

## DISTRIBUTION, RANGE EXTENSION, AND CONSERVATION OF THE ENDEMIC BLACK-HEADED BUSHMASTER (*LACHESIS MELANOCEPHALA*) IN COSTA RICA AND PANAMA

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**Abstract.**—The Black-headed Bushmaster, *Lachesis melanocephala* (Viperidae: Crotalinae), is an endemic pit viper from south-eastern Costa Rica. Despite its importance with regard to medicine and conservation, the ecology and distribution of this species are still poorly known, mainly because it was only recently recognized as a full species and records are scarce across its range. Known only from the Pacific slopes of the Talamanca mountain range, *L. melanocephala* is considered uncommon, restricted to undisturbed habitats, and likely threatened with extinction. Here we summarize its distribution, in terms of the Extent of Occurrence (EOO) and Species Distribution Model (SDM), and present a new locality record for the Las Tablas Protected Zone, at an elevation of 1,873 m, in a mixed premontane and montane oak forest habitat with steep slopes. The new record is located 14 km from the Panama border, so it is very likely that the species is also found in that country. Our results indicate that *L. melanocephala* has a very small geographic range, between 3,432 and 10,507 km<sup>2</sup>, depending on the method of assessment. It is found mostly in undisturbed habitats, including tropical, premontane and montane humid, very humid, and pluvial forests. Due to its restricted geographic range and habitat specificity, the severe and continued loss of lowland and mid-elevation forests throughout its range pose serious threats to the persistence of the Black-headed Bushmaster.

**Key Words.**—Crotalinae; endemism; Las Tablas; niche; snake; Talamanca

### INTRODUCTION

Knowledge on the geographic distribution and habitat preferences, key components of the natural history of any species, forms the basis for conservation and management of biodiversity. The analysis of species distributions is also fundamental for assessing their conservation status (Balaguera-Reina et al. 2009; González-Maya et al. 2011c). Recent tools have allowed estimating species ranges with scarce information, providing new decision-making tools, and evaluating the importance of environmental determinants to species distributions, specially based on the ecological niche concept (Peterson et al. 2011).

In Costa Rica, while the biology and ecology of most snake species is still poorly understood (González-Maya et al. 2011b), vipers have received considerable attention due to their medical and public health importance (Savage 2002). The Black-headed Bushmaster, *Lachesis melanocephala* Solórzano and Cerdas, 1986 (Fig. 1), is the largest venomous snake in Central America and the second largest venomous snake in the world (Leenders 2001). It is endemic to

southern Costa Rica (Solórzano 2004). Formerly considered a sub-species, it was raised to the species category based on biochemical, morphological, and behavioral characteristics (Solórzano and Cerdas



FIGURE 1. The Black-headed Bushmaster, *Lachesis melanocephala* from Las Tablas Protected Zone, Talamanca, Costa Rica. (Photographed by José F. González-Maya).

1986; Zamudio and Greene 1997; Savage 2002; Fernandes et al. 2004). *Lachesis melanocephala* is oviparous, reaches over 3 m, is considered nocturnal and crepuscular, and is restricted to relatively intact forests (Solórzano 2004). Considered uncommon, it is prone to disappear when forests are disturbed and is recorded rarely and opportunistically in a few localities (Solórzano 2004). Despite its ecological, medical, and conservation unique features, little is known about its ecology and distribution, and currently the species is not ranked in any threat category of the IUCN Red List of Endangered Species (IUCN. 2012. The IUCN Red List of Threatened Species Available from <http://www.iucnredlist.org>. [Accessed 14 August 2013]). Herein we analyze the distribution of *L. melanocephala*, provide a range extension record and new information on habitat use, and provide information about its conservation status according to IUCN Red List of Threatened Species criteria ([www.iucnredlist.org](http://www.iucnredlist.org)).

