific side of Panama."

LEFT: Pygmy sloth in a box back on Isla Escudo de Veraguas. Photo credit: Shannon Thomas / the Sea Turtle Conservancy. RIGHT: Radio tracking sloths on the island. Photo credit: @Craig Turner/ZSL

Potential captive breeding

Breeding programs for some threatened species have been successful. However, three-toed sloths are very difficult to maintain in captivity. They often do not survive, nor reproduce. For years, many have tried to maintain them artificially outside the Tropics, and nearly all have failed. According to Dr. Jutta Heuer, from Halle Zoo, Germany, one of the world experts in sloth husbandry in Europe, there is little to no experience with keeping, breeding and feeding three-toed sloths in captivity.

"A modern and serious zoo should never bring wild animals in without knowing this basic information. As studbook keeper for two-toed sloths in Europe I can say that because of ignorance and lack of experiences from zoos, a lot of sloths paid with their lives in the past," says Heuer.

Recently, the Dallas World Aquarium has been able to maintain a small population of three brown-throated three-toed sloth (*Bradypus variegatus*) – another sloth species that is not endangered – by providing fresh Cecropia leaves to them flown in from Hawaii. But these three animals are the only ones which survived out of the nine sloths Dallas Aquarium imported from Venezuela and Costa Rica in the past 15 years. The only baby sloth born in captivity died 7 months later and had been conceived in the wild.

To make matters worse, the critically endangered pygmy sloths themselves have never been held and bred in captivity. Even their actual diet is unknown. They are thought to eat primarily red mangroves from the coast, but the radio collar study found pygmy sloths on the interior of the island in deep forest, suggesting that other trees make up at least a portion of their diet.

"The idea of an external breeding program to increase the number of pygmy sloths sounds logical and noble at first, but when you consider that it's hard enough to just keep common three-toed sloths alive in captivity, let alone breed them, it seems highly unlikely that a satellite breeding population in Dallas would have yielded anything more than at best a few sloths surviving in captivity in a foreign zoo, but more likely eight fewer surviving pygmy sloths in the wild. The potential risks at this time do not justify the means. Promising the local community that by removing a few sloths from the island they will eventually benefit by receiving multiple captive-bred replacements is a fantasy at this point," says Voirin.

The temporary overnight enclosure for the contested pygmy sloths. Photo credit: Jahir Amir Torres via The Bocas Breeze.

The controversy

All professionals from the international sloth conservation community contacted by mongabay.com were caught by surprise by the actions undertaken by Dallas World Aquarium [5].

"I have formerly worked with the New Zealand Wildlife Service on some of the most endangered species in the world, which often involved capture of wild animals for transfer to other reserves or captive breeding. There is no way any kind of captive program for the sloths should have been established or even considered without a comprehensive management plan developed in consultation with experts on the species as well as with all relevant stakeholders. A serious conservation organization should never have undertaken this kind of project without further research and consultation with independent experts," said Dr. George Angehr from the Smithsonian Tropical Research Institute.

"I fail to understand why Dallas World Aquarium did not consult with the experienced researchers prior to exporting these animals. Furthermore, I fail to understand how ANAM approved the export of roughly 10% of the wild population if this species has never been kept in captive conditions," said Dr Mariella Superina, Chair of the IUCN/SC Anteater, Sloth and Armadillo Specialist Group.

Sigler explains that "a document called *Isla Escudo de Veraguas: a Vision for the Future*, on page 16, Section 6.1 Project Scorecard showed the proposed participation of actors."

Pygmy sloth release back on Isla Escudo de Veraguas. Photo credit: the Sea Turtle Conservancy.

This document was supposed to have been publicly shared for comments and sent electronically to all stakeholders more than a year ago. But it is not available online and apparently the only conservation organization it was emailed to (in January 2013) was the Zoological Society of London (ZSL), which promptly responded that “the current draft raises a number of questions and concerns [6]."

