Diversity, activity patterns, and habitat use of the snake fauna of Chapada dos Veadeiros National Park in Central Brazil

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Abstract: Chapada dos Veadeiros National Park (CVNP) in central Brazil is one of the most important protected areas of Brazilian Cerrado yet the diversity that this park harbors remains unknown for many taxa. From 2006 to 2009, we studied the snake assemblage of CVNP to determine the species composition, abundance, seasonal and daily activity patterns, morphology, and habitat use. We documented 47 snake species from seven families within CVNP, with the most common species being *Bothrops marmoratus*, *Oxyrhopus trigeminus*, *Crotalus durissus* and *Bothrops moojeni*. The incidence of snakes was highly seasonal and appeared to be associated mainly with rainfall. Daily activity patterns revealed that the majority of snakes are strictly diurnal, whereas others are nocturnal or active during both periods. Species richness estimators suggest that more snake species than the 47 we documented likely occur within CVNP, indicating that it harbors one of the richest snake faunas among South American open biomes studied to date.
Keywords: *snakes, assemblage, ecology, Brazilian Cerrado.*

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Resumo: O Parque Nacional da Chapada dos Veadeiros é uma das mais importantes unidades de conservação do Cerrado brasileiro apesar de sua diversidade faunística ainda não ser totalmente conhecida. Entre 2006 a 2009, nós estudamos a taxocenose de serpentes do PNCV visando determinar a composição das espécies, abundância, padrões de atividade diários e sazonais, morfologia e uso de habitat. Foram registradas 47 espécies de serpentes pertencentes a sete famílias, sendo as espécies mais comuns *Bothrops marmoratus*, *Oxyrhopus trigeminus*, *Crotalus durissus* e *Bothrops moojeni*. A incidência das serpentes foi sazonal e é associada principalmente com a precipitação. Padrões de atividade diária revelaram que a maioria das serpentes é estritamente diurno, enquanto outras são noturnas ou ativas em ambos os períodos. Os estimadores de riqueza de espécies sugerem que a riqueza é maior que as 47 espécies documentadas indicando que o PNCV mantém uma das maiores diversidades de serpentes das áreas de Cerrado da América do Sul.
Palavras-chave: *serpentes, taxocenose, ecologia, Cerrado Brasileiro.*

Introduction

In the last decade there has been an increase in knowledge of the community ecology of South American snakes, with information about species richness and natural history being published for species in different biomes, such as Amazonia (Martins & Oliveira 1998, Bernarde & Abe 2006), Atlantic Forest (Marques & Sazima 2004, Pontes & Rocha 2008), Caatinga (Vitt & Vangilder 1983), Cerrado (França et al. 2008, Sawaya et al. 2008), Chaco (Leynaud & Bucher 2001, Scrocchi & Giraudo 2005), Pantanal (Strussmann & Sazima 1993), and Pampas grasslands (Winck et al. 2007). This recent interest in snake ecology is due to an increase in the number of herpetologists working with snakes, new methods for surveying, capturing, and tracking individual snakes (Fitch 1987), and recognition of snakes as interesting ecological models (Shine & Bonnet 2000).

The Cerrado harbors a very diverse herpetofauna with numerous endemic species (Colli et al. 2002, Costa et al. 2007, Nogueira et al. 2011). This biome covers about 2,000,000 km^2 (Oliveira & Marquis 2002), and is considered to be among the most threatened biomes in the world as the result of anthropogenic activities, such as rapid and uncontrolled development for agriculture and large-scale hydroelectric projects (Alho & Martins 1995, Ratter et al. 1997, Oliveira & Marquis 2002). These activities have lead to a highly fragmented mosaic of undisturbed Cerrado patches surrounded by agricultural fields and/or pasture. Much of the Cerrado's biodiversity has been preserved in a few major protected areas scattered throughout the biome's range (Klink & Machado 2005). However, the actual species diversity that these areas are preserving remains largely unknown for many taxa.

Here, we present the results of a three-year study on the snake assemblage of Chapada dos Veadeiros National Park (CVNP), one of the most important protected areas of Brazilian Cerrado. We focus on composition, abundance, seasonal and daily activity patterns, morphology, and habitat use of snake species.

Materials and Methods

Fieldwork was conducted on 650 non-consecutive days from 15 November 2006 to 15 April 2009 in Chapada dos Veadeiros National Park (13° 51' S to 14° 10' S, and 47° 25'W to 47° 42'W) northern Goiás State, Brazil. The CVNP covers approximately 65,512 ha of relatively undisturbed Brazilian Cerrado, and is located in a mountainous region, the Planalto Central Goiano (Felfili et al. 2007), with altitudes ranging between 620 and 1,700 m, including the highest peak in Central Brazil (Pouso Alto, with 1,784 m). The climate is type Aw in the Köppen classification, receiving annually 1500-1750 mm of a highly predictable and strongly seasonal precipitation, almost entirely restricted to October–April (Nimer 1989). Long-term climatic data from the Chapada dos Veadeiros region are summarized in Figure 1. Average temperatures vary between 20 and 26 °C (Silva et al. 2001). The natural vegetation of the CVNP is characterized by a predominance of gallery forest at low elevations and Cerrado with rocky areas at high elevations (Felfili et al. 2007).

