Snakes of an urban-rural landscape in the central Andes of Colombia: species composition, distribution, and natural history

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Abstract

Snakes of an urban-rural landscape in the central Andes of Colombia: species composition, distribution, and natural history. From 2005 to 2011, I studied the composition, distribution and natural history of an Andean urban-rural snake assemblage at the Cordillera Central of Colombia, based on three data sources: (1) examination of specimens in the MHN-UC [Museo de Historia Natural, Universidad de Caldas], (2) incidental encounters by author, and (3) collection of data by other researchers. Additionally, I provide natural history notes for the species involved. A total of 14 species, including two subspecies of snakes, belonging to 12 genera and four families, have been found in the studied area (municipality of Manizales, Caldas). Taking into account this total, 10 had at least one record in the urban area, 13 in the rural area and 14 in forested areas. Only Liophis epinephelus bimaculatus was found exclusively in forest environment. Three species (21.4%) are apparently endemic to the region, six species (42.8%) correspond to a fauna representative of the Tropical-Andean range of South America, four species (28.5%) are distributed from Central America to the tropical Andes, and only one species is widely distributed in the whole continent. The snake assemblage in Manizales is mostly terrestrial, and in general, the species tend to be more active in the rainy periods of the year (mainly from October-December), and most of them may occasionally be found in urban areas, mainly close to areas of vegetation such as crops and pastures.

Keywords: Andean snakes, assemblage, distribution, diversity, natural history.

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Resumen

Serpientes de un paisaje urbano-rural en los Andes centrales de Colombia: composición de especies, distribución e historia natural. Yo estudié desde 2005 hasta 2011, la composición de especies, distribución e historia natural de un ensamblaje de serpientes andinas, en un paisaje urbanorural de la Cordillera Central de Colombia, basado en tres fuentes de información: (1) revisión de especímenes en el Museo de Historia Natural, Universidad de Caldas (MHN-UC), (2) encuentros accidentales del autor, y (3) toma de datos por otros investigadores. Adicionalmente proveo notas de historia natural para las especies incluidas. Un total de 14 especies de serpientes, incluyendo dos subespecies, pertenecientes a 12 géneros y cuatro familias, han sido encontradas en el área de estudio (municipio de Manizales, Caldas). De estas, 10 tienen al menos un reporte en el área urbana, 13 en el área rural y 14 en áreas forestadas. Solamente Liophis epinephelus bimaculatus fue encontrada exclusivamente en un ambiente boscoso. En cuanto a su distribución geográfica, tres especies (21.4%) son aparentemente endémicas de la región, seis especies (42.8%) corresponden a un grupo representativo del rango Tropical-Andino de Suramérica, cuatro especies (28.5%) están distribuidas desde Centro América hasta los Andes tropicales, y solo una especie está ampliamente distribuida en todo el continente. Según los datos sobre historia natural, el ensamblaje de serpientes de Manizales es principalmente terrestre; las especies en general tienden a ser más activas en los períodos lluviosos del año (principalmente entre octubre-diciembre), y la mayoría de ellas (71.4%) pueden ocasionalmente ser encontradas en el área urbana, principalmente cerca a zonas de vegetación como cultivos y pastizales.

Palabras Clave: distribución, diversidad, ensamblaje, historia natural, serpientes andinas.

Resumo

Serpentes de uma paisagem urbana-rural nos Andes centrais da Colômbia: composição de espécies, distribuição e história natural. De 2005 a 2011, eu estudei a composição de espécies, distribuição e história natural de uma assembleia de serpentes em uma paisagem urbana-rural andina na Cordillera Central da Colômbia, com base em três fontes de dados: (1) análise de amostras do MHN-UC [Museo de Historia Natural, Universidade de Caldas], (2) encontros ocasionais e (3) coleta de dados por outros pesquisadores. Além disso, forneci notas da história natural das espécies envolvidas. Um total de 14 espécies, incluindo duas subespécies de serpentes, pertencentes a 12 gêneros e quatro famílias, foram encontradas na área de estudo (municipio de Manizales, Caldas). Levando em conta este total, 10 tiveram pelo menos um registro na área urbana, 13 na zona rural e 14 em áreas florestais. Apenas Liophis epinephelus bimaculatus foi encontrada exclusivamente em ambiente de floresta. Três epécies (21.4%) são aparentemente endêmicas da região, seis espécies (42.8%) correspondem a representantes da fauna da faixa Tropical-Andina da América do Sul, quatro espécies (28.5%) estão distribuídas a partir da América Central até os Andes tropicais e apenas uma espécie é amplamente distribuída em todo o continente. A assembleia de serpentes de Manizales é principalmente terrestre, e em geral as espécies tendem a ser mais ativas nos períodos chuvosos do ano (especialmente a partir de outubro-dezembro), e a maioria delas pode ocasionalmente ser encontrada em áreas urbanas, principalmente perto de áreas de vegetação, tais como culturas e pastagens.

Palavras-chave: assembleia, distribuição, diversidade, história natural, serpentes andinas.

Introduction

Alteration of the land mass by humans for their own benefit has generated enormous structural changes on the natural environment, leading to fragmentation and the consequent formation of varied landscapes, which include not only remnants of original habitats, but also (and in some cases a greater proportion), areas of production and economic development for human populations (Andrén 1994, Fahrig 2003, Fletcher 2005, Lloyd et al. 2005, Santos and Telleria 2006). For this reason, in different areas of the world, species currently face the challenge of living and coexist in complex landscape mosaics that include both their own habitat, as well as new environments, including urban and agricultural zones (for snakes see Sazima and Manzani 1995, Winck et al. 2007, Urbina-Cardona et al. 2008, Knoot and Best 2011).

The assemblages of Neotropical snakes present high species richness and complex structures, related to high diversity of resource activity patterns, reproduction, morphology (see Duellman 1990, Zimmermann and Rodrigues 1990, Cadle and Greene 1993, Martins and Oliveira 1998). Moreover, the composition of Neotropical snakes in different environments presents variations in the patterns of geographical distribution of the species, coexisting in the same habitat species with large and small distributions, representing different biogeographic regions (see Duellman 1990 for a revision in Neotropical environments). Although research in recent decades has contributed substantially to knowledge about the ecology, distribution and natural history of Neotropical snakes (e.g., Dixon and Soini 1977, Duellman 1978, Rodríguez and Cadle 1990, Zimmerman and Rodrigues 1990, Strüssmann and Sazima 1993, Martins and Oliveira 1998, Bernarde and Abe 2006, Urbina-Cardona et al. 2008), there still exist information gaps for most natural areas of the Neotropics, and even more for those anthropogenically modified environments such as urban and rural landscapes.

This lack of information is much more evident to the Montane forests of the northern Andes, which have been listed as one of the most biologically diverse areas in the world, but paradoxically also one of the most threatened (Dinerstein et al. 1995, Myers et al. 2000). In Colombia, where the Andes reach their maximum geomorphological complexity dividing into three main ranges (the Occidental, Central and Oriental Cordilleras), the gamma diversity of snakes exceeds 220 species (Sánchez et al. 1995), making the Andean region the most specific and generic rich areas in the whole country, surpassing even areas of high biodiversity like the Amazon and the Pacific rainforests (Sánchez et al. 1995). However, the Andean snake assemblages appear to have low local (Alpha) diversity, following the pattern of faunal impoverishment that occurs with increasing altitude. This change in the diversity may be explained as an increase in altitude that leads to a reduction in temperature, which is a critical environmental condition that limits the distribution of ectothermic vertebrates (Navas 2003). Andean snake assemblages, however, have a high rate of endemism (especially the genus Atractus; see Passos et al. 2009, Passos and Lynch 2010), which makes them interesting faunal units from a biogeographic perspective. However, both the basic information on natural history, and patterns of diversity and biogeography of these assemblages, are still very poorly known, because in most cases these data are represented in technical reports that are not published in the scientific literature. In this regard, I aim to contribute to knowledge about the diversity and distribution patterns of an Andean snake assemblage, analyzing variation of the species composition in an urbanrural landscape, and provide notes on the natural history of the species involved. With this information, I seek to contribute to future studies on analyses of population trends, community structure. and large-scale biogeographic patterns, and to give information to guide conservation measures in the highly altered Colombian Andes.