The conservation plan-type document was not drafted by any particular conservation organization (nor the Dallas World Aquarium). Instead, it was put together and emailed around by Jason and Julia Heckathorn – the children's books authors and amateur naturalists, who were also present at the airport last Monday for the attempted pygmy sloth exportation.

The Dallas aquarium refused further explanations as to what kind of working relationship they had with the animal-loving couple [7].

Pygmy sloths being released back on Isla Escudo de Veraguas. Photo credit: the Sea Turtle Conservancy.

In the meantime, Silvano Vergara, the head of ANAM in Panama city gave an interview for local TV in which he said: "The agreement with Dallas Aquarium foresaw since 2007 that they would do research, and after doing studying the behavior, reproduction of each of these individuals, see how they could be reproduced in captivity. Precisely, they were going to export three pairs to reproduce them in captivity, and then bring back the animals and introduce them."

Back in Bocas, nobody (including the local ANAM officer) had heard about this newly surfaced agreement with Dallas World Aquarium until the incident at the airport last Monday. People were upset that nobody apparently consulted them on a matter as important as the fate of the few remaining pygmy sloths in the wild.

"If we want to protect this great species successfully we need to work openly together. We shouldn't learn about a conservation effort relating to the pygmy sloths in the middle of the night amidst violent social unrest," says Voirin.

Photo credit: Jahir Amir Torres via The Bocas Breeze

Protected legal status

Although the IUCN Red List classifies the pygmy sloth as Critically Endangered, the Convention on International Trade in Endangered Species (CITES) has not yet been updated to include the recently described species. Pygmy sloths have been known to science only since 2001 when they were formally described as a separate species, occurring only on Isla Escudo de Veraguas. This is why the Aquarium (or anyone else) needs no import permit from the U.S. federal government. They need only Panamanian export permits, which some experts claim are easily obtained [8].

"The leaders of this effort have exploited the oversight: no one ever anticipated that there would be trafficking of pygmy sloths out of the country," says Voirin.

According to him, an effort is underway since last week to have Panama immediately request that the pygmy sloths be listed as a CITES III protected species [9].

All aspects of the incident are still under active investigation in Panama.

Videos of the release shot by the Sea Turtle Conservancy

29-Sep-2013 Annotations

[1]: The sloths were never in the process of being loaded onto a plane, says Dallas World Aquarium. They didn't leave the customs area of the airport where they were easily observed by law enforcement.

[2]: The only exporter was the Dallas World Aquarium. The remaining individuals on the flight were research assistants and consultant, according to Dallas World Aquarium.

[3]: The passengers were unable to comment as they were not involved in the flight planning. They discovered later that the pilots scheduled a stop on Roatan for fuel only, and no passengers left the airport there.

[4]: Once removed from the island, the health and well-being of the pygmy sloths was carefully monitored by the researchers, according to Dallas World Aquarium.

[5]: Dallas World Aquarium says it had the prior approval of ANAM and mayor Archibold of Kusapin, under whose jurisdiction the island falls.

[6]: Dallas World Aquarium contends that it sent the plan to a number of conservationists and NGOs and received multiple comments on it. However, mongabay.com has not been able to verify who received the proposal ahead of time. All the conservationists mongabay.com reached out to stated they had no knowledge of the immediate plans to export pygmy sloths from their native habitat.

[7]: According to the Dallas World Aquarium, there is no basis for further explanation because the DWA has no formal relationship with the Heckathorns.

[8]: Formally, the exported sloths would have remained the property of Panama and could be returned at any time if the government requested them.

[9]: However, even if the pygmy sloth becomes protected under CITES III, it could still be exported with an appropriate export permit from Panamanian authorities.

DWA also provided two documents: a letter from Judy Avey Arroyo of the Sloth Sanctuary in Costa Rica to Kristin L. Vehrs, Executive Director of the Association of Zoos & Aquariums and a field report by Marcelo Espinoza and Rebecca Cliffe.

Read more at http://news.mongabay.com/2013/0920-pygmy-sloth-fiasco-dimitrova.html#szzlsKtLlb5dT1DK.99

How Did Dallas Aquarium Almost Get Away With Taking 8 Endangered Pygmy Sloths from Panama?

