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 Martinez
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 pit vipers 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 re-construct 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* (Garcia, 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* (Garcia, 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 pit vipers 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.

![Close up of the study site at Viento Frío](image)

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 Ofidología (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.

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.

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 novemcinctus*) 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. 3. The eggs laid in captivity were removed from the mother after five days and placed in an incubator (PSelecta 4000602).](image) © Vianka Martinez
Table 1. Information and results from sampling trips to Viento Frio, Provincia de Panamá, Panama.

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

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 Frio is fragmented, and significant anthropogenic intervention has occurred in the surrounding areas.

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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.

<table>
<thead>
<tr>
<th>Scale Characters</th>
<th>Female #1</th>
<th>Male #2</th>
<th>L. acrochorda (Campbell and Lamar, 2004)</th>
<th>L. stenophrys (Campbell and Lamar, 2004)</th>
<th>L. stenophrys (Fernandes et al., 2004)</th>
<th>L. acrochorda (Ripa, 2001)</th>
<th>L. stenophrys (Ripa, 2001)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canthals</td>
<td>4</td>
<td>4</td>
<td>—</td>
<td>—</td>
<td>3–5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Supralabials</td>
<td>9</td>
<td>9</td>
<td>8–10 (usually 9)</td>
<td>7–9 (usually 8)</td>
<td>8–10 ♂ 8–9 ♀</td>
<td>9–10</td>
<td>7–9</td>
</tr>
<tr>
<td>Infra labials</td>
<td>16</td>
<td>16</td>
<td>14–17 (usually 15)</td>
<td>12–16 (usually 13 or 14)</td>
<td>13–15 ♂ 12–15 ♀</td>
<td>14–17</td>
<td>12–15</td>
</tr>
<tr>
<td>Anterior Dorsal</td>
<td>40</td>
<td>40</td>
<td>—</td>
<td>—</td>
<td>34–38 ♂ 35–39 ♀</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Ventral</td>
<td>34</td>
<td>36</td>
<td>32–53</td>
<td>35–51</td>
<td>46–53 ♀ / ♂</td>
<td>35–53</td>
<td>35–49</td>
</tr>
</tbody>
</table>

### 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.

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


Rogemif Daniel Fuentes Magallón is a zoologist with a passion for Neotropical herpetology, who graduated from the Universidad de Panamá. His interests are in management and conservation, and currently his research focuses in studying the biology and distribution of the genus Lachesis in Panama, and uses venoms to develop this topic in the country. Rogemif previously has worked with anurans, crocodiles, and other ophidians.

Greivin Corrales Chaves was born and raised in Costa Rica. Introduced to nature as a child by one of his brothers, today his principal research interests are in the reproductive biology of Neotropical snakes. His specialty is in members of the genus Lachesis, of which he has written several papers on the captive reproduction of various species. He currently is employed at the Instituto Clodomiro Picado, Universidad de Costa Rica, and also is a professor at the Universidad del Turismo (UTUR) in Costa Rica. Greivin has lectured in national and international wildlife symposiums, and also has lent his expertise to several film crews in an effort to bring attention to the Costa Rican herpetofauna.