We captured snakes by hand during visual searches and driving roads by car. Almost all snakes were measured and released at or near their capture sites. We collected a few voucher specimens of each snake species, and all individuals found dead on roads (SISBIO license 15325-1). These snakes were fixed with 10% formalin and deposited in the Herpetological Collection of Universidade de Brasília (CHUNB) (Appendix 1). We marked released snakes by scale clipping (Fitch 1987) however we did not use recaptured snakes in our analysis.

We constructed species accumulation curves for snakes of CVNP using the sample- and individual-based rarefaction methods (with the nonparametric Mao Tau estimator) to evaluate collection effort and species saturation of the assemblage (Gotelli & Colwell 2001, Colwell et al. 2011). For the sample-based method, we used days with searches as the sampling period. The function of richness (Mao Tau) was calculated as the accumulation function of species throughout the number of sampling days. The species rarefaction curves were made without replacement using 1000 randomizations. In addition, we used species richness estimators (with nonparametric incidence-based estimators: Bootstrap, Chao 2, ICE, Jacknife 1 and 2, and abundance-based data: ACE and Chao 1) to determine the expected number of snake species in the area (Colwell & Coddington 1994). Richness estimators provide a likely tool to evaluate the completeness of an inventory, but they have different accuracy depending the methods of sample and the effort (Colwell & Coddington 1994). Herein, we don't want to determine the best estimator, but to present the variation in estimates to better predict the species richness that we possible

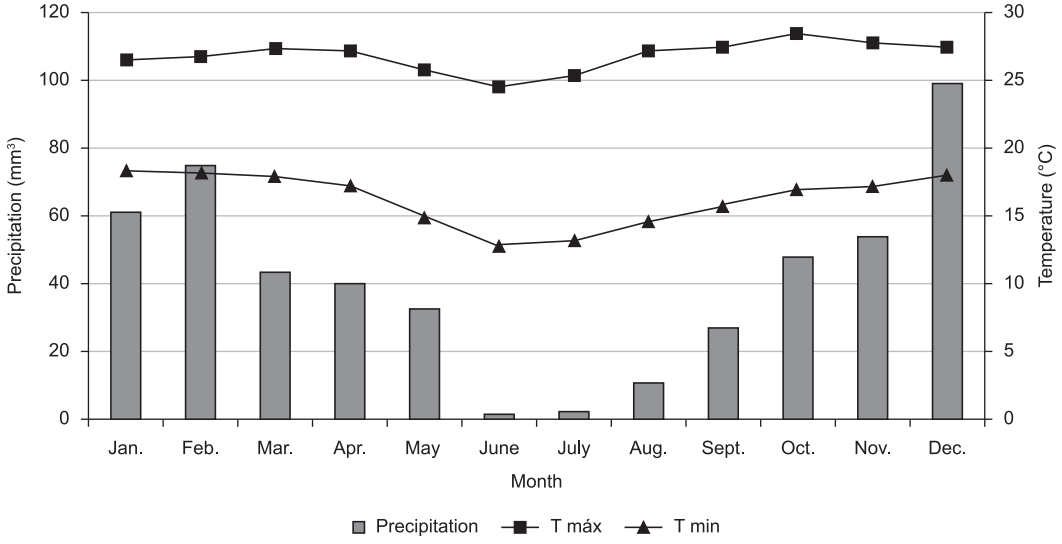

Figure 1. Long-term climatic data from the Chapada dos Veadeiros region.

find in the study area. The species rarefaction and richness estimators were performed with EstimateS 8.2.0 (Colwell 2009).

For all snakes encountered, we recorded the hour of capture and the habitat in which we found the snake. We grouped capture hours into six time periods (05:00-07:59; 08:00-11:59; 12:00-14:59; 15:00-17:59; 18:00-20:59; 21:00-24:00) to better characterize snake activity patterns. We conducted no searches between 00:00 and 04:59, and we did not use 'Brazilian summer time' (or daylight saving time when clocks of some Brazilian regions are adjusted forward one hour) during October to February. We classified habitats into one of five categories: grassland, cerrado, forest, aquatic, and anthropic. We also categorized snake species based on general habits (terrestrial, fossorial, cryptozoic, arboreal, semi-arboreal, or aquatic) using data from the literature and our collections. Finally, for all individuals, we recorded two morphological variables: snout–vent length (SVL) and tail length (TL).

We use the recent paper of Grazziotin et al. (2012) to support the taxonomy of snake species and families. We also use "*Liophis*" rather than "*Erythrolamprus*" because in Grazziotin et al. (2012) the authors comment "*Erythrolamprus* arrangement of 50 species may be challenged after a more densely sampled analysis".

Results

1. *Composition, richness and abundance*

We documented 47 species from seven families in the snake assemblage of CVNP (Table 1, Figure 2 and 3). Dipsadidae was the richest family with 28 species from seven different tribes,

Table 1. Summary of natural history information of the snakes in Chapada dos Veadeiros National Park. Abbreviations are: N = number of individuals; RA = Relative Abundance; A = arboreal, C = cryptozoic, F = fossorial, T = terrestrial, SAB = semi-arboreal, AQ = aquatic, g = grassland, ce = cerrado, fo = forest, aq = aquatic environments, an = anthropic environments. N = nocturnal, D = diurnal. Inside parenthesis in N: is number of individuals measured; and in Morphology: is minimum and maximum measurement.