- by Susan Bird
- October 14, 2013

The citizens of Panama take a hard line when it comes to their country's endangered species. If they think you're spiriting them out of the country without permission, they *will* stop you.

That's what the Dallas World Aquarium (DWA) found out recently when it arrived in Panama to capture and export eight endangered pygmy three-toed sloths. As it turns out, DWA apparently had all the appropriate paperwork to take the sloths.

The problem was that they didn't seem to have done enough prior coordination with Panamanian officials or sloth experts before showing up at Bocas del Toro in a private plane with full crates in hand. The resulting uproar became something of an international incident.

The pygmy three-toed sloth lives only on Isla Escudo de Veraguas, a small uninhabited island near Panama. Fewer than 100 of them exist. It is the smallest sloth in the world and is understood to feed mostly on mangrove leaves, though experts know little about its habits. See a YouTube video about this species here:

The DWA wanted eight of these animals and came to get them on September 9. That's when the situation almost got out of hand.

Protesters Reportedly Threw Rocks, Trapped DWA Personnel in Van

The activity on the tarmac at Isla Colón International Airport looked mighty suspicious to the morning guard. He saw the little plane and the crates sitting in the customs area containing unknown animals ready to be loaded as cargo.

Alarmed, the guard alerted his supervisor. With admirable speed, word spread to the local police chief, Bocas del Toros' mayor, the National Environmental Authority's (ANAM) regional director and local conservation organizations. That's when the crowd started forming.

The situation at the airport escalated rapidly, according to reports. A crowd of 75 to 100 protestors reportedly trapped the would-be exporters in a van, pelting them with rocks until they got an agreement that the sloths would be immediately returned to their island home.

“It got a little scary there for everybody,” Daryl Richardson, DWA’s chief executive, told the Dallas Morning News.

The sloths were to be returned to the island the next day. Two protestors stayed all night at the sloths’ temporary enclosure, guarding them to ensure they actually made it back to their island home the next day.

Sloth Conservation Experts Mystified by DWA‘s Actions

DWA says its intent was to create an “insurance population” of pygmy three-toed sloths, in case the island one day can’t support them any longer. The problem with that idea, say sloth experts, is that no one has ever successfully bred this species in captivity. It does not survive well as a captive species.

More to the point, say experts, a successful captive breeding program needs to be conducted under the auspices of a species management plan, which doesn’t yet exist for the pygmy three-tied sloth. Additionally, conservationists argue DWA didn’t bother to consult with other scientists currently studying this species on Isla Escudo de Veraguas, a group considered to be the world’s top experts on the pygmy three-toed sloth.

DWA, on the other hand, says it sent its plan to export the sloths to several conservationists and NGOs and received multiple comments on it. However, DWA has not named who these people and organizations were.

Conservation group Mongabay reached out to international sloth conservation experts for input on this situation. The experts were surprised and mystified.

“I fail to understand why Dallas World Aquarium did not consult with the experienced researchers prior to exporting these animals,” said Dr. Mariella Superina, Chair of the IUCN/SC Anteater, Sloth and Armadillo Specialist Group. “Furthermore, I fail to understand how ANAM approved the export of roughly 10 percent of the wild population if this species has never been kept in captive conditions.”

“There is no way any kind of captive program for the sloths should have been established or even considered without a comprehensive management plan developed in consultation with experts on the species as well as with all relevant stakeholders,” Dr. George Angehr of the Smithsonian Tropical Research Institute told Mongabay.

Pygmy Sloths Not Yet Protected by CITES

Unfortunately, DWA apparently had all the paperwork it needed to cart away these eight sloths: a research permit, an animal export permit and a veterinary certification. It didn’t need anything else.

This is because this species was discovered relatively recently and therefore is not yet included in the Convention on International Trade in Endangered Species (CITES). Until the pygmy three-toed sloth becomes a CITES III protected species with tougher import/export standards, it remains vulnerable to situations like this one.