Materials and Methods

Study Area

This research included snakes' registers of the urban and part of the rural area in the municipality of Manizales, Caldas, Colombia (Figure 1). The urban area of Manizales ranges from 1900-2160 m of elevation above sea level (5°01'-04' N, 75°25'-33' W) and is involved in a diverse ecological mosaic that includes remnants of Low Montane Wet Forest (sensu Holdridge et al. 1982) of different sizes and in different states of preservation; agro forestry areas mainly of Pinus patula crops, and areas of open fields used for cattle breeding (Figure 2A, B). The remnant forest fragments range from five to 4300 ha in extension, and are mostly forests in successional stages lesser of 30 years since deforested or altered (except Bosques de la Chec Forestal Reserve, Figure 2A). Its structure is complex

with an irregular canopy at 20-30 m, in which most frequent tree species include: Bocconia frutescens, Cecropia angustifolia, Cecropia telealba, Croton magdalenensis, Heliocarpus popayanensis, Saurauia cuatrecasana, Weinmannia pubescens (Orrego et al. 2008). Primary forests are absents in this area. Although in the urban area the natural vegetation has been severely altered and reduced, small fragment forests (<20 ha) are still restricted to the rivers and stream borders, even in urban expansion zones. Moreover, some eco-parks have been declared as biodiversity conservation zones and for ecotouristic purposes (e.g., Los Yarumos, Los Alcázares, Recinto del Pensamiento). In Manizales, rainfall distribution is bimodal-tetraestacional type, with two marked periods of rainfall (March-May and September-December), with an annual average of 2600 mm and a temperature ranging between 16-20°C (Corpocaldas 2002, Cenicafé 2004).

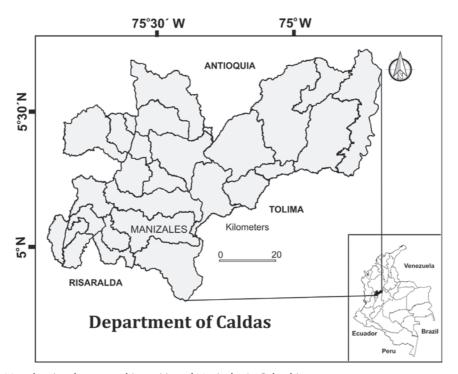


Figure 1. Map showing the geographic position of Manizales in Colombia.

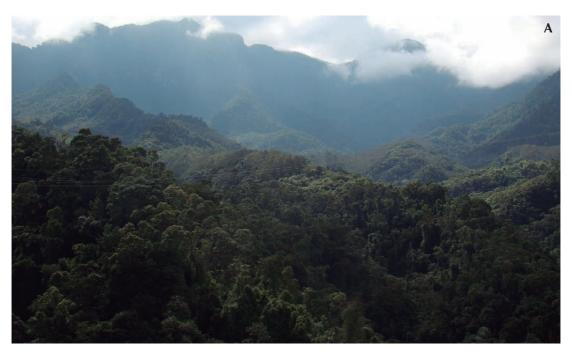




Figure 2. Panoramic images of urban and rural areas of Manizales, where **(A)** represents an Andean forest with over 60 years since reforested (Forestal Reserve Bosques de La Chec), and **(B)** shows major land uses in the municipality, showing a matrix that includes areas for urban expansion, pine plantations and pastures (north zone of Manizales).

Data Collection

From December 2005 to December 2011, I collected data on the diversity of snakes in Manizales based on three sources: (1) review of specimens deposited in the herpetological collection of the Museo de Historia Natural at the Universidad de Caldas (MHN-UC) (Appendix I), (2) incidental encounters during field work by other researches or other activities such as walking in the study area, and (3) collection of data by other researchers. I took the following data for each individual found alive or dead: day/time of capture or observation, habitat (urban, rural, forested areas) and microhabitat (arboreal, terrestrial, cryptozoic) where it was found and specific comments on behavior (for the living individuals). When conditions of dead specimens allowed, these were fixed and deposited in the collection of MHN-UC.

Species Identification, Taxonomic Considerations, and Natural History

Some recent taxonomic and systematics analysis including Neotropical snakes, were extensively carried out by Adalsteinsson et al. (2009) (Leptotyphopidae), Zaher et al. (2009) (Dipsadidae), Pyron et al. (2011) (Colubroidea), and Grazziotin et al. (2012) (Dipsadidae). Seeking to be consistent with the most widely used snakes classification (The Reptile Database: Uetz 2012; http:// www.reptile-database.org/), I follow that reference to include species to a family level, except for Dipsadidae, which I consider as a proper family in the sense of Zaher et al. (2009) and Grazziotin et al. (2012). The identification of the species was made always when possible until the subspecies level. I used the following taxonomic papers in order to properly identify the specimens: Prado (1940, 1941), Peters (1960), Roze (1966), Peters and Orejas-Miranda (1970), Dixon (1983, 1989), Pérez-Santos and Moreno (1988), Campbell and Lamar (1989), Zaher (1996) and Passos et al. (2009). I cannot even assign individuals of Atractus sp. to any recognizable

species of the genus, but they share a suite of meristic and morphometric characters with *Atractus melanogaster* (unpub. data), which inhabits Andean forest (1800–2200 m a.s.l.) at the Eastern slope of the Central Cordillera, in the departments of Caldas and Tolima (Passos and Lynch 2010). All specimens examined in the collection were measured in snout-vent length (SVL) and tail length (TAL), but due to the low sample, only total length (TL) ranges are presented for most species.

The snakes were categorized in relation to time of activity (diurnal, noctural) and microhabitat (arboreal, terrestrial, cryptozoic) where they were found following the proposal of Martins and Oliveira (1998) (Table 1). To provide objective data on microhabitat of the species, I include only the information obtained during this study; also because some species have been found in more than one category (e.g., *Bothriechis schlegelii*, *Dipsas sanctijoannis*), I include the number of individuals found in each category (Table 1). In addition, I briefly describe the coloration in life of the little-known species or the ones for which their coloration is only known in preservative (*Atractus* spp., *Chironius monticola*).

Data Analysis

The snake composition in the studied area was compared with that of other localities in different regions of Colombia (Table 2). Composition between sites was compared using the coefficient of biogeographic resemblance proposed by Duellman (1990), in which only species (not subspecies) were included. In addition, to explore the representation of the species, I assigned each one to a category of geographical distribution according to Kattan et al. (2004): Endemic (E), species with geographical ranges <50.000 km²; Tropical Andean (TA), species that are distributed in the tropical Andes; Andean-Central America (CA), species that are distributed in the tropical Andes and Central America; and wide distribution (WD), species that are widely distributed in tropical America or in the whole continent.

Table 1. Local composition of snakes at urban, rural, and forested areas in the municipality of Manizales, department of Caldas, Colombia. Microhabitat categories and time activity are: (A) arboreal, (T) terrestrial, (C) cryptozoic, (D) diurnal and (N) nocturnal (see Martins and Oliveira 1998). Asterisk represents new records for Manizales.