Species	N	RA (%)	Morphology		Habits	Habitats	Activity
			SVL	TL			
Anomalepididae (1)							
Liotyphlops ternetzii (Boulenger, 1896)	3 (2)	0.74	(31-18)	(0.5-0.6)	F	g, ce, fo, an	N
Leptotyphlopidae (1)							
Trilepida fuliginosa (Passos, Caramaschi & Pinto, 2006)	1 (1)	0.25	16.5	1.5	F	ce	N
Boidae (3)							
Boa constrictor Linnaeus, 1758	7 (4)	1.72	117.1 (100-150)	16 (15.5-16.5)	T, SAB	fo, ce, an	N, D
Epicrates crassus Cope, 1862	11 (8)	2.71	54 (35-106)	6.9 (4.5-12)	T, SAB	ce, g	N, D
Eunectes murinus (Linnaeus, 1758)	1 (1)	0.25	1574	261	AQ	fo, aq	N, D
Viperidae (4)							
Bothrops moojeni Hoge, 1966	25 (20)	6.16	66.2 (32-138)	10.5 (5-18)	T	fo, ce	N, D
Bothrops marmoratus Silva & Rodrigues, 2008	68 (58)	16.75	40.3 (19.8-63)	6 (2-8.8)	T	g, ce	N, D
Bothrops pauloensis (Amaral, 1925)	2 (1)	0.49	40.5	4.8	T	g, ce	N, D
Crotalus durissus Linnaeus, 1758	32 (22)	7.88	75.5 (30-108)	6.86 (2.2-12.9)	T	ce, g, fo, an	N, D
Colubridae (9)							
Chironius exoletus (Linnaeus, 1758)	3 (2)	0.74	(85.4-88.5)	(46.6-48)	A, SAB	fo	D
Chironius flavolineatus (Boettger, 1885)	9 (5)	2.22	66.3 (57.8-75)	42.5 (35.7-47.5)	A, SAB	g, ce, fo	D
Chironius quadricarinatus (Boie, 1827)	3 (2)	0.74	(36.6-55.5)	(39.5-61.1)	A, SAB	ce, g	D
Drymarchon corais (Boie, 1827)	3 (2)	0.74	(117.2-149.8)	(28-34.3)	T, SAB	ce, g, fo	D
Drymoluber brazili (Gomes, 1918)	2 (1)	0.49	84	39	T	ce	D
Mastigodryas bifossatus (Raddi, 1820)	5 (4)	1.23	112.9 (99-128)	44.4 (37.7-50.9)	T	g, ce, fo	D
Oxybelis aeneus (Wagler, 1824)	7 (3)	1.72	63.1 (51-78)	36.2 (26.5-47)	A, SAB	ce, g	D
Spilotes pullatus (Linnaeus, 1758)	1 (1)	0.25	1586	525	A, SAB	fo, ce	D
Tantilla melanocephala (Linnaeus, 1758)	8 (4)	1.97	26.6 (23-30.5)	9.3 (8.1-10.5)	F, C	g, ce	N
Dipsadidae (28)							
Dipsadidae incertae sedis (1)							
Xenopholis undulatus (Jensen, 1900)	1 (1)	0.25	24	3.8	T, C	fo	N
Dipsadinae (3)							
Atractus albuquerquei Cunha & Nascimento, 1983	1	0.25	-	-	C	fo	N
Leptodeira annulata (Linnaeus, 1758)	6 (3)	1.48	46.2 (41.8-54)	15.9 (14.7-18)	A, SAB	fo, ce	N
Sibynomorphus mikanii (Schlegel, 1837)	19 (14)	4.68	37.6 (14.8-49.5)	8 (3.7-11.1)	T	fo, ce, an	N
Xenodontinae (24)							
Elapomorphini (1)							
Apostolepis ammodites Ferrarezzi, Barbo & Albuquerque, 2005	3 (1)	0.74	32.4	3.5	F	ce, g	N, D

Table 1. Continued...

