

# Sexual maturation in free-ranging *Chilabothrus angulifer* (Serpentes: Boidae)

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## Abstract

**Sexual maturation in free-ranging *Chilabothrus angulifer* (Serpentes: Boidae).** The Cuban Boa (*C. angulifer*) is the only boid snake in Cuba. It is the largest member of the genus, as well as the largest snake in the West Indies (> 400 cm in snout-vent length); as such, it is an iconic species of the Cuban herpetofauna. Although the snake's natural history is poorly known, several studies describe aspects of its reproductive biology in captivity. Herein we document the sizes and ages at which both sexes reach sexual maturity in nature, and show that the Cuban Boa reaches adulthood at a much smaller size than previously reported for captive snakes. Based on the limited information on the growth rate of *C. angulifer* in nature, males must reach breeding size after 3 years and females after 5 years.

**Keywords:** Cuba, Cuban Boa, endemic snake, minimum breeding size, reproductive biology, West Indies.

## Resumen

**Maduración sexual en *Chilabothrus angulifer* (Serpentes: Boidae) en la naturaleza.** El majá de Santa María (*C. angulifer*) es el único boido en Cuba. Es el mayor miembro del género, así como el mayor ofidio del Caribe Insular (> 400 cm de longitud hocico-cloaca), esto la convierte en una especie icónica de la herpetofauna cubana. A pesar de que su historia natural se conoce muy poco, varios estudios describen aspectos de su biología reproductiva en cautiverio. Aquí documentamos las edades y tallas con que ambos sexos alcanzan la madurez sexual en la naturaleza y mostramos que el majá de Santa María alcanza la adultez con una talla mucho más pequeña de lo que previamente

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se ha reportado para especímenes de cautiverio. Basados en la escasa información sobre la tasa de crecimiento de *C. angulifer* en la naturaleza, los machos deben alcanzar la talla adulta después de los 3 años y las hembras después de los 5 años.

**Palabras Clave:** talla reproductora mínima, Cuba, serpiente endémica, biología reproductiva, Caribe Insular.

### Resumo

**Maturidade sexual de *Chilabothrus angulifer* (Serpentes: Boidae) em estado selvagem.** A jiboia-cubana, *Chilabothrus angulifer*, é o único boídeo de Cuba. É a maior serpente do gênero e também das Índias Ocidentais (comprimento rostro-cloacal > 400 cm); por essa razão, trata-se de uma espécie icônica da herpetofauna cubana. Apesar de sua história natural ser pouco-conhecida, diversos estudos descrevem aspectos de sua biologia reprodutiva em cativeiro. Documentamos aqui o tamanho e a idade em que ambos os sexos atingem a maturidade sexual na natureza e mostramos que essa serpente atinge a idade adulta com um tamanho muito menor do que previamente relatado para indivíduos cativos. Com base na informação limitada sobre a taxa de crescimento de *C. angulifer* na natureza, os machos atingem o tamanho reprodutivo após 3 anos, e as fêmeas, após 5 anos.

**Palavras-chave:** biologia reprodutiva, Cuba, Índias Ocidentais, jiboia-cubana, serpente endêmica, tamanho reprodutivo mínimo.

### Introduction

The boid snake genus *Chilabothrus* Duméril and Bibron, 1844 comprises 12 species distributed in the Greater Antilles and Bahamas (Reynolds *et al.* 2013, 2016, Rodríguez-Robles *et al.* 2015). The endemic Cuban Boa, *Chilabothrus angulifer* (Cocteau and Bibron, 1840), is the only representative of the family Boidae in Cuba. It is the largest member of the genus, as well as the largest snake in the West Indies, exceeding 400 cm in snout-vent length (reviewed by Tolson and Henderson 1993, Henderson and Powell 2009). This primarily nocturnal snake is widespread in the Cuban Archipelago, occurring in a great variety of habitats from sea level to above 1200 m elevation (Henderson and Powell 2009, Rodríguez-Schettino *et al.* 2010). It was evaluated as “Near Threatened” by the IUCN Red List of Threatened Species (Day and Tolson 1996), and retained in the same category in later evaluations (Polo-Leal and Rodríguez-Cabrera 2012). Also, this boa is listed under appendix II of CITES (e.g., UNEP-WCMC 2014).