	Urban area	Rural area	Forested area	Microhabit			Activity	
				Α	T	С		
LEPTOTYPHLOPIDAE								
<i>Trilepida joshuai</i> (Peters, 1857)*	6		1		6		?	
COLUBRIDAE								
Chironius monticola (Roze,1952)	1	3	1	1	3		D	
<i>Dendrophidion bivittatus</i> (Duméril, Bibron & Duméril, 1854)*		3	1		3		?	
Lampropeltis triangulum micropholis (Cope, 1860)*		1	1		2		;	
DIPSADIDAE								
Atractus sp.*	17	14	6		27	10	Ν	
Atractus manizalensis (Prado, 1939)	5	1	4		8	2	Ν	
Atractus titanicus (Passos et al. 2009)*	5	1	1		6	1	?	
Clelia equatoriana (Amaral, 1924)*	3	1	1		5		Ν	
Dipsas sanctijoannis (Boulenger, 1911)*	1	3	7	3	6		Ν	
Erythrolamprus bizonus (Jan, 1863)*	2	2			4		?	
Imantodes cenchoa (Linnaeus, 1758)*		1	1		1		?	
Liophis epinephelus pseudocobella (Peracca, 1914)	7	1	2		10		D	
<i>Liophis epinephelus bimaculatus</i> (Cope, 1899)*			1		1		D	
ELAPIDAE								
<i>Micrurus mipartitus decussatus</i> (Duméril, Bibron & Duméril, 1854)		1	2		3		D?	
VIPERIDAE								
Bothriechis schlegelii (Berthold, 1846)	3	1	3	2	3		D/N	
TOTAL SPECIES	10	13	14	3	15	3		
TOTAL INDIVIDUALS	50	33	32	6	88	13		

Results

Richness and Composition

During this study and considering the three methods used, there were 14 species recorded, distributed in five families and 12 genera (Table 1). Ten species (71.4%) are new records for the municipality of Manizales (Corpocaldas 2002), highlighting the presence of an additional species

of *Atractus* and *Liophis epinephelus*, the latter of which two subspecies are sympatric in the studied area (*L. e. bimaculatus* and *L. e. pseudocobella*, sensu Dixon *et al.* 1983; Table 1).

Distribution Patterns

Of the 14 species found, 10 had at least one record in the urban area, 13 in the rural area and 14 in forested areas. Only *Liophis e. bimaculatus*

Table 2. Characterization of the localities included in the analysis of biogeographical resemblance (Table 3). Characterization of the life zones follows to Holdridge (1982), and classification of the Colombian biogeographic regions follows the proposal of Camacho *et al.* (1992) (in Spanish).

L Re-	Geo reference	Biogeographic characterization				
Locality	Geo reference	Life zone	Biogeographic region in Colombia			
(1) PNN Gorgona, Cauca	2°47'-3°06' N, 78°06'-78°18' W, 0-330 m	Tropical Wet Forest (bh-T)	Territorio oceánico insular del Pacífico			
(2) Pacurita, Chocó	5°41' N, 76°40' W, 53 m	Tropical Very Wet Forest (bmh-T)	Provincia del Chocó-Magdalena			
(3) Neguanje, PNN Tayrona, Magdalena	11°18'–11°21' N, 74°4'–74°7' W, 0–700 m	Tropical Dry Forest (bs-T)	Cinturón árido precaribeño			
(4) Pueblo Nuevo, Córdoba	8°17'–8°25' N, 75°03'–75°21' W, 38–54 m	Tropical Dry Forest (bs-T)	Provincia del Chocó-Magdalena			
(5) Ciénaga Grande del Bajo Río Sinú, Córdoba.	9°10'–9°13' N, 75°50'–75°54' W	Tropical Dry Forest (bs-T)	Provincia del Chocó-Magdalena			
(6) Yacopí, Cundinamarca	5°33'–5°41' N, 74°17'–74°24' W, 190–1500 m	Tropical Wet Forest (bh-T)	Provincia del Chocó-Magdalena			
(7) Bosque de Yotoco, Valle del Cauca	3°53'18" N, 76°24'05" W, 1200–1700 m	Pre-montane Wet Forest (bh-PM)	Provincia Norandina			
(8) PNN Selva de Florencia, Caldas	5°29'8.17" N, 75°04'7.18" W 900–2400 m	Very Humid Pre-montane Forest (bmh-PM)–Low Montane Very Humid Forest (bmh-MB)	Provincia del Chocó-Magdalena			
(9) Manizales, Caldas	5°01'–5°04' N, 75°25'–75°33' W, 1900–2160 m	Low Montane Wet Forest (bh-MB)	Provincia Norandina			

was found exclusively in forest environment, and the species *Dendrophidion bivittatus*, *Lampropeltis triangulum micropholis* and *Micrurus mipartitus decussatus*, were not recorded in the urban area (Table 1). The locality with the highest coefficient of biogeographic resemblance in relation to Manizales, was Yotoco Forest (CBR = 0.5), followed by the Selva de Florencia

Natural National Park (CBR = 0.260); contrary, localities more dissimilar in species composition with respect to Manizales were Neguanje and Ciénaga Grande, which there was not shared species (CBR = 0.00; Table 3). According to the geographical distribution patterns, three species (21.4%) are apparently endemic to the central region of the Cordillera Central, six species

Table 3. Biogeographic similarity coefficients among Colombian snakes' assemblages. Number of common species above the diagonal; total species in bold (along the diagonal) and biogeographic similarity coefficients are below the diagonal (follows to Duellman 1990). Localities: MA = Manizales (this study); GOR = Gorgona National Natural Park (Urbina-Cardona *et al.* 2008); PA = Pacurita, Chocó (Moreno *et al.* 2003, Moreno 2005); NE = Tayrona National Natural Park (Rueda-Solano and Castellanos-Barliza 2010); PN = Pueblo Nuevo, Córdoba (Carvajal-Cogollo and Urbina-Cardona 2008); CG = Ciénaga Grande del bajo Río Sinú, Córdoba (Carvajal-Cogollo *et al.* 2007); YA = Yacopí, Cundinamarca (Moreno-Arias *et al.* 2008); YO = Bosque de Yotoco forestal reserve, Valle del Cauca (Castro-Herrera *et al.* 2007, Vargas-Salinas *et al.* 2011); SF = Selva de Florencia National Natural Park, Caldas (Rueda-Almonacid 2000). *Data in parentheses indicate total number of taxa (including subspecies) recorded for the sites, but the CBR was only performed with the number of taxa identified to species level.

	MA	GOR	PA	NE	PN	CG	YA	YO	SF
MA	14 (15)*	2	2	0	2	0	4	9	3
GOR	0.148	13	5	4	4	4	9	7	2
PA	0.102	0.263	25 (26)*	2	6	7	7	5	2
NE	0.00	0.296	0.102	14 (17)*	2	7	4	4	1
PN	0.16	0.333	0.333	0.16	11	7	6	5	1
CG	0.00	0.25	0.318	0.424	0.466	19	8	5	1
YA	0.25	0.58	0.325	0.25	0.413	0.432	18 (19)*	9	3
YO	0.5	0.4	0.212	0.222	0.303	0.243	0.45	22	1
SF	0.260	0.173	0.114	0.083	0.095	0.068	0.214	0.125	10

(42.8%) correspond to a fauna representative of the Tropical–Andean range, four species (28.5%) are distributed from Central America to the tropical Andes, and only one species is widely distributed in America (Table 4).

Natural History: Species Accounts

Leptotyphlopidae.—Trilepida joshuai "Culebra ciega". A small fossorial species (Total length range 99.4–320 mm; N = 5). All individuals, except MHN-UC 0162, were founded dead on the ground in the urban area of Manizales. MHN-UC 0162 was found within an area of *Pinus patula* plantations at the Botanical Garden of the Universidad de Caldas (Rojas-Morales and González-Durán 2011). The species was found on both, dry and rainy periods, but mostly in October (N = 3) when the second rainy period of the year begins. In Manizales, adults are dark silvery grey on the dorsum, and uniformly creamish white on the venter, while juveniles

have the head pink, silvery grey on the dorsum and the venter totally white (see fig. 2 in Rojas-Morales and González-Durán 2011).