#### MATERIALS AND METHODS

**Study site.**—Costa Rica and Panama are in the southernmost portion of Central America with an area of 51,100 and 75,515 km<sup>2</sup>, respectively. These countries harbor diverse climates and a complex orography that, along with their geographic position, support one of the richest biodiversity areas in the world (Myers et al. 2000; Olson and Dinerstein 2002). Our area of interest ranges from the Central Pacific region in Costa Rica, approximately at 9°42' N and 84°39' W, southwards to the Chiriqui province in Panama, approximately at 8°30' N and 82°20' W. The study area is included in the Isthmian-Pacific moist forests ecoregion, with a smaller portion within the Talamancan montane forests ecoregion, both considered within the Tropical and Subtropical Broadleaf Moist Forests biome (Olson et al. 2001). The area is one of the most biologically diverse regions in Mesoamerica, including the largest forest remains in both countries, and one of the 200-priority ecoregions for global conservation (Olson and Dinerstein 1998). Most of the area corresponds to the piedmont of the Talamanca mountain range, extending from southeastern Costa Rica to western Panama, with elevations from 0 to 3,820 m, mean annual precipitation of 3,500 mm, and mean temperature of 27 °C. The region contains the largest protected, intact forests patches of the country (González-Maya and Mata-Lorenzen 2008), some of the most important areas in terms of endemism and conservation (Rodríguez-Herrera et al. 2012), and was identified as a priority irreplaceable area for

conservation for many groups of animals (González-Maya et al. 2012a, 2012b, 2013; Le Saout et al. 2013).

**Methods.**—Here we present two complementary approaches to describe the distribution of *L. melanocephala*. First, we collected all available records of the species from the literature and online databases of national and international collections. For the literature review, we extracted the information from the two most comprehensive herpetological accounts for the country (Savage 2002; Solórzano 2004) and the species descriptions (Solórzano and Cerdas 1986). Additionally, we searched for specimens hosted at zoological collections through the Global Biodiversity Information Facility online database. All records were geographically referenced and mapped. We also included a new record for the species from Zona Protectora Las Tablas, Costa Rica, obtained opportunistically from extensive routine hunting-control patrols.

To determine the geographic range and habitat of the Black-headed Bushmaster, we entered the available records and our new record in a Geographic Information System (ESRI 2013). After georeferencing all records, we assessed the characteristics of each locality according to land-use type, elevation, and life-zone based on the information available from the Costa Rica National Digital Atlas (Instituto Tecnológico de Costa Rica 2008) and the Global Land Cover (European Space Agency and Université Catholique de Louvain 2009). As a first approach, based on IUCN Red List of Threatened Species guidelines, we generated a Minimum Convex Polygon (MCP) as an estimate of the Extent of Occurrence (EOO) with the outermost records, creating the smallest polygon containing all the sites of occurrence (IUCN 2012, [www.iucnredlist.org](http://www.iucnredlist.org)). Additionally, we built a species distribution model (SDM) based on maximum entropy using MaxEnt v.3.3.3K (Phillips et al. 2006) using the occurrence data, 19 bioclimatic variables from World Clim (Hijmans et al. 2005), and three topographic variables (DEM-Slope-Aspect; USGS 2012) at 1 km<sup>2</sup> resolution. We divided the occurrence data into a calibration set (75% random selection as training data) and a test dataset (25%) to run 100 replicates with different random partitions (bootstrap). We used the Receiver Operator Characteristic (ROC) curve and the Area Under the Curve (AUC) to determine model adjustment, and whether or not the model was better than chance (Phillips et al. 2006). We then generated a binary polygon (presence-absence) based on the logistic threshold and the fractional predicted area (Anderson and Martínez-Meyer 2004). With the binary polygon,

**TABLE 1.** List of records and related information used for the estimation of distribution for the Black-headed Bushmaster (*Lachesis melanocephala*) in Costa Rica (CR) and Panama. Collection abbreviations: UK-BI: University of Kansas Biodiversity Institute, NHMLAC: Natural History Museum of Los Angeles County, SDNHM: San Diego Natural History Museum, MVZ: Museum of Vertebrate Zoology.

