A neonate of the Chocoan Bushmaster, *Lachesis acrochorda*, born in captivity after 72 days of incubation; it measured 47.5 cm in total length and its body mass was 52.7 g. The mother was captured at a study site in Viento Frío, Provincia de Panamá, Panama, a new locality for this species. The *in situ* reproductive biology of *L. acrochorda* remains largely unknown. © Vianka Martínez

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New distribution record and reproductive data for the Chocoan Bushmaster, *Lachesis acrochorda* (Serpentes: Viperidae), in Panama

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Abstract: We report finding three individuals (including one gravid female), a clutch of eggs, and a new locality in Panama for the rare pitviper, *Lachesis acrochorda* (García, 1896). The new locality represents a notable range extension. Additionally, we collected *in situ* reproductive data and provide information on oviposition, egg incubation, and captive husbandry.

Key words: Bushmasters, egg incubation, *ex situ* conservation, *in situ* reproductive biology

Resumen: Reportamos el encuentro de tres individuos (incluyendo una hembra grávida), una puesta de huevos, y una nueva localidad en Panamá para la rara víbora *Lachesis acrochorda* (García, 1896). La nueva localidad representa una clara extensión para la distribución de la especie. Adicionalmente, colectamos datos reproductivos *in situ*, y suministramos información sobre la oviposición, incubación de los huevos y cuido en cautiverio.

Palabras Claves: Biología reproductiva *in situ*, conservación *ex situ,* incubación de huevos, matabuey, verrugosa

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INTRODUCTION

The longest members of the family Viperidae are in the genus *Lachesis* (Daudin, 1803). Commonly known as bushmasters, the distribution of these terrestrial pitvipers is restricted to relatively undisturbed tropical wet forests in Central- and South America (Vial and Jimenez-Porras, 1967; Solórzano and Cerdas, 1986; Campbell and Lamar, 2004).

Campbell and Lamar (1989) presented an overview of *Lachesis muta* (Linnaeus), and noted the following subspecies: *L. m. stenophrys* from the Atlantic lowlands of Costa Rica and Panama, crossing over to the Pacific central in Panama; *L. m. melanocephala* from the Pacific lowlands of southeastern [= southwestern] Costa Rica; *L. m. muta* from the equatorial forests of Colombia, Venezuela, Trinidad, Guyana, Suriname, French Guyana, Brazil, Ecuador, Peru, and Bolivia; and *L. m. rhombeata* from the Atlantic forests of east-central Brazil. Zamudio and Greene (1997) subsequently conducted a phylogeographic study on *L. muta*, using mtDNA gene sequences to reconstruct phylogenetic relationships among the subspecies, and based on morphological, behavioral, and molecular evidence recognized three species of *Lachesis* (*L. melanocephala*, *L. muta*, and *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. Subsequently, Ripa (1999) described a fourth species, *Lachesis darienensis*, named after the locality of the holotype (KUMNH 75767; Laguna, Serranía del Darién, Panama), and indicated its distribution as eastern Panama and the Pacific coast of Ecuador and Colombia. Campbell and Lamar (2004), however, indicated that the name "*Bothrops acrochordus* García, 1896)" was available for this species, and used the new combination *Lachesis acrochorda*. Furthermore, based on information in Ripa (2001), Silva (2001), Zamudio and Greene (1997), and their own data, Campbell and Lamar (2004) hypothesized the relationships among the bushmasters as ((*stenophrys*, *melanocephala*) (*acrochorda* (*muta*, *rhombeata*))). In a concurrent study, Fernandes et al. (2004) supported the recognition of *L. melanocephala* and *L. stenophrys* as distinct species and regarded *L. muta* as monotypic. Additionally, in a study of snake venomics across *Lachesis*, Madrigal et al. (2012) revealed a close relationship between *L. stenophrys* and *L. melanocephala*, and their data supported the elevation of *L. acrochorda* to species status. Thus, the four species of *Lachesis* are: *L. acrochorda* (García, 1896); *L. melanocephala* Solórzano and Cerdas, 1986; *L. muta* (Linnaeus, 1766); and *L. stenophrys* Cope, 1875. Campbell and Lamar (2004) noted that the specific name of this viper, *acrochordus*, is derived from the Greek word "akrochordon," meaning "wart," in reference to the raised tubercular scales on the dorsum. In Panama and Colombia, this species commonly is known as the Chocoan Bushmaster or Verrugosa (warty). *Lachesis acrochorda* is known to teach a total length of 300 cm (Campbell and Lamar, 2004).

Campbell and Lamar (2004) indicated the distribution of *L. acrochorda* as in both versants of western Panama and into northwestern Colombia on the Atlantic coast, extending southward into the Cauca (Antioquia) and Magdalena (Caldas) River valleys, and along the Pacific versant of Colombia into northwestern Ecuador. Further, they noted this species occurring at elevations from near sea level to 1,600 m, in tropical wet and moist forest with rainfall regimes ranging from about 2,500 to 6,000 mm per year; in eastern Panama, however, the habitat of *L. acrochorda* is relatively dry.