Had DWA merely done a bit more coordination ahead of time, it would easily have been able to export the eight sloths it wants. DWA says it will return at some future point and try again, because it can. Panama, however, is already acting to get the sloth added under CITES III, which it has the unilateral ability to do.

DWA Threatens Legal Action for Mongabay‘s Story on this Incident

Mongabay broke this story shortly after the events at the airport. According to Mongabay’s website, DWA made legal threats and complained that its side of the story had not been included. Mongabay has since added annotations to its original article that express DWA’s inputs and correct some details. Interestingly, Mongabay says it asked DWA for such input before its story ran, but got little from DWA. So why the legal threats later?

DWA has attracted the wrong kind of attention for export attempts before. In 1997, they tried to capture and export four Amazon River dolphins from Venezuela, but had to pull back and abandon that idea after some heavy hitting conservationists, including primatologist Jane Goodall, voiced objections.

One good thing to come out of this fracas is that the conservationists of the world are now watching DWA’s activity in Panama a little more closely.

Read more: http://www.care2.com/causes/how-did-dallas-aquarium-almost-get-away-with-taking-8-endangered-pygmy-sloths-from-panama.html#ixzz2i12pGTfo

SERVICIO VETERINARIO - MASCOTAS

Changuinola, Bocas del Toro, Panamá. 7 de Septiembre de 2013.

CERTIFICADO DE SALUD

No: 070913.

El suscrito Médico Veterinario **NICOLAS AGUERO MURILLO**, CERTIFICA QUE: hasta donde me fue posible determinar los animales descritos a continuación se encuentran clínicamente libres de enfermedades infecto – contagiosas, así como libres de parásitos externos e internos; realizando un examen clínico y desparasitación el día Viernes 6 de setiembre 2013.

Especie: *Bradypus pygmaeus*

Nombre común: Perezosos de tres dedos

Cantidad: 6 animales

Sexo: 2 machos y 4 Hembras

Los ejemplares fueron identificados con pintura de diferente color en sus uñas: roja, blanco, rosa amarillo, verde y azul. Para su posterior identificación definitiva con su respectivo Chip.

Atentamente:

Dr. Nicolás Agüero M
Reg. 581
GRANMA CUB.

Dr. Nicolás Agüero Murillo

Médico Veterinario

Registro No. 581

Celular: 6601-1134 Changuinola, Bocas del Toro, Panamá. E-mail: todoveterinario_2712@hotmail.com

MIDA
Ministerio de Desarrollo Agropecuario
Dirección Nacional de Salud Animal

DSA-TE- 0876-13

Panamá, 9 de septiembre de 2013

CERTIFICADO INTERNACIONAL PARA EXPORTAR PEREZOSOS PIGMEOS A DALLAS – USA.

I. IDENTIFICACION EL ANIMAL

ESPECIE	NUMERO	SEXO	MARCAS QUE LO IDENTIFICAN
Bradypus pigmaeus	6	4 hembras 2 machos- VIVOS	Uñas pintadas con colores rojo, blanco, rosa, amarillo, verde y azul

II. ORIGEN DEL ANIMAL(S)
Nombre del consignador: DARYL RICHARDSON
Dirección: Hotel SANDOLLAR BEACH PANAMÁ. CIUDAD DE PANAMA
Fecha programada de embarque y puerto de embarque (si se conoce)
9 DE SEPTIEMBRE DE 2013 Aeropuerto INTERNACIONAL DE TOCUMEN
Aerolínea programada y número de vuelo (si se conoce)
Nº de VUELO: NO SE CONOCE

III. DESTINO DEL ANIMAL (S)
Nombre del consignatario: DARYL RICHARDSON
Dirección: DALLAS WORLD AQUARIUM, DALLAS, TX- USA

Fecha programada y puerto de llegada (si se conoce): 9 DE SEPTIEMBRE DE 2013 Aeropuerto DALLAS INTERNATIONAL-USA .

