



# The Bushmasters (*Lachesis* spp.): Queens of the Rainforest. An Overview of the Taxonomy, Distribution, Natural History, Lore, and Conservation of the Largest Vipers in the World

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**Abstract.**—We herein provide an overview of the bushmasters (*Lachesis* spp.), the longest vipers in the world. We address taxonomy, distribution, etymology, lore, natural history (reproduction, defense, behavior, activity, prey and predators), and, for the first time, conservation issues, suggesting that *Lachesis melanocephala* is a Critically Endangered species under IUCN criteria.

**Key words:** Bushmaster, Amazon, Central America, rainforest, Neotropics, Viperidae, Crotalinae.

**Resumen.**—Proporcionamos aquí una descripción general de las verrugosas (*Lachesis* spp.), las víboras más largas del mundo. Abordamos su taxonomía, distribución, etimología, folklore, historia natural (reproducción, defensa, comportamiento, actividad, presas y depredadores) y, por primera vez, su conservación, sugiriendo a *Lachesis melanocephala* como una especie en peligro crítico según los criterios de la UICN.

**Palabras clave:** Amazonas, América Central, bosque primario, Neotrópico, Viperidae; Crotalinae.

Snakes have fascinated and inspired fear since ancestral primates first encountered ophidian predators (Isbell 2006), and the venomous species are arguably the most intriguing of all. Inhabiting the last remnants of primary rainforests from Nicaragua to Bolivia, the magnificent bushmasters (*Lachesis* spp.) incite mystery and lore while much remains unknown about their natural history.

## Bushmasters, *Lachesis* Daudin 1803

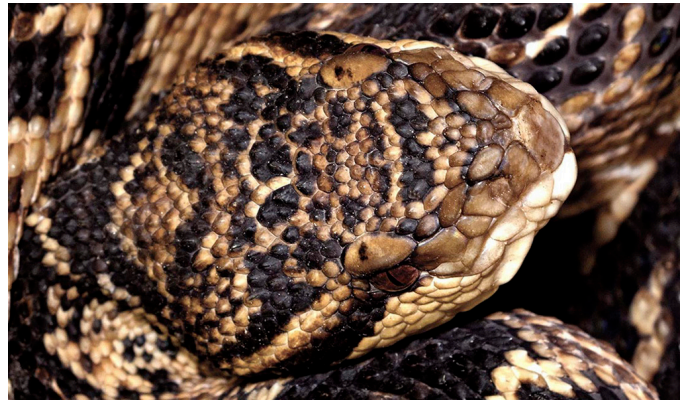
With total lengths that can exceed 3 m, bushmasters are the largest vipers in the world and the longest venomous snakes in the Americas. In cross-section, the body can be rounded or triangular and relatively compressed laterally. The skin is coarsely rough, with dorsal scales bearing extended knoblike



A Black-headed Bushmaster (*Lachesis melanocephala*). Acrylic and ink by Mexican artist René Villanueva Maldonado, whose eighteenth-century style is reminiscent of plates in classic works like those of Albertus Seba. The original depicts the snake at life size.



**Fig. 1.** Knoblike scales of a Central American Bushmaster (*Lachesis stenophrys*). Photograph by Cristian Porras (CRWild).



**Fig. 2.** Dorsal view of the head of a South American Bushmaster (*Lachesis muta*) from Loreto, Peru. Photograph by William W. Lamar.



**Fig. 3.** Eye of a Chocóan Bushmaster (*Lachesis acrochorda*) from Morromico, Chocó, Colombia. Photograph by José Vieira (Tropical Herping).



**Fig. 4.** Terminal spike-like scale on the tail of a South American Bushmaster (*Lachesis muta*) from Camamu, Bahía, Brazil. Photograph by Marco A. de Freitas.

keels (Fig. 1) that collectively resemble the surface of a pineapple (from which common names are derived in many countries). Heads bear small protruding scales (Fig. 2) and small, dark eyes are typical, although they vary in color depending on species and geographic area (Fig. 3). The unique scale at the tip of the tail is spike-like and as long as the preceding 3–4 subcaudal scales (Fig. 4). Fangs in large individuals can be as long as 5 cm (Fig. 5). The hemipenial morphology is conservative. The ground color of all species varies from tan to yellow to orange on which is superimposed a pattern of inverted black triangles; tails in juveniles can be pink to orange. Bushmasters are the only oviparous Neotropical viperid. Females coil around clutches of 6–20 large eggs inside dens until they hatch. Hatchlings 34–54 cm in total length appear to remain in dens for months (Campbell and Lamar 2004).

The genus *Lachesis* currently comprises four species (see the species accounts at the end of the article). The bushmaster was described initially by Carl von Linné (1766) as *Crotalus mutus* (“silent rattlesnake”). Daudin (1803) proposed the genus *Lachesis* for Linnaeus’s *C. mutus* (as *Lachesis mutus*) but Schinz (1822) noted that *Lachesis* was a feminine noun and

appropriately used *Lachesis muta*. Until recently, *Lachesis* was regarded as monotypic, with *L. muta* containing the subspe-



**Fig. 5.** Sheathed fangs of a captive Central American Bushmaster (*Lachesis stenophrys*). Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild), courtesy of Quetzal Dwyer (Parque Reptilandia, Costa Rica).



cies *L. m. melanocephala* Solórzano and Cerdas 1986, *L. m. muta* (Linnaeus 1766), *L. m. rhombeata* Wied-Neuwied 1824 (see also Hoge et al. 1978), and *L. m. stenophrys* Cope 1876. Zamudio and Greene (1997) elevated *L. melanocephala*, and *L. stenophrys* to specific status but retained *L. m. rhombeata* as they could not test it.

Populations west of the Andes in South America and nearby Panama were regarded as *L. stenophrys*. Campbell and Lamar (1989) noted that the status of snakes from eastern Panama, Pacific Colombia and Ecuador, and the inter-Andean valleys of Colombia had never been determined satisfactorily. Ripa (1999) considered these snakes sufficiently divergent to warrant the status of a new species. He was preparing a formal description but it was never published. Ripa (2004) resuscitated the name *Botrops [sic] acrochordus* García 1896 as *Lachesis acrochorda* to accommodate those populations west of the Andes in Colombia, Ecuador, and eastern Panama, but Campbell and Lamar (2004) made the new combination official. Employing morphological characters, Fernandes et al. (2004) also concluded that *L. melanocephala* and *L. stenophrys* warranted recognition as species but synonymized *L. m. rhombeata* into *L. muta*. Additionally, in a study of snake venomomics across *Lachesis*, Madrigal et al. (2012) revealed a close relationship between *L. stenophrys* and *L. melanocephala* venoms and supported the elevation of *L. acrochorda*.

In the most recent genetic phylogenies of the Viperidae (Alencar et al. 2016; Zaher et al. 2019), *Lachesis* appeared as basal in the subclade *Lachesis* + *Ophryacus* + *Mixocoatlus* + *Bothriechis* and sister to the subclade *Agkistrodon* + *Sistrurus* + *Crotalus* in the subfamily Crotalinae). The common ancestor of *Lachesis* appeared around 7 mya, while the Centroamerican clade (*L. melanocephala* + *L. stenophrys*) diverged about 3 mya and the South American clade (*L. acrochorda* + *L. muta*) about 1 mya, suggesting a Mesoamerican origin of the genus, contrary to the idea that *Lachesis* had a South American origin (Ripa 1999). Unfortunately, neither Alencar et al. (2016) nor Zaher et al. (2019) examined specimens from the Brazilian Atlantic forest; consequently, the synonymy of Fernandes et al. (2004) must still be tested.

**Etymology:** The generic name *Lachesis* (pronounced Lá-kē-sis) was coined by Daudin (1803) in reference to Lachesis, the second of the three Greek fates. Lachesis was the apportioner who decided how much time was allotted to each person or being (Graves 2017), an obvious allusion to the potentially fatal bite of this snake.

**Lore:** Garcia (1896) recorded many legends believed by locals in western Colombia. One described an exaggerated abundance of bushmasters in the forests, where they often call like hens. These snakes snore during the day as they appear to

sleep while actually stalking travelers along the paths. The claw-like tip of the tail was used to dig into trees so the snake could pull itself up and strike a victim with all its force. If a person stands close enough to a snake, then a strike is imminent; if the person has no weapons, he will need to strangle the snake in order to kill it before it can coil around him.

Eatherly (2015) relayed stories based on R.R. Mole's conversations with Raymond Ditmars on Trinidad. Snakes would be attracted by the light of a campfire, then strike their victims, paralyzing them, and leaving them to be eaten alive by ants and worms; or they would sting people to death with the spikes on their tails. These snakes were considered supernatural, able to inflict deadly bites even after death. If one is killed, its mate will seek revenge. Similarly, gold miners in Guayanese Venezuela indicated that bushmasters were attracted to light and would follow and even attack the beam of a flashlight (CBA, pers. obs.). Similar stories have been related by local people in Ecuador and Colombia to the authors and colleagues.

