



Revista de Biología Tropical

ISSN: 0034-7744

ISSN: 2215-2075

Universidad de Costa Rica

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Revista de Biología Tropical, vol. 68, no. 4, 2020, October-, pp. 1387-1400
Universidad de Costa Rica

DOI: <https://doi.org/10.15517/RBT.V68I4.42359>

Available in: <https://www.redalyc.org/articulo.oa?id=44966323031>

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Redescription of the snake *Lachesis melanocephala* (Squamata: Viperidae): Designation of a neotype, natural history, and conservation status

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Received 18-VI-2020.

Corrected 18-VIII-2020.

Accepted 11-IX-2020.

ABSTRACT. Introduction: The Black-headed Bushmaster (*Lachesis melanocephala*) is a large venomous snake that inhabits tropical moist forest, wet forest, montane and premontane wet forest in Southwestern Costa Rica and extreme Western Panama. **Objective:** We assign a neotype for the species due to the loss of the original holotype and update the information on its geographical distribution, natural history, and conservation status. **Methods:** To determine the conservation status of *L. melanocephala*, we modeled its potential distribution using the species' locality records and distribution modeling analysis implemented in MaxEnt. Based on the species' potential distribution, we evaluate the loss of its original habitat and estimate the percentage of its distribution area that is currently protected by the country's protected area system. **Results:** The potential distribution of the species was estimated at 10 139 km², including areas where the species currently occurs and historical areas where the species has been registered but is nowadays considered locally extinct. About 29 % of that potential distribution overlaps with protected wild areas, so less than a third of the potential distribution of the species is under protection. **Conclusions:** During the last decade, accelerated habitat loss and growing evidence of declining natural populations indicate the need for urgent protective measures to prevent the extinction of this species in the foreseeable future.

Key words: Neotropical pitvipers; snake conservation; species distribution model.

Solórzano, A., & Sasa, M. (2020). Redescription of the snake *Lachesis melanocephala* (Squamata: Viperidae): Designation of a neotype, natural history, and conservation status. *Revista de Biología Tropical*, 68(4), 1384-1400.

The genus *Lachesis* (n.f., Daudin, 1803) represents a clade of Neotropical pitvipers that includes four nominal species distributed in the rainforest of South America and Isthmian Central America (Campbell & Lamar, 2004; Wallach, Williams, & Boundy, 2014). These are the longest venomous snakes in the Western Hemisphere and are considered the longest vipers in the world (Campbell & Lamar, 2004). Besides their large size, species within *Lachesis* share several external characteristics that

allow distinguishing them. In its distal part, the caudal region has small, bristling scales, even in the sub-tail area (Fernandes, 2001). The tail ends on a spine-shaped scale; some authors suggest it is involved in producing a warning sound when vibrates against the leaf litter (Ripa, 1994). The dorsal scales are warty, almost pyramidal, giving it a rough and warty appearance (the vernacular name assigned to bushmasters in Panamá and Colombia refers to that appearance). The dorsal coloration consists

of a background of light brown, cream, or clay tones depending on the species and has a pattern of dark rhomboid designs that extends from the dorsal spine to the sides. These designs also vary interspecifically. The bushmaster species also share a unique feature among Neotropical pitvipers: they are oviparous, conceivably the only members of Viperidae that lay eggs in the New World (Campbell & Lamar, 2004; see this same reference for a possible exception in *Bothrocophias colombianus*).

Among the bushmaster species, the Black-headed Bushmaster (*Lachesis melanocephala*) is considered the most distinctive: the back of its head is heavily pigmented, forming a unique black cap (Fig. 1A, Fig. 1B, Fig. 1C). This characteristic makes this species locally known as Plato Negro (black plate), and the epithet “*melanocephala*” refers precisely to that dark coloration on the back of the head

(Solórzano & Cerdas, 1986). The dorsal ground color is light, cream-white to yellowish, with rhomboidal markings that are dark gray or black (Fig. 1D). *Lachesis melanocephala* has the most restricted distribution, occurring in Southern and Southwestern Costa Rica (Savage, 2002; Solórzano, 2004; Sasa, Chaves, & Porras, 2010). This species also occurs near the border with Costa Rica in Western Panama, in the Province of Chiriquí (Dwyer & Perez, 2009, see below).

Populations currently assigned to *L. melanocephala* were first considered a synonymy of *Lachesis muta* (Daudin, 1803). In Costa Rica, early researchers did not distinguish between bushmaster populations at each side of the Cordillera Volcánica Central and the Talamanca mountain range, but they were aware of their presence (Picado, 1931; Taylor, 1954). Later, Vial & Jiménez-Pórras (1966)