IV. INFORMACIÓN SANITARIA Y CERTIFICACIÓN

1. Permiso Científico **Nº SEX/A-61-13** emitido por Dirección de **Áreas Protegida y Vida Silvestre-** ANAM.
2. Certificado de Salud **Nº 070913** emitido por Dr. **Nicolás Agüero Murillo, M.V; Reg. 581.**
3. Los animales se encuentran clínicamente libre de enfermedades infectocontagiosas.
4. Los animales han sido examinados y no presentan síntomas clínicos de parásitos externos e internos.
5. Los animales han sido examinados y desparasitados el día 6 de septiembre de 2013.

DR. FAUSTINO SANCHEZ
Nombre del Veterinario Oficial
Registro 646
Lugar Changuinola-Bocas del Toro, Panamá

Sello y firma del Veterinario Oficial

Fecha: 9 de septiembre 2013

VÁLIDO POR SIETE (7) DÍAS.

GOBIERNO NACIONAL
REPÚBLICA DE PANAMÁ
Teléfonos (507) 266-2012 220-2801 Fax: (507) 266-2943

REPUBLICA DE PANAMA

Autoridad Nacional del Ambiente

anam

Apartado C, Zona 0843, Balboa, Ancón, Panamá

PERMISO CIENTÍFICO
SCIENTIFIC PERMIT

No. SC/A-23-13

VALIDO HASTA 09-11-2013
VALID UNTIL

FAUNA / FLORA / HONGOS / BACTERIAS / OTROS ORGANISMOS

FAUNA

INVESTIGADOR RESPONSABLE
MAIN RESEARCHER
Daryl Richardson

IDENTIFICATION
I.D.
483840935-USA

ASISTENTE (S)
ASSISTANT (S)
Luis Sigler
Francisco Arroyo
Jason Heckathorn,
Julia Heckathorn
Sebastian Castillo

IDENTIFICATION
I.D.

COLECTA OBSERVACION
COLLECT OBSERVATION
MARCADO OTROS
MARKING OTHERS

COLECTA

INSTITUCION QUE RESPALDA LA INVESTIGACION
INSTITUTE SUPPORTING THE RESEARCH
The Dallas World Aquarium

OBJETIVO
PURPOSE
Iniciar estudios de adaptación en cautiverio con miras a conformar una población ex situ. Los mismo se exportaran al DWA y un par quedara en las instalaciones de un Zoológico en Panamá. Este recurso es de patrimonio de la República de Panamá y en Cualquier momento puede ser solicitado por su país de origen.

LUGAR DEL ESTUDIO
STUDY
Bocas del Toro, Escudo de Veraguas.

NOMBRE COMUN COMMON NAME	NOMBRE CIENTÍFICO SCIENTIFIC NAME	CANTIDAD QUANTITY	DESCRIPCIÓN DESCRIPTION
Perezoso	Bradypus pygmaeus	10	Individuos vivos

DURACION DEL ESTUDIO
TIME OF STUDY
09-08-2013 Hasta 09-11-2013

ESTE PERMISO ES EMITIDO POR:
THIS PERMIT IS ISSUED BY:

Dirección de Áreas Protegidas y Vida Silvestre

FECHA: 09-08-2013

ING. IBELICE AÑINO N.
Directora de Áreas Protegidas y Vida Silvestre

Elaborado por: Alexander Montero

FIRMA RESPONSABLE Y SELLO

TODO INVERSTIGADOR DEBE: 1. REPORTARSE A LA REGION CORRESPONDIENTE ANTES DE INICIAR SU TRABAJO; 2. PORTAR EN TODO MOMENTO EL PERMISO CORRESPONDIENTE; 3. ENVIAR INFORME DE COLECTA A LA ANAM; 4. ENTREGAR MUESTRAS DE CADA ESPECIE A LA UNIVERSIDAD DE PANAMA; 5. ENVIAR A LA ANAM, A MAS TARDAR EN UN AÑO, AVANCE O INFORME FINAL DEL ESTUDIO, CON RESUMEN EN ESPAÑOL DE LO CONTRARIO NO SE LE OTORGARA OTRO PERMISO.