Bushmasters often are thought to be extremely aggressive and chase people; however, the authors could not find anyone who could corroborate this claim. Ripa (1999) wrote that he was pursued by a male *L. melanocephala* on the Osa Peninsula in Costa Rica, but a conversation with QD determined that this was not true. Steffen Reichle, a German herpetologist living in Bolivia, described a bushmaster in the Chiquitania that he was photographing alongside a dirt road that became quite agitated and tried to bite the tires of a slowly passing trailer (S. Reichle, pers. obs.) We are uncertain how *Lachesis* earned this reputation, as we perceive it to be one of the calmest of the Neotropical vipers (see also Solórzano 2004). Even when awake and alert, it strikes or pursues an aggressor only in exceptional situations or as a defensive response (de Plecker and Dwyer 2020). For example, during recent encounters with three different individuals of *L. melanocephala* on the Peninsula de Osa in September 2020 (CBA, pers. obs.), all were very alert but calm and not at all aggressive. Compared to *L. stenophrys*, de Plecker and Dwyer (2020) did note that *L. melanocephala* is more nervous and alert, elevating its head and directing it toward a perceived threat. QD shipped several young Black-headed Bushmasters in individual cages to the late Dean Ripa in the mid 2000s. All had fed before shipping. After arrival at the destination some 48 hours later, those that had defecated were very aggressive, whereas those with clean cages were calm (de Plecker and Dwyer 2020). Maybe the reason why Ditmars and others thought that bushmasters were aggressive was that they were dealing with snakes that had been caged and lying in their feces while en route for weeks on their way from Trinidad to New York.

The Chaima natives from the area surrounding the Cueva del Guácharo in the Venezuelan state of Monagas considered bushmasters the cave's guardians (Civrieux 1998) that detected

hunters while scouting the forest, pursuing them by biting their own tails and rolling like a wheel down the mountain.

The Shuar natives from Amazonian Ecuador believed that Yamung, the queen of the night (as they refer to *Lachesis muta*) is the only entity that can repel Ibiash, a demon of the night, and the Shuars therefore do not kill bushmasters (D. Núñez, pers. comm.). However, modern Shuars readily kill them when encountered.

Although snakes cannot emit sounds other than hissing or by mechanical means (e.g., rubbing their skin against itself or another surface or the rattling of rattlesnakes), Ripa (2001) stated that bushmasters sing or produce non-hissing sounds to communicate with one another or to attract prey, specifically describing a shrill, rapidly descending whistle-like sound, which he failed to record. A possible explanation proposed by Campbell and Lamar (2004), recalling information from Ulrich Kuch about captive bushmasters emitting a whistling sound, was that the whistle was attributable to respiratory infections. Most likely, anything heard and attributed to the snakes originated from another animal, like a frog, gecko, insect, or nocturnal bird.

In Bahia (and probably the rest of Brazil), bushmasters are commonly called “Pico de Jaca,” because the texture of the skin resembles that of Jackfruit (*Artocarpus heterophyllus*), a common introduced fruit. People also say that they smell like jackfruit (DAF, pers. obs.).

Lima da Silva et al. (2019), based on a series of interviews with natives in the Upper Juruá Region of the Brazilian Amazon about perceptions of dangerous snakes, revealed that the South American Bushmaster is considered the most venomous, although the “Jararaca” (*Bothrops atrox*) is the most feared due to its abundance and the number of fatal encounters.

**Defense:** The only defensive displays we have observed, which also were described by Ditmars (1910) and Greene (1983), in *L. muta*, *L. melanocephala*, and *L. stenophrys* are a sudden coiling into an S-shaped pose with the head not much higher than the rest of the body, and a sound produced by the tail vibrating in dry leaf litter (the latter not observed in *L. melanocephala* in nature). The tail-vibrating behavior produces a sound reminiscent of that made by rattlesnakes. Barrio-Amorós (2005) and Barrio-Amorós et al. (2011) described this behavior by a *L. muta* in Triunfo in southeastern Venezuela, which also is evident in a video made by Pedro Gómez Murillo (<https://www.youtube.com/watch?v=4ugf6feEyY>) of another *L. muta* in Villa Tunari, Cochabamba, Bolivia. Valencia et al. (2016) described a defensive behavior involving the elevation of the anterior body while vibrating the tail in both *L. acrochorda* and *L. muta*.

However, in our combined experience, the only strike observed in natural conditions by any of the four species was

JC’s claim that he saw a *L. stenophrys* striking at an unaware CBA. Valencia et al. (2016) reported that captive female *L. acrochorda* and *L. muta* excreted small amounts of bloody fluid and that male and female *L. muta* generated an offensive odor, which also had been mentioned by Beebe (1946).

Although generally inoffensive (see comments in the previous section on lore), males engaged in reproductive behavior become aggressive toward other males, with which they engage in ritual combat (de Plecker and Dwyer 2020), but mating males also are aggressive toward females during courtship (de Plecker and Dwyer 2020; GC, pers. obs.). In addition, GC has repeatedly observed aggressive responses of captive males toward hot objects (like cameras and lights) during courtship. One male *L. stenophrys* in the breeding program at the Instituto Clodomiro Picado (ICP) aggressively attacked the flash of a camera during mating, striking it repeatedly until it was turned off. This could explain the origin of tales describing bushmasters being attracted to light (although most probably to heat) (see the previous section on lore).

In 1,200 h of fieldwork involving South American Bushmasters in Brazil, DAF has observed only two strikes, perhaps attributable to the removal of structure in which the snakes had sought refuge. Also in the field, Konrad Mebert (pers. comm. to DAF) occasionally approached to within 40 cm of snakes that made no attempt to strike, despite being awake and active. In addition to a typically calm temperament, we suggest that snakes that interact frequently with humans (such as captives) become conditioned to their presence and no longer associate them with risk, although new captives can and sometimes do react aggressively toward keepers (C. Porras, pers. comm.). Generally, however, sudden aggressive behavior in normally quiet individuals could merely be a feeding response (de Plecker and Dwyer 2020).

**Tail-luring:** No published reports document young snakes using their pinkish tails to attract prey. In September 2017, JC and CBA filmed a calm adult female *Lachesis stenophrys* (Fig. 6) making slow luring motions with her tail (<https://www.youtube.com/watch?v=DJ2Jtm5c7qo>). Two days later, we were informed by J. Solís, a naturalist guide in the area, that two other snakes (probably males) were seen in the exact same area. Perhaps those males were nearby because the female had been releasing pheromones to attract a potential mate (see also the Activity and Reproduction section below).

**Reproduction:** Bushmasters are the only oviparous pitvipers in the Western Hemisphere (Amaral 1925), laying 6–20 (usually 7–10) eggs (Campbell and Lamar 2004). Relatively little is known about reproductive activity, with most of the available information collected from captive snakes (see below). The few data pertaining to snakes in nature are in studies by





**Fig. 6.** An adult female Central American Bushmaster (*Lachesis stenophrys*) tail-luring. Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild).

Alves et al. (2014), who addressed reproduction of *Lachesis muta* in the Brazilian Atlantic forest; Fuentes and Corrales (2016), who presented data on reproduction of *L. acrochorda* in Panama; and an unpublished account by Héctor de Burgos (pers. comm.), who found a clutch of seven *L. muta* eggs inside a hollow log near Iquitos, Peru, on 20 November 2018. Also inside the same log were seven older hatched eggs presumably from another clutch. He incubated the fresh eggs and seven hatchlings emerged on 1 January 2019. All were healthy and eating well one year later.

Successful *ex-situ* reproduction has been reported in all four species of *Lachesis*. Ripa (1994), Chacón and Valverde (2004), Corrales et al. (2014), and Camina et al. (2020) documented reproduction in *L. stenophrys*; Ripa (1994) and de Plecker and Dwyer (2020) in *L. melanocephala*; Boyer et al. (1989), Corrales et al. (2016), and de Souza (2007) in *L. muta*, the latter on animals from Brazilian Atlantic populations formerly assigned to *L. m. rhombeata*; and Henao-Duque and Corrales (2015) and Fuentes and Corrales (2016) in *L. acrochorda*.

The serpentarium of the ICP is currently working on a display with cameras in each breeding enclosure, allowing the staff a non-invasive view of the reproductive behavior of *L. stenophrys*. In videos of the most recent breeding attempts by *L. stenophrys*, GC repeatedly noted tail-luring behavior in four different females, indicating a receptive response during the presence of a male (see above about tail luring). This behavior

also was observed once in *L. melanocephala* at the same facility. In order to stimulate a male, he would be introduced into the enclosure of a female after she had shed. The male would then take the initiative, sliding onto the coiled female, probably encouraging her tail-luring motions. This might stimulate the female to release pheromones into the environment and lead to courtship, during which the male is normally very aggressive. He will dominate the female with rough movements, rubbing his dorsal scales against those of the female, and later embracing the female's vent with his tail and moving it up and down. This behavior triggers a response by the female, stimulating her to mate (Corrales et al. 2014, 2016). Turner (1997) also noted violent breeding behavior in the same species, during which a male courts the female by writhing about the enclosure on its dorsum and actually flipping the female over in his efforts.

The period from mating until ovipositioning for bushmasters has been reported by Ripa (1994) and Corrales et al. (2016) as 95–101 days for *L. melanocephala*, *L. stenophrys* and *L. muta*. Various techniques are used to stimulate breeding in adult pairs before they are put together, and these require keeping them together for at least two months. Since bushmasters can mate several times during this process, without direct observation, it is impossible to know exactly when the female becomes gravid and to accurately calculate the time until eggs are laid. In 2018, the ICP serpentarium staff bred two female *L. stenophrys* with the same male, recording the

whole process on camera. The two females laid eggs 147 and 148 days later (GC, unpubl. data). Although several courtships attempts were recorded on camera, only one copulation event by the male with each female was recorded. Camina et al. (2020) reported a span of 141 days in *L. stenophrys* from the first copulation (which is not guaranteed to be the right one) until egg deposition.