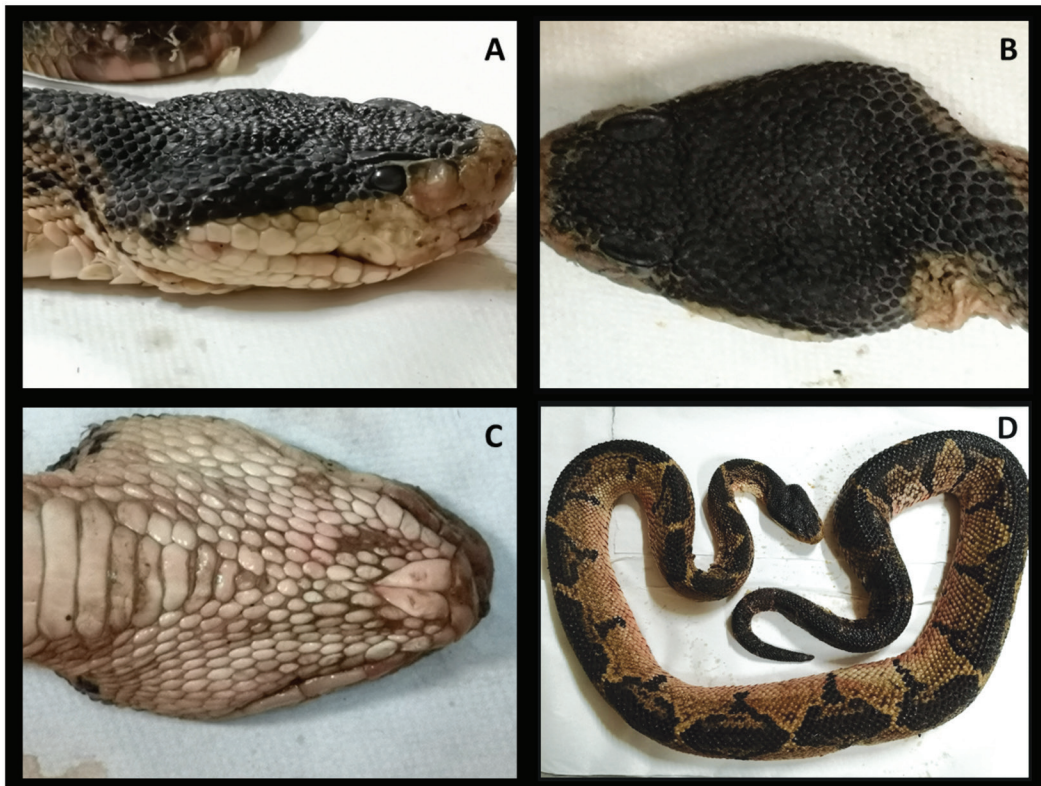


Fig. 1. Neotype of *Lachesis melanocephala* MZUCR-23185. **A.** Lateral view of head. **B.** Dorsal view of the head. **C.** Chin region. **D.** Full view. Note the dorsal body blotches.

and Bolaños (1982) distinguished the Pacific and Caribbean forms, although they did not offer a formal taxonomic proposal. During those years, differences in venom characteristics between the Caribbean populations (= *Lachesis stenophrys*) and the South Pacific population were recognized by Roger Bolaños and collaborators at Instituto Clodomiro Picado (ICP), Universidad de Costa Rica (Bolaños, Muñoz, & Cerdas, 1978).

Solórzano & Cerdas (1986) first described *Lachesis melanocephala* as a subspecies of *Lachesis muta*. Besides their venom immunological differences, the authors found morphological evidence to support that Caribbean and Pacific bushmaster populations were distinct forms that warrant different taxonomic status. In the original description, the type series was collected from 1984 to 1986 in the Southern region of Puntarenas Province, Costa Rica. All specimens were deposited in the Museo Instituto Clodomiro Picado (MICP), a snake collection established in 1984 by one of us (ASL) at ICP in San José. The holotype MICP-301 was an adult male (1969 mm snout-vent length), collected 9 km Northern of Ciudad Neily. The paratypes localities were: MICP-302: Palmar Norte; MICP-303: Corcovado National Park on Península de Osa; MICP-304: Golfito; MICP-305: Palmar Sur; MICP-306: Sabalito de Coto Brus; MICP-307: Alturas del Río Cotón, East from Valle de Coto Brus (Solórzano & Cerdas, 1986).

It would take another decade before the Black-headed Bushmaster was recognized as a full species. Ripa (1994) first suggested the convenience of elevating both *L. melanocephala* and *L. stenophrys* as valid species but did not take action on his proposal. Zamudio and Greene (1997) used mitochondrial gene sequences to reconstruct the phylogenetic relationships and historical biogeography of populations then assigned to *Lachesis muta*, including *L. m. melanocephala*, *L. m. stenophrys*, *L. m. muta* and *L. m. rhombeata*. Their results support a deep divergence between the Central and South American lineages, separated from 18 to 6 million years ago. These authors

propose the species status for *L. melanocephala* and *Lachesis stenophrys*. Subsequently, Fernandes (2001) and Fernandes, Franco, & Fernández (2004) confirm the Central American forms as valid species, separated from *L. muta*, from morphological characters related to squamation, hemipenes morphology, and coloration patterns.

The ICP museum collection was neglected during 1996-2000, resulting in the loss of many specimens during that period. One of the most painful losses was the holotype and paratypes of *Lachesis melanocephala*. These losses forced the cessation of maintaining the scientific collection at the Institute and the decision to send the remaining specimens to the Museum of Zoology, at the Universidad de Costa Rica (MZUCR).

Probably due to its relatively recent description and coupled with the fact that it is an uncommon species, the biology, and conservation status of *L. melanocephala* has not received much attention by the scientific mainstream (Solórzano, 2004). In fact, much of the information available on the ecology and behavior of this species comes from observations in captivity (see the section on Natural history, below).

In recent years, interest in this species has grown. Using ecological niche modeling, González-Maya, Castañeda, González, Pacheco, & Ceballos (2014) estimated the extent of occupation for *L. melanocephala* in less than 10500 km². According to these authors, the restricted distribution and high specificity to undisturbed habitats impose risky conditions for the survival of this species, suggesting that this situation coincides with the IUCN criteria for categorizing a species as Endangered (IUCN, 2012). So far, however, only *L. muta rhombeata* from the Atlantic of Brazil is listed by IUCN, as Vulnerable, whereas no other Bushmaster species is included in any other category.

The loss of forest cover throughout the distribution of *L. melanocephala* is significant (García, Obando, & Murillo, 2005), contributing to the notion that populations of this species

are threatened and restricted to the few protected areas in the region (González-Maya et al., 2014). In fact, the establishment and maintenance of a network of protected areas is the most substantial conservation action that Costa Rica has taken to preserve its snake diversity, including the Bushmasters (Sasa et al., 2010). The protection of areas is carried out by the Sistema Nacional de Áreas de Conservación (SINAC, 2020), the state agency in charge of policies, planning, and execution of processes aimed at the sustainability of the country's natural resources. SINAC administers the national parks and reserves and also regulates activities that involve the management of wild species. Conservation strategies based on protected areas assume that these areas represent the minimum amount of land that might remain for many wildlife species if current deforestation and urbanization patterns continue. However, it is not clear whether these protected areas are enough to support viable populations of *L. melanocephala* or if other conservation strategies should be implemented for its protection.

