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Article

Potential seed dispersers: a new facet of the ecological role of *Boa constrictor constrictor* Linnaeus 1758

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Abstract: The boa (*Boa constrictor*) is considered a top predator and its diet includes a wide variety of birds, mammals, and other reptiles, all related directly to their availability in the environment inhabited by the snake. Seven boas were found roadkilled on highways adjacent to conservation units in the semi-arid region of Rio Grande do Norte state, in northeastern Brazil. Their digestive tract was analyzed to identify food items and classify them according to their orientation in the tract. Among the food items found, the white-eared opossum (*Didelphis albiventris*) and the black-and-white tegu (*Salvator merianae*) were ingested head-first, while teeth of a punaré (*Thrichomys laurentius*) and a Spix's yellow-toothed cavy (*Galea spixii*) and hairs of an unidentified rodent were found in the intestinal tract. In addition, two novel items were identified: the plain-breasted ground-dove (*Columbina minuta*), which were ingested tail-first, and carnauba palm seeds (*Copernicia prunifera*). The orientation of the prey (head-first or tail-first) followed what was expected for each type of prey. In addition, the presence of carnauba palm seeds indicates that, while being a top predator, the boa may also be a potential disperser of seeds, which would constitute a previously unrecorded ecological role for this species.
Keywords: *Caatinga, Feeding behavior, Snake, Seed dispersal, Zoochory.*

Potenciais dispersores de sementes: uma nova faceta do papel ecológico de *Boa constrictor constrictor* Linnaeus 1758

Resumo: A jiboia (*Boa constrictor*) é considerada um predador de topo e a sua dieta inclui uma grande variedade de aves, mamíferos e outros répteis, todos relacionados diretamente com a sua disponibilidade no ambiente por ela habitado. Sete jiboias foram encontradas atropeladas em estradas no entorno de unidades de conservação da região semiárida do estado do Rio Grande do Norte, no nordeste brasileiro. O seu trato digestivo foi analisado de modo a identificar itens alimentares e a classificá-los de acordo com a sua orientação no trato. De entre os itens alimentares encontrados, o gambá-de-orelha-branca (*Didelphis albiventris*) e o teju (*Salvator merianae*) foram ingeridos no sentido ântero-posterior, enquanto que dentes de punaré (*Thrichomys laurentius*) e de preá (*Galea spixii*) e pelos de um roedor não identificado foram encontrados do trato intestinal. Dois itens novos foram identificados: a rolinha-de-asa-de-canela (*Columbina minuta*), que foi ingerida no sentido póstero-anterior, e sementes de carnaúba (*Copernicia prunifera*). A orientação dos itens (ântero-posterior ou póstero-anterior) seguiu o que era esperado para cada tipo de presa. A presença de sementes de carnaúba indica que, além de ser um predador de topo, a jiboia também pode ser um potencial dispersor de sementes, o que constitui um papel ecológico previamente não descrito para esta espécie.
Palavras-chave: *Caatinga, Comportamento alimentar, Serpente, Dispersão de sementes, Zoocoria.*

Introduction

The boa constrictor (*Boa constrictor* Linnaeus, 1758) is a large, robust snake of the Boidae family Gray, 1825a (Pizzatto et al. 2009, Mesquita et al. 2013) and is widely distributed in the Neotropical region, including South and Central America (Hynková et al. 2009, Card et al. 2016). In Brazil, this species can be commonly found in several biomes such as the Amazon and Atlantic forests (Pizzatto et al. 2009) the Cerrado (Pizzatto et al. 2009) and the Caatinga (Loebmann & Haddad 2010, Marques et al. 2017). Boas are primarily nocturnal, although daylight activity has also been reported, and present terrestrial or semi-arboreal behavior (Strüssmann & Sazima 1993, Martins & Oliveira 1999, Freitas 2003, Pizzatto et al. 2009, Bernarde 2012, Mesquita et al. 2013, Guedes et al. 2014). They are non-venomous snakes with aglyphous dentition and are considered mostly ambush predators, although they can also actively forage (Montgomery & Rand 1978, Greene 1997, Martins & Oliveira 1999, Freitas 2003). Similarly to other members of the Boidae family, boas detect their prey using infrared radiation, visual cues and chemoreception (Buning 1983, Gracheva et al. 2010). Once the prey is captured, it is subdued by constriction (Vanzolini et al. 1980, Scartozzoni & Molina 2004, Bernarde 2012) which causes circulatory arrest followed by death (Boback et al. 2015).