Colubridae.—Chironius monticola "Jueteadora". A large-sized species (for length see Dixon et al. 1993, La Marca and Soriano 2004) (TL range 387–640 mm; N = 3) mostly found in the rural area (N = 3), where is highly vulnerable to be killed by farmers (local people pers. com). It is a diurnal and semiarboreal species like other Chironius species (Dixon et al. 1993), but was often found on the ground (Table 1). Of three juvenile individuals, two were found in April and the other in October, suggesting a possible hatchling in the rainy months. The juveniles are brown-yellowish on the dorsum, with a lighter banded pattern, becoming dark brown on the posterior part of the body (see fig. 44 in La Marca and Soriano 2004), while adults are totally emerald green with yellow rostral and supralabials scales. The venter, in both juvenile

Table 4. Patterns of geographic distribution of the snake species of Manizales, department of Caldas, Colombia. Categories are: Apparently endemic (AE), Tropical Andean (TA), Andean-Central American (CA) and wide distribution (WD).

Consider	Distribution category						
Species	AE	TA	CA	WD			
Atractus sp.	X						
Atractus manizalensis	X						
Atractus titanicus	Χ						
Bothriechis schlegelii			Χ				
Chironius monticola		Χ					
Clelia equatoriana		Χ					
Dendrophidion bivitattus		Χ					
Dipsas sanctijoannis		Χ					
Erythrolamprus bizonus			Χ				
Imantodes cenchoa			Χ				
Lampropeltis triangulum				X			
Liophis epinephelus			Χ				
Micrurus mipartitus		Χ					
Trilepida joshuai		Χ					

and adults, is totally white-cream. For a detailed description of the coloration in preservative see Dixon *et al.* (1993).

Dendrophidion bivittatus "Guardacamino". A medium-sized species (see Pérez-Santos and Moreno 1988) (TL range 741–839 mm; N=2) rarely seen, and never found in the urban area of Manizales. All individuals with the exception of MHN-UC 0038, were found dead by farmers on unpaved roads in a rural area at north of municipality. In addition, the individual MHN-UC 0163 was found on April 8, 2010, killed by domestic cat within a house in this same area. No data on living individuals are available to determine its period of activity and microhabitat use.

Lampropeltis triangulum micropholis "Falsa coral". This large species appears to be rare in Manizales, and I accumulated only two records during this study. An adult was found on July 26, 2008 at 10:30 h, rolled at the base of a bamboo plant near a crop of beans, and the other individual was found dead by a farmer, on August 31, 2011 at 16:20 h, on the edge of an unpaved road within a secondary forest. It is possible that populations in Manizales, like other at highlands in Ecuador, face greater risks of decline than those located in the lowlands, due to loss of habitat, high rates of urbanization, and direct killing because of its coral snake pattern (Cisneros-Heredia 2007).

Dipsadidae.—Atractus sp. "Culebra tierrera" (Figure 3A). A small species (SVL $\overline{X} = 244$ mm, range 101–379 mm; TAL $\bar{x} = 30.9$ mm, range 12-45 mm; N = 12), most frequently found in the urban area, usually at the edge of pastures and forest fragments (N = 27), but can also be found in house gardens (N = 4). On December 23, 2006 during a fieldwork of two hours between 9:00-11:00 h, I found seven individuals (four juveniles and three adults) of Atractus sp., all inactive under rocks and debris in a grassland area of ca. 2 ha. This could indicate that individuals tend to aggregate leading to highly localized populations. This species is primarily nocturnal, because during the study period, five individuals were observed moving actively at night (19:00–22:00 h) on different paved roads and even inside houses. However, three individuals, who were recently run over by vehicles, were found at dawn in different areas, indicating that it may also be active in the early hours of the morning, as also it has been observed in other Andean Atractus (e.g., A. emigdioi, A. erythromelas, A. univittatus; see Esqueda and La Marca 2005). Atractus sp. can be preyed in the wild by the sympatric snake Clelia equatoriana, as an individual in captivity was consumed by the latter species when offered as potential prey (see account for Clelia equatoriana). Atractus sp. appears to be the most tolerant snake of



Figure 3. Some snake species recorded at the urban, rural, and forested areas in the municipality of Manizales, department of Caldas, Colombia. (A) Atractus sp.; (B) Atractus manizalensis; (C) Clelia equatoriana; (D) Dipsas sanctijoannis; (E) Liophis epinephelus bimaculatus, and (F) Bothriechis schleguelii (Photo by Sergio Escobar-Lasso).

environmental disturbance agents such as deforestation and urbanization, because individuals were found in all years of study, even in areas heavily impacted by industrial pollution. Throughout the year, Atractus sp. is more often sighted between June and December, but proves to be more active between the months of October to December (N = 25), when the maximum of annual precipitation is reached.

The defensive behavior of Atractus sp. includes immobility, hiding head, elevating head and neck, body thrash when handled, and balling; the latter corresponds to the first report for the genus Atractus. A detailed description of the behaviors exhibited by Atractus sp. and other species is in preparation (González-Durán et al. unpubl. data.; see also accounts for A. manizalensis, Liophis e. bimaculatus and L. e. pseudocobella). In life, juveniles of Atractus sp. are dark brown dorsally and ventrally are white with black spots distributed through the venter to the tail. The head has the same coloration of the body, except for an incomplete creamy yellow occipital band, that covers the distal posterior part of the parietal and temporal scales. The front of the head (rostral, nasal, internasals and part of the prefrontals scales) is creamy yellow with diffuse black spots. Adults are dark brown on the dorsum and have three rows of black scales (vertebral and paravertebrals), forming three longitudinal lines along the body. The venter is yellow with diffuse black spots distributed to the tail. The coloration of the head is similar to the juveniles, but the incomplete occipital band has a dark brown color almost indistinguishable from the rest of body (Figure 3A).

Atractus manizalensis "Culebra tierrera" (Figure 3B). A small species (SVL \overline{x} = 252.33 mm, range 131–336 mm; TAL \overline{x} = 30.33 mm, range 16–44 mm; N = 7), that is also relatively common in urban and forested areas of Manizales. Individuals of A. manizalensis usually were found dead on paved roads near individuals of A. titanicus,

which may suggest that these species have a period of activity and habitat use similar. Within forests, individuals of *A. manizalensis* were found between 08:30–10:00 h, inactive under rocks. The defensive behavior of this species includes as in *Atractus* sp., immobility and hide head, but also presents dorsoventral body compression accompanied with elevated body (González-Durán *et al.* unpubl. data).

Juveniles of Atractus manizalensis are light brown dorsally, with small black spots of one scale in length distributed on either sides of body, some of which are joined medially, forming a zigzag pattern on the paravertebral region. The head is dark brown on parietal scales and creamy covering supralabials, postocular and temporal scales. The venter is creamish white with dark brown spots profusely distributed throughout the body. Adults are dorsally red with black spots distributed only on either sides of body, not forming a distinct vertebral line. The head is dark brown dorsally, but the bottom, including supralabials is yellow. The venter is yellow background with profuse black spots that cover almost all scales even the tail (Figure 3B).

Atractus titanicus. This snake (TL range 273–445 mm; N = 5) was recently described by Passos et al. (2009) and is known only from two localities. This is the first record of the species in Manizales, filling a geographical gap between the towns of Villamaría (department of Caldas) and Sonsón (department of Antioquia, type locality). In Manizales, all individuals except one were found dead on paved roads in diurnal hours 05:30-09:00 h. The only living individual was found on April 6, 2009 at 11:30 h under a rock, on the edge of a forested area. Like other Atractus of Manizales, individuals of A. titanicus were found at sites close to each other (<500 m distance), which may suggest that tend to remain aggregated in localized areas. Coloration in life of A. titanicus corresponds to a pattern of red and black bands covering the entire dorsal surface to the tip of the tail. The red bands have one or two scales in width, while the black usually have three scales. Ventrally individuals are creamish white, accentuating more towards the front and with diffuse black spots distributed throughout the body (see Passos *et al.* 2009 for a detailed description of the color in preservative).