Lachesis are large nocturnal pitvipers that often employ a "sit-and-wait" (ambush) predatory strategy, usually next to the trails and runways of such specific prey as rice rats (*Oryzomys* sp.) and spiny rats (*Proechimys* sp.), which makes them selective predators (Greene and Santana, 1983; Greene, 1997; Ripa, 1999; Campbell and Lamar, 2004; Turner et al., 2008). Little information is available on the natural history and *in situ* reproductive biology of *L. acrochorda* (Ripa, 1999; Campbell and Lamar, 2004; Fernandes et al., 2004; Henao Duque and Corrales, 2015). Members of the genus *Lachesis* are the only oviparous vipers in the New World; they deposit their eggs in hollow logs and mammal burrows, and use these sites as seasonal refugia (Mole, 1914; Ripa, 1994; Greene, 1997; Campbell and Lamar, 2004; de Souza, 2007). Henao Duque and Corrales (2015) provided the first report on the captive (*ex situ*) reproduction of this species. In this paper we report new distributional information for *L. acrochorda* in Panama, record new reproductive data, and promote *in situ* and *ex situ* breeding programs for this species to assist with its conservation.

MATERIALS AND METHODS

The study was conducted at Viento Frío (8°57'4.50"N, 78°36'32.70"W; datum UTM), an area of primary forest located in the Provincia de Panamá, ca. 10 km from the Panamerican Highway (Fig. 1). To the north and east the area is bounded by the community of San José, and to the south and west by a mountain chain, the Serranía de Maje. Large deforested areas that have been converted for agricultural use and raising livestock surround San José and the Serranía de Maje. Access to the study area required four-wheel drive vehicles for approximately two thirds of the distance, and thereafter we had to proceed on foot. Along the road, houses were surrounded by patches of forest and cleared areas.