Based on the loss of the holotype (Solórzano & Cerdas, 1986), herein, we provide a re-description of this species *Lachesis melanocephala* and assign a neotype. We also update the information on the geographic distribution and natural history of this species. In addition, we use species distribution modeling to assess the state reserves' role in the conservation of this species. To make this assessment, we tried to answer two specific questions: Is Costa Rica's protected area system enough to protect the Black-headed Bushmaster? Are these protected areas large enough to support viable populations of this species?

MATERIALS AND METHODS

Taxonomic and natural history account:

We reviewed specimens of *L. melanocephala* deposited in the Museum of Zoology, Universidad de Costa Rica (MZUCR, <http://museo.biologia.ucr.ac.cr/>). Scutellation followed Fernandes et al. (2004). For the natural history

account, we drew on our observations in the field or captivity from close to 15 specimens observed in more than 40 combined years of snake biology studies in Costa Rica. We complement our notes with information from published scientific references.

Potential distribution estimation: We gathered occurrence data for the Black-headed Bushmaster from locality records at MZUCR, the literature, and our field observations (Table 1). To estimate the potential distribution of *L. melanocephala*, we performed a species distribution model using the maximum entropy algorithm program MaxEnt (Phillips, Anderson, & Schapire, 2006). MaxEnt is a presence-background approach that uses information from climatic conditions on occurrence datasets. This algorithm allows discriminating between suitable non-suitable areas by assigning a probability of occurrence for the study species (Phillips et al., 2006).

To generate the model, we used environmental data from 19 bioclimatic variables from WorldClim (2020). These layers described annual means of environmental conditions and were generated by land area interpolations of monthly precipitation and temperature data at weather stations worldwide from 1950 to 2000 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). For data extraction and model construction, we calibrated the model to the extent of Costa Rica by cropping the bioclimatic layers within a defined bounding box (7.750-11.500N, 82.150-86.250W).

We developed the model with ENMeval (Muscarella et al., 2014). This package facilitates the construction and evaluation of MaxEnt-generated SDMs with tuned settings, therefore avoiding the selection of overfitted models. We generated a series of candidate models using linear, quadratic, hinge, product and threshold feature classes, and regularization multipliers ranging from 0.5 to 5 (with increases of 0.5), resulting in a total of 60 models. For data partition, we used the method "block." To select the most robust model, we used two metrics: 1) AUCTEST (AUC) to evaluate environmental

TABLE 1
Localities records for the Black-headed Bushmaster (*Lachesis melanocephala*) in Southern and Southwestern Costa Rica

Country	Locality	Latitud	Longitud	Elevation (m)
CR	Tinamastes, Pérez Zeledón, San José	9.3029	-83.7953	700
CR	Dominical, Puntarenas	9.2564	-83.8551	122
CR	Uvita, Puntarenas	9.2262	-83.8267	153
CR	Buenos Aires, Puntarenas	9.1717	-83.3003	455
CR	Cajón Sur, Buenos Aires, Puntarenas	8.9492	-83.3406	298
CR	Curré, Buenos Aires, Puntarenas	8.9904	-83.2683	215
CR	Palmar Norte, Osa, Puntarenas	8.9803	-83.4594	368
CR	Los Mogos, Península de Osa	8.7430	-83.3200	179
CR	Rincón, Península de Osa	8.7042	-83.5044	181
CR	San Juan de Rincón, Península de Osa	8.7659	-83.4720	267
CR	Rancho Quemado, Península de Osa	8.6918	-83.5567	370
CR	Cerro Chocuaco, Rancho Quemado, Península de Osa	8.7425	-83.5611	549
CR	Dos Brazos de Río Tigre, Puerto Jiménez	8.5334	-83.4000	119
CR	La Palma, Puerto Jiménez, Península de Osa	8.6588	-83.4403	9
CR	Playa Blanca, Puerto Jiménez, Península de Osa	8.6373	-83.4399	11
CR	Los Patos, Parque Nac. Corcovado, Península de Osa	8.5802	-83.5046	215
CR	La Gamba, Golfito, Puntarenas	8.6998	-83.1864	122
CR	Piedras Blancas, Golfito, Puntarenas	8.7835	-83.2330	108
CR	Cerro Adams, Golfito, Puntarenas	8.6487	-83.1573	279
CR	Cerro Paraguas, Las Cruces, San Vito de Coto Brus	8.4715	-82.5916	1 105
CR	Jardín Botánico Wilson, Las Cruces, San Vito de Coto Brus	8.7889	-82.9583	1 150
CR	Sabalito, San Vito de Coto Brus, Puntarenas,	8.8168	-82.9132	946
CR	Alturas de Cotón, Puntarenas	8.9500	-82.8333	1 227
CR	Las Tablas, Talamanca, Puntarenas	8.9444	-82.7528	1 873
CR	Ciudad Neily, Corredores, Coto 47, Puntarenas	8.6038	-82.9672	152
CR	Villa Briceño	8.7200	-83.1639	90
CR	Ciudad Cortés	8.9681	-83.5233	20
Panamá	Chiriquí, Cantón Racimiento, Finca Hartmann	8.84504	-82.7607	1 200

discrimination and 2) minimum training present omission rate (ORMTP) to evaluate overfitting (Muscarella et al., 2014).

To estimate the geographic area occupied by the Black-headed Bushmaster, we transformed our prediction into a binary map to visualize the relative distribution of suitable and unsuitable conditions across Costa Rica. We employed a 10th percentile presence (Radosavljevic & Anderson, 2014). This rigorous criterion sets the threshold value that it discards as “suitable habitat,” the 10 percent of the localities predicted with the lowest suitability values. We found this threshold was appropriate after testing other more conservative limits that tend to over predict the geographic distributions.

Conservation assessment: To assess whether the protected areas system in Costa Rica is sufficient to keep populations of *L. melanocephala*, we followed two approaches. First, we evaluated the proportion of the species distribution area under some land protection category. We plotted the extent of occurrences of the Black-headed Bushmaster over the layers of forest types and SINAC protected areas; then, we estimated the proportion of area that lies under some protection category. The forest and protected areas layers were obtained from ATLAS Costa Rica of the Technological Institute of Costa Rica (Ortiz-Malavasi, 2014).