Clelia equatoriana "Cazadora" (Figure 3C). This medium-sized species (see Zaher 1996) (TL range 239.5–402 mm; N = 3) is a rare snake in Manizales. All individuals except two were found dead on the edge of paved roads adjacent to forested or cultivated areas. The two live individuals were found on November 20, 2007 and May 17, 2008 at night. One individual was found moving on the ground at the edge of a paved road, next to a forested hillside; the other individual was also found on the ground moving into secondary forest (Botanical Garden, Universidad de Caldas) and was maintained in captivity for 15 days until its release. During this time, it consumed an individual of Atractus sp. indicating the occurrence of ophiophagy in this species, a widely distributed food pattern in the genus Clelia (see for revision Cunha and Nascimento 1978, Vitt and Vangilder 1983, Pinto and Lema 2002).

Dipsas sanctijoannis "Caracolera" (Figure 3D). A medium-sized species (see Peters 1960) (TL range 241–515 mm; N = 3) frequently found in rural areas and to a lesser extent in forested areas (Table 1). Only one individual was found in the urban area (July 27, 2011 at 09:10 h), moving on the edge of a paved road next to a cultivated area. Dipsas sanctijoannis is nocturnal and was found mainly on the ground crossing small, unpaved roads (Morales and Lasso 2010). On January 17, 2010 at 19:00 h, one individual was observed moving slowly on the ground, foraging on the edge of a *Pinus patula* plantation. Near, there were high abundance of the rain frog Pristimantis achatinus (Boulenger 1898) in reproductive activity and accounted for up to five individuals per m². However, there was no predatory event on frogs, possibly because D. sanctijoannis is a specialized snail-eater like

other species of the genus (Peters 1960, Duellman 1978, Sazima 1989, Martins and Oliveira 1998). This species has been found in both dry and rainy months, with the majority of individuals in June when apparently hatchling occurs (newborns MHN-UC 0102 and 0103 captured in June 2009). The complex defensive behavior of this species, which include both arboreal and terrestrial displays, is described in Morales and Lasso (2010). For description of the coloration in life see Boulenger (1911) and Peters (1960).

Erythrolamprus bizonus. A false coral snake species (TL range 313–522 mm; N = 4) rarely seen in Manizales, although all individuals were found in urban and rural areas. Two of the four specimens observed were killed by people, because they confused this snake with a true coral snake considering it a venomous species; however, both the color pattern, and body proportions between $E.\ bizonus$ and $Micrurus\ m.\ decussatus$ (the only coral snake in Manizales), are very distinct to each other. For description of the coloration in life of $E.\ bizonus$, I recommend Roze (1966).

Imantodes cenchoa "Bejuquillo". This large species (TL range 1001–1073 mm; N = 2), very common in many places of Colombia, is a rare snake in Manizales. The two individuals deposited in the MHN-UC were found dead in a rural and forest area respectively (see Figure 2C where the specimen MHN-UC 0047 was found).

Liophis epinephelus bimaculatus (Figure 3E). A single individual was sighted recently, on 30 October 2011, on an unpaved road into a secondary forest at 2500 m (see Figure 2A). The individual was found at 14:00 h, moving actively on the ground, and then rose rapidly up a shrub to 50 cm approx. when the observer tried to capture it (S. Escobar-Lasso pers. comm.). This report and other from the municipality of Salamina, department of Caldas (ca. 30 km to northeast from Manizales), agrees with Dixon

(1983) since *L. e. bimaculatus* is a subespecies that inhabits high Andean valleys (2600–3000 m) in the Tropical Andes. The defensive behavior of this species includes body compression, head and neck elevation and gaping (González-Durán *et al.* unpubl. data.).

Liophis epinephelus pseudocobella. This medium-sized species (Dixon 1983) (TL range 128-582 mm; N=3) is the second most common snake in the urban and rural area of Manizales, sighted in most cases on the edge of paved roads and grassland urban parks (N = 7), which makes it highly susceptible to direct killing and running over by vehicles. In addition, because they have combined black and orange bands, they are commonly mistaken with coral snakes (local people, pers. com.). This species is terrestrial and diurnal, as I have observed individuals foraging actively between 9:00–13:00 h (N = 4). A juvenile was found on September 29, 2006 at 23:50 h, inactive under debris inside a bush in the Botanical Garden of the Universidad de Caldas. Throughout the year, L. e. pseudocobella is most frequently observed between August and December, when apparently hatchling occurs (N= 2); adult individuals have been found in the months of January and April. The defensive behavior of this species includes lateral neck expansion, body thrash and cloacal discharge (González-Durán et al. unpubl. data.).

Elapidae.—Micrurus mipartitus decussatus "Rabo de ajî". A medium-large species (Roze 1996) (TL range 660–827 mm; N=2) rarely sighted in Manizales. During this study only three individuals were found from 2005–2010; one individual was killed on an unpaved road in a rural area, and two live individuals were found in forest fragments within the urban area. All individuals were observed during the day (6:30–14:00 h) and on the ground, suggesting diurnal activity, as reported by Ayerbe *et al.* (1990) for specimens in southwestern Colombia. According to Roze (1966), *M. m. decussatus* feeds on blind snakes and *Atractus* species, which was corro-

borated by Ayerbe *et al.* (1990), who also showed that in captivity, this species can feed on juveniles of *Leptophis ahaetulla* and *Dendrophidion bivittatus*. Ayerbe *et al.* (1990) also reported tail display with flattening of the anal part as defensive behavior for some individuals observed in the wild.

Viperidae.—Bothriechis schlegelii "Cabeza de candado" (Figure 3F). A medium-sized species (TL range 604–691 mm; N = 2) rarely sighted in the municipality of Manizales. From 2002-2010, seven individuals were found: three in the urban, one in rural and three in forested areas. In the urban area, individuals were found dead, run over on paved roads near small bushes, even adjacent to an industrial area (N = 1). In rural area, a juvenile was seen moving along the rocky ground at the edge of a river at 08:30 h on a sunny day. In forested areas, two individuals were observed on day (10:10-13:00 h) perched on bushes ca.1.5 m in height, while another individual was observed in the afternoon (17:06 h) moving on the ground at the edge of a small creek. Although generally docile, individuals of B. schlegelii defend themselves with frontal display and striking when repeatedly stimulated (pers. obs.).

Discussion

Richness and Composition

The richness of snakes species (N=14) reported in Manizales corresponds to 10.9% of the species known from the Andean region of Colombia and 6.3% for the whole country (N=128 for Andean region, and N=222 for Colombia in general, Sánchez-C *et al.* 1995). Such richness is much less than that found in different regions of the Amazonia (e.g., Dixon and Soini 1977 [88 species], Duellman 1978 [52 species], Zimmerman and Rodrigues 1990 [62 species], Martins and Oliveira 1998 [66 species]), in the Brazilian Cerrado (Sawaya *et al.* 2008 [36 species], Araujo *et al.* 2010 [21 species]), and is

less than that reported in the Colombian Pacific lowlands (Moreno et al. 2003 [25 species]), and in one locality at the Cordillera Occidental (Castro-Herrera et al. 2007 [22 species]). However, different environmental factors such as climate, topography, landscape configuration and environmental productivity, besides the factors associated with the type of sampling and data collection, can directly influence the diversity patterns observed in Manizales (see Rocha et al. 2008, Sawaya et al. 2008, Urbina-Cardona et al. 2008). Therefore, making comparisons of species diversity is extremely complicated when related to dissimilar environmental areas, and when different sampling methods have been used (Feisinger 2001). Additionally, this problem can be much more pronounced in snakes, as these are relatively difficult to find, because they usually occur in low densities, most species are cryptic, and many have secretive habits (Sazima and Manzani 1995, Martins and Oliveira 1998, Bernarde and Abe 2006, Sawaya et al. 2008). In Manizales, however, it is almost certain that the richness of snakes is greater than that reported here, considering that large areas of natural habitats have not been adequately sampled, and that an intensive effort of collection has not been made. As such, the results presented in this paper (although with a time of extensive data collection), should be considered preliminary, and therefore, I recommend that the development of diversity studies incorporate the estimate of snake richness in relation to efforts and area sampled.