EVERY RESEARCHER MUST: 1. REPORT TO THE NEAREST ANAM OFFICE BEFORE START WORKING; 2. CARRY THE PERMIT AT ALL TIMES; 3. SEND A REPORT OF COLLECTED MATERIAL TO ANAM; 4. SEND SAMPLES OF REPRESENTATIVE MATERIAL TO THE UNIVERSITY OF PANAMA; 5. SEND AN INTERMEDIATE OR FINAL REPORT TO ANAM WITHIN A YEAR, WITH A SPANISH SUMMARY. NO MORE PERMITS WILL BE ISSUED TO THOSE WHO DO NOT COMPLY WITH THESE REGULATIONS.

Max-Planck-Institut für Ornithologie
Max Planck Institute for Ornithology

October 16, 2013

Ms. Kristin L. Vehrs
Association of Zoos & Aquariums
8403 Colesville Road, Suite 710
Silver Spring, MD 20910-3314

Dear Ms. Vehrs,

Since the attempted exportation of the Critically Endangered pygmy sloth (*Bradypus pygmaeus*) on September 9th, members of the international scientific community have been working hard to gather the facts surrounding the situation, and to present them openly, without bias, and with the utmost regard to transparency. Although many of us have been working on the biology, ecology, and conservation of pygmy sloths for years, none of us were aware, consulted, or involved whatsoever with Dallas World Aquarium and Aviarios del Caribe Sloth Sanctuary's plan to remove 10 pygmy sloths from the island of Escudo de Veraguas for *ex-situ* husbandry and study. There was no prior discussion of any such plan, nor was any proposal circulated for review or comments, nor was any attempt made to notify any of us about their plans in advance. While we were shocked at the initial news that such an attempt had been made to remove these fragile animals to a foreign location in the name of science, we have since become very concerned about the complete lack of transparency and unwillingness to discuss with us their motives, scientific rational and justification, and ethical standards which they were operating under. Moreover, there has been a significant amount of conflicting and contradictory information being presented on behalf of the involved parties, much of which is not based on any facts or simply false. We would like to clarify the following points that were made in the letter from Judy Arroyo addressed to you (and the AZA) dated September 20th (available online at http://mongabay-images.s3.amazonaws.com/13/DWA_A-letter-to-Ms-Vehrs.pdf), as well as some points made in the field report by Marcelo Espinoza and Rebecca Cliffe (available online at http://mongabay-images.s3.amazonaws.com/13/DWA-Pygmy-sloth-field-report.pdf):

- Although Aviarios del Caribe claims that they are the only facility to maintain a sustained population of *Bradypus* sloths, this is incorrect. There are several additional rescue and rehab centers that specialize specifically on sloths (Fundación AIUNAU in Colombia, Green Heritage Fund in Suriname, as well as several other well-known sloth rescue and rehabilitation centers in Costa Rica). Mrs. Arroyo and members of her sloth center are well aware of the existence of these centers, all of which have rescued and successfully reintroduced many three-toed sloths, including hand-reared individuals. It is misleading to omit reference to these additional experts on sloth husbandry, as they have a great deal of knowledge relevant to this matter, yet were not consulted.

- Mrs. Arroyo mentions "several, well known institutions sit by idly, with no cohesive or contingent conservation plan". May we point out that this is a clear example of the lack of communication between DWA / Aviarios and our represented institutions - which is unilateral, as all other institutions have repeatedly tried to communicate with DWA / Aviarios, but to no avail. In fact, these institutions have been and are currently carrying out a comprehensive, community-integrated conservation plan. For example, the Zoological Society of London is supporting and funding an EDGE fellow, Panamanian veterinarian Dr. Diorene Smith, who is doing excellent, extensive work throughout the local community. Diorene has ensured that all stakeholders were aware of her project from the start, informing ANAM, the president and members of the Ngöbe - Buglé congress, the Mayor of Kusapin, local community members, and both local and international scientists in order to discuss the long-term conservation of pygmy sloths and Escudo as a whole. Unfortunately, the recent actions of DWA / Aviarios have put this internationally recognized and transparent conservation program at risk, as the local community is now on heightened alert for foreigners claiming to be there to “help the sloths.” Moreover, this incident will likely have a lasting impact on other, non-sloth related science and conservation in the region. The repercussions of these recent actions are not to be underestimated, and will likely be profound within the community for an extended period.