Although *Chilabothrus angulifer* is an iconic species of the Cuban herpetofauna, its natural history is poorly known; however, aspects of its reproductive biology in captivity have been described in several studies (Huff 1976, Nowinski 1977, Murphy *et al.* 1978, Bloxam and Tonge 1981, Tolson 1980, 1983, 1992, 1994, Tolson and Teubner 1987, Tolson and Henderson 1993, Morell *et al.* 1998, Polo-Leal and Moreno 2007, Morell 2009). Nevertheless, there are important gaps in our knowledge of the snake’s reproductive biology, such as the size and age at which both sexes reach sexual maturity in nature. Tolson and Teubner (1987) suggested that reproductive maturity in females of some West Indian *Chilabothrus* (referred therein as *Epicrates*, but see work of Reynolds *et al.* 2013), is determined by body size and not age. These authors concluded that *C. angulifer*, given adequate size and lipid reserves, can reproduce as early as 3 years of age, and mentioned two females born in captivity that contained ovarian follicles more than 40 mm in diameter shortly after having reached this age. Moreover, Tolson (1992) and Tolson and

Henderson (1993) argued that males can reproduce at shorter lengths (and presumably younger ages) than females, and reported a male that reached breeding size at 3 years, with snout-vent length (SVL) of 1613 mm and a body mass of 2960 g.

However, these reports are based on captive specimens raised with *ad libitum* food and water (Tolson and Teubner 1987, Tolson 1992, Tolson and Henderson 1993); the energy expenditure of these individuals would be minimal because of confinement. There are no data on the sexual maturation of *Chilabothrus angulifer* in the wild (Tolson 1992, Tolson and Henderson 1993). We predict that in nature, the age at sexual maturity may vary individually in Cuban Boas and that it is directly correlated with feeding rates. Thus, snakes that are good hunters with access to plentiful trophic resources and that live in thermally stable environments (e.g., associated to hot caves with abundance of prey) will grow faster and therefore reach breeding size earlier. Herein we report the minimum size and age required for wild *C. angulifer* to reach sexual maturity, based on histological analysis of male reproductive organs, some morphological characters, estimates of growth rate, and direct observations of reproductive activity (i.e., copulation, parturition).

## Materials and Methods

We kept male and female *Chilabothrus angulifer* in captivity to observe their reproductive behavior. Management of captive specimens largely followed the protocol of Tolson and Teubner (1987) and Tolson (1994), except for social grouping; we kept pairs isolated from conspecifics. The animals were surveyed twice a day (early in the morning and late in the afternoon) during the study period. We weighed juvenile snakes to the nearest 5 g and adults to the nearest 100 g with Pesola® spring scales. We also measured SVL and tail length with a string and a flexible measuring tape to the nearest 1 mm. Smaller quantities of tissue such as fat were

weighed with a Gram Precision® (BH-1200) electronic scale to the nearest 0.01 g.

We also checked the reproductive maturity of a small, road-killed male *Chilabothrus angulifer* by removing the testes, epididymis, and vas deferens, and fixing them in buffered neutral formalin (10%) for 72 h. Then we transferred the samples to ethanol (75%) for preservation. Histological preparations followed the methodology of Torre (1985). We sectioned the middle regions of the testes and the epididymis at a thickness of 5 µm with a manual rotary microtome, and then stained the resulting sections with hematoxylin-eosin following the protocol of Ganter and Jollès (1970). We focused our observations mainly on epididymis because sperm cells are stored here after spermatogenesis (Estrada and Uribe 2002, Gribbins and Rheubert 2011).

We also observed a group of 15 small to medium-sized Cuban Boas (970–1840 mm SVL) from a hot cave at the Ecological Reserve “Mogotes de Jumagua” (22°49'06" N, 80°08'06" W; 20 m a.s.l.), Sagua La Grande, Villa Clara Province. They were monitored at 3-month intervals during 2009. Recaptures of eight individuals (ranging in size from 970–1400 mm SVL) allowed estimates of growth rate (length) presented herein.

Geographic reference of all coordinates is WGS 84. Means are presented ± one standard deviation (SD).