Boa constrictor is considered a dietary generalist, typically consuming preys available in its local environment (Pizzatto et al. 2009) such as birds, mammals, and reptiles (Vitt & Vangilder 1983, Martins & Oliveira 1999, Freitas 2003, Quick et al. 2005, Mesquita et al. 2013, Guedes et al. 2014, Marques et al. 2017). Hence, boas usually reside in higher trophic levels (Campbell & Campbell 2001) and they are considered top-predators, since they are generally free of predation, particularly in the adult stage (Sergio et al. 2014). Because of their ecological role as top-predators, boas can exert strong top-down pressure on the food webs associated with trophic cascades (Schmitz et al. 2000), affecting both species abundance and composition. This effect on community structure has also been observed in areas were boas were introduced (Martínez-Morales & Cuarón 1999, Snow et al. 2007).

The present study describes prey items found in the digestive tracts of boas found roadkilled on highways in the vicinity of two federal conservation units in the state of Rio Grande do Norte, northeastern Brazil. These records provide a preliminary analysis of the diet composition of *Boa constrictor*, for this region of the Brazilian Caatinga biome. In addition, a review on the feeding habits of this species for its Brazilian distribution was conducted to provide a general overview on the ecological role of this species, also considering the new data presented.

Materials and Methods

The *B. c. constrictor* specimens were obtained from highways adjacent to two federal conservation units in the Brazilian state of Rio Grande do Norte: (i) the Açu National Forest (5°03’15.53”S, 37°30’39.85”W, altitude: 123 m) in the municipality of Açu, located in the Vale do Açu microregion (IBGE 1992), and (ii) the Seridó Ecological Station (6°35’15.43”S, 37°15’19.63”W, altitude: 214 m) in the municipality of Serra Negra do Norte, located in the West Seridó microregion (IBGE 1992). Highways were surveyed by motor vehicle, traveling at a speed of 40–60 km/hour. Collected specimens were preserved in ice-filled coolers, and then taken to the Laboratory of Wildlife Ecology and Conservation at the Federal Rural University of the Semi-Arid in Mossoró, Rio Grande do Norte, Brazil.

In the laboratory, snout-vent length (SVL) and tail length (TL) were measured using a ruler (precision 1 mm) and body mass was determined using a 5000 g Pesola Macro-Line Spring Scale (precision 50 g). Sex of specimens was determined through the examination of the gonads. Food items were weighed using a Shimadzu AUW220 digital bench-top balance (precision 0.0001 g) and then identified to the lowest taxonomic level possible. Those items still largely intact were measured with a caliper (precision 0.05 mm) and their direction of ingestion classified as head-first or tail-first (Sazima 1989, Ruffato et al. 2003), according to the orientation of the prey item in relation to the body of the snake. The intestinal content in an advanced digestive stage was placed in a plastic sieve (1 mm mesh) and washed under running water. Its remaining content was then examined using a stereomicroscope (PHYSIS) with a WF10X wide-angle lens for the identification of hairs, feathers, bones, and teeth to the lowest possible taxonomic level. All material collected was fixed in 70% alcohol and stored in glass containers in the laboratory.

Results

Of the seven boas obtained from highways adjacent to the two federal conservation units considered, two of them were found in the Açu region and five in the Seridó region (Table 1). Two of the boas (B3 and B5) presented empty stomachs and digestive tracts, while the remaining five presented food items at different states of digestion (Table 2). Specimens B1 and B6 contained food items, in both the stomach and the digestive tract, that could be classified quantitatively and qualitatively. In specimen B1, both the white-eared opossum (*Didelphis albiventris* Lund, 1840) and the black-and-white tegu (*Salvator merianae* Duméril & Bibron, 1839) were ingested head-first. Additionally, its digestive tract also contained two seeds of the carnauba palm tree (*Copernicia prunifera* (Miller) H.E. Moore, 1963; Arecales: Arecaceae). The digestive tract of specimen B6 contained two plain-breasted ground-doves (*Columbina minuta* Linnaeus, 1766), which were both ingested tail-first. Although specimens B2 and B4 had empty stomachs, their digestive tracts did contain hairs and teeth of rodents (order Rodentia). In specimen B2, the material could only be identified to order (Greene 1959), whereas in specimen B4, the teeth could be identified as belonging to a punaré (*Thrichomys laurentius* Thomas, 1904) and a Spix’s yellow-toothed cavy (*Galea spixii* Wagler, 1831), based on available identification keys (Neves & Pessôa 2011, D’Elía & Myers 2014, Ubilla & Rinderknecht 2014).