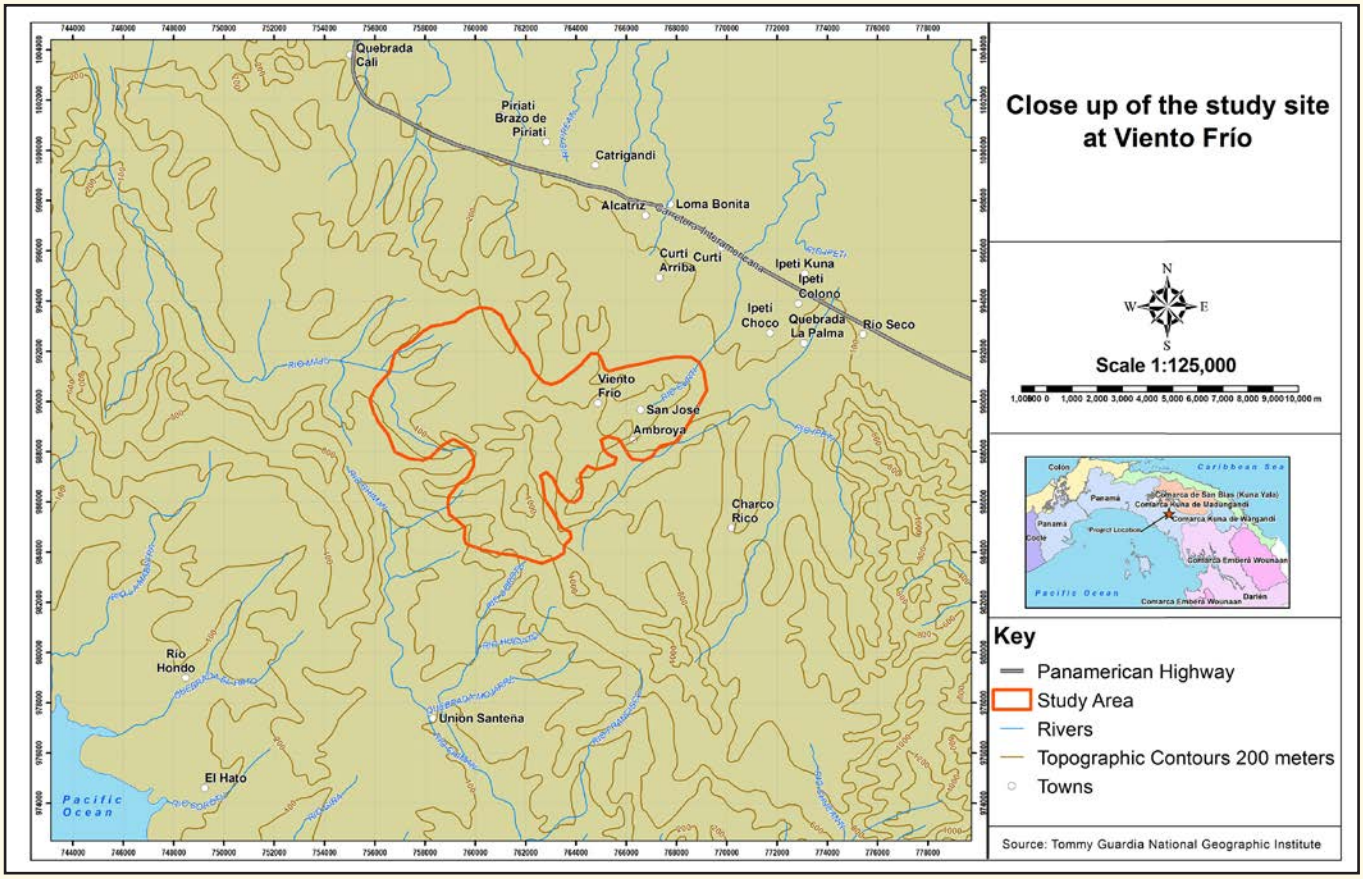

Fig. 1. Close up of the study site at Viento Frío, Provincia de Panama, Panama.

We focused our sampling in forest remnants and along major streams (Fig. 2). Specifically, for 20 months, we made field trips to the study site and collected individuals of *L. acrochorda* with the help of students, professors, and local villagers. We performed our searches along the streamside vegetation and in the forested areas up to 50 m away from the water; we also searched along steep banks, especially in hollow tree trunks and subterranean cavities or burrows, where we attempted to identify mammal activity or snake tracks. Where it was dark and difficult to see, we used flashlights to confirm the presence of a snake, and sometimes excavated some distance into the burrows. Most of our fieldwork took place at night, from 1900 to 0100 h.

On 23 January 2015 we transported the two individuals of *L. acrochorda* we collected (see below) to the Centro para Investigaciones y Respuestas en Ofidiologia (CEREO) of the Universidad de Panamá. Later, once they shed, we conducted a lepidosis analysis of the shed skins to confirm their identity as *L. acrochorda*. At CEREO, we placed them in terraria measuring 133 L × 83 W × 83 H cm in an effort to simulate their natural environment. To

reduce the possibility of stress from their new conditions, we furnished their enclosures with branches, water bowls, and maintained ideal temperatures (23–26°C) and humidity (95–98%) levels based on conditions in their microhabitats. Additionally, we covered the terrariums with black plastic to reduce visual contact with people. We offered the snakes laboratory rats (*Rattus norvegicus*) with a body mass of 100–150 g as food, but they refused to eat.

Fig. 2. Tropical Rainforest habitat of *Lachesis acrochorda* at Viento Frío, Provincia de Panamá, Panama. © Rogemif Daniel Fuentes

When eggs were laid in captivity, we numbered and placed them in an incubator (PSelecta 4000602, CO_2) with tiered racks (Fig. 3). We positioned them on the upper level, on trays with a substrate of absorbent paper, and placed trays of water on the lower level. Although the incubator was designed for use with CO_2, we did not use this component. We set the average temperature of the incubator at 26°C and the average humidity at 95%, and used thermo-hydrometers to control the settings. Once the neonates piped and emerged (hatched), we housed the neonates in individual enclosures. We waited until they shed their skin for the first time before offering them laboratory mice (*Mus musculus*) as food; they fed readily, and we maintained them on a feeding schedule of every two weeks. The body mass of the food items on the first week, fourth week, and the fourth month was 5 g, 7 g, and 15 g, respectively.

RESULTS

The study site contains remnant patches of Tropical Rainforest, where the elevation is ca. 600 m and the rainfall ca. 3,360 mm per year (Fig. 2). The sampled areas consist mainly of primary forest with trees ranging from 20 to 60 m in height, and temperatures ranging from 26 to 30°C during the day and 22 to 24°C at night. These temperatures are only for the forested areas; in deforested areas they vary according to the elevation. The Viento Frío camp is located in an area of converging air currents, where diurnal temperatures range from 22 to 25°C and fall to 18 to 20°C at night. The area consists of few isolated islands of forest, as significant anthropogenic intervention has occurred in the surrounding areas (Fig. 4). Additionally, we interviewed landowners in the study area and concluded that during each dry season the habitat is further reduced by 60–80 ha.

During a field trip to the study site in September of 2014, we found a clutch of 14 newly hatched *Lachesis acrochorda* eggs about 25–30 cm within a mammal burrow, located in a steep bank (Fig. 5; Table 1). We recorded the temperature within the burrow at 24°C; the eggs measured an average of 8 L × 4.5 W cm. We searched the area for the neonates, but found none.

Fig. 3. The eggs laid in captivity were removed from the mother after five days and placed in an incubator (PSelecta 4000602).