The incubation time reported in captivity for all species of *Lachesis* ranges from 74 to 79 days (Switak 1969; Boyer et al. 1989; Ripa 1994, 1999; Eisele 2009; de Souza 2007; Corrales et al. 2014, 2016; Fuentes and Corrales 2016; Camina et al. 2020), extended to 65–98 in *L. melanocephala* (Ripa 1994; de Plecker and Dwyer 2020). New data for *L. stenophrys* at the ICP report 83 days of incubation at a temperature range of 24–28 °C and relative humidity of 85–95% (GC, unpubl. data). At Parque Reptilandia, which is situated within the range of the species, de Plecker and Dwyer (2020) reported that reproductive activity for *L. melanocephala* was highest in October, although ritual combat and/or mating can extend into January. Eggs are laid 138–144 days after mating and incubation lasts 74–98 days. Hatching usually coincides with the beginning of the rainy season (May–July), which offers an abundance of possible prey for young snakes.

After two years unsuccessfully attempting to breed *L. muta* at the Dallas Zoo, adjustments in temperature and humidity levels eventually led to successful reproduction (Boyer et al. 1989), suggesting that environmental conditions are critical. However, no definitive evidence suggests that reproduction in bushmasters is seasonal. In Venezuela, Corrales et al. (2016) found no well-defined breeding season for *L. muta* and hatchlings can be found at different times of the year. In Brazil, de Souza (2007:41) reported that “there is no such thing as a ‘breeding season’ for *L. m. rhombeata* in the wild.” Bushmasters do appear to be sexually stimulated

by cold fronts and storms that trigger reproductive behavior rather than a specific period of fertility (Ripa 1994; Boyer et al. 1989; de Souza 2007; Turner et al. 2008; Henao-Duque and Corrales 2015; Corrales et al. 2016; Fuentes and Corrales 2016). However, at least in Costa Rica, breeding activity appears to peak during the rainy season in both *L. stenophrys* and *L. melanocephala* (CBA, GC, QD, pers. obs.).

**Juveniles:** Hatchlings probably stay underground for weeks or even months in the burrow where the eggs had incubated (Antonio Suzart Argolo and Carlos Coronado, pers. comm. to DAF) and we know little about their activities early in life. Bert Jonckheere encountered a young *L. stenophrys* (Fig. 7) at 0945 h on 14 January 2016, another at 1845 h on 23 December 2015, and yet another at 1035 h on 30 December 2016 at the same locality in southern Caribbean Costa Rica. In Panama, Edgar Pérez found a young snake in Parque Nacional Chagres (Fig. 8). Carlos Martínez Rivera, observed a young *L. acrochorda* (Fig. 9) coiled during the day in the Canandé Forest Reserve of the Ecuadorian Choco and Abel Batista saw another young *L. acrochorda* in Panama (Fig. 10). In Municipio Caripe, Monagas, Venezuela, DAF reported eight *L. muta* hatchlings on different dates at an elevation of about 1,000 m asl in various terrestrial microhabitats (under logs, rocky substrate, buttresses, and leaf litter) (Fig. 11). Steffen Reichle photographed a young snake in the transition area between rainforest and dry forest in Chiquitania, Bolivia (Fig. 12). Subadults about 1 m in length are even more rarely encountered. Omar Entiauspe saw one at Bahia, Brazil (Fig. 13) and Marisa Ishimatsu photographed another subadult near Iquitos, Peru (Fig. 14). We are not aware of any juvenile *L. melanocephala* photographed in nature, but a very young individual about 50 cm in length hatched at Parque Reptilandia, Costa Rica (Fig. 15).



**Fig. 7.** This juvenile Central American Bushmaster (*Lachesis stenophrys*) from southern Costa Rica was found during the morning. Photograph by Bert Jonckheere.



**Fig. 8.** This juvenile Central American Bushmaster (*Lachesis stenophrys*) from Parque Nacional Chagres, Panama, was encountered around midnight in March 2011. Photograph by Edgar Pérez.





**Fig. 9.** This juvenile Chocoan Bushmaster (*Lachesis acrochorda*) from Canandé Reserve, Esmeraldas, Ecuador was found during the day. Photograph by Carlos Martínez Rivera.



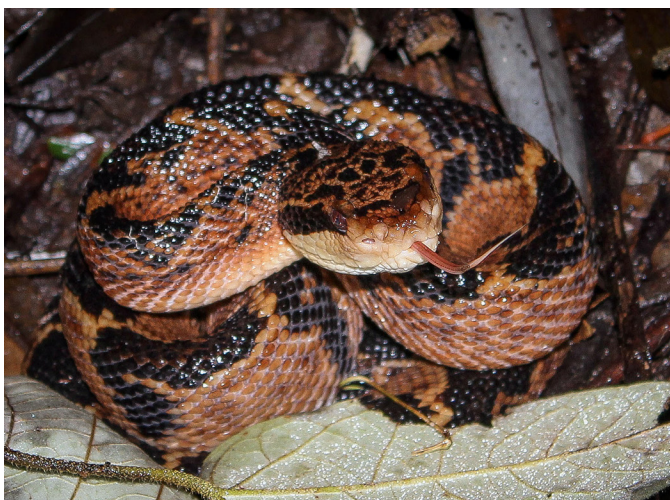
**Fig. 10.** This juvenile Chocoan Bushmaster (*Lachesis acrochorda*) was found in the middle of a forest path at midday in Comarca Kuna de Wargandi, Panamá. Photograph by Abel Batista.



**Fig. 11.** This juvenile South American Bushmaster (*Lachesis muta*) at the entrance of a den in Municipio Caripe, Monagas, Venezuela, measured 52 cm. Photograph by Diego A. Flores.



**Fig. 12.** A juvenile South American Bushmaster (*Lachesis muta*) about 60–70 cm in length from Chiquitania, Bolivia. Photograph by Steffen Reichle.



**Fig. 13.** A juvenile/subadult South American Bushmaster (*Lachesis muta*) about 90–100 cm in length from Itacaré, Bahia, Brazil. Photograph by Omar Entiauspe.

**Use of mammalian burrows:** Bushmasters are known to spend time in subterranean cavities or burrows (Fig. 16) made by Agoutis (*Dasyprocta* spp.), Pacas (*Cuniculus paca*), and Armadillos (*Dasytus novemcinctus*) (GC, DAF, pers. obs.), information reinforced by frequent reports from hunters who have found bushmasters guarding eggs in mammal burrows (pers. comm. to CBA, GC, and DAF). Subterranean cavities provide suitable conditions for egg incubation, and maternal guarding is an important response against active mammalian burrowers such as armadillos, which are known to prey on snake eggs in the wild (Ditmars 1910; Mole 1924; Ripa 1994; Wainwright 2002; Campbell and Lamar 2004; de Souza 2007; Turner et al. 2008; Henao Duque and Corrales 2015; Fuentes and Corrales 2016). Nevertheless, we know that bushmasters share burrows with armadillos, agoutis, and Pacas, sometimes simultaneously (DAF, pers. obs.). Dean Ripa (pers. comm. to GC) stated that two hunters digging





**Fig. 14.** A subadult South American Bushmaster (*Lachesis muta*) about 100 cm in length from near Iquitos, Loreto, Peru. Photograph by Marisa Ishimatsu.



**Fig. 15.** A young Black-headed Bushmaster (*Lachesis melanocephala*) hatched at Parque Reptilandia, Costa Rica. Photograph by Roel de Plecker.

a Paca den on the Osa Peninsula found three coiled Black-headed Bushmasters (*L. melanocephala*), but provided no evidence of this occurrence. On 3 April 2014 in the area surrounding Corcovado National Park on the Osa Peninsula of Costa Rica, two hunters killed two female Black-headed Bushmasters guarding 22 eggs, likely from at least two clutches, in a den (GC, pers. obs.).

**Activity:** Bushmasters are almost entirely nocturnal and are rarely active during the day (Campbell and Lamar 2004), when individuals can be seen coiled and well-camouflaged, presumably resting and waiting for nightfall before resuming activities like hunting and searching for mates. One female *L. melanocephala* on the Osa Peninsula of Costa Rica was

seen resting every day for at least two months (May and June) without entering a den (E. Castro, pers. comm.). A recently encountered *L. melanocephala* on the Osa Peninsula remained in the same area five days, moving only a few meters, before totally disappearing. An adult female *L. stenophrys* coiled close to a forest trail in Braulio Carrillo National Park in Costa Rica apparently had released pheromones (see the tail-luring section above). Two days later, at about 0800 h at the same location, J. Solís, a naturalist guide, saw two very active bushmasters and spotted another that escaped without being properly identified. The latter were very likely males searching for the female observed earlier.