The results of richness and composition in the different landscape units analyzed (urban, rural, and forested areas), show while forested areas provide habitats for all species recorded, both rural and urban areas represent zones that are used by most snakes (92.8 and 66.6% of the species, respectively), whether as places for temporary displacement. This can be attributed to that in disturbed areas, the distribution of the herpetofauna is associated with changes in temperature (Urbina-Cardona and Londoño-

Murcia 2003), which tends to increase in open areas, thereby facilitating thermoregulation (Urbina-Cardona *et al.* 2006), or also due to ecological attributes of the species as vagility and plasticity in microhabitat use (see discussion on distribution patterns below) (Winck *et al.* 2007, Urbina-Cardona *et al.* 2008, Hartmann *et al.* 2011).

Distribution Patterns

It is well known that urbanization can impact herpetofauna via three key ecological processes: habitat loss, habitat fragmentation and isolation, and the degradation of habitat quality (Hamer and McDonnell 2008). At the level of species assemblages, changes in the spatial configuration of a landscape due to urbanization can cause changes not only in the species diversity, but also in their distribution, reconfiguring the composition of the assemblages in the remaining landscape units (Santos and Tellería 2006. Urbina-Cardona et al. 2008, Hamer and McDonnell 2010). The results in Manizales, however, show a slight difference in the distribution of snakes between urban, rural, and forested areas (see Table 1), which could indicate that the change in the configuration of the original habitat has not change the species distribution. However, it should be noted that for this study, the absence of an intensive, randomized, and strict sampling, prevents statistical comparisons of the results obtained, and therefore represent occasional data on particular observations.

It is interesting to note that species such as Liophis e. bimaculatus, L. t. micropholis and Micrurus m. decussatus (never observed in urban areas), correspond strictly to taxa that inhabit forests or areas of secondary vegetation, and therefore can be seriously affected by urbanization. For other species, the occurrence in urban areas does not mean that they completely tolerate the environmental conditions of this new habitat, but their presence in the city may be due to the proximity to rural and forested areas

(Rojas-Morales and González-Durán 2011), which would indicate that sightings of snakes in urban areas can be casuistic. However, it is likely that nocturnal species as Atractus sp., A. manizalensis, Clelia equatoriana and Dipsas sanctijoannis, use the paved areas of the city as substrates for thermal regulation overnight (see Shine et al. 2004, Pinowsky 2005), and in the case of *C. equatoriana*, that also forage for other snakes. Unlike urban areas, in rural areas (crops, pastures, unpaved roads), some snakes can find more abundant food resources (e.g., high densities of frogs such as Colostethus fraterdanieli, Dendropsophus columbianus, Pristimantis achatinus, pers.obs.), plus to suitable microhabitats for sleeping and nesting, which surely allows snakes to remain in these habitats for long periods of time.

At present, the fauna of snakes in Colombia is still poorly known in terms of diversity, distribution and biogeography, and for this reason comparative analysis between areas are difficult. In this regard, I recommend the reader to review the document of Cadle (1992), on the criticism of the book Ofidios de Colombia [Museo regionale di Scienze Naturali, Monographie VI. Torino, Italia]), which remains as major reference for the identification and distribution of the Colombian snakes. Results of the coefficient of biogeographic resemblance (CBR) between sites indicate generally low species similarity between them (mean 0.25; see Table 3), which can show high beta diversity reflected in the geographic replacement of species; however, the CBR values are affected by the largest number of species in areas such as Pacurita (tropical Wet Forest) and Yotoco (sub-Andean Wet Forest), which increases the denominator of the factor and decreases the similarity between localities. Therefore, these results are much lower compared to those obtained in different areas of the Amazon (mean 0.65; Bernarde and Abe 2006), and are even lower than those obtained by Duellman (1990) when he compared forests of Central and South America (mean 0.36). For Manizales specifically, the localities more similar in snake composition

corresponds to two Andean areas: (1) Bosque de Yotoco Forestal Reserve, which is a sub-Andean forest area located on the eastern flank of the Cordillera Occidental, between 1200-1700 m elevation (Vargas-Salinas et al. 2011), and (2) Selva de Florencia Natural National Park, which is geographically close to Manizales (ca. 75 km linear) located on the eastern flank of the Cordillera Central (Rueda 2000). Comparing the snake composition of Manizales with the other sites analyzed, it may be noted that the assemblage of Manizales is more similar to those of the tropical rainforests, with which it shares an average of two species (see Tables 1 and 3), and is totally different from the tropical dry forest because the absence of shared species (except Pueblo Nuevo, Córdoba). Such results are predictable if considers that in Manizales almost half of the species correspond to a representative group of the Tropical-Andean range (Table 4), which inhabit mostly above 1000 m elevation (with the exception of Dendrophidion bivittatus and Micrurus mipatitus; Roze 1996, Moreno-Arias et al. 2008). In addition, three species appear to be distributed along the area studied, in the central portion of the Central Cordillera (Atractus sp., A. manizalensis and A. titanicus); however, taxonomic status of many Andean Atractus species has not been adequately evaluated, and one of the problems is that there is a high proportion of species known only from, or near the type locality. This is the case for A. manizalensis and A. titanicus, which are only known from municipalities of Villamaría and Manizales (both contiguous), and to localities ca. 100-150 km to the north of Caldas and southeast of Antioquia (see Prado 1940, 1941, Passos et al. 2009).

Natural History

Ecology an ethology descriptive (= natural history in the sense of Green 2005), includes a robust body of data that includes various aspects of the biology of organisms (e.g., diet, reproductive cycles, microhabitat use, activity time),

which constitute a fundamental basis for understanding the structure of biological communities, and therefore is a key element to consider in implementing environmental conservation programs (Green 1993, 2005). The data presented in this manuscript include observations on the habits, activity time, seasonal occurrence, landscape distribution, and notes on the behavior of snakes, although with lack of uniformity in the information presented, due to insufficient data for most species. Still, the accumulation of observations over the period of time analyzed shows that: (1) the snake assemblage in Manizales is primarily terrestrial, although species such as Bothriechis schlegelii, Chironius monticola and Dipsas sanctijoannis also use the vegetation during day and night; (2) in general, most species tend to be more active in the rainy periods of the year (mainly from October to December), during which the rate of mortality increases due to running over and killing indiscriminately (Rojas-Morales in. prep); (3) all species except three that were observed only in forested areas, can occasionally be found in urban areas, in most cases close to areas of vegetation such as crops and pastures (Table 1).

It is essential to obtain additional information on the composition, ecology and behavior of Andean snakes, especially related to their diet and reproduction, to make comparisons with respect to the assemblages of other areas such as tropical rainforests. This information will undoubtedly lead us to know how the diversity and the ecological segregation of species vary through the gradients of elevation in the Neotropical environments.

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References

- Adalsteinsson, S. A., W. R. Branch, S. Trape, L. J. Vitt, and S. B. Hedges. 2009. Molecular phylogeny, classification, and biogeography of snakes of the family Leptotyphlopidae (Reptilia, Squamata). Zootaxa 2244: 1–50.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Araujo, C. O., D. T. C. Filho, and R. J. Sawaya. 2010. Snake assemblage of Estação Ecológica de Santa Bárbara, SP: a Cerrado remnant in Southeastern Brazil. *Biota Neotropica* 10: 235–245.
- Ayerbe, S., M. A. Tidwell, and M. Tidwell. 1990. Observaciones sobre la biología y comportamiento de la serpiente coral "Rabo de Ají" (*Micrurus mipartitus*). Descripción de una subespecie nueva. *Novedades* Colombianas 2: 30–41.
- Bernarde, P. S. and A. S. Abe. 2006. A snake community at Espigão do Oeste, Rondônia, southwestern Amazon, Brazil. *South American Journal of Herpetology 1:* 102–113.
- Boulenger, G. A. 1911. Descriptions of new reptiles from the Andes of South America, preserved in the British Museum. *Annals and Magazine of Natural History* 7: 19–25.
- Cadle, J. E. 1992. On Colombian snakes. Herpetologica 48: 134–143.
- Cadle, J. E. and H. W. Greene. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pp. 281–293 in E. Ricklefs and D. Schluter (eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. Chicago. University of Chicago Press.
- Camacho, J. H., A. H. Guerra, R. O. Quijano, and T. Walshburger. 1992. Unidades biogeográficas de Colombia. Pp. 105–151 in G. Halffter (ed.), La diversidad Biológica de Iberoamérica. Xalapa. Instituto de Ecología.