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In January of 2015, we returned to our study site and collected two adult *L. acrochorda*. We found the first individual (Female #1) in the shade of a tree fern (*Cryosophila* sp.), at an elevation of 694 m. We recorded the following measurements: head length (HL) = 7 cm; body length (BL) = 176 cm; tail length (TaL) = 16.2 cm; and total length (TL) = 199.2 cm. We found another individual (Male #2) in the entrance of a mammal burrow (probably *Dasypus novecinctus*) located within a steep bank. We recorded the following measurements (in cm): HL = 7; BL = 174; TaL = 17.6; and TL = 198.6 (Fig. 6). We also conducted a lepidosis analysis of both individuals and confirmed their identity as *L. acrochorda* (Table 2). On 25 April 2015, locals killed an adult *L. acrochorda* (Female # 3) at the study site.

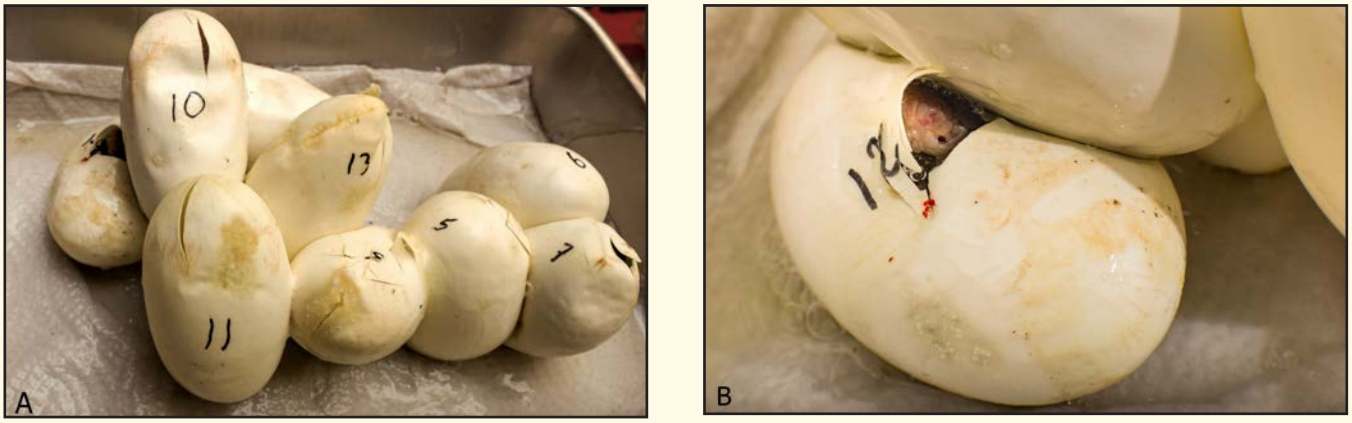

Fig. 4. (A) Piping began after 70 days of incubation; and (B) a close up of an egg. © Rogemif Daniel Fuente

Table 1. Information and results from sampling trips to Viento Frío, Provincia de Panamá, Panama.

Individuals	UTM Coordinates	Elevation (m)	Field Trips	Season	Time (h)	Number of Persons in Trip	Observations
Clutch of Eggs	8°57'6.9"N, 78°36'25.6"W	706	20 September 2014	Rainy season	2138	10	14 newly hatched eggs
Female #1	8°58'6.10"N, 78°36'54.10"W	694	19 January 2015	Dry season	1109	10	Gravid female
Male #2	8°58'2.90"N, 78°36'47.40"W	660	21 January 2015	Dry season	1319	10	Adult male
Female #3	8°57'43.7"N, 78°35'40.5"W	232	25 April 2015	Dry season	2000	5	Dead individual

On 19 February 2015, 27 days after arriving in the laboratory, Female # 1 deposited a clutch of 13 eggs (Fig. 7). The eggs were left with the female for five days, but then removed, numbered, and placed in the incubator (Fig. 3). Mean egg measurements were 7.1 L × 4.25 W cm, with a mean weight of 63.53 g (Table 3).

On the 70th day after the eggs were deposited they started to hatch (Figs. 8–10). By the 74th day 12 neonates had emerged from their eggs; all appeared healthy and in good condition except for egg #1, which never hatched. This egg contained an underdeveloped neonate, which we fixed in 10% formalin and placed in 70% ethanol before depositing it in the CEREO collection. At birth, the mean TL and mean body mass of the neonates was 44.40 cm and 49.91 g, respectively (Table 3). The sex ratio of all the neonates was five males (38.46%) and eight females (61.4%). Presently, all of the neonates are feeding on laboratory mice (12–15 g). We attempted to feed both of the adult individuals laboratory rats, but they refused food and died about four months after arriving at CEREO.