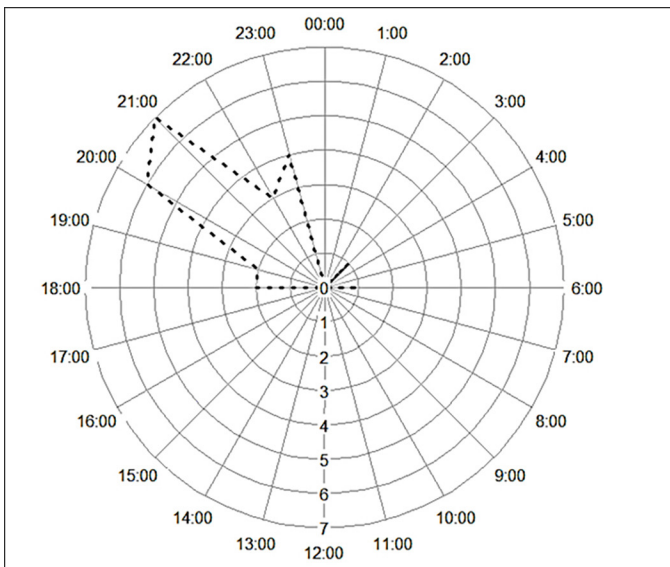
Twenty-one of 28 snakes in northeastern Venezuela were active from 2000–2300 h (DAF, 28 records with precise times noted; Fig. 17). One male was still active at 0300 h and another at 0625 h. These data, however, are likely biased, as search effort was generally concentrated between 2000 h and 0000 h. However, a similar pattern of peak activity early in the night was observed in six radio-tracked bushmasters in the Brazilian Atlantic forest (DAF, unpubl. data). This peak in activity period has been observed in other Neotropical pitvipers (Sazima 1988; Oliveira and Martins 2001; Tozetti and Martins 2013) and appears to be correlated with higher environmental and body temperatures during the early nighttime hours when snakes are searching for a spot from which to either ambush prey or avoid becoming prey (Gibbons and Semlitsch 1987; Bonnet et al. 1999). Males usually are the first to become active early at night and the last to rest.

Those records from forested areas, roads, and anthropogenically altered areas from throughout the range of *L. muta* suggest that this activity pattern is broadly applicable to bush-





**Fig. 16.** An adult South American Bushmaster (*Lachesis muta*) sharing a den with an Armadillo (*Dasypus novemcinctus*) in Igrapiuna, Bahia, Brazil. Photograph by Diego A. Flores.



**Fig. 17.** Circular plot showing the activity of South American Bushmasters (*Lachesis muta*) during a 24-h period in northeastern Venezuela; internal number describes the frequency and external numbers the hours of the day.

masters. An exception exists in the Suriname coastal plain, where the sandy substrate effectively conserves heat and where bushmasters emerge from burrows much later than elsewhere (sometimes as late as midnight) (D. Ripa, pers. comm. to QD; D. Lock, pers. comm.).

Regardless of evident patterns, when necessary, *Lachesis muta* can be active at any time in a variety of situations, even as extreme as swimming across a river as wide as the Essequibo in Guyana (Fig. 18).

**Movements:** In Costa Rica, campesinos report daytime encounters with sleeping bushmasters. We unfortunately do not know if these snakes are males or females. We believe that individuals resting outside of burrows during the day are usually males, whereas females typically remain in or very close to their underground refugia. One radio-tracked female *L. melanocephala* moved within a maximum area of only 50 m<sup>2</sup> over a period of three months; she had probably just laid eggs (E. Castro, pers. comm.).



**Fig. 18.** An adult South American Bushmaster (*Lachesis muta*) swimming across the Río Essequibo in Guyana. Photograph by Steve Townson (Amazon-Angler).



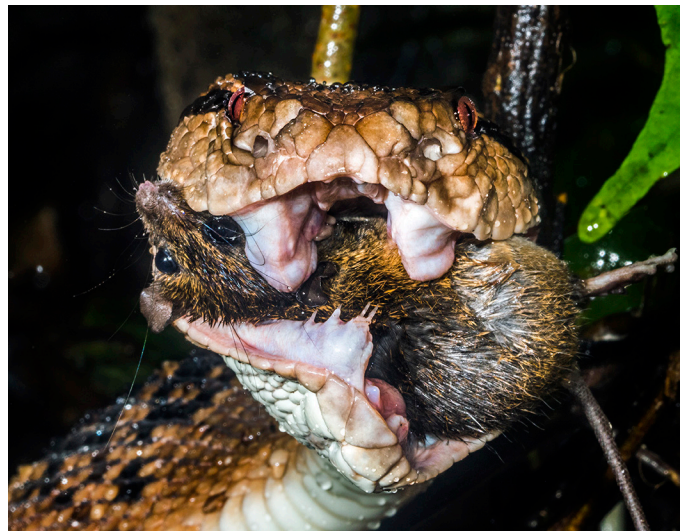
Greene and Santana (1983) followed one radio-tagged *Lachesis stenophrys* (length 90 cm) from La Selva, Sarapiquí, Costa Rica, that spent 3, 6, and 25 days at three different sites, also moving in an area of only 50 m<sup>2</sup>. She moved only 1% of the time and this was always at night; otherwise, she was immobile, spending the day under small plants. On night 24 she ate a rodent weighting 40% of her own body mass (which is not typical, see below under Prey and Predators), after which she remained inactive for nine more days.

During 2017, DAF monitored six *Lachesis muta* at the Michelin Ecological Reserve, IGRAPIUNA, in Bahia, Brazil. Movements were invariably along mammalian trails made by agoutis or other medium-size mammals. Snakes used one trail to move to a site and a different trail to return. Trails passed through both canopy-covered areas and forest gaps. Such movements were observed eight times, indicating a nonrandom pattern.

**Prey, predators, and parasites:** Viperids in general are snakes able to swallow prey many times the diameter of their bodies (e.g., Ripa 2001; Morgan and Barrio-Amorós 2015). However, bushmasters of moderate size of about 200 cm tend to consume prey that is usually not larger than 200–250 g (maximum 525 g; Ripa 1999), with major prey items comprised of small to medium-sized marsupials and rodents. Spiny rats (*Proechimys*, *Orozomys*, *Droechemys*), which are attracted to the seeds and fruits of palms (e.g., *Welfia* sp.), are common prey items in Central America, where, along with suitable habitat, the abundance of snakes is largely dependent on the availability of this food source (Greene and Santana 1983). To our knowledge, no records exist of any bushmasters preying on amphibians, birds, or other reptiles, but we cannot rule out the possibility that at least young individuals might exploit the amphibians (contrary to Diniz-Sousa et al. 2020, citing Carrillo de Espinoza 1970) that can be phenomenally abundant in habitats where bushmasters occur. Note, however, that even hatchling bushmasters are large enough to swallow small rodents. Carrillo de Espinoza (1970) cited birds and amphibians as part of the diet of *L. muta* in Peru, but provided no details.

Bushmasters maintain their bite until the end of envenomation (Fig. 19) before swallowing prey. This appears to minimize the loss of small and fast prey items. A Central American Bushmaster in Caribbean Costa Rica did not release the hand of a victim for 5–10 seconds. Surprisingly, that person survived (M. Solano to C. Porras, pers. comm.), although tissues in the hand and arm were severely damaged.

On the other hand, especially young or subadult bushmasters can themselves become prey to certain predators, such as the Mussurana (*Clelia* spp.), a colubrid that can swallow prey larger than itself (Barrio-Amorós and ter Harmse 2017), and the “Sabanera real” or “Rabo negro” (*Drymarchon*



**Fig. 19.** An adult South American Bushmaster (*Lachesis muta*) from near Iquitos, Peru, with rodent prey. Photograph by Christopher Gillette.

*melanurus*), which is sympatric with *L. melanocephala* on the Osa Peninsula and with *L. stenophrys* along the Caribbean versant. An unconfirmed report documented by a photograph of poor quality from near Turrialba in Limon Province described a *D. melanurus* (approx. 1.80 m in length) regurgitating a subadult *L. stenophrys* (approx. 1.20 m in length) (Minor Camacho and Miguel Solano to Esteban Arrieta, pers. comm.). In Amazonia, the Indigo Snake (*Drymarchon corais*) is a likely predator for *L. muta*. Alexander Blanco (pers. comm. to DAF) found pieces of *Lachesis* in Harpy Eagle (*Harpia harpyja*) nests in Imataca, Venezuela. Large owls as well as mustelids, peccaries, and wild cats also are possible predators of small bushmasters. In the 1980s, La Selva Biological Reserve near Sarapiquí, Costa Rica, was known to have a substantial bushmaster population (Greene and Santana 1983) as well as a large population of Collared Peccaries (*Pecari tajacu*) (C. de la Rosa, former director of La Selva Biological Station, pers. comm. to CBA). The Collared Peccary population was stable at that time due to the presence of large predators. Today, Jaguars (*Panthera onca*) have become very scarce at La Selva and the population of peccaries has grown considerably. Central American Bushmasters have not been seen at La Selva since the early nineties, even though it is one of the most extensively explored tropical biological stations in the world.

Humans, predictably, are the major threat to bushmasters. As they rest during the day, snakes are easy prey for native peoples, such as the Achuar in Ecuador or the Yanomamo in Brazil and Venezuela, who exploit large bushmasters for food (Fig. 20) or preserve the skins as trophies. Bushmasters also are killed merely because they are serpents. Nevertheless, the most critical threat for all species is habitat destruction (Maxwell et al. 2016), resulting in the forced coexistence





**Fig. 20.** Bushmaster as food. An unfortunate South American Bushmaster (*Lachesis muta*) in Amazonas, Venezuela, cooks while a Yanomami native waits to eat. Photograph by Charles Brewer-Carías.