We also take a heuristic approach to investigate if the protected areas within the species distribution are capable of maintaining

sustainable populations of Black-headed Bushmasters. Our approach takes advantage of the concept of Minimum Viable Populations (MVP), the smallest size that a population must have to persist (Gilpin & Soule, 1986). This concept has been used as a useful framework to assess the risk of extinction in wildlife populations. Reed, O'Grady, Brook, Ballau, & Frankham (2003) presented MVP for several reptiles and other vertebrates; their adjusted MVP mean (\pm SD) estimated for large pitvipers is 13 212 (\pm 649) individuals. If we assume a similar MVP for bushmasters, we need to determine the minimum viable area (MVA) that will support them. Since we lack estimates of bushmaster density in their habitat, we used density estimates for *Bothrops asper*, the most common pitviper in humid environments in

Costa Rica. For this last species, mean density estimations are around 0.48 individuals/hectare (Sasa, Wasko, & Lamar, 2009). Densities for bushmasters should be much smaller, as suggested by their extremely low relative abundance. Using two density conditions and the confidence interval around the MVP means approximating the minimum area that state protected reserves should have to ensure viable *L. melanocephala* populations (Table 2).

RESULTS

Synonymy

Crotalus mutus Linnaeus, 1776

Lachesis mutus Daudin, 1803

Lachesis muta Picado 1931

Lachesis muta stenophrys Taylor 1951

TABLE 2
Proportions of the total area of SINAC protected areas on the estimates of the minimum viable area (MVA) for *Lachesis melanocephala*

Protected area ¹ \MVP	Total area (Ha)	MVA ²			
		Low density ³ (0.048 ind./Ha)		High density ³ (0.48 ind./Ha)	
		Lower limit	Higher limit	Lower limit	Higher limit
Humedal Terraba-Sierpe	26 779	0.102	0.093	1.023**	0.928
PN Corcovado	42 469	0.162	0.147	1.622**	1.471**
PN Piedras Blancas	14 133	0.054	0.049	0.540	0.490
PN La Amistad	198 293	0.758	0.687	7.574**	6.869**
PN Carara	5 330	0.020	0.018	0.204	0.185
PN La Cangreja	2 574	0.010	0.009	0.098	0.089
Reserva Forestal Golfo Dulce	61 959	0.237	0.215	2.367**	2.146**
RVS Carate	141	0.001	0.000	0.005	0.005
RVS Golfito	2 877	0.011	0.010	0.110	0.100
RVS Pejeverro	763	0.003	0.003	0.029	0.026
RVS Preciosa Platanares	257	0.001	0.001	0.010	0.009
RVS Punta Rio Claro	320	0.001	0.001	0.012	0.011
RVS Cerro Redondo	680	0.003	0.002	0.026	0.024
RVS Finca Barú	327	0.001	0.001	0.012	0.011
RVS Hacienda Avellana	500	0.002	0.002	0.019	0.017
RVS Portalón	449	0.002	0.002	0.017	0.016
ZP Las Tablas	19 981	0.076	0.069	0.763	0.692

¹ Only protected areas within the potential distribution of the species (see text) are shown. Protection categories include National Park (PN), Wildlife Reserve (RVS), National Wetland (H), Protective Zone (ZP).

² MVA confidence limits estimated from values of minimum viable populations for snakes from Reed et al. (2003) under two density conditions³: low (0.048 individuals/Ha) and high (0.48 ind./Ha). * = protected areas large enough to support a minimum viable population.

Lachesis muta stenophrys Taylor 1954
Lachesis muta Vial & Jiménez-Porras 1967
Lachesis muta stenophrys Bolaños 1982
Lachesis muta melanocephala
 Solórzano & Cerdas 1986
Lachesis muta melanocephala
 Campbell & Lamar 1989
Lachesis melanocephala
 Zamudio & Greene 1997
Lachesis melanocephala
 McDiarmid, Campbell, & Touré 1999
Lachesis melanocephala Savage 2002
Lachesis melanocephala
 Fernandes, Franco & Fernandes 2004
Lachesis melanocephala
 Campbell & Lamar 2004
Lachesis melanocephala Solórzano 2004

Description of the neotype: MZUCR-23185 (Fig. 1A), is an adult male from San Juan de Rincón, Península de Osa, province of Puntarenas, along the Pacific South of Costa Rica (8.78363; -83.47683, 267 m elevation); collected on June 18, 2008. The dorsal coloration is a pale yellow, on which lies a pattern of 26 black rhomboidal blotches (Fig. 1D), the dorsal part of the head is uniform black (Fig. 1B), chin region is clear (Fig. 1C), and the venter is uniformly white. The measurements and scutellation are as follows: snout-vent length (SVL) = 1 890 mm; total length (TL) = 2 050 mm; head length (HL) = 71 mm; ventrals = 215; cloacal plate = single; divided subcaudals = 44; dorsal scales (keeled and protuberant) at midbody = 36; interoculars = 9-11; supralabials = 9-9; and infralabials = 13-13.

Additional specimen: MZUCR-1589, and adult female from Playa Blanca, Puerto Jiménez, Península de Osa, province of Puntarenas, collected on August 1966; SVL = 1 650 mm; TL = 1 820 mm; HL = 70 mm; ventrals = 215; subcaudals = 38; dorsal scales at midbody = 41; interoculars = 9-10; supralabials = 8-9; and infralabials = 13-13.