## Results

At 10:00 h, on 30 March 2008, we collected a male *Chilabothrus angulifer* (Figure 1A) of unknown age (1272 mm SVL, 158 mm tail length, 900 g) on the ground of a semi-deciduous forest at Cariblanca (22°03'54" N, 79°40'19" W, 200 m a.s.l.), Fomento, Sancti Spíritus Province. Despite its small size, we suspected that it was reproductively active. The snake was active by day (the species is primary nocturnal) at the onset of the reproductive season reported for this species (discussed below) and had well-

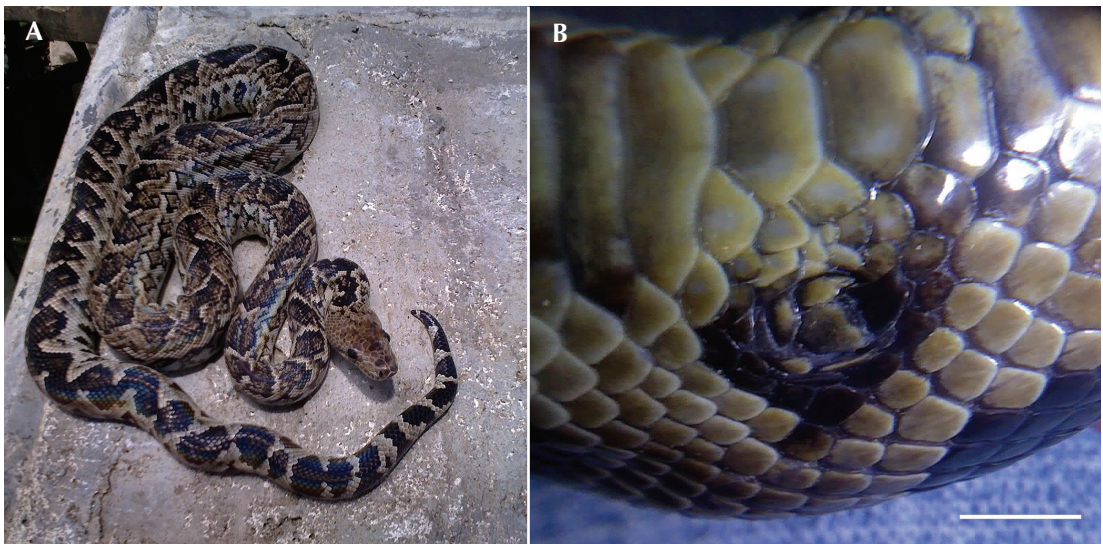
developed pelvic spurs (> 5.5 mm long, 2.5 mm wide at the base of claw vs. 2.5 mm long, 1.2 mm wide in females of equivalent size) (Figures 1B, 2). We placed this individual into captivity together with a captive-born adult female approaching 8 years of age (2233 mm SVL, 217 mm tail length, 9525 g). We recorded copulations on 19 April, 24 April, 2 May, and 8 May 2008. By 13 October 2008, the female gave birth to 13 neonates ranging in SVL from 593–646 mm, 53–67 mm in tail length, and 140–157 g. We estimated the gestation period to be anywhere between 169 and 177 days (approaching 6 months) owing to multiple copulations.

Around 08:00 h, on 27 April 2013, a mating aggregation of nine *Chilabothrus angulifer* (1 female, 8 males) was found by a local person inside a fallen hollow log of royal palm tree, *Roystonea regia* (Kunth) O. F. Cook, in a second-growth forest about 3 km west of Arimao (22°04'25" N, 80°20'25" W, 50 m a.s.l.), Cienfuegos Province. Although the local person killed the snakes, he told us the exact place of this finding so that we could examine them. All

of the snakes were engaged in courtship (i.e., males intertwined around the female) when found (R. Martínez Jr., pers. comm.). The female was 1520 mm SVL (170 mm tail length) and weighed 1800 g; a ventral incision revealed two mature ovarian follicles about 100 mm long. The males ranged in SVL from 1150–1580 mm, 140–175 mm in tail length, and 800–1600 g. All males had well-developed pelvic spurs, enlarged turgid testis, and considerable amounts of lipid reserves.