- Genetic analyses to estimate levels if genetic diversity and demographic parameter to confirm that *B.pygmaeus* is a true species have been done by several labs, and a corresponding manuscripts is currently being submitted (Dr. Nadia Moraes-Barros (Brazil). These studies are done with a minimal amount of genetic sample (i.e. hair). As such, there is absolutely no justification to keep pygmy sloths in captivity to perform genetic analyses. A simple hair sample is sufficient.

- There is absolutely no evidence to claim an "inexplicable and rapid decline in pygmy sloth numbers." We do now know the origin of the population estimates cited by Mrs. Arroyo (“Daryl approached me years ago about the precarious position of the Pygmy Sloth in Panama, when purportedly there were over 500 on the island.”), as population estimates have always been lower than this number. Neither the IUCN Red List of Threatened Species nor the ZSL website state that the population ever consisted of 500 animals, but rather that there are *less than* 500 individuals without providing an exact number due to the lack of exhaustive field surveys. Three mangrove surveys of pygmy sloths, from 2011, 2012, and 2013, found a nearly identical population estimate (~80) for sloths in the mangroves (Kaviar *et al* 2012; Turner et al *in prep*). These studies all admitted a bias for only sampling the mangrove patches of the island, which consist of less than 3% of the island’s landmass, and acknowledged they were likely an underestimate. Recent work has found pygmy sloths in non-mangrove habitat (including observations by the DWA / Aviarios) and locals on the island have reported seeing pygmy sloths on parts of the island far away from any mangroves. Surveying a cryptic and largely sedentary mammal is difficult in tropical rainforests, as typical means like camera trapping are ineffective. While searching for radio-collared sloths in the forest with an antenna, sloths are typically visible less than 20% of the time. Currently we are discussing a population model for the island where we can overlay botanical data from the island with known sloth densities in other forests of Panama. A scientific approach to the whole island is needed to accurately assess the overall population size.

- Initially, hunting of pygmy sloths was listed as a *possible* threat to their numbers, as local indigenous camp out on the island periodically throughout the year while fishing. This was based on a few anecdotal hearsay reports from locals, but nothing conclusive. Social data collected during numerous interviews and meetings with locals both on the island and on the mainland has so far revealed that hunting pygmy sloths is not an immediate threat. No evidence of any hunting pressure on pygmy sloths has been found, and the locals were generally taken back that anyone would imply they were doing so. Mrs. Arroyo, Dr. Espinoza, and

Ms. Cliffe cite hunting pressure from up to 1200 locals as the driving force for the imminent collapse of the species, yet are unable to produce any evidence to support such a claim. Many of us have been working on Escudo for years, and know that there is no way 1200 people have ever been on the island at once. Both the population decline and the claim that fishermen are eating sloths (instead of eating their catch) are wholly unsubstantiated scientifically, and Diorene's work will continue to address this and other potential threats directly with the great indigenous community.

- The Dallas World Aquarium informed ANAM that after a March census on Escudo, there remained only 30 pygmy sloths. The Director of ANAM reported in a TV interview that after receiving this data, and understanding that hunting was primarily to blame, ANAM decided to act in the best interest of the sloths, and allowed DWA to take some sloths back with them to Dallas, where they could be bred. Acknowledging that such a breeding facility does not exist in Panama, ANAM allowed this foreign export under the assumption that the captive bred offspring would be introduced back to the island. This information was further reported in the local newspaper, Panama America.

  In their own field reports, DWA and their associates acknowledge that although they counted 30 sloths in their March fieldwork lasting only 2 days, "There was no attempt to conduct a comprehensive survey." This misrepresentation of the population estimate is critical, and is being widely used to highlight the impending collapse of the species. However, no such data exists, even when reading the group's own field reports.