Fig. 5. The habitat of *Lachesis acrochorda* at Viento Frío is fragmented, and significant anthropogenic intervention has occurred in the surrounding areas. © Rogemif Daniel Fuentes

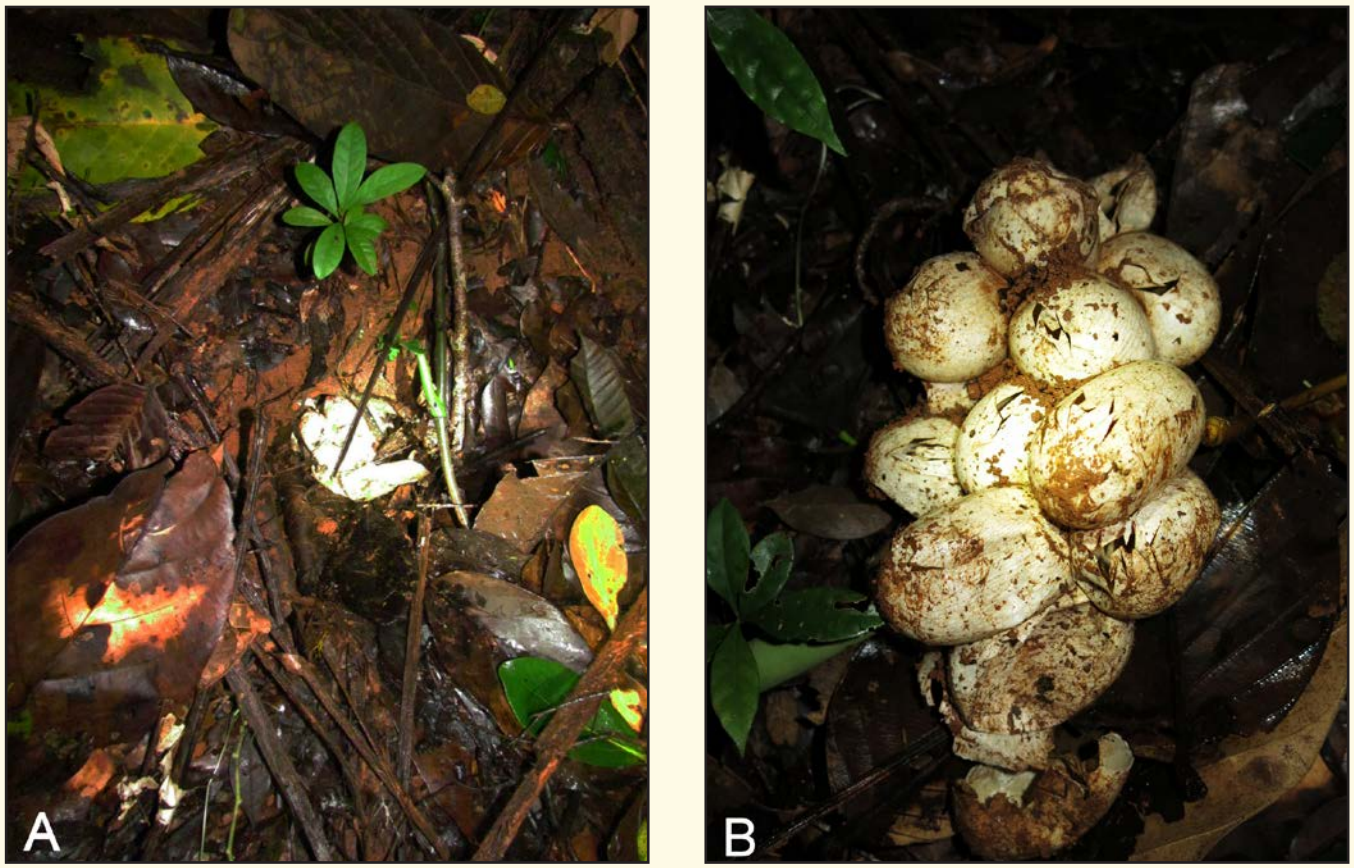

Fig. 6. (A) A clutch of eggs found inside a mammal burrow on 20 September 2014, during the rainy season; and (B) the same clutch (14 eggs) showing that the eggs had hatched. © Eileen Rivera (A) and Rogemif Daniel Fuentes (B)

Table 2. Data obtained from collected individuals (Female #1, Male #2) and literature information used in the lepidosis analysis.

Scale Characters	Female #1	Male #2	*L. acrochorda* (Campbell and Lamar, 2004)	*L. stenophrys* (Campbell and Lamar, 2004)	*L. stenophrys* (Fernandes et al., 2004)	*L. acrochorda* (Ripa, 2001)	*L. stenophrys* (Ripa, 2001)
Canthals	4	4	—	—	3–5	—	—
Supralabials	9	9	8–10 (usually 9)	7–9 (usually 8)	8–10 ♂ 8–9 ♀	9–10	7–9
Infralabials	16	16	14–17 (usually 15)	12–16 (usually 13 or 14)	13–15 ♂ 12–15 ♀	14–17	12–15
Anterior Dorsal Scale Rows	40	40	—	—	34–38 ♂ 35–39 ♀	—	—
Dorsal Scale Rows at Midbody	33	33	31–39	33–38	31–37 ♂ 33–37 ♀	31–36	33–38
Posterior Dorsal Scale Rows	25	25	—	—	24–25 ♂ 24–26 ♀	—	—
Ventrals	219	216	211–228 ♂ 211–215 ♀	191–209	198–204 ♂ 197–211 ♀	211–226	191–209
Subcaudals	34	36	32–53	35–51	46–53 ♀/♂	35–53	35–49

Table 3. Data for eggs laid in captivity, including egg measurements, number of incubation days, date of hatching, and length, weight, and sex of the neonates.