Record	Source	Voucher number	Collection	Date of collection	Country	Locality	Geographic Reference		Elevation (m)
							Long.	Lat.	
		102539	UK-BI	1966	CR	Rincón de Osa	-83.500	8.633	99
2		154514	NHMLAC	1963	CR	Villa Briceño	-83.167	8.717	89
3	GBIF 2013	102539	UK-BI	1966	CR	Rincón de Osa	-83.500	8.633	99
4		46013	SDNHM	1963	CR	Palmar Norte	-83.533	8.983	49
5		229858	MVZ	1987	CR	Wilson Botanical Garden	-82.976	8.653	59
6		154532	NHMLAC	1962	CR	Villa Neily	-82.933	8.650	152
7		154666	NHMLAC	1962	CR	Buenos Aires	-83.333	9.167	342
8		N/A	N/A	N/A	CR	Corcovado National Park	-83.532	8.468	449
9	N/A	N/A	N/A	CR	Corcovado National Park	-83.563	8.523	82	
10	N/A	N/A	N/A	CR	Rincón de Osa	-83.532	8.679	100	
11	N/A	N/A	N/A	CR	Puerto Cortes	-83.583	9.005	57	
12	N/A	N/A	N/A	CR	Puerto Cortes	-83.569	8.960	1	
13	Savage 2002	N/A	N/A	N/A	CR	Puerto Cortes	-83.515	8.947	9
14		N/A	N/A	N/A	CR	Puerto Cortes	-83.464	8.903	11
15		N/A	N/A	N/A	CR	Pilas	-83.470	9.120	776
16		N/A	N/A	N/A	CR	Los Mogos	-83.320	8.743	179
17		N/A	N/A	N/A	CR	Piedras Blancas	-83.170	8.797	1095
18		N/A	N/A	N/A	CR	La Guaría	-83.136	8.753	558
19		N/A	N/A	N/A	CR	San Vito de Coto Brus	-82.935	8.874	912
20		N/A	N/A	N/A	CR	Sabalito	-82.815	8.938	1399
21	This study	N/A	N/A	2013	CR	Las Tablas	-82.874	8.980	1873