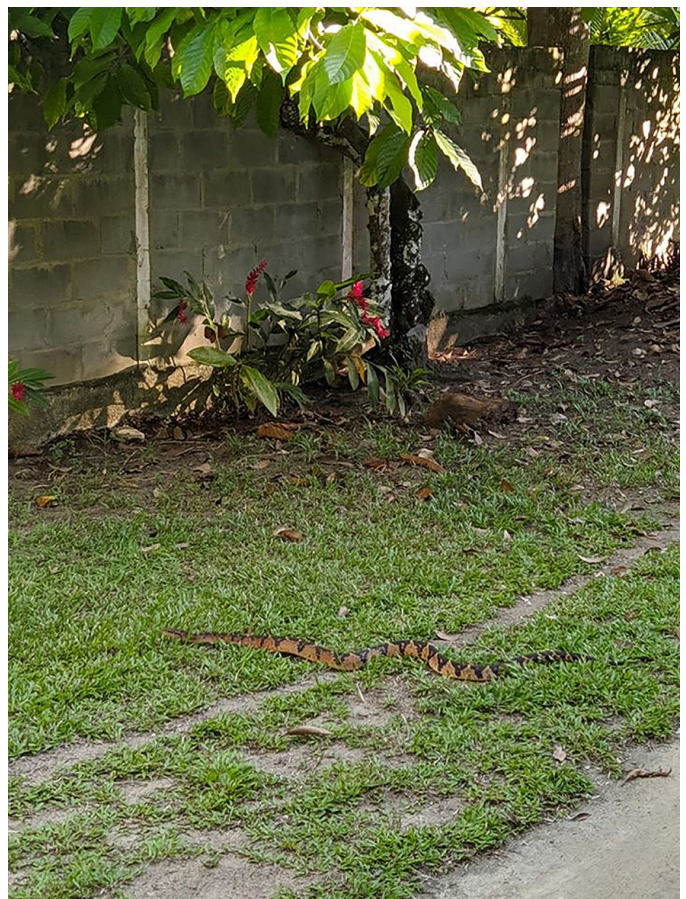
of humans and snakes in regions where forests have been destroyed (Fig. 21) or in recently constructed areas of expanding towns, like the subadult *L. muta* found near an old house near Bahia, Brazil (Fig. 22), and killed immediately thereafter.

Bushmasters are known to harbor a wide variety of parasites ranging from mild infestations of pentastomids (*Porocephalus crotali*) (Barrio-Amorós et al. 2011) to heavy infestations of nematodes (*Hastospiculum onchocercum*) (Araujo-Filho 2013). Parasites can be lethal in wild-caught (Araujo-Filho 2013) and captive bushmasters (Eatherley 2015), with infestations of lung worms (*Rhabdias*) especially virulent (Campbell and Lamar 2004).

**Are bushmasters rare or just difficult to find?:** A substantial handicap when searching for bushmasters is their impressive crypsis, which renders them essentially invisible when outside of burrows (Fig. 23), so determining whether they are truly rare is a challenging task. In the mid-20th Century, Taylor (1951) considered *L. stenophrys* a rare snake



**Fig. 21.** An adult Central American Bushmaster (*Lachesis stenophrys*) crossing a dirt road during the day in a recently cleared area near Turrialba, Cartago, Costa Rica. Photograph by Minor Camacho.



**Fig. 22.** A subadult South American Bushmaster (*Lachesis muta*) in the outskirts of a small town near Bahia, Brazil. Unfortunately, like nearly all snakes discovered close to human settlements, it was killed. Photograph by Rogerio Borges.

in Costa Rica. Even earlier, in 1910, the Trinidadian collector Howel Mole wrote Raymond Ditmars (in charge of the Bronx Reptile House at that time) apologizing because bushmasters were not as abundant as they had been before the introduction of mongooses to the island (Eatherley





**Fig. 23.** Bushmaster microhabitat of *Lachesis* in Costa Rica is comprised of low bushes, palms, and a thick layer of leaf litter. Finding a snake in such a situation can be challenging. Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild).

2015). On the contrary, Beebe (1952) stated that bushmasters were more common at Arima Valley of Trinidad than *Bothrops atrox*. J. Danch (in Boos 2001), reported finding four *L. muta* in the Arima Valley in a two week period in 1987. In fact, many herpetologists active during the 1950s through the 1980s or even 1990s considered bushmasters a fairly common element of the primary forests they studied (Beebe 1952; Greene and Santana 1983; Solórzano 2004). However, field data from the 21st century indicate otherwise. In Venezuela, South American Bushmasters (*L. muta*) are considered very rare in general (comments from researchers and campesinos to CBA and DAF), although they can be common in some areas. During a three-month study in a gold-mining concession surrounded by primary rainforest south of the Orinoco River to El Manteco, Bolívar, Barrio-Amorós et al. (2011) recorded only three individuals. In the Turimiquire Massif along the northeastern Venezuelan coast, this species is not as rare as it appears to be in the south of the country and in the Atlantic forest of Brazil. DAF counted one individual per 12.3 h of search time in the Turimiquire Massif compared to one individual per 32.5 hours in the Atlantic forests. Snake population densities in general are highly correlated with habitat conditions, the availability of prey, the density of predators or disturbing elements, and the availability of microhabitat that is not used by sympatric snakes species (e.g., Perrin and Bodbijn 2001; Lind et al. 2005; Luiselli 2006).

In Costa Rica, the situation is different for each of the two species. The Black-headed Bushmaster is known from an area of only 4,828.15 km<sup>2</sup>, the smallest range of the four species of bushmasters (see also the Conservation section below). Despite some old reports from the central Pacific (Solórzano 2004), the currently accepted distribution is confined to southern Costa Rica at elevations from 0 to 1,873 m asl (González-Maya et al. 2014; Solórzano and Sasa 2020) and nearby Panama. Even within that area, the species' abundance has always been considered low (Solórzano 2004). During the 1980s, collectors removed many *L. melanocephala* out of the country, establishing the current breeding populations in the U.S. and Europe (Ripa 2001). Interviews with local people clearly indicate that this trend of diminishing population sizes is largely attributable to habitat loss and an increase in illegal hunting (interviews with farmers and local hunters conducted by CBA at many localities within the distribution of the species). Farmers say that the “plato negro” was not uncommon in the 1960s to 1980s, when they would encounter and kill 1–10 snakes each year; now say they have not seen one in 20 or 30 years. A major predator, the Collared Peccary originally inhabited the lowlands close to the coast, in the mangroves, and in the riparian areas of larger rivers. Due to tourism and other development along the coasts, peccaries have invaded areas farther inland, even to the tops of many mountains (G. Núñez, pers. comm. to CBA) — and locals confirm that peccaries will kill any snake they encounter. Very recently



(September 2020), CBA and colleagues located three individuals in two consecutive nights at what we suppose is a stable population on the Península de Osa.

On the other hand, the Central American Bushmaster can still be fairly common in appropriate and undisturbed areas in the Caribbean versant of Talamanca. We recently were informed of four snakes seen along a single path in a period of a few days (three during a single morning) in Parque Nacional Braulio Carrillo in early September 2017. The same is true for a site in southern Caribbean Costa Rica, where locals are starting to be interested and are collecting data about the species, and where 16 anecdotal observations were made at a single location in 2017.

South American Bushmasters are considered rare throughout their range, although certain locations, such as the area around Iquitos, Peru, support higher densities of snakes than others (M. Cage, M. Ishimatsu, C. Gilette, B. Lamar, D. Fenolio, pers. comm. to CBA). Since 2008, Darwin Núñez, a herpetologist in Zamora Chinchipe Province of Ecuador, has observed 18 bushmasters: 15 *L. muta*, 11 in the upper Nangaritza (Zamora-Chinchipe Province), two in Yasuni National Park (Napo-Pastaza), and two in Llanganates National Park (Pastaza-Napo), plus three *L. acrochorda*, two in Tesoro Escondido (Esmeraldas), and one in the Mashpi Lodge Forest, Pichincha Province. Also in the Mashpi Reserve in western Ecuador, during eight months in 2015, JC found two adult *L. acrochorda* while spending five nights per month in the reserve. Another four individuals were reported in 2016 by guides and tourists (Carlos Morozch, pers. com). In Nuquí, Choco Department, Colombia, three *L. acrochorda* (two in the same night, one early in the morning) were found in a period of seven days in April 2020 (Pablo Montoya, pers. comm.).

**Conservation:** Venomous snakes are difficult to protect. Even species known to be rare in the wild or restricted to small ranges are frequently not protected by local, national, or international legislation. Of all *Lachesis*, only the subspecies *L. muta rhombeata* is included on the IUCN Red List as Vulnerable (Martins and Marques 2000). However, that taxon is no longer valid, leaving the isolated Atlantic populations of *L. muta* totally unprotected in the remaining 7% of the original Atlantic Forest as of 2008 (Turner et al. 2008).