Species	N	RA (%)	Morphology		Habits	Habitats	Activity
			SVL	TL			
Echinantherini (1)							
Taeniophallus occipitalis (Jan, 1863)	1 (1)	0.25	38.5	13.5	T	ce, fo	D
Hydropsini (1)							
Helicops angulatus (Linnaeus, 1758)	1 (1)	0.25	41.6	2.2	AQ	fo, aq	N
Tachymenini (2)							
Thamnodynastes hypoconia (Cope, 1860)	17 (11)	4.19	39.6 (31.5-51.5)	12.5 (10.5-16.7)	T	ce	N
Thamnodynastes sp.	1 (1)	0.25	38.6	10.5	T	fo	N
Xenodontini (8)							
Erythrolamprus aesculapii (Linnaeus, 1758)	3 (1)	0.74	58	7.5	T	fo	D
Liophis almadensis (Wagler, 1824)	9 (5)	2.22	31.2 (24-36.2)	9.3 (7-10.5)	T	ce, g	D
Liophis maryellenae Dixon, 1991	5 (4)	1.23	38 (37-39.2)	11.2 (10.3-11.5)	T, AQ	aq	D
Liophis poecilogyrus (Wied-Neuwied, 1825)	6 (5)	1.48	34 (17.5-49.2)	7.6 (4-10.5)	T	ce, g, fo, an	D, N
Liophis reginae (Linnaeus, 1758)	1 (1)	0.25	37.6	5.7	T	fo	D, N
Lygophis meridionalis (Schenkel, 1902)	10 (7)	2.46	44.8 (30-52.5)	16.3 (11.2-21.2)	T	ce, g	D
Xenodon merremii (Wagler, 1824)	9 (3)	2.22	31.4 (18.3-41.5)	4.2 (3-6.2)	T	ce, g, fo, an	D
Xenodon nattereri (Steindachner, 1867)	1 (1)	0.25	25.3	5	T	ce, g	D
Pseudoboini (6)							
Boiruna maculata (Boulenger, 1896)	1 (1)	0.25	47	9.5	T	ce	N
Oxyrhopus guibei Hoge & Romano, 1977	15 (10)	3.69	38.4 (19.4-68)	10.1 (5-16.5)	T, SAB	g, ce, fo	N
Oxyrhopus rhombifer Duméril, Bibron &Duméril, 1854	10 (9)	2.46	41 (37.5-48)	11 (8.5-12.7)	T	ce, g, fo	N
Oxyrhopus trigeminus Duméril, Bibron &Duméril, 1854	39 (25)	9.61	48.4 (25.5-83)	13.6 (6.5-45.5)	T	ce, g, fo	N
Phimophis guerini (Duméril, Bibron &Duméril, 1854)	5 (3)	1.23	57.2 (53-62)	14.5 (13.6-15.5)	T, C	ce, g	N
Pseudoboa nigra (Duméril, Bibron &Duméril, 1854)	3 (1)	0.74	108	29	T	ce, g	N
Philodriadini (5)							
Philodryas aestivus (Duméril, Bibron &Duméril, 1854)	8 (7)	1.97	45.4 (30.3-59)	21.1 (14-26.5)	T	g	D
Philodryas agassizii (Jan, 1863)	5 (4)	1.23	30.6 (17.8-35.6)	10.6 (6.5-13.5)	T	g	D
Philodryas nattereri Steindachner, 1870	11 (8)	2.71	76.9 (29-118)	29.7 (11.3-49.5)	T	g, ce, an	D
Philodryas olfersii (Lichtenstein, 1823)	5 (3)	1.23	70.7 (48-82)	25.3 (20.5-28)	T, SAB	ce, g, fo	D
Philodryas patagoniensis (Girard, 1858)	17 (7)	4.19	71.4 (54-89)	26.7 (22.5-31)	T, SAB	ce, g, fo, an	D
Elapidae (1)							
Micrurus frontalis Duméril, Bibron &Duméril, 1854	2 (1)	0.49	80	4.5	C	ce, g, fo	D, N

while Anomalepididae, Elapidae, and Leptotyphlopidae were each represented by a single species. The dominant dipsadid lineages were the subfamily Xenodontinae (51.1% of total richness), and the tribe Xenodontini, which comprised 33.3% of the Xenodontinae species.

The most common species was the viper *Bothrops marmoratus* followed by a false-coral snake *Oxyrhopus trigeminus*, a rattlesnake *Crotalus durissus*, and another viper *Bothrops moojeni* (Table 1). The species abundance distribution curve showed a sigmoid pattern resembling a lognormal distribution (Whittaker 1970, Krebs 2009) (Figure 4).

2. *Rarefaction*

The rarefaction curves (Mao Tau), both sample-based and individual-based, did not reach stability (Figure 5), and the various species richness estimators produced different estimates, all of which were greater than the observed richness of 47 species (Table 2). The estimates produced by the species-based method varied between 53.77 ± 0.28 with a Bootstrap estimator and 79.0 ± 23.32 with a Chao 1 estimator. The estimates produced by the individual-based method varied between 52.3 ± 0.24 with a Bootstrap estimator and 86 ± 30.45 with a Chao 1 estimator (Table 2).

3. *Natural history*

The snakes of CVNP exhibit a diversity of natural history traits (Table 1). Twenty-five species are strictly terrestrial, six are fossorial or cryptozoic, six are arboreal or semi-arboreal, six are terrestrial but use arboreal habitats frequently, and two are mainly aquatic. All scolecophidian, elapomorphine and elapid snakes have fossorial or cryptozoic habits, while all vipers, pseudoboines, and most philodryadines and xenodontines are primarily terrestrial. Most

Figure 2. Some snake species recorded in the Chapada dos Veadeiros National Park. a) *Liotyphlops ternetzii*; b) *Epicrates crassus*; c) *Bothrops marmoratus*; d) *Bothrops moojeni*; e) *Crotalus durissus*; f) *Micrurus frontalis*; g) *Chironius exoletus*; h) *Chironius quadricarinatus*; i) *Oxybelis aeneus*; j) *Sibynomorphus mikanii*; k) *Xenopholis undulatus*; l) *Apostolepis ammodites* (Photos by F.G.R. França).

arboreal snakes are colubrid species, and only *Eunectes murinus*, *Helicops angulatus*, and *Liophis maryellenae* are aquatic.

A majority of the snake fauna occurred in open and interfluvial areas of cerrado and grassland, but a small portion were found exclusively in forest (e.g., *Chironius exoletus*, *Xenopholis undulatus*, *Atractus albuquerquei*, *Erythrolamprus aesculapii*, *Liophis reginae*; Table 1). Only six species were found in all Cerrado habitats (*Liotyphlops ternetzii*, *Chironius flavolineatus*, *Mastigodryas bifossatus*, *Oxyrhopus guibei*, *Philodryas patagoniensis*, and *Xenodon merremii*). Most snakes of Viperidae and Colubridae inhabited principally open habitats, with the exception of *Bothrops moojeni*, *Chironius exoletus* and *Spilotes pullatus*, which were commonly found in forest.