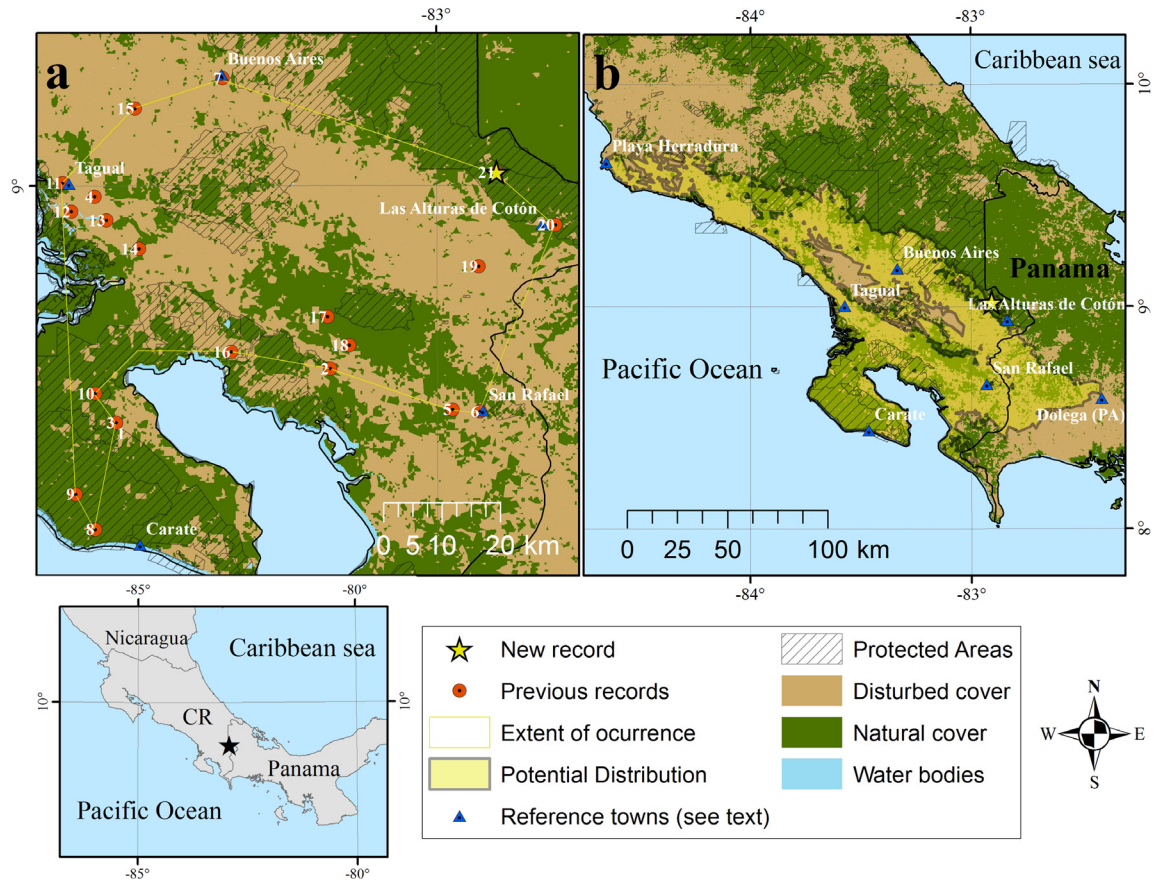
we estimated distribution parameters for Costa Rica, and proposed potential areas where ideal environmental conditions occur for the species in Panama. Using both polygons, we analyzed the available natural forested habitat for the species according to the Global Land Cover (ESA and UCLovain 2009), and considering the species as restricted to forests (Solórzano 2004). Further, we analyzed the extent of the species' distribution currently within national-level protected areas using the World Database on Protected Areas data (UNEP and IUCN 2009). Finally, we estimated the extent of available habitat by both methods, and provided the data necessary for status assessment according to the IUCN Red List of Threatened Species Category and Criteria (citation).

**RESULTS**

We obtained 21 records, including 13 records by Savage (2002), seven from the Global Biodiversity Information Facility database (The Global Biodiversity Information Facility. 2013. GBIF Backbone Taxonomy. Available from <http://www.gbif.org/species/5221064>. [Accessed 10 September 2013]), and our new locality (Table1).

Our record was obtained on 27 April 2013, during extensive routine hunting control patrols in the Las Tablas Protected Zone, an 11,000 ha reserve situated on the Pacific slopes of the Talamanca region. The male *Lachesis melanocephala* was accidentally killed

by an ATV on a dirt road during the patrols at approximately 1520. The snout-vent length of the individual was 1,665 mm, and total and tail lengths were 1,840 and 175 mm, respectively. Coloration follows that of the type specimen (Solórzano and Cerdas 1986) with a complete dorso-cephalic black coloration and yellow colored-dorsum. The specimen had 40 rows of dorsals at midbody, 214 ventrals, 37–37 divided sub-caudals, 11 infralabials, and 9–28 supralabials. The locality where the individual was collected is a transition zone between Low Montane Forest and High Montane Oak Forest (Kappelle 1996), at an elevation of 1,873 m (8°58'47.59"N, 82°52'26.75"W). It is 8 km south and 14 km west of the Panama border, in a steep area near the Cedro River (Fig. 2), characterized by mixed stands dominated by Lauraceae trees (*Persea* sp., *Ocotea tenera* and *O. mollicella*), *Clusia* sp., and oak trees (Fagaceae; *Quercus* spp. - five species), with sparse understory dominated by dwarf palms and *Chusquea* spp. bamboos (Kappelle 1996). The slope is pronounced, up to 40% on mountainsides, and elevation up to 1,920 m. The records of *Lachesis melanocephala* range from Las Tablas (our record) in the north, to the Osa Peninsula (Corcovado National Park) in the south, and from the slopes of the Talamanca cordillera near Pueblo Nuevo, Canton of Buenos Aires, Puntarenas province in the west, to near San Rafael, Canton of Canoas, Puntarenas province in the east, from sea-level up to 1,680 m of elevation. All records are located in four life zones:



**FIGURE 2.** Extent of Occurrence and records of the Black-headed Bushmaster (*Lachesis melanocephala*) (a), Species Distribution Model (b) over land-use cover (disturbed/undisturbed), and protected areas in southeastern Costa Rica and western Panama. Inset map indicates location of Costa Rica and Panama. Note that most of the known localities are located outside protected areas and natural forest cover within the species' distribution is scarce.

Premontane Humid Forests (n = 1), Very Humid Premontane Forests (n = 10), Very Humid Tropical Forests (n = 8) and Low Montane Pluvial Forests (n = 2). The habitat of these locality records includes forests (n = 8), succession areas (n = 1), forested pastures (n = 1), wood plantations (n = 1), pastures (n = 5), palm, coffee and rice crops (n = 4), and urban areas (n = 1). All collections, except our new record, were made between 1962 and 1987 and, therefore, specimens were not necessarily collected in the habitat type we report, considering severe changes in land-use from those times to the present. Records are mostly located in lowlands (15 records below 500 m of elevation), three records occurred between 500 and 1,000 m, and only three records above 1,000 m (one record at 1,400 and our record at 1,873 m; Table 1).

We estimated an EOO of 3,432 km<sup>2</sup>, mostly composed by a natural cover or mixed stands of forest and shrublands (43%; Table 2). The resulting polygon extends from near Tagual, canton of Osa, northeast to Buenos Aires, canton of Buenos Aires,

southeast to Las Alturas de Coton, canton of Coto Brus, southwest to San Rafael, canton of Canoas, southwest to near Carate, canton of Puerto Jimenez, all within Puntarenas province (Fig. 2). Nearly 440 km<sup>2</sup> or 13% of the EOO is currently protected, with the largest proportion within Golfo Dulce Forest Reserve (270.3 km<sup>2</sup>, 61.5 %) and Corcovado National Park (73 km<sup>2</sup>, 16.6 %; Table 3).

The SDM performed significantly better than random (mean AUC = 0.98), with precipitation variables (BIO13 and BIO16; Hijmans et al. 2005) contributing the most to model gain and AUC. The SDM covers 10,507 km<sup>2</sup>, with a non-continuous distribution from Playa Herradura, Puntarenas province, Costa Rica, south to Dolega, Chiriqui Province, Panama, and from the Talamanca mountains south to Osa Peninsula, from sea level to elevations of 2,000 m (Fig. 1). The SDM spans about 9,240 km<sup>2</sup> in Costa Rica and about 1,266 km<sup>2</sup> in Panama, mostly of natural forest cover or forest-shrubland mix stands (47.6 %), the rest representing



**TABLE 2.** Land-cover within the estimated range of the Black-headed Bushmaster (*Lachesis melanocephala*) in Costa Rica and Panama based on Extent of Occurrence (EOO) and Species Distribution Modeling (SDM). % indicates the percentage of each land-use cover of the total estimated distribution.