*Lachesis melanocephala*, with a total range of 4,828.15 km<sup>2</sup>, is the bushmaster with the smallest distribution and the most threats to its survival. When only the actual forest cover, which does not correspond to primary rainforest, is considered, the range diminishes dramatically to 1,920.71 km<sup>2</sup>. If old reports from Alto Los Guarumos near Puriscal and the Quepos area are included, the range grows considerably, but no sightings have been reported since at least 1968 from near Puriscal and since the 1970s from the Quepos area. Reverting

to what we consider the actual range and in light of the many obvious threat to this species, we suggest that the species qualifies for Critically Endangered (CR A2ac+4; see IUCN 2020 for an explanation of the criteria for listing).

We further suggest that *Lachesis stenophrys*, *L. achrochorda*, and *L. muta* deserve NT (Near Threatened) status due to their scarcity and a multitude of threats, despite all having extensive ranges. However, conditions within nations vary considerably. For example, while *L. acrochorda* in the Colombian Choco probably deserves a LC (Least Concern), its dramatically reduced distributions in Ecuador and Panama must be reviewed (see below). Similarly, *Lachesis stenophrys* in Nicaragua should be considered CR A1ac+B1, but those criteria are not applicable in Costa Rica or Panama. However, IUCN Red List assessments are complex and considerably more data are needed to document the threats and current populations trends in all four species.

Another qualification for determining the conservation status of species is the Environmental Vulnerability Score (EVS), which has been used recently as an alternative to IUCN Red List criteria to assess the state of Mexican reptiles (Wilson et al. 2013) and the Central American herpetofauna (Johnson et al. 2015). Those authors noted that the IUCN system is expensive (reliant on meetings of regional specialists), time consuming, often fails to consider systematic advances, and leaves too many species in the DD (Data Deficient) category. On the other hand, the EVS system is quick, simple to elaborate, cheap, predictive, and can be applied to poorly known species or even after a new species has been described. Johnson et al. (2015) provided EVS valuations for the three Central American bushmasters. On a scale of 0–20 in which the higher the number, the more threatened the species, *Lachesis acrochorda* was rated 14 and *L. stenophrys* and *L. melanocephala* both were rated 17. Considering the substantial difference in the extent of their ranges, that *L. stenophrys* and *L. melanocephala* earned the same score was surprising. Using EVS criteria, our own evaluation is that *L. stenophrys* has an EVS value of 17 (5 + 7 + 5 = distribution only within Central America, but not restricted to the vicinity of the type locality + occurs in two formations + venomous species or mimics thereof, killed on sight = 17), whereas *L. melanocephala* has a value of 18 (6 + 7 + 5 = distribution limited to Central America in the vicinity of the type locality + occurs in two formations + venomous species or mimics thereof, killed on sight = 18). The difference between the two assessments is minimal, but we consider it crucial to emphasize the actual status of *L. melanocephala*. We also recommend a more detailed system depending on as much objective information as possible on, for example, the estimated abundance of individuals, which should indicate that, in appropriate habitats, *L. stenophrys* is more abundant and/or detectable than *L. melanocephala*. In addition, we believe that the sec-



**Fig. 24.** A road-killed South American Bushmaster (*Lachesis muta*) in Caripe, Monagas, Venezuela. Because vehicles cannot speed on rough rural roads, roadkills are likely intentional. Photograph by Diego A. Flores.

ond component, which earns eight points if a species occurs in only one vegetative formation and seven if it occurs in two, can be misleading, especially if a species that occurs in two formations has a smaller range than a species that occurs in one. *Lachesis melanocephala*, for example, has a very restricted distribution but occurs in two formations, lowland wet rainforest and upland cloud forest.

In southern Bahia, Brazil, habitat fragmentation is one of the main causes of biodiversity loss and some taxa have been reduced and restricted to primary forest in protected areas (DAF, pers. obs.). Bushmasters, however, occur in all successional stages and many farms, including both forms of Cocoa (*Theobroma cacao*) plantations (agroforestral farms and cocoa monoculture) and rubber plantations (*Leopoldinia piasaba*) (DAF, unpubl. data), where they are important predators of crop-eating rats (*Rhipidomys* spp., *Hylaiamys* spp., *Oligoryzomys* spp.). Consequently, encounters with humans, including road mortality, appear to be the principal cause of declining bushmaster populations (Fig. 24). Despite being on the state Red List of vertebrates (Bahia 2017), during a two-year period, DAF and collaborators encountered seven bushmasters while searching for the species and recorded 11 opportunistic encounters by people associated with the study plus three by hunters, five by rangers, four snake accidents in urban areas, and one accident in a rural area.

Efforts dedicated to the conservation of these snakes must be focused on preserving habitat and connectivity and reducing the number of interactions between humans and bushmasters. However, to better evaluate population trends and genetic variability of increasingly isolated populations, considerably more research is needed. Finally, ongoing efforts to maintain and study these snakes in captivity can help to understand breeding cycles, behaviors, and other aspects of their biology.

## SPECIES ACCOUNTS

### Chocoan Bushmaster, *Lachesis acrochorda* (García 1896) (Fig. 25)

**Type locality:** “las selvas del Chocó, a orillas de los ríos Atrato, San Juan, Dagua, Telembí y ... el camino a Buenaventura,” Colombian Chocó.

**Vernacular names:** Verrugosa, diamante, mapaná rayo, guascama, martiguaja, montuno (Colombia), verrugosa, guascama (Ecuador), verrugosa (Panama).

**Etymology:** The specific name *acrochorda* comes from the Greek *acrochordon* (= wart), a reference to the warty dorsal scalation of the species.

**Taxonomic remarks:** Populations of *Lachesis* in South America west of the Andes were regarded as *L. stenophrys* until Ripa (1999) claimed striking differences between *L. stenophrys* and the Darien-Chocoan form. Ripa (2004) and Campbell and Lamar (2004) resurrected the name *Botrops* [*sic*] *acrochordus* García 1896 as *Lachesis acrochorda*.

**Description:** Head tan brown with black postocular stripes (1–2 scales wide); supralabials usually yellowish tan and spotless; head dorsally marked with irregular spots or “arabesques”; throat white; body ground color is dark brown to beige usually with 23–31 irregular or incomplete black dorsal rhombuses separated by ivory to dirty white scales, seen laterally as inverted triangles, and the interior of each rhombus (or triangle) basically the same as the ground color or darker; iris red-brown, becoming darker with age. Ground color in hatchlings and juveniles tan brown to orange-brown, rhom-



**Fig. 25.** A Chocoan Bushmaster (*Lachesis acrochorda*) from Chocoan Ecuador. Photograph by Jaime Culebras.





**Fig. 26.** An adult male Chocoan Bushmaster (*Lachesis acrochorda*) from Viento Frío, Panama Province, Panama. Photograph by Kevin Martínez.



**Fig. 27.** A Chocoan Bushmaster (*Lachesis acrochorda*) from Bahía Solano, Chocó, Colombia. Photograph by Mateo Giraldo.

buses or triangles dark brown and usually incomplete, tail pinkish. Head scales are small, barely smooth to tuberculate; dorsals keeled and in 31–39 rows; vertebral and paravertebral scale rows very tuberculate, appearing as a vertebral keel; ventral scales in males 204–228, in females 202–221; subcaudals 46–58 in males, 49–55 in females (Valencia et al. 2016). Valencia et al. (2016) reported maximum total lengths of 2,327 mm for males and 2,342 mm for females in Ecuador. The maximum total length reported for the species is 300 cm (Campbell and Lamar 2004).

*Lachesis acrochorda* and *L. stenophrys* are externally similar but usually can be distinguished by the latter having 191–209 ventrals (202–228 in *L. acrochorda*) and usually few if any dark spots on the top of the head (distinctly marked with dark spots and lines or “Ripa’s arabesques” in *L. acrochorda*; Ripa 1999; Campbell and Lamar 2004). *Lachesis acrochorda* is most similar to *L. muta*, although Campbell and Lamar (2004) indicated that they differ in body shape (*L. muta* round in cross-section, *L. acrochorda* tall and compressed); however, we cannot corroborate this distinction, as our experiences indicated that the body shapes of all congeners can vary in response to different factors.

**Distribution and habitat:** The species ranges from Panama (northwest of Darien; see Fuentes and Corrales 2016; Fig. 26) through the Magdalena and Cauca river valleys in Colombia and south into the Chocó in Colombia (Fig. 27) and northwestern Ecuador (Fig. 28) at elevations from sea level (two individuals were close to the beach at Golfo de Tribugá, Chocó, Colombia) to 1,600 m asl (Campbell and Lamar 2004) in tropical wet and moist forest with annual rainfall of about 2,500–6,000 mm; in eastern Panama, however, the habitat is relatively drier (Fuentes and Corrales 2016). Reports in Ecuador are in primary forest, secondary forest



**Fig. 28.** The distributions of South American bushmasters. The range of the Chocoan Bushmaster (*Lachesis achrochorda*) is indicated by dark gray and that of the South American Bushmaster (*Lachesis muta*) by light gray. The isolated populations of *L. muta* in eastern Brazil were previously considered subspecifically distinct as *L. m. rhombeata* (see text).

with low levels of disturbance (Yáñez-Muñoz et al. 2010), cocoa plantations, and pastures but always near primary forest. The conservation of Ecuadorian Chocó rainforest is critical due to deforestation, with only 2% of the native rainforest (CEPF 2005) and 19% of the lowland habitat remaining. Consequently, a review of the conservation status of *L. acrochorda* in Ecuador should be considered as a priority. In Colombia, about 20% of the primary Chocó rainforest is extant.