Discussion

Both the reviewed (Table 2) and the new data here presented confirm that *Boa constrictor constrictor* acts as a top predator in the Caatinga by preying upon higher vertebrate taxa, such as mammals, birds and other reptiles. Some food items identified in this study had already been described for the diet of boas in the Caatinga, including *Galea spixii* (Vitt & Vangilder 1983) and rodents (Mesquita et al. 2013). Moreover, other food items identified were already recorded as part of the diet of Boas in other biomes (Table 1): rodents of the family Echimyidae

Table 1. Collection sites, sex, morphometric measurements and diet of the seven Boa constrictor specimens retrieved from highways of the semi-arid zone of the Brazilian Northeast. Measurements are given in millimeters (mm) and body mass in grams (g). SVL = Snout-Vent Length; TL = Tail Length; Missing values of mass, SVL and TL indicate measurements that could not be determined due to the advanced stage of decomposition of either the boa (predator found roadkilled) or its food items (digestive decomposition).

Ind.	location	Lat/long.	sex	Mass (g)	SVL (mm)	TL (mm)	Food items		
							identification	TL (mm)	Mass (g)
B1	BR 304, Açu	5°37'06.95" S, 36°53'13.77" W	F	4250	1770	185	*Didelphis albiventris*	339	123.22
							Salvator merianae	–	–
							Copernicia prunifera (seed)	20.9	1.997
							Copernicia prunifera (seed)	17.5	1.456
B2	RN 118, Açu	5°29'33.01" S, 36°51'16.15" W	F	–	–	91.7	Rodentia: teeths and hairs	–	–
B3	RN 288, Seridó	6°22'59.63" S, 37°19'41.16" W	M	–	572	70	–	–	–
B4	RN 288, Seridó	6°22'03.20" S, 37°24'36.90" W	M	2500	1435	205	*Thrichomys laurentius*	–	–
							Galea spixii	–	–
B5	RN 288, Seridó	6°23'57.72" S, 37°16'20.42" W	F	1200	1129	189	–	–	–
B6	BR 427, Seridó	6°26'24.55" S, 37°10'58.71"W	F	3000	1510	161	*Columbina minuta*	137	39.24
							Columbina minuta	–	–
							Galea spixii	–	–
							Thrichomys laurentius	–	–
B7	RN 118, Seridó	6°37'01.37" S, 37° 08'57.80" W	F	318	842	81	Mammal: hairs	–	–

Table 2. Known diet of *Boa constrictor*, *B. constrictor amarali* and *B. constrictor constrictor* for their Brazilian distribution, including biome, prey category (Aves, Mammalia and Reptilia/Squamata) and food items.

Species/subspecies	Biome	Locality, State	Prey category	Food items	Reference
B. constrictor	Amazon Forest	Ilha de Germoplasma, PA	Mammalia	*Chiropotes satanas utahicki* Hershkovitz, 1985	Ferrari et al. (2004)
B. constrictor	Amazon Forest	Oriximiná, PA	Reptilia/Squamata	*Iguana iguana* Linnaeus, 1758	Oliveira et al. (2015)
B. constrictor	Amazon Forest	Espigão do Oeste, RO	Aves	*Volatinia jacarina* Linnaeus, 1766	Bernarde and Abe (2010)
			Aves	unspecified	
			Mammalia	Rodentia Bowdich, 1821 (undet.)	
			Reptilia/Squamata	*Ameiva ameiva* Linnaeus, 1758	
B. constrictor	Amazon Forest	Cacaulândia, RO	Aves	*Ara severus* Linnaeus, 1758	Begotti and Marcos Filho (2012)
B. constrictor	Amazon Forest	Rolim de Moura, RO	Mammalia	*Alouatta puruensis* Lönnberg, 1941	Quintino and Bicca-Marques (2013)
B. constrictor	Amazon Forest	Manaus, AM	Aves	unspecified	Martins and Oliveira (1999)
			Mammalia	unspecified	
			Reptilia/Squamata	unspecified	
B. constrictor	Caatinga	Fortaleza, CE	Aves	*Troglodytes musculus* Naumann, 1823	Gondim et al. (2012)
B. constrictor	Caatinga	Pentecoste, CE	Aves	*Passer domesticus* Linnaeus, 1758	Mesquita et al. (2013)
			Mammalia	Rodentia (undet.)	
			Reptilia/Squamata	*Cnemidophorus ocellifer* Spix, 1825	
B. constrictor	Caatinga	Exu, PE	Aves	*Tinamus* sp. Hermann, 1783	Vitt and Vangilder (1983)
			Mammalia	*Galea spixii* Wagler, 1831	

Continuation Table 2.