Land-use cover	EOO		SDM	
	Area (km <sup>2</sup> )	%	Area (km <sup>2</sup> )	%
Natural or semi-natural				
Closed broadleaved forest permanently flooded	170.99	4.98	765.4	7.28
Closed broadleaved deciduous forests	-	0.00	0.47	0.00
Closed-open broadleaved evergreen or semi-deciduous forests	1198.85	34.93	3823.5	36.39
Mosaic Forest-Shrubland/Grassland	20.27	0.59	73.05	0.70
Mosaic Grassland/Forest-Shrubland	104.74	3.05	336.25	3.20
Intervened				
Closed to open grassland	187.13	5.45	399.94	3.81
Closed to open shrubland	0.19	0.01	0.32	0.00
Mosaic Vegetation/Croplands	1367.70	39.85	3797.0	36.14
Mosaic Croplands/Vegetation	288.95	8.42	981.0	9.34
Rain watered croplands	83.49	2.43	237.1	2.26
Water bodies	10.17	0.30	93.0	0.89
Total	3432.49		10507.13	

intervened land-use covers (Table 2). Protected areas covering the SDM represent 1,539 km<sup>2</sup> or approximately 14.6%, where Corcovado National Park (28%) and Golfo Dulce Forest Reserve (40%) in Costa Rica are the largest areas. Only one area in Panama, Lagunas de Volcan Wildlife Refuge, covers 0.12% of the estimated distribution of the species (Table 3). Potential areas for the presence of the species in Panama, not yet confirmed, include regions between and around Piedra Candela, Rio Sereno, Monte Lirio, Plaza de Caisán, Gomez, Potrerillos Abajo, and Canoas, all within Chiriqui Province.

## DISCUSSION

Here we provide a new record for *Lachesis melanocephala*, expanding its currently known distribution, elevation range, and habitats. Based on this new record, it is likely that the species is also present in Panama, because no significant natural or anthropogenic barriers exist between this locality and

the Panamanian territory. Furthermore, our SDM indicates a high probability of presence in areas near the border. Anecdotal accounts of local residents from the new locality indicate only two additional sightings in nearly 35 years of living and intensively walking in these forests, both in the last 10 years. The new altitudinal limit defined by our record expands the current known limit for the genus of 1500 m (Solórzano and Cerdas 1986; Zamudio and Greene 1997) to 1,873 m of elevation. To our knowledge, no physiological barriers or similar have been proposed for the species. This locality also corresponds to a whole new habitat, the forest transition along the Talamanca range, which may be extremely important for the conservation of *L. melanocephala* because of its large area and good conservation status. Little research effort has focused on mid elevations, and it is likely the species may have been overlooked. Additionally, forests on the Pacific slopes of the Talamanca region have suffered intensive pressure, with clear-cutting of most of the lowland and mid-elevation slopes for extensive mono-crops and cattle production. Most of the habitat below 1500 m of elevation has been destroyed, with habitat remaining only in areas officially under protection (Zamudio and Greene 1997; Gonzalez-Maya et al. 2012b).

The Talamanca mountain range constitutes a significant natural barrier for many species, including *L. melanocephala* and *L. stenophrys* (Solórzano and Cerdas 1986; Zamudio and Greene 1997; Savage 2002; González-Maya et al. 2011a). *Lachesis melanocephala* is the only species in the genus that reaches elevations above 1,000 m, but it is the most restricted in terms of range and habitat. Interestingly, considering the potential niche conservatism between *L. melanocephala* and *L. stenophrys* (Zamudio and Greene 1997; Wiens et al. 2010), the former could be expected to inhabit areas between the Caribbean and Pacific slopes of the Talamanca range. However, our SDM only identified areas on the Pacific slopes, probably indicating a history of population isolation in the near past between both species (Peterson et al. 1999).

Based on our estimations, the EOO and the estimated available habitat or Area of Occupancy (AOO) could be used as an input for species conservation assessment following the IUCN Red List of Threatened of Species criteria (IUCN 2012). According to geographic range thresholds from IUCN, the Endangered category (EN) is applicable to species with an EOO estimated to be < 5,000 km<sup>2</sup>, while the Vulnerable category (VU) requires an estimated EOO of < 20,000 km<sup>2</sup>; thresholds for AOO for both categories are defined as < 500 km<sup>2</sup> (EN)

**TABLE 3.** Protected areas and area size in the estimated range of the Black-headed Bushmaster (*Lachesis melanocephala*) in Costa Rica and Panama based on Extent of Occurrence (EOO) and Species Distribution Model (SDM). % indicates the percentage of each land-use area in the total estimated distribution.