Nothing is known about the natural history of this species beyond anecdotal reports on reproduction (Fuentes and Corrales 2016) and general accounts (Campbell and Lamar 2004; Valencia et al. 2016).



**Black-headed Bushmaster, *Lachesis melanocephala***  
Solórzano and Cerdas 1986 (Fig. 29)

**Type locality:** “tropical forests 9 km northern of Ciudad Neily in southeastern Provincia Puntarenas, Costa Rica.” Since the type series was lost, Solórzano and Sasa (2020) provided a neotype from San Juan de Rincón, Península de Osa, Provincia de Puntarenas, Costa Rica.

**Vernacular names:** Matabuey, plato negro (Costa Rica).

**Etymology:** The specific name *melanocephala* is derived from the Greek *melanos* (= black) and *kephalos* (= head), an allusion to the solid black top of the head in this species.



**Fig. 29.** A Black-headed Bushmaster (*Lachesis melanocephala*) from southern Pacific versant of Costa Rica. Photograph by Jaime Culebras, courtesy of Instituto Cloromido Picado.

**Description:** The most distinctive of the bushmasters, with the black top of the head fused with the postocular stripe; body ground color light tan to yellow with 20–32 regular and/or irregular black dorsal rhombuses, seen laterally as inverted triangles, and the interior of each rhombus (or triangle) brown and often with some black scales; iris red-brown. Rhombuses and triangles in hatchlings and juveniles usually incomplete, tail pinkish. Head scales are smooth to tuberculate; dorsals keeled and in 36–40 rows; vertebral and paravertebral scale rows very tuberculate, appearing as a vertebral keel; ventral scales 209–216; subcaudals 43–56. Savage (2002) reported a maximum length of 3,900 mm for *Lachesis* in general without citing references, listing vouchers, or making any specific reference to species. Maximum recorded total lengths for *L. melanocephala* are 2.3 m (Solórzano 2004) or 240 cm (Ripa 2001).

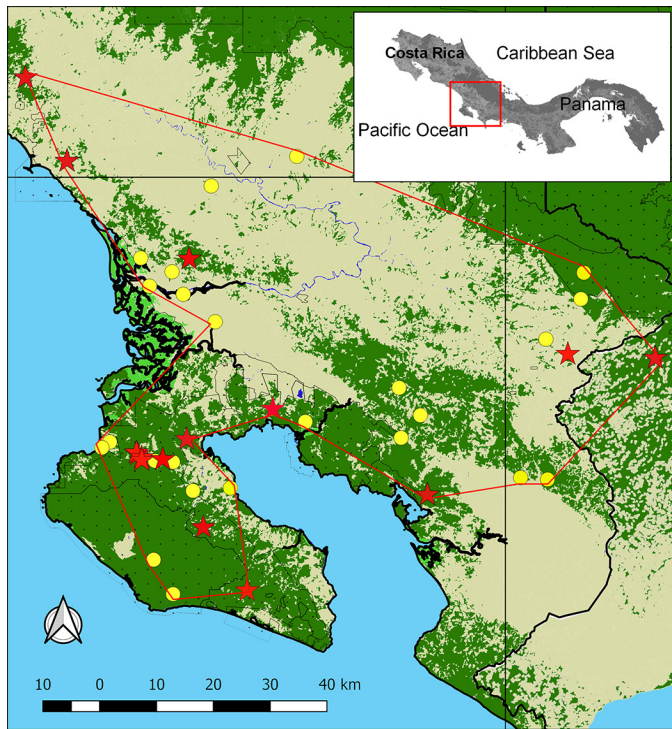
**Distribution:** This species, with the smallest distribution of all congeners, is endemic to the Pacific versant of the Talamanca Mountain range in Costa Rica (Savage 2002; Campbell and Lamar 2004; González-Maya et al. 2014; Solórzano and Sasa 2020) and adjacent Panama (Dwyer and Pérez 2009), a biogeographic zone known as Tropical Evergreen Forest (Holdridge 1966) or Isthmian Pacific moist forest (Leenders 2019). We suggest that, due to the small range and the alarming rate at which the primary rainforest inhabited by this species is disappearing, it should be considered Critically Endangered by the IUCN (see the Conservation section below).

Solórzano’s (2004) Figure 280 depicts an individual from Tinamastes de Pérez Zeledón in San José Province, but his



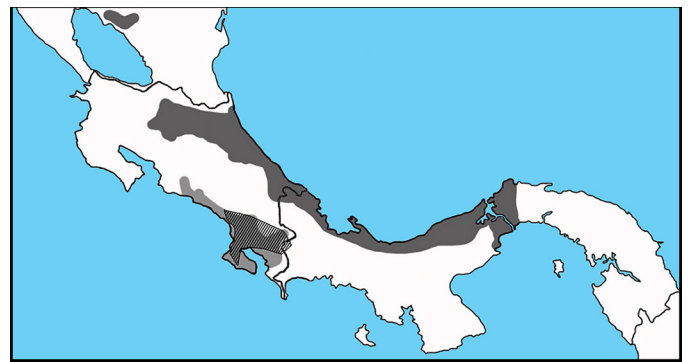
**Fig. 30.** An adult Black-headed Bushmaster (*Lachesis melanocephala*) from the Osa Peninsula, Costa Rica. Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild).





**Fig. 31.** A Minimum Convex Polygon based on known localities of the Black-headed Bushmaster (*Lachesis melanocephala*). Previously published records by Gonzalez-Maya et al. (2014) are indicated by yellow dots and additional new records by red stars. Pale green denotes disturbed areas, bright green wetlands, and dark green vegetated areas (mostly forest). Map by S. Rodriguez-Abarca using QGIS 2.18 with shape files Costa Rica 2014 v.1.2.

distribution map and that of González-Maya et al. (2014) did not include this record. Because we recently received photographs of dead snakes from Tinamastes (09°17'N, 83°46'W; 860 m asl) and from an area near Uvita (09°09'N, 83°42'W; 590 m asl) in Puntarenas Province, we do not doubt that the extent of the species' distribution is larger than had been depicted previously. An old report from Alto Los Guarumos near Puriscal (Solórzano 2004) extends the known distribution presented herein 84 km northwestward (to an extent of ~9.164 km<sup>2</sup>). However, that area is currently devoid of primary forest capable of sustaining populations (M. Matarrita, pers. comm.). Campbell and Lamar (2004) showed another locality near Quepos that had been reported by Bolaños et al. (1978). Suitable habitat exists in the area between Quepos and Tinamastes, but to date we are unaware of any confirmed records. However, due largely to protection provided by the Parque Nacional Corcovado and the remote inaccessibility of much of the Osa Peninsula, the species remains well represented in that area (Fig. 30), which might support the bulk of the extant populations. We generated a Minimum Convex Polygon (MCP; Fig. 31) as an estimate of the Extent of Occurrence (EOO) but avoided mangroves, because they are not known to provide suitable habitat. Our calculated range for the species is 4,828.15 km<sup>2</sup>, which differs substantially from the EOO of 3,434 km<sup>2</sup> in González-Maya et al. (2014).



**Fig. 32.** The distributions of Central American bushmasters. The range of the Central American Bushmaster (*Lachesis stenophrys*) is indicated by dark gray. The historical distribution of the Black-headed Bushmaster (*L. melanocephala*) is indicated by light gray and the current distribution (see Fig. 12) is marked with diagonal lines.

Their Species Distribution Model (SDM) extended for 9,240 km<sup>2</sup> in Costa Rica and 1,266 km<sup>2</sup> in Panama. Fig. 32 depicts the current and historical distribution of *L. melanocephala*.

### South American Bushmaster, *Lachesis muta* (Linnaeus 1766) (Fig. 33)

**Type locality:** “Surinam.”

**Vernacular names:** Apaga fogo, pico de jaca (Bahia, Brazil); surucucú (Amazonian Brazil; Mota da Silva et al. 2019); surucucú de fogo (northeastern Brazil); surucutinga/surucutinga (central Brazil); pucarara, cascabel púa (Bolivia); sibucano, diamante, macaurel, mapaná rayo, martiguaja, montuno, pudridora, riega (Colombia); yamunga (shuar), motolo (kichua), yamung/a (shuar), genenenka (huaroani) (Ecuador); maitre de la brousse, urukuku (French Guiana); coonocooshe, counacouchi, patiesak (Guyana); shushupe, cuanira, dueño del monte, macapé, monare (Peru); bosmeester, kapasisneki, maka sneki, makkaslang (Surinam); maepire z'annana, maepire zanana, pine-apple maepire, maepire ananas,



**Fig. 33.** A South American Bushmaster (*Lachesis muta*) from Zamora-Chinchipe, Ecuador. Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild), courtesy of D. Nuñez.





**Fig. 34.** A South American Bushmaster (*Lachesis muta*) from Santa Cruz, Bolivia, probably the only population living in transitional habitat between primary rainforest and dry forest in the Chiquitania region. Photograph by Steffen Reichle.

pineapple snake (Trinidad and Tobago); cuaima, cuaima piña, cuaima concha de piña, daya (Venezuela).