Species/subspecies	Biome	Locality, State	Prey category	Food items	Reference
B. constrictor	Cerrado	Distrito Federal, DF	Mammalia	Muridae Illiger, 1811 (undet.)	França et al. (2008)
			Reptilia/Squamata	*Ameiva ameiva*	
B. constrictor	Cerrado	Campos Belos, GO	Mammalia	*Callithrix penicillata* É. Geoffroy, 1812	Teixeira et al. (2016)
B. constrictor	Cerrado	Campo Grande, MS	Aves	*Turdus rufiventris* Vieillot, 1818	Rocha-Santos et al. (2014)
			Aves	*Pitangus sulphuratus* Linnaeus, 1766	
B. constrictor	Cerrado	Itirapina e Brotas, SP	Aves	unspecified	Sawaya et al. (2008)
			Mammalia	*Didelphis albiventris* Lund, 1840	
B. constrictor	Atlantic Forest	Cachoeiro de Itapemirim, ES	Aves	*Furnarius* sp. Vieillot, 1816	Giori et al. (2016)
B. constrictor	Atlantic Forest	São Paulo, SP	Aves	*Diopsittaca nobilis* Linnaeus, 1758	Travaglia-Cardoso et al. (2016)
B. constrictor	Pantanal	Cuiabá, MT	Mammalia	*Noctilio albiventris* Desmarest, 1818	Esbérard and Vrcibradic (2007)
B. constrictor amarali	Atlantic Forest	Botucatu, SP	Mammalia	Erethizontidae Bonaparte, 1845 (undet.)	Cherubini et al. (2003)
B. constrictor amarali	–	Several unspecified locations	Aves	*Gallus gallus* Linnaeus, 1758	Pizzatto et al. (2009)
			Aves	*Zonotrichia capensis* Cabanis & Heine, 1850	
			Aves	Passeriformes (undet.)	
			Aves	unspecified	
			Mammalia	*Akodon cursor* Winge, 1887	
			Mammalia	*Didelphis albiventris* Lund, 1840	
			Mammalia	Cricetidae G. Fischer, 1817 (undet.)	
			Mammalia	Echimyidae Gray, 1825b (undet.)	
			Mammalia	Rodentia (undet.)	
			Reptilia/Squamata	*Ameiva ameiva*	
B. constrictor constrictor	Amazon Forest	Alta Floresta, MT	Reptilia/Squamata	*Tupinambis teguixin* Linnaeus, 1758	Rocha and Bernarde (2012)
B. constrictor constrictor	–	Several unspecified locations	Aves	unspecified	Pizzatto et al. (2009)
			Mammalia	Echimyidae (undet)	
			Mammalia	*Didelphis marsupialis* Linnaeus, 1758	
			Mammalia	Rodentia (undet.)	
			Mammalia	unspecified	
			Reptilia/Squamata	*Ameiva ameiva*	
			Reptilia/Squamata	*Tropidurus* sp Wied-Neuwied, 1825	
			Reptilia/Squamata	unspecified	

(Pizzatto et al. 2009), represented by *Thrichomys laurentius*; marsupials of the family Didelphidae Gray, 1821 (Sawaya et al. 2008, Pizzatto et al. 2009), represented by *D. albiventris*; and lizards of the family Teiidae (Pizzatto et al. 2009, Bernarde & Abe 2010, Rocha & Bernade 2012, França & Braz 2013, Mesquita et al. 2013), represented by *Salvator merianae*. However, while boas are known to prey on birds, *Columbina minuta* doves (family Columbidae Leach, 1820) had not been previously recorded in the diet of *B. constrictor*.

Food items such as *S. merianae* (this study) and *Iguana iguana* Linnaeus, 1758 (Oliveira et al. 2015) emphasizes the capacity of *Boa constrictor* for the ingestion of relatively large prey, which is a characteristic of the boids (Sazima & Martins 1990), and reinforces their ecological role of top predators. Furthermore, snakes may ingest their prey head-first, tail-first or sideways, depending on the type of animal being preyed upon (Greene 1976, Rodriguez-Robles & Leal 1993, Rodríguez-Robles et al. 1999). Boas tend to ingest more reactive animals (which are able to respond to attacks with defensive behaviors, such as biting) head-first, as observed by Scartozzoni & Molina (2004). This would be consistent with the head-first orientation of the *D. albiventris* and *S. merianae* prey items recorded in the present study. By contrast, columbiform birds, such as *C. minuta*, are more passive, and much less likely to wound a predator such as the boa. Hence, the tail-first ingestion position of *C. minuta* observed in this study is consistent with previous observations regarding preys with low relative mass ratios and small diameters when compared to snake head size, albeit for other serpent species (Greene 1976, Rodriguez-Robles & Leal 1993, Rodríguez-Robles et al. 1999).