Egg Number	Egg Width (cm)	Egg Length (cm)	Days of Incubation	Date of Hatching	Total Length (cm)	Body Mass (g)	Sex
1	4.0	8.4	75	—	41.5	58.8	♂
2	4.0	6.5	73	2 May 2015	36.1	29.8	♀
3	4.1	7.0	70	29 April 2015	44.5	44.8	♀
4	4.0	6.8	72	1 May 2015	47.0	53.4	♂
5	4.7	6.7	72	1 May 2015	47.5	52.7	♀
6	4.3	6.7	75	4 May 2015	42.5	48.1	♀
7	4.4	6.2	72	1 May 2015	45.4	49.4	♀
8	4.0	6.9	73	2 May 2015	43.1	48.4	♀
9	4.7	6.9	72	1 May 2015	46.5	52.5	♂
10	4.6	7.3	72	1 May 2015	43.5	50.4	♀
11	4.2	7.3	72	1 May 2015	46.5	53.0	♂
12	4.3	7.2	72	1 May 2015	46.0	52.1	♀
13	4.0	8.4	72	1 May 2015	47.2	55.5	♂

DISCUSSION

Based on the information reported in Campbell and Lamar (2004), the individuals and eggs of *Lachesis acrochorda* we found at Viento Frío represent a notable range extension for the species. In addition, the northernmost record for *L. acrochorda* in Panama was on the northwest side of Golfo de San Miguel, in the Darién (J. Campbell, pers. comm.), and the records from Viento Frío, in the Provincia de Panamá, represent a range extension of ca. 120 km to the NW from the Golfo de San Miguel locality (Fig. 11).

Henao Duque and Corrales (2015) noted that although *L. acrochorda* is found in remote areas of primary forest, fragmentation and destruction of the natural habitat and the largely negative reaction by humans to venomous snakes have impacted populations. The population of *L. acrochorda* at Viento Frío occurs in a fragmented area, bounded by large tracts of land that have been deforested for livestock grazing and other agricultural uses (Fig. 4). An analysis of the maps produced by Autoridad Nacional del Ambiente (now Ministerio de Ambiente) indicates that an estimated 48% of the forest has been lost since 1992, and thus this area has been reduced to a few biogeographic islands of forest. Because primary forest in this area continually is being lost, a policy of *in situ* conservation should be established for this population, as the loss of habitat has placed it at a high risk of disappearing. Strategies for preventing the loss of habitat fragmentation should be promoted, such as ecological tourism and implementation of private natural reserves, with an option for reforestation and the re-introduction of native species.

At the Dallas Zoo, after two years of unsuccessful breeding attempts with captive *L. muta*, changes in temperature and humidity levels eventually led to reproduction (Boyer et al., 1989). In Venezuela, a well-marked breeding season apparently is not evident for *L. muta*, for in the wild neonates can be found at different times of the year (G. Corrales, D. Flores, and A. Gómez, unpublished). In Brazil, de Souza (2007: 41) reported that, "there is no such thing as a 'breeding season' for bushmasters (= *L. rhombeata*) in the wild." Further, de Sousa (2007) noted that the idea of no breeding season was supported by the fact that in any 12-month period there was no pattern as to the size (thus age) of animals encountered. Collectively, these data suggest that a specific breeding season might not be present in *L acrochorda*, and that clutches and hatchlings can be found throughout the year.