Snake daily activities occurred from 0500 h to 2400 h and varied among species. Most snakes were strictly diurnal (20 species), but many were nocturnal (16 species) and others were active during both periods (11 species; Table 3). Most snakes (with ≥5 observations) were found during two or three time periods and only *Crotalus durissus* was found in all six time periods throughout the day. Almost all species of diurnal snakes were observed from 0800 to 1800 h, but few snakes were active between 1200 and 1459 h, as seen in all species of *Philodryas*. Several diurnal species exhibited

Figure 3. Some snake species recorded in the Chapada dos Veadeiros National Park. a) *Oxyrhopus trigeminus*; b) *Oxyrhopus rhombifer*; c) *Phimophis guerini*; d) *Philodryas nattereri*; e) *Philodryas olfersii*; f) *Thamnodynastes hypoconia*; g) *Liophis almadensis*; h) *Liophis maryellenae*; i) *Lygophis meridionalis* (Photos by F.G.R. França).

bimodal activity periods, such as species of *Liophis* and *Chironius*. Most nocturnal snakes commenced activity around 1800 h or earlier in twilight, and some had activity periods extending to 2400 h or later. Three individuals of nocturnal species (*Bothrops marmoratus*, *Sibynomorphus mikanii*, and *Oxyrhopus trigeminus*) were captured around 2400 h.

The annual activity of snakes in CVNP was highly seasonal. Although snakes were found in all months, most captures occurred during the rainy season (end of September to April) with March having the highest number. Snake captures showed a significant decrease during the dry season (May to beginning of September) with August having the lowest number (Figure 6).

Table 2. Species richness estimates of the snake assemblage in Chapada dos Veadeiros National Park using different estimators and the sample- (SBM) and individual-based rarefaction methods (IBM).

Estimators	Mean ± SD	
	SBM	IBM
ACE	61.81 ± 0.6	57.01 ± 0.43
ICE	61.97 ± 0.01	57.03 ± 0.42
Chao 1	79.0 ± 23.32	86 ± 30.45
Chao 2	72.6 ± 17.9	85.9 ± 30.37
Jacknife 1	62.95 ± 5.21	59.97 ± 3.54
Jacknife 2	73.9 ± 0.8	71.91 ± 0.6
Bootstrap	53.77 ± 0.28	52.3 ± 0.24

Discussion

The snake assemblage of CVNP is composed of a high number of species. In comparison to other well-sampled localities in Cerrado, that range from 22 to 61 snake species (Vanzolini 1948, França et al. 2008, Sawaya et al. 2008, Araújo et al. 2010) or with other South American open formations, such as Caatinga (19 species, Vitt & Vangilder 1983), Chaco (21 species, Leynaud & Bucher 2001), Pampas (20 species, Winck et al. 2007), and Pantanal (26 species, Strüssmann & Sazima 1993), snake diversity of CVNP is among the most species rich. Nevertheless, we certainly did not record all snake species that occur in the region. Snakes are notoriously difficult to sample because they usually occur at low densities, are cryptic, and have secretive habits (Greene 1997). We did not use methods such as pitfall traps or funnel traps, which are often effective at detecting cryptic and secretive species (Jorgensen et al. 1998, Sutherland 2006).

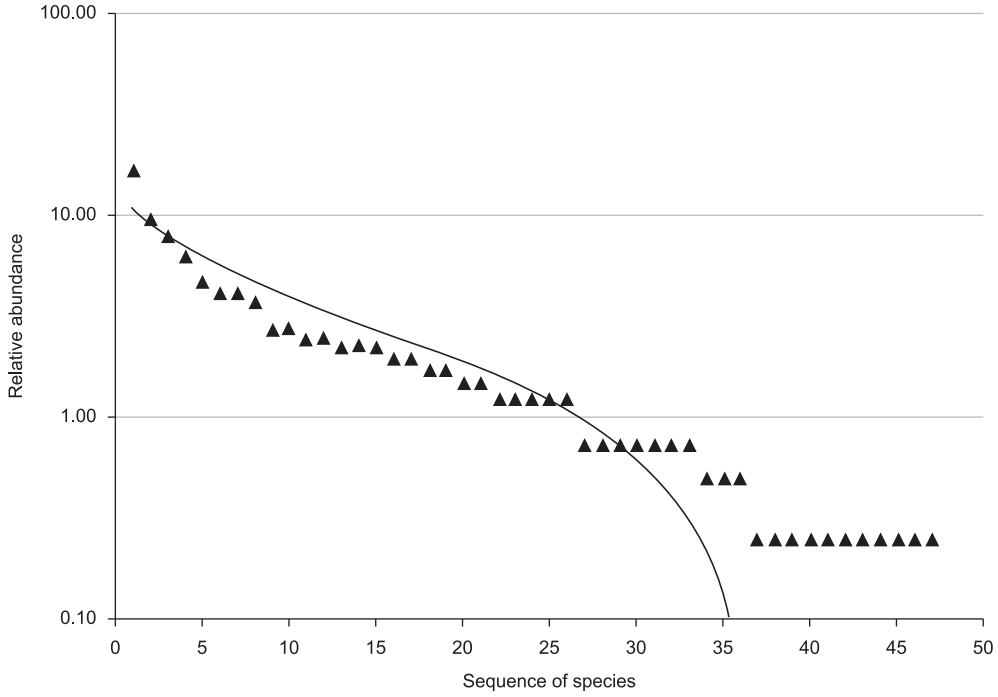

Figure 4. The snake species abundance distribution curve showing a sigmoid pattern resembling a lognormal distribution.