Natural history account: *Lachesis melanocephala* is a terrestrial species that is

mainly active at dusk or night (Solórzano, 2004), although a series of recent observations suggest that this species can be active also during the day. The species often hides among the roots of large trees, under logs, and in patches of dense vegetation mostly in primary and undisturbed secondary forests (Fig. 2A, Fig. 2B, Fig. 2C). The Black-headed Bushmaster also occupies subterranean cavities and mammal burrows, where it resides for indefinite periods. It appears to select strategic locations from which it can passively observe potential prey, a behavior characteristic of other species in the genus (Greene & Santana, 1983; Greene, 1997; Solórzano, 2004, Diniz-Sousa, Moraes, Rodrigues-da-Silva, Oliveira, & Caldeira, 2020). When hunting, it bites and holds on to its prey until it becomes immobilized by the venom, as is reported for other Bushmaster species (Diniz-Sousa et al., 2020). Both adults and juveniles seem to feed exclusively on small mammals, although not much information is available about their diet. Our few stomach contents and fecal analysis reveal rodents such as spiny rats (usually *Heteromys desmarestianus* and *Proechimys semispinosus*) and marsupials (family Didelphidae) as common prey items.

Its defensive behavior includes raising the head and coiling the body in a threatening posture while vibrating the tail forcefully against the ground. The Black-headed Bushmaster has a bad reputation among the species of its genus being an irascible or nervous snake, an idea that prevails even among people accustomed to its handling or capture (Ripa, 1994; Campbell & Lamar, 2004). This reputation possibly derives from the fact that it is a species that is much more willing to lift its head and part of its body during defensive movements and escapes (Fig. 2D). Despite this, in our experience, it seldom shows a disposition to strike.

Adults of this species attain a maximum total length of 2.3 m, with a mean of 1.9-2.0 m (Solórzano, 2004). Reproduction in *L. melanocephala* is seasonal, and, in captivity, copulation has been reported from October to January and hatching from May to early



Fig. 2. Different resting sites for *Lachesis melanocephala*. (A, B, and F) Under palm leaves on the forest floor. (C) In tree buttress. (D, E) Periscopic displacement by raising the head. (A, B, C, D and E - Photos by Roel De Plecker; F - photo by Jacobo Mesén Sandoval).

July (De Plecker & Dwyer, 2020). Mating includes violent movements in which the male could knock the female off the ground with his coils (Ripa, 1994, Ripa, 2004). As seen in other vipers, the male first advances toward the female and rubs his chin in her dorsum. An unusual behavior, however, is that at some point, the male turns around and, with his back on top of her, venter upwards, begins with his own back to rub the female's back forward and

backward as if sawing (De Plecker & Dwyer, 2020). This “upside-down sailing” is presumably behavior to stimulate copulation. Ripa (1994) suggests that the prominent spinal ridge observed in *L. melanocephala* and *L. stenophrys* might serve this stimulation function.

The combat between males occur during the breeding period, but there is no field description of it. However, comprehensive observations come from captivity. According

to Ripa (1994), the combat between males is not explicit, and it is not as spectacular or violent as the behaviors described for courtship. However, De Plecker and Dwyer (2020) described how a captive male lost its life due to stress from ritual combat. Males try to coiling on top of each other, and this behavior is repeated for several nights before copulation.

In *L. melanocephala*, clutches are between 6-16 eggs, with an incubation period between 74-101 days in captivity (Ripa, 2004; De Plecker & Dwyer, 2020). This period is similar to that observed for *L. stenophrys* (75-106 days) on the Caribbean versant (personal observation, Chacon-Gutiérrez & Valverde, 2004). Females generally use holes in the ground or abandoned burrows to deposit their eggs. Eggs are deposited directly into the substrate within the burrow. The female protects them by wrapping them with her coils, and as she laid them, she frequently flicks her tongue over the surface of the egg, as in recognition (De Plecker & Dwyer, 2020).

Maternal care has been suggested in all bushmaster species; *L. melanocephala* is no exception. The female bushmaster protects her eggs by staying with them in the burrow throughout the entire incubation period, hardly ever leaving them to drink water. Females become more restless, even more irascible, during this period; in captivity, it is still a delicate task to separate them from their egg clutches (personal observation, De Plecker & Dwyer, 2020).

As in other vipers that protect their eggs and offspring from predators (Greene, May, Hardy, Scituro, & Farrell, 2002), maternal care in this species has an associated cost. Throughout the incubation period, the female fasts, this causes her to lose a significant fraction of her weight. The prolonged fast can last up to six months in total, and the reduction is estimated between 15 and 30 % of body mass (Ripa, 1994). It is not clear how long it takes for females to regain their weight in the field or the effect this reproductive cost has on the population level. Still, it possibly means that the females must wait more than a year to

reproduce again (see Alves, Argôlo, & Carvalho, 2014 for a similar situation in *L. muta*). This hypothesis contrasts with the fact that in captivity, it is possible to breed females of this and other *Lachesis* species annually (Corrales, Meidinger, Rodríguez, Chacón, & Gómez, 2014). At birth, neonates' mean total length is 44.2 cm, with an average weight of 72.9 g (De Plecker & Dwyer, 2020).

Distribution: As stated before, the distribution of this species in Costa Rica is currently restricted to the South Pacific region (Fig. 3A). However, in the past, *L. melanocephala* reached at least the Central Pacific of the country, as evidenced by a 1967 record from Alto Los Guarumos (elev. ca. 500 m) near Puriscal, San José province (Solórzano, 2004). At that time, the natural vegetation in this region was not as altered as it is today, and forest cover was extensive. In Panama, *L. melanocephala* is known from a single specimen collected in Chiriquí, near the border with Costa Rica (Dwyer & Perez, 2009); another specimen, deposited in the Museum of Vertebrate Zoology (MVZ 27321) is from an unknown Panamanian locality (Campbell & Lamar, 2004). In this country, the Black-headed Bushmaster likely occurs in Western locations adjacent to the edge of Costa Rica, on the Pacific hillside of the Talamanca mountain range, since no significant topographic and bioclimatic barriers are present in the region.