Country	IUCN category	National category	Name	EOO		SDM			
				Area (km <sup>2</sup> )	%	Area (km <sup>2</sup> )	%		
Costa Rica	II	National Park	Corcovado	73.01	16.60	458.25	29.81		
			Piedras Blancas	47.92	10.90	137.88	8.97		
			Internacional La Amistad	10.98	2.50	129.09	8.40		
			Chirripó	-	-	53.20	3.46		
			Marino Ballena	-	-	10.06	0.65		
			Manuel Antonio	-	-	8.55	0.56		
			Golfito	-	-	27.44	1.78		
	IV	National Wildlife Refuge	Cataratas de Cerro Redondo	-	-	5.05	0.33		
			Portalón	-	-	4.13	0.27		
			Rancho La Merced	-	-	3.44	0.22		
			Finca Barú del Pacífico	-	-	3.30	0.21		
			Hacienda Copano	-	-	2.59	0.17		
			Donald Peter Hayes	-	-	2.10	0.14		
			Aguabuena	1.82	0.41	1.71	0.11		
			Forestal Golfito S.A.	-	-	0.87	0.06		
			RHR Bancas	-	-	0.59	0.04		
			Transilvania	-	-	0.57	0.04		
			Punta Río Claro	-	-	0.37	0.02		
			VI	Forest Reserve	Golfo Dulce	270.37	61.48	610.22	39.70
					Las Tablas	35.64	8.10	48.07	3.13
Cerro de La Cangreja	-	-			8.29	0.54			
Panama	IV	Wildlife Refuge	Lagunas de Volcán	-	-	1.89	0.12		
Total				439.74	0.13	1537.17	0.15		

and < 2,000 km<sup>2</sup> (VU; IUCN 2012). Our EOO estimates derived from both methods would categorize the species as Endangered according to EOO or Vulnerable according to SDM; based on our available habitat or AOO estimate (EOO derived = 1,495 km<sup>2</sup> and SDM derived = 4,999 km<sup>2</sup>) only our EOO estimate would fall under the Vulnerable threshold. However, the current AOO based on available habitat is probably declining across the range (see IUCN 2012 for Category and Criteria details). Furthermore, some aspects such as threats and species requirements, the heavily fragmented habitat extent, and the fact that known localities are no longer within the expected habitat of the species, should be considered for the species assessment. The current range of *L. melanocephala* confirms its restricted distribution and the serious threats suffered

by the species. Despite the method used, it is clear that the species range is highly fragmented, and the low frequency that this species is detected warrants further analysis and management of current populations. Our approach has multiple considerations depending on the objectives of the management and conservation planning for the species. The EOO approach is a conservative estimate of the distribution, providing arguments for the endangerment status and setting alarms for urgent conservation actions. However, incorporating the ecological determinants of species distributions seems to be a sensible approach for range assessment (Gaston 2009). In this sense, despite the limiting factors and unresolved assumptions (Bedia et al. 2013), SDMs are some of the most adequate tools for assessing distributions from an ecological perspective

(Peterson et al. 2011). In our study, however, this approach could lead to an over-estimation of the species range, which can lead to erroneous conclusions about its conservation status. Thus ecological niche modeling represents a useful tool that should be used cautiously, and researcher expertise and critic assessments should be a requirement when applying SDMs to conservation (Elith et al. 2011). As the species range is highly restricted (around 100 km linear), mostly to undisturbed forests that have been seriously reduced, mid-elevations and isolated forest patches are potentially the only remaining habitat for the species. We suggest that intensive efforts should be invested in recording and surveying the species in new areas, to adequately understand not only the species basic ecology, range, and natural history, but also the conservation requirements for its long term survival.

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## Herpetological Conservation and Biology



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