- Campbell, J. A. and W. W. Lamar (eds.). 1989. The Venomous Reptiles of Latin America. Ithaca. Comstock Publishing Associates. 425 pp.
- Carvajal-Cogollo, J. E. and J. N. Urbina-Cardona. 2008. Patrones de diversidad y composición de reptiles en fragmentos de Bosque seco Tropical en Córdoba, Colombia. Tropical Conservation Science 1: 397–416.
- Carvajal-Cogollo, J. E., O. V. Castaño-Mora, and G. Cárdenas-Arévalo. 2007. Reptiles asociados a humedales de la planicie del departamento de Córdoba, Colombia. Caldasia 29: 427–438.
- Castaño, O., E. Hernández, and G. Cárdenas. 2000. Reptiles. Pp. 612–616 in O. Rangel-Ch (ed.), Colombia Diversidad Biotica III: La Región Paramuna de Colombia. Bogotá. UNAL, IAvH.
- Castro-Herrera, F., W. Bolívar-García, and M. I. Herrera-Montes (eds.). 2007. Guía de los Anfibios y Reptiles del Bosque de Yotoco, Valle del Cauca-Colombia. Cali. Grupo de Investigación Laboratorio de Herpetología, Universidad del Valle. 70 pp.
- Cenicafé (Centro Nacional de Investigación de Café). 2004.
 Anuario Metereológico Cafetero. Chinchiná. Federación Nacional de Cafeteros de Colombia. 554 pp.
- Cisneros-Heredia, D. F. 2007. On the distribution and conservation of *Lampropeltis triangulum* (Lacépède, 1789) in Ecuador. *Herpetozoa 19*: 182–183.
- Corpocaldas. 2002. Agenda para la Gestión Ambiental del Municipio de Manizales. Manizales, Colombia. Subdirección Planeación y Sistemas. 232 pp.
- Dinerstein, E. D., D. Olson, D. Graham, A. Webster, S. Primm, M. Bookbinder, and G. Ledec (eds.). 1995. A Conservation Assessment of the Terrestrial Ecoregions of Latin America and Caribbean. Washington. The World Bank. 129 pp.
- Dixon, J. R. 1983. Systematics of the Latin American snake,
 Liophis epinephelus (Serpentes: Colubridae). Pp 132–149 in A. G. Rhodin and K. Miyata (eds.), Advances in
 Herpetology and Evolutionary Biology. Boston. Museum of Comparative Zoology, Harvard University.
- Dixon, J. R. 1989. A key and checklist of the Neotropical snake genus *Liophis* with country list and maps. Smithsonian Herpetological Information Service 79: 1-40.
- Dixon, J. R. and P. Soini. 1977. The reptiles of the upper Amazon basin, Iquitos region, Peru. II. Crocodilians, turtles, and snakes. Contributions in Biology and Geology Milwaukee Public Museum 12: 1–91.

- Dixon, J. R., J. A. Wiest Jr, and J. M. Cei (eds.). 1993.
 Revision of the Neotropical Snake Genus Chironius Fitzinger (Serpentes, Colubridae). Torino. Museo Regionali di Scienze Naturali. 279 pp.
- Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *University of Kansas, Museum of Natural History, Miscellaneous Publication* 65: 1–352.
- Duellman, W. E. 1990. Herpetofaunas in Neotropical rainforests: comparative composition, history, and resource use. Pp. 455–505 in A. H. Gentry (ed.), Four Neotropical Rainforests. New Haven. Yale University Press.
- Esqueda, L. F. and E. La Marca. 2005. Revisión taxonómica y biogeográfica (con descripción de cinco nuevas especies) del género *Atractus* (Colubridae: Dipsadinae) en los Andes de Venezuela. *Herpetotropicos* 2: 1–32.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34: 487–515.
- Feisinger, P (ed.). 2001. El Diseño de Estudios de Campo para la Conservación de la Biodiversidad. Editorial FAN. 242 pp.
- Fletcher, R. J. 2005. Multiple edge effects and their implications in fragmented landscapes. *Journal of Animal Ecology* 74: 342–352.
- Green, H. W. 1993. What's good about good natural history. Herpetological Natural History 1: 3.
- Green, H. W. 2005. Organisms in nature as a central focus for biology. Trends in Ecology and Evolution 20: 23–27.
- Hamer, A. J. and M. J. McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: a review. *Biological Conservation* 141: 2432–2449.
- Hamer, A. J. and M. J. McDonnell. 2010. The response of herpetofauna to urbanization: inferring patterns of persistence from wildlife databases. *Austral Ecology 35*: 568–580.
- Hartmann, P. A., M. T. Hartmann, and M. Martins. 2011. Snake road mortality in a protected area in the Atlantic forest of southeastern Brazil. South American Journal of Herpetology 6: 35–42.
- Holdridge, L. R. (ed.). 1982. Ecología Basada en Zonas de Vida. San José. IICA. 215 pp.
- Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography 31*: 1829– 1839.

- Knoot, T. G. and L. B. Best. 2011. A multiscale approach to understanding snake use of conservation buffer strips in an agricultural landscape. *Herpetological Conservation* and Biology 6: 191–201.
- La Marca, E. and P. J. Soriano (eds.). 2004. Reptiles de los Andes de Venezuela. Mérida. Fundación Polar, Conservación Internacional, CODEPRE-ULA, Fundacite Mérida, BIOGEOS. 173 pp.
- Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental sourcesink dynamics. *Ecological Applications* 15: 1504–1514.
- Martins, M. and M. E. Oliveira. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History 6: 78–150.
- Morales, J. A. R. and S. E. Lasso. 2010. Defensive behavior of *Dipsas sanctijoannis* (Serpentes: Dipsadidae). *Phyllo-medusa* 9: 147–150.
- Moreno, F. J. 2005. Nuevos reportes de ofidios (Squamata: Serpentes) para el departamento del Chocó. Revista Institucional Universidad Tecnológica del Chocó 22: 37–44.
- Moreno, F. J., E. A. M. Mosquera, Y. R. García, Y. D. M. García, and J. T. R. Mosquera. 2003. Caracterización ecológica de la ofidiofauna en el corregimiento de Pacurita, Chocó-Colombia. Revista Institucional Universidad Tecnológica del Chocó 19: 45–49.
- Moreno-Arias, R. A., G. F. Medina-Rangel, and O. V. Castaño-Mora. 2008. Lowland reptiles of Yacopí (Cundinamarca, Colombia). Revista de la Academia de Ciencias Exactas, Físicas y Naturales 32: 93–103.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Navas, C. 2003. Herpetological diversity along Andean elevational gradient: links with physiological ecology and evolutionary physiology. Comparative Biochemistry and Physiology part A 133: 469–485.
- Orrego, O., J. E. Botero, J. C. Verhelst, A. M. Pfeifer, J. A. López, V. M. Franco, and J. G. Vélez. 2008. Plantas vasculares del municipio de Manizales, Caldas, Colombia. Boletín Científico, Museo de Historia Natural, Universidad de Caldas 8: 61–106.
- Passos, P. and J. D. Lynch. 2010. Revision of *Atractus* (Serpentes: Dipsadidae) from middle and upper Magdalena drainage of Colombia. *Herpetological Monographs* 24: 149–173.
- Passos, P., J. C. Arredondo, R. Fernandes, and J. D. Lynch. 2009. Three new *Atractus* (Serpentes: Dipsadidae) from the Andes of Colombia. *Copeia 2009*: 425–436.