The altitudinal distribution of *L. melanocephala* ranges from sea level to 1 873 m in elevation, the highest record from Las Tablas, in the Talamanca hillside, Puntarenas province (González-Maya et al., 2014). This record exceeds the maximum reported elevation for *L. stenophrys* and -quite possibly- the other two bushmaster species (Campbell & Lamar, 2004; but see Lancini, 1986 for a high elevation record for *L. muta*). From our records, the species is more likely to be found in the interior foothills than in the outer coastal portion of Osa Peninsula. These observations, in addition to recent reports in the foothills of Talamanca (González-Maya et al., 2014), suggest that

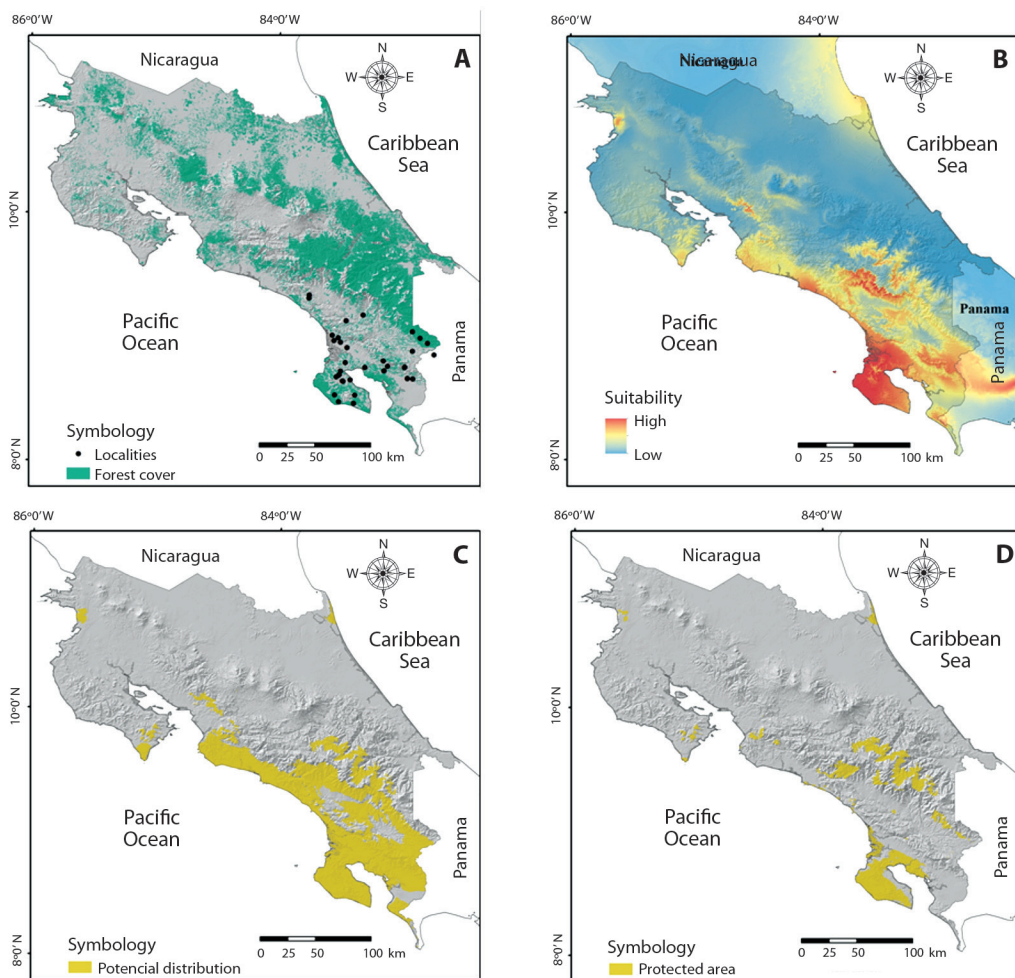


Fig. 3. **A.** Forest cover and locality records for *L. melanocephala*. **B.** Environmental niche model for *L. melanocephala* using Maxent. Localities mentioned in the text are shown. **C.** Potential distribution of *L. melanocephala* as recovered from the model. **D.** Protected wildlife areas included within the potential distribution of the species.

L. melanocephala possibly prefers drained slopes over flatlands.

Our potential distribution model ($\geq 50\%$ probability of presence) indicates 10 139.24 km² (19.84 % of the country's territory) of habitat with favorable conditions for the Black-headed Bushmaster to survive (i.e., vegetation cover and similar climatic conditions) (Fig. 3A, Fig. 3B). As expected, the model predicts areas where the species exists: the interior portion of the Osa Peninsula, the montane region of Coto Brus, the Talamanca foothills, and the

Fila Costeña region. It also includes the mountainous region in the Central Pacific, where the species existed in the past. Also, it retrieved some unexpected locations: Southern tip of the Nicoya Peninsula, the base of the Santa Elena Peninsula, and the Tortuguero region in the Northeast of the country (Fig. 3C). These locations might have suitable conditions for the species, but there is no evidence of occurrence there. For instance, the climatic conditions and forest cover on the Southern extreme of the Nicoya Peninsula are humid enough

to maintain a variety of wet forest species still found there (Laurencio, 2009), but *L. melanocephala* has never been recorder in that area.

Within the potential distribution of the species, 18 SINAC protected areas are included, counting five national parks and nine wildlife-refuges (Table 2). Approximately 2 936.10 km² of the potential distribution of *L. melanocephala* lies within these protected areas (Fig. 3D). This represents 29 % of the species possible range, thus less than a third of the black-headed Bushmaster distribution is currently under some category of protection.

To assess if these protected areas are large enough to support viable *L. melanocephala* populations, we use two density conditions and the confidence interval around the MVP mean as depicted in Table 2. Under the high-density condition, Corcovado National Park, La Amistad International Park, and the Golfo Dulce Reserve are large enough to maintain viable populations. However, suppose the low-density condition is used, which would be more likely in rare species such as *L. melanocephala*. In that case, none of the protected areas is large enough to maintain a viable *L. melanocephala* population (Table 2). This exercise demonstrates that protected areas in Costa Rica might not be sufficient to guarantee viable populations of Black-headed Bushmaster.

DISCUSSION

Lachesis melanocephala is a distinctive species with a restricted distribution and a close affinity to environments with forest cover. These characteristics make it susceptible to changes in their environment and increase the risk of extinction. Below, we present aspects that we consider relevant to its conservation, based on our analysis results.