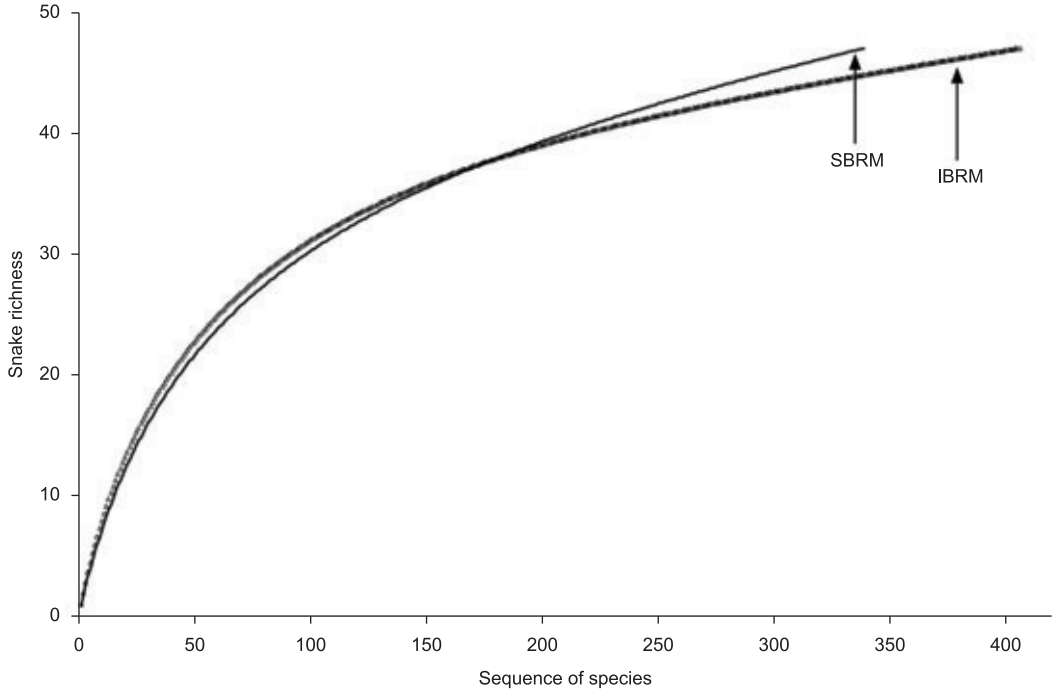

Figure 5. Sample- and individual-based rarefaction curves of snakes of Chapada dos Veadeiros National Park.

Future studies using these methods would likely add more species to the list of snakes occurring in CVNP.

A number of snake species that we did not record in this study are known from Central Brazil and are likely to occur within CVNP, including *Micrurus brasiliensis*, *Micrurus lemniscatus*, *Atractus pantostictus*, *Atractus edioi*, *Apostolepis flavotorquata*, *Phalotris nasutus* (Souza 2003, Jorge da Silva 2007, Jorge da Silva et al. 2005, Lema 2002, Lema & Renner 2005). With the addition of those species whose ranges include Central Brazil, the snake richness for the region of Chapada dos Veadeiros (an area that encloses the National Park plus 12 Particular Reserves of the Natural Patrimony – RPPN and some hydroelectric power plants and their reservoirs such as Serra da Mesa and Cana Brava; see Felfili et al. 2007) is likely to be more than 70 species. This is supported by our results showing

Table 3. Number of individuals found active during different times of the day for snake species in Chapada dos Veadeiros National Park.

Species	05:00-07:59	08:00-11:59	12:00-14:59	15:00-17:59	18:00-20:59	21:00-24:00
Liotyphlops ternetzii	0	0	0	0	2	0
Boa constrictor	1	0	0	0	0	2
Epicrates crassus	1	0	0	0	2	5
Eunectes murinus	1	0	0	0	0	1
Bothrops moojeni	2	0	0	0	19	1
Bothrops marmoratus	2	0	0	3	41	12
Bothrops pauloensis	1	0	0	1	0	0
Crotalus durissus	0	1	1	1	14	2
Chironius exoletus	0	2	0	0	0	0
Chironius flavolineatus	1	2	0	3	0	0
Chironius quadricarinatus	0	0	0	1	0	0
Drymarchon corais	0	0	1	0	0	0
Drymoluber brazili	0	1	0	0	0	0
Mastigodryas bifossatus	0	3	0	1	0	0
Oxybelis aeneus	0	4	0	1	0	0
Spilotes pullatus	0	1	0	0	0	0
Tantilla melanocephala	0	0	0	0	4	2
Apostolepis ammodites	0	0	0	0	1	0
Boiruna maculata	0	0	0	0	1	0
Taeniophallus occipitalis	0	1	0	0	0	0
Erythrolamprus aesculapii	0	3	0	0	0	0
Helicops angulatus	0	0	0	0	1	0
Leptodeira annulata	0	0	0	0	1	2
Liophis almadensis	0	1	0	4	0	0
Liophis maryellenae	0	1	0	1	0	0
Liophis meridionalis	0	3	0	4	0	0
Liophis poecilogyrus	0	0	0	0	2	0
Liophis reginae	0	0	0	0	1	0
Oxyrhopus guibei	2	0	0	1	4	2
Oxyrhopus rhombifer	0	0	0	0	5	1
Oxyrhopus trigeminus	0	0	0	0	11	11
Philodryas aestivus	0	3	1	0	3	0
Philodryas agassizii	0	2	2	1	0	0
Philodryas nattereri	0	4	3	2	0	0
Philodryas olfersii	0	3	1	0	0	0
Philodryas patagoniensis	1	4	3	3	0	0
Phimophis guerini	1	0	0	0	2	1
Pseudoboa nigra	1	0	0	0	1	1
Sibynomorphus mikanii	0	0	0	0	6	9
Thamnodynastes hypoconia	0	0	0	0	7	1
Thamnodynastes sp.	0	0	0	0	0	1
Xenodon merremii	0	0	1	4	0	0
Xenodon nattereri	0	0	0	0	1	0
Xenopholis undulatus	0	0	0	0	1	0
Micrurus frontails	1	1	0	0	0	0