- Pérez-Santos, C. and A. Moreno (eds.). 1988. Ofidios de Colombia. Torino. Museo Regionale di Scienze Naturali. 517 pp.
- Peters, J. A. 1960. The snakes of the subfamily Dipsadinae. Miscellaneous Publications, Museum of Zoology, University of Michigan 114: 1–224.
- Peters, J. A. and B. Orejas-Miranda (eds.). 1970. Catalogue of the Neotropical Squamata. Part I. Snakes. Washington. Smithsonian Institution Press. 347 pp.
- Pinowski, J. 2005. Roadkills of vertebrates in Venezuela. Revista Brasileira de Zoologia 22: 191–196.
- Prado, A. 1940. Notas ofidiologicas 4. Cinco espécies novas de serpentes colombianas do gênero Atractus Wagler. Memórias do Instituto Butantan 13: 15–19.
- Prado, A. 1941. Notas ofiológicas 8. Dois novos Atractus da Colombia. Memórias do Instituto Butantan 14: 25–27.
- Pyron, R. A., F. T. Burbrink, G. R. Colli, A. N. Montes de Oca, L. J. Vitt, C. A. Kuczynski, and J. J. Wiens. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics* and Evolution 58: 329–342.
- Rocha, C. F. D., H. G. Bergallo, C. F. V. Conde, E. B. Bittencourt, and H. Santos. 2008. Richness, abundance, and mass in snake assemblages from two Atlantic Rainforest sites (Ilha do Cardoso, São Paulo) with differences in environmental productivity. *Biota Neotropica* 8: 117–122.
- Rodríguez, L. B. and J. E. Cadle. 1990. A preliminary overview of the herpetofauna of Cocha Cashu. Pp 410– 425 in A. H. Gentry (ed.), Four Neotropical Rainforests. New Haven. Yale University Press.
- Rojas-Morales, J. A. and G. A. González-Durán. 2011. Description of the colouration in life of *Tricheilostoma joshuai* (Serpentes, Leptotyphlopidae). A species tolerant of disturbed habitats? *Salamandra* 47: 237–240.
- Roze, J. A. 1966. La Taxonomía y Zoogeografía de los Ofidios de Venezuela. Caracas. Universidad Central de Venezuela. 362 pp.
- Roze, J. A. 1996. Coral snakes of the Americas. Biology, Identification and Venoms. Malabar, Florida. Krieger Publishing Company. 328 pp.
- Rueda-Almonacid, J. V. 2000. La Herpetofauna de los "Bosques de Florencia" Caldas: una Visión Integrada Sobre su Composición, Diversidad y Relaciones Ecológicas. Santafé de Bogotá. Corporación Autónoma Regional de Caldas (CORPOCALDAS). 212 pp.
- Rueda-Solano, L. A. and J. Castellanos-Barliza. 2010. Herpetofauna de Neguanje, Parque Nacional Natural Tayrona, Caribe colombiano. Acta Biológica Colombiana 15: 195–206.

- Sánchez-C. H., O. Castaño-M, and G. Cárdenas-A. 1995.
 Diversidad de los reptiles en Colombia. Pp. 277–325 in
 J. O. Rangel (ed.), Colombia Diversidad Biótica I.
 Bogotá. Editorial Guadalupe Ltda.
- Santos, T. and J. L. Tellería. 2006. Pérdida y fragmentación del hábitat: efecto sobre la conservación de las especies. *Ecosistemas* 15: 3–12.
- Sawaya, R. J., O. A. V. Marques, and M. Martins. 2008. Composition and natural history of a Cerrado snake assemblage at Itirapina, São Paulo state, southeastern Brazil. *Biota Neotropica* 8: 129–151.
- Sazima, I. 1989. Feeding behavior of the snail-eating snake, *Dipsas indica. Journal of Herpetology* 23: 464–468.
- Sazima, I. and P. R. Manzani. 1995. As cobras que vivem numa reserva florestal urbana. Pp. 78–82 in P. C. Morellato, and H. F. Leitä-Fihlo (eds.), Ecologia e Preservação de uma Floresta Tropical Urbana. São Paulo. Editora Unicamp.
- Shine, R., M. Lemaster, M. Wall, T. Langkilde, and R. Mason. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). *Ecology and Society* 9: 9–21.
- Strüssmann, C. and I. Sazima. 1993. The snake assemblage of the Pantanal at Poconé western Brazil: faunal composition and ecological summary. Studies on Neotropical Fauna and Environment 28: 157–168.
- Uetz, P. (ed.). 2012. The Reptile Database: an Online Reference. Electronic Database accessible at http://www.reptile-database.org/>. Captured on 27 June 2012.
- Urbina-Cardona, J. N. and M. C. Londoño-Murcia. 2003.
 Distribución de la comunidad de herpetofauna asociada a cuatro áreas con diferente grado de perturbación en la Isla Gorgona, Pacífico colombiano. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 27: 105–113.

- Urbina-Cardona, J. N., M. C. Londoño-Murcia, and D. G. García-Ávila. 2008. Dinámica espacio-temporal en la diversidad de serpientes en cuatro hábitats con diferente grado de alteración antropogénica en el Parque Nacional Natural Isla de Gorgona, pacífico colombiano. *Caldasia* 30: 479–493.
- Urbina-Cardona, J. N., M. Olivares-Pérez, and V. H. Reynoso. 2006. Herpetofauna diversity and microenvironment correlates across the pasture-edge-interior gradient in tropical Rainforest fragments in the region of Los Tuxtlas, Veracruz. *Biological Conservation* 132: 61–75.
- Vargas-Salinas, F., I. Delgado-Ospina, and F. López-Aranda. 2011. Mortalidad por atropello vehicular y distribución de anfibios y reptiles en un bosque subandino en el occidente de Colombia. *Caldasia 33*: 121–138.
- Winck, G. R., T. G. Santos, and S. Z. Cechin. 2007. Snake assemblage in a disturbed grassland environment in Rio Grande do Sul state, southern Brazil: population fluctuations of *Liophis poecilogyrus* and *Pseudablabes* agassizii. Annales Zoologici Fennici 44: 321–332.
- Zaher, H. 1996. A new genus and species of Pseudoboine snakes, with a revision of the genus Clelia (Serpentes, Xenodontinae). Bolletino Museo Regionale di Scienze Naturali 14: 289–337.
- Zaher, H., F. G. Grazziotin, J. E. Cadle, R. W. Murphy, J. C. Moura-Leite, and S. L. Bonatto. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American xenodontines: a revised classification and descriptions of new taxa. Papéis Avulsos de Zoologia 49: 115–153.
- Zimmermann, B. L. and M. T. Rodrigues. 1990. Frogs, snakes and lizards of the INPA/WWF reserves near Manaus Brazil. Pp 426–454 in A. H. Gentry (ed.), Four Neotropical Rainforests. New Haven. Yale University Press.

Appendix I. Specimens Examined.

Colubridae: Chironius monticola (MHN-UC 0182, 0186, 0195); Dendrophidion bivittatus (MHN-UC 0038, 0163); Dipsadidae: Atractus sp. (MHN-UC 0035, 0039, 0101, 0107, 0108, 0118, 0119, 0167, 0181, 0187, 0189, 0192); Atractus manizalensis (MHN-UC 0037, 0073, 0165, 0166, 0179, 0180, 0184); Atractus titanicus (MHN-UC 0048, 0055, 0164, 0177, 0188); Clelia equatoriana (MHN-UC 0191, 0193, 0194); Dipsas sanctijoannis (MHN-UC 0102, 0103, 0190); Erythrolamprus bizonus (MHN-UC 0071, 0072, 0082, 0185); Imantodes cenchoa (MHN-UC 0047, 0173); Liophis epinephelus pseudocobella (MHN-UC 0050, 0036, 0178). Elapidae: Micrurus mipartitus decussatus (MHN-UC 0078, 0104). Leptotyphlopidae: Trilepida joshuai (MHN-UC 0040, 0051, 0160, 0161, 0162). Viperidae: Bothriechis schlegelii (MHN-UC 0014, 0015).