Fig. 7. An adult (Male #2) *Lachesis acrochorda* found at Viento Frío, Provincia de Panamá, Panama.
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Fig. 8. Photo of *Lachesis acrochorda* (Female #1) taken three days after she deposited a clutch of 13 eggs.
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Fig. 9. A neonate of *Lachesis acrochorda* that just hatched.
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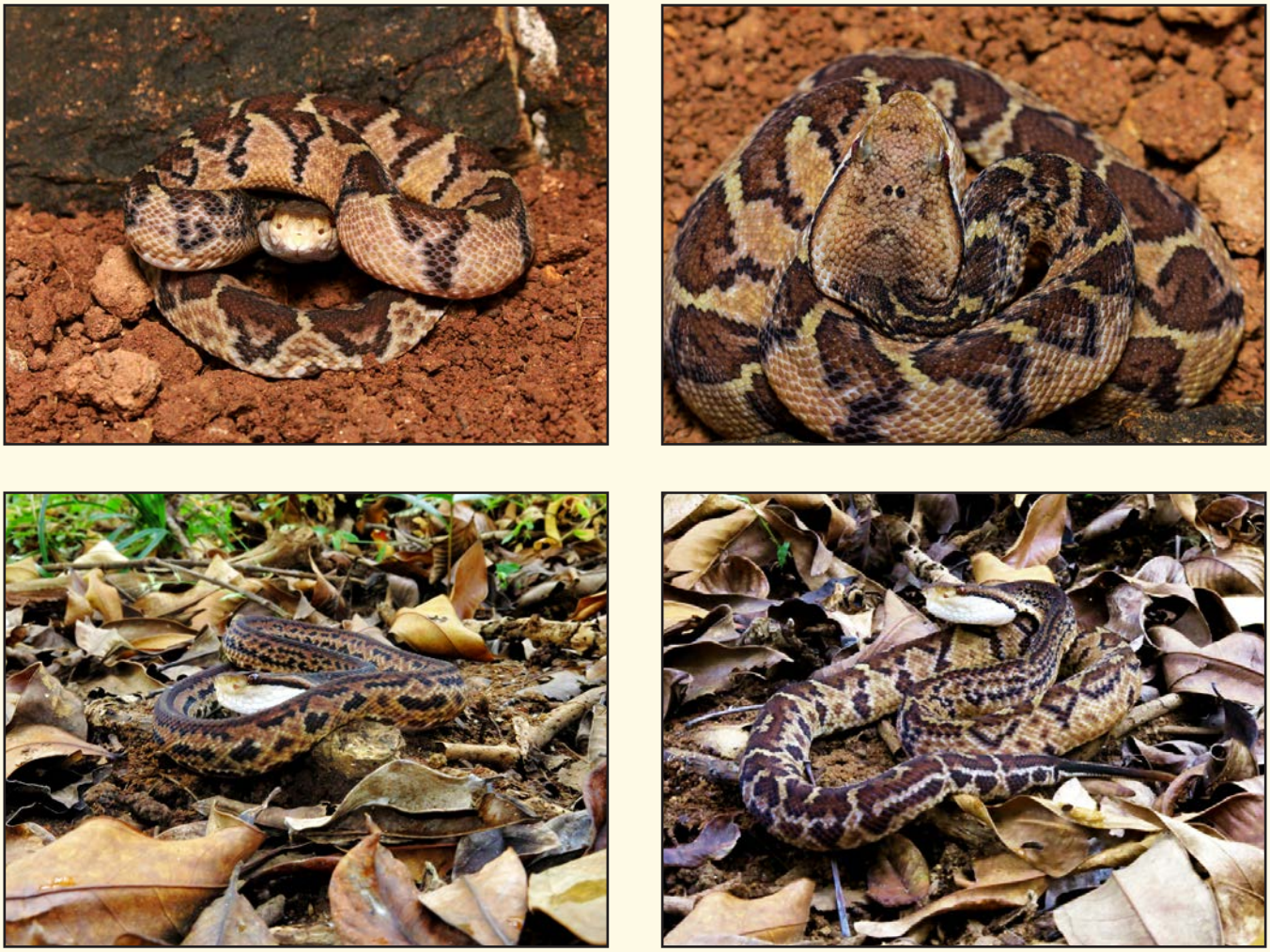

Fig. 10. Variation in color pattern seen in neonates of *Lachesis acrochorda*.

© Vianka Martínez (top) and Rogemif Daniel Fuentes (bottom)

The average measurements of the eggs found in the wild are similar to those oviposited by Female #1. Additionally, the individuals we collected came from an isolated forest, without connection to other regions occupied by *Lachesis*, such as Colón and the western end of Comarca Kuna Yala where *L. stenophrys* has been found, or the Darién where *L. acrochorda* has been reported (Campbell and Lamar 2004). Hence, both *L. stenophrys* and *L. acrochorda* apparently are allopatric, as dry forest and the large deforested areas prevent movements by these species (Ripa, 1999). Nonetheless, a site within the Kuna Yala region potentially contains suitable habitat where *L. acrochorda* and *L. stenophrys* might occur in sympatry (R. Fuentes and G. Corrales, pers. observ.).

Several authors have reported captive reproduction in bushmaster species (Boyer et al., 1989; Ripa 1994; de Souza 2007; Corrales et al., 2014). Only a single report of captive reproduction, however, is available for *L. acrochorda* (Henao Duque and Corrales, 2015), who recorded a clutch of 11 eggs that were maintained at temperatures from 21.3 to 27.1°C and a relative humidity of 78.7–95.6%, and in which the incubation period lasted 93–96 days and seven eggs hatched. As a result of the low incubation temperatures, the period of incubation was longer than the one recorded here. Herein we report the successful incubation of eggs for *L. acrochorda* using the information obtained *in situ* from the mammal burrow where the eggs were found to apply suitable conditions for incubating the eggs in captivity. Furthermore, here we report the mean body mass of neonates as 49.9 g, whereas Henao Duque and Corrales (2015) reported a mean body mass of 42 g.