that the species accumulation curve was not asymptotic and that all species richness estimators were higher than the observed number of species (47). Taken together, our results indicate that central Brazilian Cerrado has high species richness of snakes and that CNVP is an important area for biodiversity conservation (França & Araújo 2006, França et al. 2008).

The snake assemblage of CVNP is dominated by a few abundant species, with three of the four most common species being venomous. The CVNP is a highly frequented tourism and conservation unit in Brazil due to the beautiful scenery including many rivers and waterfalls (Felfili et al. 2007). Even though snake activity periods may not coincide with peak times of human visitation, the dominance of venomous snakes is important information for park management and tourists should take precautions to avoid potentially hazardous encounters with snakes while inside the park. We also found a high number of snakes and other vertebrates dead on paved and unpaved roads surrounding the park (unpublished data), suggesting the need for increased public awareness and possibly conservation actions

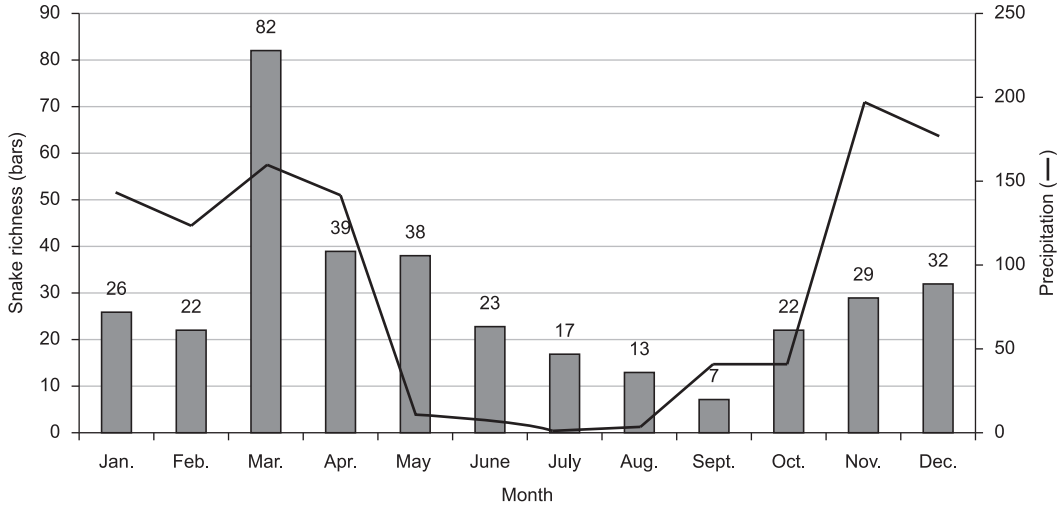

Figure 6. Seasonal activity patterns of snakes of Chapada dos Veadeiros National Park.

to reduce the negative impacts of roads on wildlife in the region (Forman et al. 2003, Shepard et al. 2008).

The species abundance curve shows a sigmoid pattern resembling a lognormal distribution (Whittaker 1970). This pattern is typical of species-rich and highly equitability communities, and is commonly observed in Central and South American snake assemblages (Leynaud & Bucher 2001, Sawaya et al. 2008). Most Neotropical snake assemblages, in different environments and biomes, are characterized by a dominance of venomous species, mainly vipers, and a high number of rare harmless snakes (Martins & Oliveira 1999, Duellman 2005, Sawaya et al. 2008, Hartmann et al. 2009a), with some exceptions in wetlands of the Pantanal (Strussmann & Sazima 1993) and in subtropical grasslands (Winck et al. 2007). Venomous snakes, such as species of *Bothrops*, usually have a high number of offspring and occupy a diversity of habitats (Campbell & Lamar 2004), which contributes to this dominance.

Habitat selection has been frequently reported as one of the most important factors affecting snake assemblage diversity and structure (Reinert 1984, 2001). The habitat complexity of the Cerrado biome, which consists of a mosaic of open habitats (grasslands and cerrado-savanna) and forest environments (gallery forests and cerradão) (Felfili et al. 2007), likely helps to maintain the high diversity of snake species in central Brazil. In our study, we found that only six species (12.8% of 47 species) were encountered in all Cerrado habitats, with most species being found in only one habitat type. Snake species occurring in CVNP were found principally in open habitats with comparably few species encountered exclusively in forested habitats. The higher number of snakes inhabiting open environments is also seen in other snake assemblages in the Cerrado biome (França et al. 2008, Sawaya et al. 2008).