Association to forested environments:

The strong connection between bushmasters and undisturbed forest habitats has been previously noted (Greene, 1997; González-Maya et al., 2014). It is one of the most outstanding characteristics of this group of snakes. On some

occasions, however, snakes of the genus *Lachesis* can be found in slightly more disturbed environments, such as abandoned pastureland and cocoa plantations, but always close to forest covers. From our records, *L. stenophrys* inhabit abandoned cacao plantations in the Northeast of Costa Rica, and *L. melanocephala* has been found in a small cacao plantation near Aguabuena, in the Osa Peninsula in Southern Costa Rica. Large patches of mature forest surrounded both sites. Besides, Argôlo (2004) also reports the presence of *L. muta* in cocoa plantations in the Atlantic of Brazil. Those findings are not surprising if we consider the structure of cacao plantations: although they exhibit simpler vertical structure and understory than the mature forest, their greater leaf-litter depth and the dense canopy provides similar abiotic conditions to those recorded in a forest (Lieberman, 1986). As a result, these environments can support an essential component of herpetofauna diversity in tropical regions (Argôlo, 2004; Heinen, 1992).

The reason for the close association between bushmasters and forest is not apparent: the climatic requirements (temperature, humidity) do not seem to differ from that of other species of tropical pitvipers that -in contrast- manage to survive in more altered spaces (for instances, *Bothrops asper*, Sasa et al., 2009). Little information is available on these animals' ecophysiological needs, on aspects of their diet selection and their spatial requirements. However, it seems that their home ranges are narrow (see Greene & Santana, 1983 for *L. stenophrys*). Despite the limited information available, it appears that it is in mature forest cover that bushmasters manage to find suitable nesting sites and adequate prey.

As we have seen from our experience in keeping animals in captivity, bushmasters, in general, need humid environments with dry substrates as well as hiding places for optimal maintenance. In very wet substrates, or if adequate dens are unavailable, individuals become stressed and susceptible to infections that end up killing them. These observations are consistent with the preference -at least in the case

of Central American bushmasters- to inhabit burrows located on slopes, which allow better drainage in the rainy places where they live.

Deforestation impact in *Lachesis melanocephala*: Species strongly linked to mature forest cover have the disadvantage of being susceptible to deforestation and its consequences (Sorvari & Hakkarainen, 2007; Scott et al., 2006). Forest degradation has direct (i.e., the reduction of the potential habitat of a species) or indirect (disable other components of its ecological niche, such as availability of resources) effects on forest dwellers. In the case of *L. melanocephala*, the reduction of wet lowland forests and premontane and low montane forests (see below), are responsible for its local disappearance in many sites.

The pattern of deforestation in Costa Rica is connected with the country's economic development and migration history (Locher, 1997). Most deforestation occurred in the 20th century, especially in the sixties and seventies. It was led by state policies promoting the cutting of trees and the development of land for agriculture (see Sasa et al., 2010 for a summary of historical deforestation patterns and their impact in Costa Rican herpetofauna). Driven by foreign companies and the dynamics of the international marketplace, banana plantations replaced much of the forest on the South Pacific lowlands. By the late seventies, Lowland Moist Forest in this region was limited mostly to the Osa Peninsula. Up North, in the foothills of Talamanca, the colonization process that began in the 1950s with the arrival of Italian settlers for agricultural production in the Java River Valley evolved into a critical coffee industry that continues today.

The impact of the Coto Brus mountain region's development was the substantial loss of premontane and low montane forests (Sansonetti, 1995; Quesada-Román & Díaz-Bolaños, 2019), today restricted to the protected La Amistad International Park.

The deforestation rate declined by the mid-eighties (Garcia et al., 2005), allowing the forest in some areas of the country to recover,

although much of the cover that remains is heavily fragmented (Sanchez-Azofeifa et al., 2001; Garcia et al., 2005). Forest fragmentation affects populations and ecological functionality of the system and is one of the leading causes of biodiversity reduction. Thinning of vertebrate species, known as defaunation (Dirzo & Miranda, 1991), is the norm in many forest fragments. The decline in abundance and occurrence of animals in a community can have cascading effects, affecting the dynamics of other animals and plants (Kurten, 2013). Although we do not have supporting data, it is easy to imagine that a decline in small mammals that dig burrows (agoutis, pacas, armadillos) by hunting or habitat fragmentation may severely limit refuge availability for bushmasters.

Anecdotal evidence supports the marked decline in bushmasters' relative abundance in Costa Rica, even in forested areas. During the first three years of its foundation in 1970, the Clodomiro Picado Institute (University of Costa Rica) received close to 300 individuals *L. stenophrys* from the country's Caribbean region (Taylor, Flores, Flores, & Bolaños, 1973). Today, the number of records is less than one every two years. At La Selva Biological Station, one of the best-known tropical forests in the Neotropics (McDade & Hartshorn, 1994), the species went from being seen with some frequency in the eighties and nineties (Greene & Santana, 1983; Greene, 1997; Guyer & Donnelly, 2004), to be infrequent at the turn of the century. The last *L. stenophrys* reported for this place date from 2003; ever since, it has not been observed again, despite our intensive search there in the last 17 years.

Similarly, *L. melanocephala* is now an extremely rare snake through what is left of its range. With the rise of ecotourism, the forested areas of the Southern Pacific of the country have become centers of attraction (Hunt, Durham, Driscoll, & Honey, 2015), promoting not only more people in the bushmaster habitat but also people who are actively looking for animals to display them. Despite this increase in the search effort, encounters with the Black-headed

Bushmaster are very few and sporadic, limited to only but a few locations.

Black-headed Bushmaster conservation: Our analyses suggest that the protected areas along the distribution of *L. melanocephala* may not be sufficient to guarantee viable populations. Consequently, we need to complement conservation strategies based on the protection of areas, as traditionally carried out by the SINAC, with other conservation strategies. Two approaches that could improve the species' chances of survival are ex-situ conservation (through captive breeding programs) and the establishment of a robust environmental education program (Morgan, 1992) specifically aimed at protecting the Black-headed Bushmaster. We consider these strategies to be explored or internalized in SINAC's work plans if the conservation objectives of species that do not have much chance of achieving sustainable populations in the environment are met.