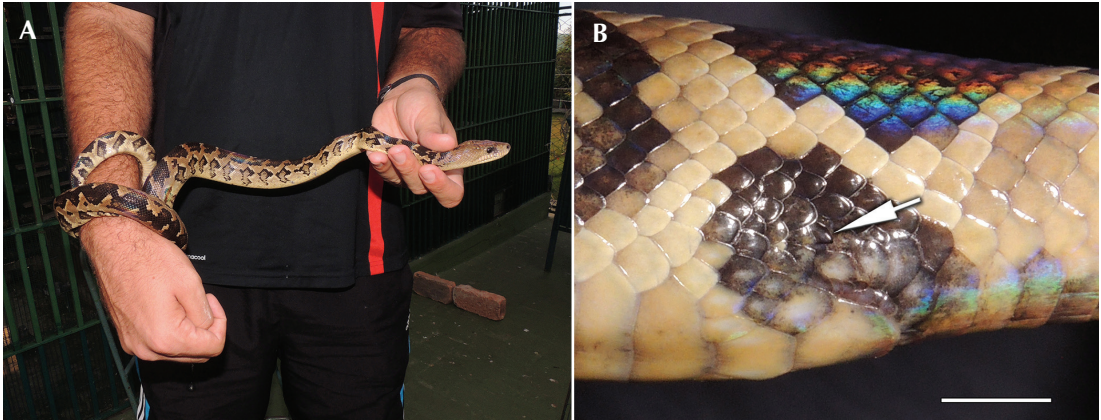
At 22:00 h, on 20 May 2013, we discovered a pair of Cuban Boas *in copula* inside a bat cave (22°24'16" N, 79°23'25" W, 75 m a.s.l.) at “Lomas las Tasajeras”, Yaguajay, Sancti-Spíritus Province. The female SVL was 1300 mm (155 mm tail length, 1700 g) and the male SVL was 1520 mm (210 mm tail length, 1500 g).

On 14 July 2013, we collected a pregnant female *Chilabothrus angulifer* (1320 mm SVL, 160 mm tail length, 1730 g) at “Las Breas” path (22°24'16" N, 79°23'25" W, 75 m a.s.l.), Camajuaní, Villa Clara Province. On 4 November 2013, it gave birth to 3 neonates in captivity;



**Figure 1.** Mature male *Chilabothrus angulifer* collected at Cariblanca, Fomento, Sancti Spíritus Province (A), and details of the vent region showing pelvic spur (B). Scale bar = 5 mm. Photographs by TMRC.





**Figure 2.** Female *Chilabothrus angulifer* (995 mm SVL, 550 g) approaching the size of the smaller males reported in this paper (A), with detail of lateral vent region (B) depicting reduced pelvic spurs (arrow). Scale bar = 5 mm. Photographs by TMRC.

they ranged in SVL from 617–635 mm, 57–65 mm in tail length, and 141–150 g.

At 08:30 h, on 30 March 2014, we found a freshly road-killed male Cuban Boa (1180 mm SVL, 145 mm tail length, 833 g) (Figure 3A) at the Cienfuegos Botanical Garden (22°07'36" N, 80°19'51" W, 70 m a.s.l.), Cienfuegos Province. A thorough examination of the snake revealed well-developed pelvic spurs (Figure 3B), considerable amount of lipid reserves (42 g = 5% of body mass) (Figure 3C), and enlarged turgid testes (Figure 3D). These features suggested sexual maturation, which we confirmed after observing sperm cells in the cross sections from the testis and epididymis. The latter structure in particular showed great amount of sperm and secretion in the lumen (Figure 4).

Seven individuals from the Ecological Reserve “Mogotes de Jumagua” were recaptured once (2 in the 3<sup>rd</sup> month, 3 in the 6<sup>th</sup> month, 1 in the 9<sup>th</sup> month, and 1 in the 12<sup>th</sup> month), and one was recaptured twice (3<sup>rd</sup> and 9<sup>th</sup> month, respectively). They increased from 7–20 mm in length per month (mean =  $14.8 \pm 4.1$  mm). All the above cases are summarized in the Table 1.