**Etymology:** The specific name *muta* is from the Latin *mutus* (= mute), probably a reference to the species' superficial similarity with rattlesnakes in the genus *Crotalus*, to which the species was originally assigned by Linnaeus (1766); but lacking a rattle it was presumed to be silent or mute.

**Description:** Top of the head more or less spotted in black, apparently darker on western Amazonian individuals and lighter on northeastern snakes (Venezuela, French Guiana, Guyana, Surinam, Trinidad); postocular stripe black; body ground color light tan to yellow to pink or orange with 25–35 regular and/or irregular black dorsal rhombuses, seen laterally as inverted triangles and thicker posteriorly, sometimes fused dorsally or separated by one or two scales, usually outlined by one row of scales paler than the ground color, and with the light scales inside the rhombuses or triangles the same as the



**Fig. 36.** A South American Bushmaster (*Lachesis muta*) about 1.20 m in length from San Jose de Anacoco, Bolívar, Venezuela. Photograph by David Briceño.



**Fig. 35.** A South American Bushmaster (*Lachesis muta*) from Eliseo Medrado, Bahia, Brazil. Photograph by Marco A. de Freitas.

ground color, lighter, darker, or absent and becoming totally black (Fig. 34); iris black, brown, red-brown, or burgundy red. Rhombuses and triangles in hatchlings and juveniles can be complete or incomplete; tail black to reddish. Head scales are smooth to tuberculate; dorsal scales keeled and in 31–38 rows; vertebral and paravertebral scale rows very tuberculate, appearing as a vertebral keel; ventral scales 213–231 in males, 220–236 in females; subcaudals 44–51 in males, 41–49 in females.

Although Fernandes et al. (2004), noting that snakes from Mato Grosso in Brazil were more similar to those that had been assigned to *L. m. rhombeata* from the Atlantic forests than to other populations from south or north of the Amazon, synonymized *L. m. rhombeata* with *L. muta*, differences in pattern and morphology could represent unresolved taxonomically significant differentiation among populations. For example, Ripa (1999) reported notable morphological differences between Guianan and western Amazonian populations. The postocular stripe is substantially wider in Atlantic (2–3 scales wide; Fig. 35) than in Amazonian or Orinoquian (1–2 scales wide; Fig. 36) populations (CBA, pers. obs.) and heads of Guianan snakes are relatively smaller than those in Amazonia (Campbell and Lamar 2004).

Although Sandner-Montilla (1994) claimed that a snake from Venezuela was 5.28 m in length and other possibly exaggerated measurements abound in the literature (Ditmars 1937; Amaral 1948), the maximum accepted length has been 291 cm (Campbell and Lamar 2004). Herein we report a male from Yasuni National Park, Ecuador in the zoological collection at the Universidad Católica de Quito, Ecuador (QCAZR5989) with a total length of 315 cm, the longest South American Bushmaster documented with a voucher. Males are larger than females (Ripa 1994, 1999; Alves et al. 2014) and this probably applies to all other species in the genus.



**Distribution:** The South American Bushmaster has an extensive distribution that includes the entire Amazon, Essequibo, and southern Orinoco basins in Brazil (Fig. 37), Bolivia (Fig.

38), Peru (Fig. 39), Ecuador (Fig. 40), Colombia, Venezuela (Fig. 41), Guyana (Fig. 42), Surinam (Fig. 43), French Guiana (Fig. 44), ultimately reaching the Turimiquire Massif and



**Fig. 37.** A South American Bushmaster (*Lachesis muta*) from Acre, Brazil. Photograph by Paulo R. Melo-Sampaio.



**Fig. 38.** A South American Bushmaster (*Lachesis muta*) from Chapare, Cochabamba, Bolivia. Photograph by Pedro Gómez Murillo.



**Fig. 39.** A South American Bushmaster (*Lachesis muta*) from near Iquitos, Loreto, Peru. Photograph by William W. Lamar.



**Fig. 40.** A South American Bushmaster (*Lachesis muta*) from Nangaritza, Zamora-Chinchipec, Ecuador. Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild), courtesy of Darwin Núñez.



**Fig. 41.** A South American Bushmaster (*Lachesis muta*) from Cueva de El Fantasma, Aprada Tepui, Bolívar, Venezuela. Photograph by Philippe Kok.



**Fig. 42.** A South American Bushmaster (*Lachesis muta*) about 120 cm in length from Parabara, Guyana. Photograph by Andrew Snyder.



Paria Peninsula in northeastern Venezuela (Fig. 45) and the island of Trinidad in the Caribbean (Fig. 46) (Roze 1966; Pérez-Santos and Moreno 1988; Visinoni 1995; Murphy 1997; Campbell and Lamar 2004; Natera-Mumaw et al. 2014; Murphy et al. 2018) (Fig. 9). Disjunct populations (formerly known as *L. m. rhombeata*) occur in the Mata Atlantica

in the Brazilian states of Ceará, Rio Grande do Norte, Paraíba, Sergipe, Pernambuco, Alagoas, Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro (Figs. 47–48). The elevational range extends from sea level (an individual close to the beach in the Paria Peninsula of Venezuela; DAF, pers. obs.) to 2,100 m asl in Caripe, Venezuela (Corrales et al. 2016).



**Fig. 43.** A South American Bushmaster (*Lachesis muta*) about 1.5 m in length from near Saramacca, Suriname. Photograph by Dick Lock.



**Fig. 44.** A South American Bushmaster (*Lachesis muta*) from Saul, French Guiana. Photograph by Vincent Prémel.



**Fig. 45.** A male South American Bushmaster (*Lachesis muta*) about 1.70 m in length from Caripe, Monagas, Venezuela. Photograph by Diego A. Flores.



**Fig. 46.** A South American Bushmaster (*Lachesis muta*) from the Northern Range, Trinidad. Photograph by Rainer Deo.



**Fig. 47.** A South American Bushmaster (*Lachesis muta*) 1.89 m in length from Igrapiuna, Bahia, Brazil. Photograph by Verena Pietzsch.



**Fig. 48.** A South American Bushmaster (*Lachesis muta*) from near Recife, Pernambuco, Brazil. Photograph by Marco A. de Freitas.



**Central American Bushmaster,**  
*Lachesis stenophrys* Cope 1875 (Fig. 49)

**Type locality:** Sipurio, Provincia de Limón, Costa Rica.

**Vernacular names:** Matabuey, cascabel muda, bocaracá de jabillo (Cabecares, Costa Rica); matabuey, cascabel muda (Nicaragua); verrugosa, mapaná, íja (Guaymies, Panama).

**Etymology:** The specific name *stenophrys* comes from the Greek *stenos* (= narrow) and *ophrys* (= brow), a reference to the small supraocular scales (Campbell and Lamar 2004).

**Description:** Head light brown and immaculate or with only a few irregular dark spots; black postocular stripes 2–3 scales wide; supralabials usually yellowish tan and spotless; throat white; ground color dark brown to beige usually with 20–37



**Fig. 49.** A Central American Bushmaster (*Lachesis stenophrys*). Photograph by Cristian Porras (CRWild).



**Fig. 50.** An adult female Central American Bushmaster (*Lachesis stenophrys*) from Braulio Carrillo National Park, Heredia, Costa Rica. Photograph by César Barrio-Amorós (Doc Frog Photography/CRWild).

irregular or incomplete dorsal black rhombuses, seen laterally as inverted triangles; dorsal rhombuses separated dorsally by ivory to dirty white scales; interior of the rhombuses or triangles essentially the same as the ground color; iris red-brown. Ground color orange and rhombuses or triangles usually incomplete in hatchlings and juveniles; tail pinkish. Head scales small, smooth to tuberculate; dorsal scales keeled and in 33–38 rows; vertebral and paravertebral scale rows very tuberculate, appearing as a vertebral keel; ventral scales 198–209; subcaudals 36–49.

Savage (2002) reported a length of 3,900 mm in this species, but without citing a reference or listing a voucher, probably a general statement about bushmasters. Solórzano (2004) stated that the maximum length in this species is 2.5 m, but historically could be as long as 3.6 m. The only references to life span in the genus corresponds to two unsexed individuals of this species that lived in captivity at least 8.5 years (Bowler 1975) and 31 years (Slavens and Slavens 2000).

**Distribution:** Currently, this species is regarded as endemic to lower Central America in Caribbean Costa Rica (Fig. 50) and Panama (mainly Caribbean but reaching Pacific slopes near the city of Panama and the Valle de Antón; Fig. 51) to slightly east of the Panama Canal (Fuentes and Corrales 2016) (Fig. 13). Ripa (1999) distinguished a widely distributed western form from a central Panamanian form, but this must be further tested. A specimen, ostensibly from Nicaragua, was mentioned by Vial and Jimenez-Porras (1967), who believed it was mislabeled and had actually originated in Panama. However, Köhler (1999) examined a specimen (University of Kansas Natural History Museum, KU 174464) from Chontales, Nicaragua, and Sunyer et al. (2014) also considered Nicaragua part of the species' distribution. However, its survival in Nicaragua is questionable. The elevational range extends from near sea level to around 1,000 m asl (Campbell and Lamar 2004).



**Fig. 51.** This Central American Bushmaster (*Lachesis stenophrys*) was found in a garden in El Valle de Antón, Panamá, and rescued. Photograph by Mario Urriola (Cecib-SEMAT).



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