The two seeds of the carnauba palm tree (*C. prunifera*) found in the digestive tract of a boa (B1, Table 2) raise the question of whether its ingestion was voluntary or accidental. The carnauba palm fruit presents a dark colored epicarp (when it is mature), a fleshy mesocarp (rich in nutrients) and a hard endocarp that protects the seed (Braga 2001). Since dark-colored items heat more and faster than lighter ones, it is possible that carnauba palm fruits retain more heat due to their dark coloration. Even though boas detect their prey's heat using infrared radiation (Buning 1983, Gracheva et al. 2010), they also use visual and Jacobson's organs (chemoreception), which makes the scenario of a boa mistaking these fruits for a potential prey and purposefully ingesting them highly unlikely to occur.

A more likely scenario is that the ingestion of the carnauba palm seeds/fruits by the boa was accidental, occurring during the maneuvering and swallowing of a prey (direct ingestion) or they were already within the stomach and digestive tract of the prey (indirect ingestion). Boas are known to prey on relatively large animals, such as the marsupial *D. albiventris*, which are capable of ingesting and dispersing *C. prunifera* seeds. Cantor et al. (2010) and Cáceres & Lessa (2012) found seeds of a size similar to those of *C. prunifera* in the digestive tracts of *D. albiventris*. In a camera-trap study of two areas of Caatinga (Furna Feia National Park and the TRIPOL trail on the Rafael Fernandes Experimental Farm in the municipality of Mossoró), Torquato (Torquato 2015) recorded the ingestion of *C. prunifera* seeds by: two birds, the white-naped jay (*Cyanocorax cyanopogon* Linnaeus, 1766) and rufous-bellied thrush (*Turdus rufiventris* Viellot, 1818); a mammal, the crab-eating fox (*Cerdocyon thous* Linnaeus, 1766); and a lizard, the black-and-white tegu (*S. merianae*). While it is unlikely that *C. thous* can constitute part of the boa's diet, *S. merianae* certainly is (Table 2) and the bird species most likely are. Indirect ingestion of seeds/fruits and other plant structures can be relatively common, as the two plain-breasted ground-doves found in the digestive tract of another boa (B6, Table) also contained unknown seeds.

Prior to the present study, there are no published records that describe the ingestion of fruits or seeds by boas, in its Brazilian distribution (Table 1). This lack of records could be the result of no seeds being found on the stomach and digestive tract of boas or simply because they were not considered food items, and thus unreported. However, regardless of how these fruits/seeds are ingested, the boa could have benefited from its nutritional content, in particular if the fruits possess a fleshy mesocarp. Furthermore, seeds may survive the digestive process of these snakes, in particular those which present a fruit with a hard endocarp that protects the seed, such as the carnauba palm (Braga 2001). Even though boas can carry seeds, the effectiveness of dispersal must still be confirmed, including by assessing whether these seeds can survive and become adult plants (Schupp 1993, Schupp et al. 2010). If the effectiveness of seed dispersal is confirmed, these snakes can become seed rescuers and secondary dispersers of different plants, as seen in other species (Reiserer et al. 2018). Hence, the findings of this study not only expand the list of prey known to be exploited by *B. constrictor*, reinforcing its capacity to adapt to different environments and the availability of prey (Martins & Oliveira 1999, Pizzatto et al. 2009), but also indicate that, in addition to being a top predator that feeds on terrestrial and arboreal vertebrates, the boa may also be a potential disperser of carnauba palm seeds, a previously unrecorded ecological role.

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Author Contributions

Sofia de O. Cabral: Bibliographical survey; Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Itainara da S. Freitas: Contribution to data collection.

Viviane Morlanes: Contribution to data collection; Bibliographical survey.

Marco Katzenberger: Contribution to data analysis and interpretation; Contribution to critical revision, adding intellectual content.

Cecilia Calabuig: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

All studied specimens of *Boa constrictor constrictor* were found roadkilled (dead) and were collected under the license 40620, attributed by Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio. Further ethic requirements do not apply to this study.

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