## Discussion

Ectotherms allocate a high proportion of their energy budget to growth (*e.g.*, Parry 1983, Peterson *et al.* 1999). However, free-living, non-reproductive reptiles must partition their energy budgets in other aspects besides growth, such as a more intense mobility during foraging periods, competition, defense, and interaction with unpredictable physical environments like temperature and relative humidity (*e.g.*, Vitt and Caldwell 2014). Thus, it is expected that wild animals show lower growth rates than those under captivity conditions, subjected to a forced sedentary lifestyle and usually not affected by the above mentioned factors. Also, differential hunting success must be a crucial factor affecting growth of free-living immature Cuban Boas (P. J. Tolson, *in litt.*, 14-XI-2012). The average increase in total length of the Cuban Boas recaptured in nature did not exceed 15 mm per month, in contrast to the near 30 mm per month showed by some immature captive boas under maximized food intake (Tolson 1992, Tolson and Henderson 1993, Morell *et al.* 1998, Polo-Leal and Moreno 2007). Notoriously, those eight

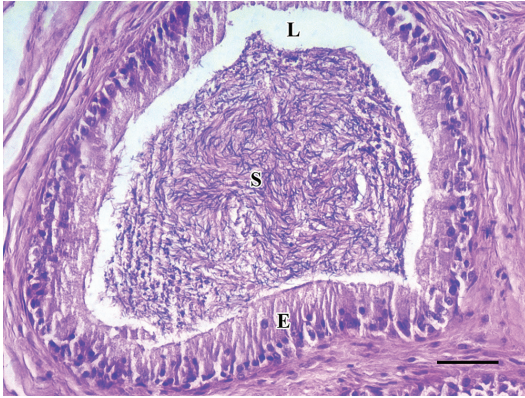


**Figure 3.** Road-killed mature male *Chilabothrus angulifer* (A) from the Cienfuegos Botanical Garden, Cienfuegos Province, showing pelvic spurs (B, arrow), lipid packages inside the body cavity around mid-region (C), and enlarged turgid testes (D): LP, lipid packages; G, gut; and T, testes. Photographs by TMRC.

**Table 1.** Summary of cases presented in this work with compelling evidences on sexual maturation of the Cuban Boa.

Case	Male (s)		Female		Evidence	Date
	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)		
1	1272	900	2233	9525	Successful fertilization	30 March
2	1150–1580	800–1600	1520	1800	Mating aggregation	27 April
3	1520	1500	1300	1700	Mating pair	20 May
4	-	-	1320	1730	Pregnant female	14 July
5	1180	833	-	-	Mature male	30 March





**Figure 4.** Cross sections of an epididymis duct of the road-killed male *Chilabothrus angulifer* from the Cienfuegos Botanical Garden, Cienfuegos Province: E = epithelium with columnar cells, L = lumen, and S = sperm cells embedded in secretions. Scale bar = 300  $\mu\text{m}$ . Photograph by JTL.

wild boas recaptured inhabited a hot cave and surroundings, a suitable habitat with large concentration of bats and apparently good shelter conditions.

There is evidence that reproductive activity in the genus *Chilabothrus* is seasonal (Vitt and Vangilder 1983, Tolson and Henderson 1993), which is consistent with most boid snakes (e.g., Fitch 1982, Vitt and Vangilder 1983, Bertona and Chiaraviglio 2003, Pizzatto *et al.* 2006a, Pizzatto and Marques 2007, Rivas *et al.* 2007; review in Reed and Rodda 2009). Courtship and mating in wild populations of *C. angulifer* occurs mainly at the onset of the rainy season, from April to June (e.g., Tolson and Henderson 1993, Morell *et al.* 1998, this paper). This allows embryos to develop during warmer months (Tolson and Henderson 1993), probably the most suitable period for thermoregulatory activity of gravid females. Parturition occurs frequently from September to December, with most in October and November (e.g., Tolson and Henderson 1993, Morell *et al.* 1998, this paper). This synchronous appearance of neonates during

the late rainy season and early dry season (“fall and early winter”) could seem controversial regarding most West Indian reptiles, which normally born at the beginning or during the core of the wet season (“spring and summer”; see Henderson and Powell 2009 for a review). However, due to the large size of neonate Cuban Boas (usually exceeding 600 mm SVL and 150 g; Tolson 1992, Polo-Leal and Moreno 2007, Morell 2009, this paper), they can consume relatively large prey almost immediately after birth, including small endotherms such as bats (Rodríguez-Cabrera *et al.* 2015), and probably rodents and birds of equivalent size. This would translate in a year-round food supply for this age class, which would not necessarily limit births during a time of the year when insects, hatchling anoles and small frogs are plentiful and thus determine the most favorable period for most reptiles in the region (see Henderson and Powell 2009 for review). Also, yolk reserves at birth must allow neonate Cuban Boas to withstand several months of starvation, without any apparent sign of health damage other than mass loss even after seven months (T. M. Rodríguez-Cabrera pers. obs. in captivity), a considerable span through which the probability to find a meal should be high.