Habitat selection of the snake assemblage is also correlated with habits and morphology of species. In forest biomes, such as Amazonia and Atlantic Forest, snake assemblages are composed of many arboreal and semi-arboreal species (Martins & Oliveira 1998, Marques & Sazima 2004), whereas in Cerrado most snakes are terrestrial or fossorial/cryptozoic species (França et al. 2008, Sawaya et al. 2008). The vegetation of CVNP is predominated by grasslands and other open cerrado environments (Felfili et al. 2007), which leads to a dominance of terrestrial and fossorial/cryptozoic snake species. This is exemplified by our findings that arboreal and semi-arboreal colubrids within CVNP were usually found in forest habitats whereas fossorial scolecophidians and species of Apostolepis inhabited open environments.

Daily activity patterns revealed that most species are diurnal and this appears to be related to phylogeny. All Dipsadinae, Tachymenini and Pseudoboini are nocturnal species while all Philodryadini and most Colubridae (with exception of Tantilla melanocephala) are diurnal. So, the majority of diurnal species in the assemblage is probably due the richness of phylogenetic groups that encompass more diurnal species than due the ecological factors. Future studies using ecological and phylogenetic analysis, such as canonical phylogenetic ordination, can support this result. Some diurnal species showed two periods of daily activity likely because the sun becomes too intense at mid-day; for example, almost no snakes were found active between 12:00 to 14:59 h. In addition, many nocturnal snakes were active during twilight (i.e., crepuscular activity), a common pattern in vipers and elapids (Shine 1979).

Data on captures throughout the year revealed that snake activity was highly seasonal with most captures occurring during the summer rainy season and few captures during the cold and dry winter months. This highly seasonal activity pattern has been found in other studies on snakes in South America, with drier months typically showing lower activity (Vitt & Vangilder 1983, Winck et al. 2007, Hartmann et al. 2009b). During the rainy summer months an increase in water availability leads to vegetation growth (principally in grasslands) and increased activity of snake prey such as small mammals, frogs, and invertebrates, which in turn would affect snake activity (Yanosky et al. 1996).

The CVNP is a large, well-preserved representative of Cerrado physiognomic forms in Central Brazil (Felfili et al. 2007). Additionally, its connectivity with other preserved natural areas (at least 22 other smaller preserved areas are found near CVNP) underscores its importance. The rich snake fauna of CVNP documented here reaffirms this region as a key area for the conservation of Cerrado biodiversity.

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Appendix

Appendix 1. Snake species collected at the Chapada dos Veadeiros National Park, state of Goiás, Brazil and housed in the Coleção Herpetológica da Universidade de Brasília (CHUNB).

Anomalepididae: *Liotyphlops ternetzii* (CHUNB 59180-59181, 59559); Boidae: *Boa constrictor* (CHUNB 59520); *Epicrates crassus* (CHUNB 59571-59573); Colubridae: *Chironius exoletus* (CHUNB 09583); *Chironius flavolineatus* (CHUNB 03755, 12426, 19699, 59125, 59555-59558); *Chironius quadricarinatus* (CHUNB 20327, 20330); *Drymarchon corais* (CHUNB 03811, 20404); *Drymoluber brazili* (CHUNB 03839); *Mastigodryas bifossatus* (CHUNB 59517); *Oxybelis aeneus* (CHUNB 59560-59561); *Spilotes pullatus* (CHUNB 20396); *Tantilla melanocephala* (CHUNB 59154-59484); Dipsadidae: *Apostolepis ammodites* (CHUNB 59155, 59483); *Boiruna maculata* (CHUNB 20375); *Helicops angulatus* (CHUNB 20355); *Leptodeira annulata* (CHUNB 59123); *Liophis almadensis* (CHUNB 59143-59145); *Liophis maryellenae* (CHUNB 17591-17592); *Liophis poecilogyrus* (CHUNB 59139-59141); *Lygophis meridionalis* (CHUNB 59135-59138); *Oxyrhopus guibei* (CHUNB 59161-59167); *Oxyrhopus rhombifer* (CHUNB 59156-59160); *Oxyrhopus trigeminus* (CHUNB 59168-59179); *Philodryas agassizii* (CHUNB 59124, 59576-59577); *Philodryas aestivus* (CHUNB 59126-59127); *Philodryas nattereri* (CHUNB 59119, 59522, 59578-59579); *Philodryas olfersii* (CHUNB 59133-59134); *Philodryas patagoniensis* (CHUNB 59128-59132, 59523); *Phimophis guerini* (CHUNB 59120-59121, 59482); *Pseudoboa nigra* (CHUNB 59521); *Sibynomorphus mikanii* (CHUNB 59147-59153); *Thamnodynastes hypoconia* (CHUNB 59562-59570); *Thamnodynastes* sp. (CHUNB 59574); *Xenodon merremii* (CHUNB 59122, 59575); *Xenodon nattereri* (CHUNB 59142); Leptotyphlopidae: *Trilepida fuliginosa* (CHUNB 50422); Viperidae: *Bothrops moojeni* (CHUNB 59516, 59546-59554); *Bothrops marmoratus* (CHUNB 53313, 59524-59529, 59531-59533, 59535-59542); *Bothrops pauloensis* (CHUNB 59530, 59534);