- DWA / Aviarios is claiming their actions are in the best interest of the species survival, and that captive pygmy sloths in Dallas would form a contingency / breeding population for a possible reintroduction to the island. They do not account for the additional pygmy sloths collected which were to remain in Colon, Panama. While in principle such a breeding population sounds like a positive step towards species survival, several significant downsides have yet to be addressed by the group. Although DWA currently maintains a small number of three-toed sloths in Dallas, they experience significant mortality with imported three-toed sloths (an estimated overall death rate of >85%). Records show that up until a few years ago, only 1 of 16 imported sloths survived at their facility.

Moreover, according to Luis Sigler at DWA, the only three-toed sloth born in captivity died after 7 months, and was conceived in the wild, There is no verifiable record of any sloth being conceived, born, and survived in captivity, let alone released back into the wild. Centro de Reabilitação Reserva Zoobotânica, a sloth rescue center in Brazil, successfully reintroduced 60% of received sloths (B. torquatus and B. variegatus) after receiving them. Very few sloths remain in their center for more than a few weeks, as maintaining them artificially results in their eventual mortality. Professionals working in Brazilian Zoos and universities report that Bradypus sloths cannot be kept in captivity for more than 1.5 years.

Certainly with any of our institutes, a rigorous and peer-reviewed animal care committee would have to approve any such captive breeding program. Given the high rate of mortality in sloths outside the tropics, and the lack of proof that three-toed sloths can even be bred in captivity (within or outside the tropics), it is highly doubtful that any of our organizations would have supported such a high-risk program. Moreover, promising the local community and wildlife officials that by removing a few sloths from the island they will eventually benefit by receiving captive bred replacements is severely misleading on behalf of the group.

- Although DWA / Aviarios had the permission from the local mayor of Kusapin, they did not notify or consult the local indigenous congress (Congreso Regional Ño Kribo), which is responsible for such matters. Their president, Willy Jiménez, has sent an official letter to ANAM, stating that the Congress does not support the removal of any pygmy sloths from the island, and is demanding a formal explanation from ANAM, as well as the suspension of all further activities on Escudo. Escudo de Veraguas is a national marine protected area, but its stewardship is shared by the indigenous territory. The support of the regional congress is critical for our conservation program, and unfortunately DWA / Aviaros's action has jeopardized any future conservation work on the island.

We would like to stress that collectively, we are committed to continuing to providing accurate, scientifically sound information to the local community, regional and national government agencies, and the general public about the current status of the pygmy sloth, as well as information about the conservation work being conducted by our international consortium of scientific and conservation experts. We are committed to institutional transparency, and have been and will continue to share all related information with any interested parties.

Sincerely,

Dr. Bryson Voirin
Scientist, The Max Planck Institute, Germany
Research Associate, Smithsonian Tropical Research Institute, Panama

Mariella Superina, Dr.med.vet., Ph.D.
Chair, IUCN/SSC Anteater, Sloth and Armadillo Specialist Group

Dr. Diorene J. Smith C. Veterinarian Doctor, EDGE Fellow

Tinka Plese, MSc
Director, Foundation AIUNAU, Colombia

Lenin Riquelme Quintero, MSc Tropical Conservation and Development
Fundación CONAVI, Panama

Monique Pool, Chairman, Green Heritage Fund Suriname

Dr. Craig Turner, MIEEM FRGS FLS
Consultant and Co-Founder, Wychwood Environmental

Matthew C. Manupella

Matthew C Manupella,
Community Environmental Conservation Expert,
US Peace Corps, Panama

Ryan K Tisdale, US Fulbright Scholar and Biologist
The Max Planck Institute, Germany

Nadia Moraes-Barros, PhD
Associate Researcher, CIBIO/InBIO, Laboratório Associado
Centro de Investigação em Biodiversidade e Recursos Genéticos
Campus Agrário de Vairão
Universidade do Porto, Portugal
Member, IUCN/SSC Anteater, Sloth and Armadillo Specialist Group

Ana Salceda, M.S.
Director, Founder, BelugaSmile
Wildlife filmmaker