This seasonal pattern is consistent with that observed in most viviparous snakes (Boidae, Tropicophiidae) in the West Indies (for review see Tolson and Henderson 1993, Henderson and Powell 2009), which suggests that natural selection might have favored seasonality prioritizing the occurrence of gestation during warmer months (temperature is a critical factor for embryos development). Despite year-round air temperatures in Cuba could seem high enough as to ensure adequate rates of embryonic development in Antillean viviparous snakes (Tolson and Henderson 1993), the synchrony observed in parturitions suggest that even the small differences between seasons have significant effects in animal behavior and reproductive cycles. Mean air temperatures in Cuba can drop more than 5°C during the coolest

months of the dry season (December–February), although extreme values below 10°C in winter and above 35°C in summer are not rare (data provided by the Instituto de Meteorología of Cuba, at the request of the authors), triggering even winter aggregation in highly territorial reptiles like anoles (Marrero *et al.* 2016). Also, despite hot caves (with year-round favorable and stable thermal conditions) are widespread in Cuba (Longueira 2006), we consider they are not representative enough of the species range and thus insufficient to shelter females from all subpopulations during pregnancy, being unlikely that this caves have functioned as selective pressure toward a trend for females to reproduce year-round using this sites for thermoregulation.

Some of the males described herein were by far the smallest reported for reproductively-mature *Chilabothrus angulifer*. Whether such small males found engaged in breeding aggregations could mate successfully or not is open to question; nonetheless, we consider the fact that they allocated energy to reproductive activity as enough evidence of sexual maturation. One of these males was indeed very small (i.e., 1150 mm SVL, 800 g), being probably near the lowest limit of breeding size for a male of this species. All these small males showed well-developed pelvic spurs, enlarged and turgid testis and great amount of lipid reserves (see also Pizzatto *et al.* 2006b), similar to the individual from the Cienfuegos Botanical Garden, on which we confirmed sperm production (Figure 3). Finally, the behavior observed in the male collected at Cariblanca (active by day) is consistent with the increased restlessness described for captive mature males at the onset of the reproductive season (Tolson 1992, 1994).

Gundlach (1880) commented that some male Cuban Boas aggregate around a single female during the breeding season, which he hypothesized might have led to a folk legend on a snake with multiple heads. This behavior was corroborated by other authors in captivity (Tolson 1983, Tolson and Henderson 1993) and by us in the wild (this paper), although it is

common to hear farmers and other field people in Cuba to talk about this phenomenon. Breeding or mating aggregations are relatively common in snakes (e.g., Bertona and Chiaraviglio 2003, Rivas *et al.* 2007, Jellen and Aldridge 2011, Nilson 2011). Other West Indian boids for which this behavior has been reported in the wild are the Saint Lucia boa, *Boa constrictor orophias* (note that some authors consider *Boa* populations from the Lesser Antilles as full species) and the congeneric Jamaican boa, *Chilabothrus subflavus* (Gosse 1851, Henderson and Powell 2009, Henderson and Breuil 2012). Teubner (1986) and Tolson and Teubner (1987) found that in captive Haitian boas (*C. striatus*) mean plasma testosterone levels of alpha-males (usually of larger size) increase with male-male agonistic interactions, whereas plasma testosterone levels of smaller males tend to decrease. This suggests that mating success of young mature males during their first breeding season might be lower, particularly while engaging in ritualized combat with larger males during breeding aggregations. Nonetheless, the optimum size required for a male to succeed in male-male combat or in interference competition is independent of the reproductive condition (maturity) of its gonads, even the looser (usually smaller) males are sexually mature and thus potentially able to fertilize. Thus the chance of smaller mature males to reproduce will probably depend on the occurrence of larger and/or more competitive males around a particular female.