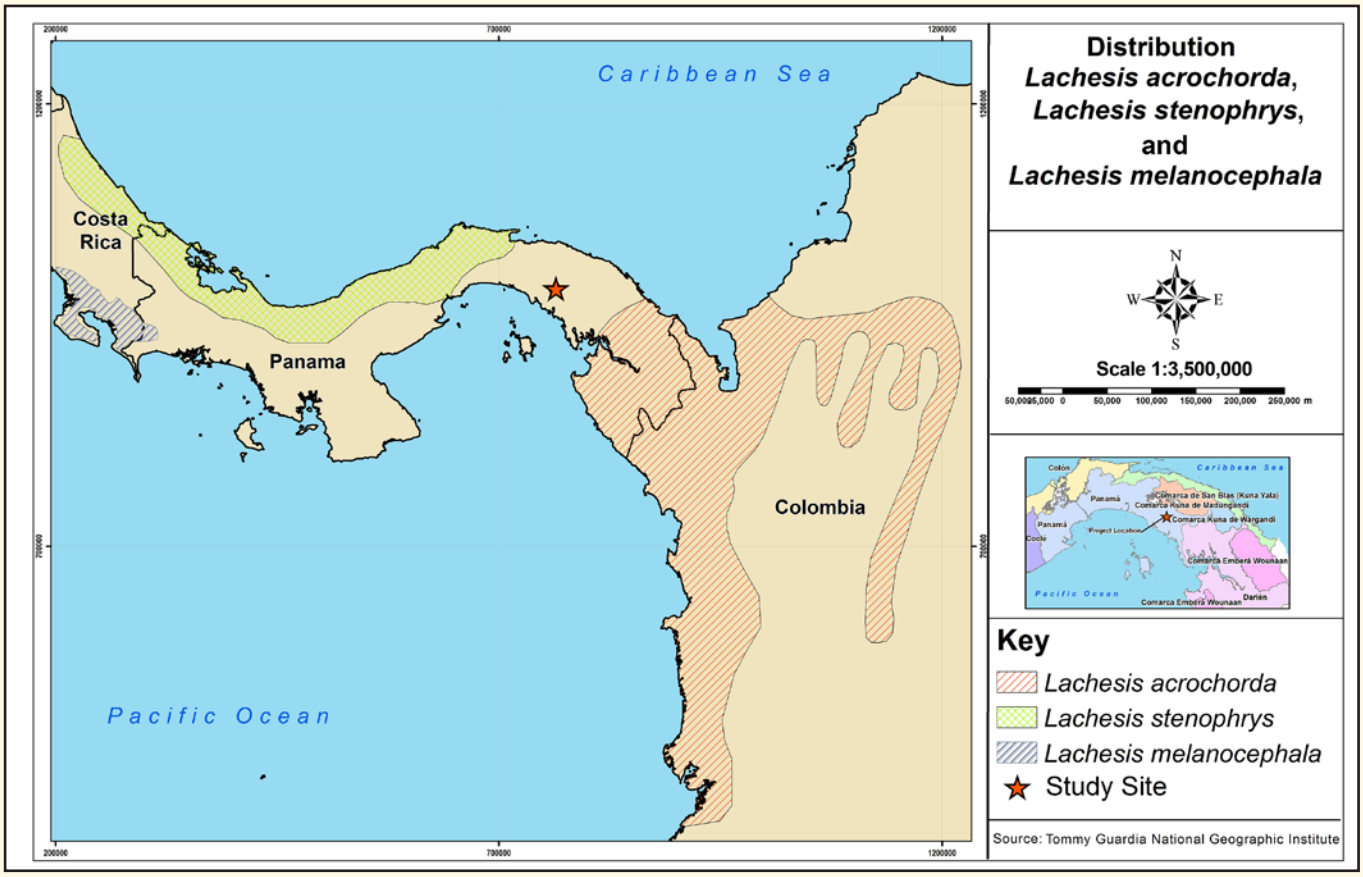

Fig. 11. Distributions of the Chocoan Bushmaster (*Lachesis acrochorda*), the Central American Bushmaster (*Lachesis stenophrys*), and the Black-headed Bushmaster (*Lachesis melanocephala*). A star indicates the new locality of Viento Frío.

In conclusion, we believe that *ex situ* reproduction and *in situ* conservation efforts in *L. acrochorda* are necessary to maintain viable populations of these uncommon, reclusive, and highly specialized snakes, particularly in areas where the destruction of its natural habitat has become a major problem.

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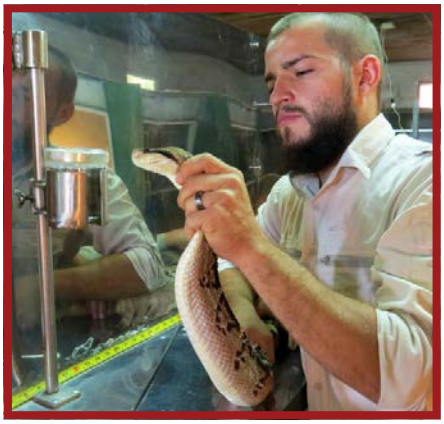

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