Ex-situ conservation of threatened snakes is a strategy with a long tradition in North America and European countries (Barker & Barker, 2014; Odum & Reinert, 2015). Still, it has not received the same attention in tropical countries. In Costa Rica, for example, 21 out of 33 reptile centers maintain bushmasters, mainly *L. stenophrys* (Arias-Ortega, Bonilla-Murillo, & Sasa, 2016). However, only two of them attempt to breed these snakes, and only in one, Reptilanda, the captive reproduction of *L. melanocephala* has been successful (De Pleck & Dwyer, 2020). Promoting the production of *L. melanocephala* in this and other centers should be considered an essential step toward its conservation.

On the other hand, educational projects focused on snake species are currently non-existent in the country, although such programs have been implemented in other regions (Morgan & Gramann, 1989; Ballouard, Provost, Barré, & Bonnet, 2012). However, there is an experience to raise public awareness about the conservation of other reptiles, such as sea turtles, through education programs that focus on them (Sasa et al., 2010). As a first step in

establishing an educational program of this nature aimed at protecting a venomous snake, it would be necessary to determine if it can be seen as a flagship species, attracting the target audience's interest.

The Black-headed Bushmaster as a flagship species: Surrogate species is an essential complementary strategy in biodiversity conservation schemes at different scales (Bowen-Jones & Entwistle, 2002; Schlegel & Rupf, 2010). Some species are attractive because they can be used as an index of environmental attributes that are difficult, inconvenient, or expensive to measure. They can be used as a symbol that gives identity to a group. The general idea is that if resources can be allocated to protect a few attractive species, other species could also be protected. Flagship species should attract public interest in a way that no other species does. Often, the criteria used to select emblematic species are based on aesthetic condition, state of conservation, or if the species is a cultural or an indicator species (Bowen-Jones & Entwistle, 2002). According to Jepson & Barua (2015), flagship species must have characteristics that allow the public to form coherent associations with concepts located in pre-existing cultural settings. For example, species with traits that are part of the networks that incorporate human fears, such as being venomous, will be less likely to become emblematic species due to the restrictions they have to align with the frameworks that incorporate collective aspirations (Jepson & Barua, 2015). This prediction would assume that a venomous snake feared due to its large size and the potency of its venom (Jorge et al., 1997, Madrigal et al., 2012, Diniz-Sousa et al., 2020), possibly has little chance of becoming a successful iconic species.

However, attitudes about those same snake species may change in a different context (Bowen-Jones & Entwistle, 2002), for example, if the associations are perceived in a positive cultural setting. Snakes in the genus *Lachesis* are considered as indicators of pristine or mature humid forests, which have led

international and local groups to suggest their potential as flagship species (REF). Before we do so, it is necessary to create a link between bushmasters and the general public.

The scarcity of Black-headed Bushmasters and the fact that they are associated with mature forest environments in a restricted region in Southern Costa Rica are already making them enigmatic animals that attract ecotourism. In the Osa Peninsula, the search and observation of this species are promoted. The same is happening on the Caribbean side of the country with its sister species. The unexpected attraction that bushmasters generate can catapult them to the public; that could adopt them as a local emblematic species. A similar situation is already happening with the scarlet macaw and the jaguar in the region. The conservation approach of traditionally negative groups, such as snakes, must include a diagnosis of the affinity generated in the target audience and, from there, design better awareness campaigns. Therefore, we highlight the need to approach bushmaster conservation from an inclusive perspective: promote awareness of the importance of this and other species of snakes and their value to society, enhance partnerships with different stakeholders, and empower communities to act in their protection. Only then will the magnificent Black-headed Bushmaster have a chance to survive.

Ethical statement: authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements section. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

We thank Louis W. Porras, William W. Lamar, Quetzal Dwyer and Gerardo Chaves (Cachí) for their criticisms and suggestions for this manuscript and for providing us with

related data. Marcelo Carvajal shared his experiences in the field with this species. We are indebted to Roel De Plecker and Jacobo Mesén Sandoval for allowing us to use some of his photographs and to Sofia Granados for performing the spatial analyzes.

RESUMEN

Redescripción de la serpiente *Lachesis melanocephala* (Squamata: Viperidae): designación del neotipo, historia natural y estado de conservación. Introducción:

La serpiente Plato Negro (*Lachesis melanocephala*) es una especie venenosa de gran tamaño, endémica de los bosques lluviosos del Pacífico sur y suroeste de Costa Rica y el extremo oeste de Panamá. **Objetivo:** Se asigna un neotipo para la especie debido a la pérdida del holotipo original y se presentan datos actualizados de su distribución geográfica, historia natural y estado de conservación. **Métodos:** Para determinar el estado de conservación de *L. melanocephala*, reconstruimos su distribución potencial utilizando los registros de localidad de la especie y el análisis de modelado de distribución implementado en MaxEnt. En función de la distribución potencial de la especie, evaluamos la pérdida de su hábitat original y calculamos el porcentaje de su área de distribución que actualmente está protegida por el sistema de áreas protegidas del país. **Resultados:** La distribución potencial de la especie se estimó en 10 139 km², incluyendo áreas donde la especie se encuentra actualmente y áreas históricas donde la especie se ha registrado, pero se considera localmente extinta. Cerca del 29 % de esa distribución potencial se traslapa con áreas silvestres protegidas, por lo que menos de una tercera parte de la distribución potencial de la especie está bajo protección. **Conclusiones:** La degradación acelerada de su hábitat y la disminución evidente de sus poblaciones durante la última década señalan la necesidad de tomar medidas urgentes de protección para evitar el riesgo de extinción a corto plazo o mediano plazo.

Palabras clave: víboras neotropicales; conservación de serpientes; modelo de distribución de especies.

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