We have observed that female Cuban Boas apparently require higher sizes to reach the minimum required for sexual maturity, as seems the rule for viviparous snakes (Shine 1978, 1994, Tolson 1992, Tolson and Henderson 1993, Rivas and Burghardt 2001, 2005, Bertona and Chiaraviglio 2003). Shine (1978) suggested two main selective pressures as the causes for this female-biased sexual size dimorphism in snakes: (1) “female fecundity is proportional to body size, so natural selection may favor females that grow to a large size before reproducing”; and (2) “reproducing necessarily involves a



female in a high energy expenditure, and risk, even if she only produces a small clutch” (see also review of Rivas and Burghardt 2001). Female fecundity is proportional to coelomic capacity, which allows larger clutches with greater possibility of larger offspring, thus with the subsequent greater chances of survival (Rivas and Burghardt 2001). Male reproductive maturity does not strongly depend on body size, mainly because of the minor cost of spermatogenesis (Shine 1978). Also, a very large body size in males could be disadvantageous because of the higher energetic cost for locomotion when tracking potential mates during the breeding season (Rivas and Burghardt 2001). Rivas and Burghardt (2001) also reasoned that there must be selective pressures toward a male local size optimum, where they are large enough as to succeed in male-male combats in the breeding aggregation, and yet small enough as to be distinguished from breeding females. These last authors also concluded that a large size would be selected in male snake species that do not show male-male combat during breeding aggregations. They mentioned that sexual size dimorphism could be the key for sex identification where a chemosensorial system is useless because both males and female in the breeding ball are impregnated in the same pheromones. However, both highly ritualized male-male combats (and/or intense agonistic behavior) and interference competition during breeding aggregations have been reported in the Cuban Boa (Tolson 1983, Tolson and Henderson 1993, this paper). Therefore, the optimum body size in males of this species appears to be selected by a combination of both types of selective pressures.

Reproduction imposes a high energetic demand to females of viviparous snakes, mainly due to catabolism and mobilization of a considerable amount of fat and structural protein (Lourdais *et al.* 2002, 2004, 2005). This can compromise seriously the performance of post-reproductive females, to the point that many of them have to reproduce at least biennially in order to guarantee a proper recovery (fat stores


and functional muscle) before the next reproduction (Lourdais *et al.* 2004). Tolson and Teubner (1987) and Petersen *et al.* (2015) have found evidence for free-ranging female Cuban Boas to reproduce at least biennially, which suggest that this species invest a large proportion of energy during pregnancy (see Bertona and Chiaraviglio 2003 for similar results with *Boa constrictor occidentalis*). So, there is a minimum optimum size required for females of each snake species at first reproduction, and that for the Cuban Boa seems to be around 1300–1400 mm SVL. A small female Cuban Boa (1460 mm SVL) was mentioned by B. R. Sheplan and A. Schwartz (in Tolson and Henderson 1993) as already containing three embryos on early August, but two of the females (1300 and 1320 mm SVL, respectively) reported herein represent the smallest mature females known for this species.

Therefore, a wild Cuban Boa with a SVL around 600 mm at birth and assuming a subsequent average growth rate of about 15 mm in length per month, could be near the size attained by the smaller reproductively-mature male reported herein (1150 mm SVL) by the spring following the third year of age. A female will require at least two more years and a larger size (ca. 1300 mm SVL and > 1700 g, minimum) to reproduce. Sex-dependent differential growth rates have not been demonstrated in immature Cuban Boas, but it probably occurs in adults as females can attain much larger sizes than males (T. M. Rodríguez-Cabrera, pers. obs.).

We do not exclude the possibility of other factors such as human predation pressure (selective killing of larger specimens), habitat (abiotic factors, food resources), and the incidence of introduced feral mammals (competition, predation) directly affecting the minimum size and age at which Cuban Boas reach sexual maturity. For example, Sasaki *et al.* (2008) found that populations of the Japanese Mamushi Pitviper, *Gloydius blomhoffii* (Boie, 1826) (Viperidae) can respond very fast to human predation pressure by significantly

changing in body size, life-history traits (i.e., litter size, mean neonate SVL, mass loss in pregnant females), and antipredation behavior. But proving a similar trend in the Cuban Boa would require long-term investigations and extensive comparisons among populations subjected to different selective pressures, including captive (control) populations.

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