Herpetological Conservation and Biology 14(1):212–222.
Submitted: 1 February 2018; Accepted: 25 February 2019; Published: 30 April 2019.

Snake Diversity (Squamata: Serpentes) In Quebrada González Sector of Braulio Carrillo National Park, Costa Rica

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***Abstract*.—Within Braulio Carrillo National Park (BCNP) of Costa Rica, there is a lack of quantitative data regarding the snake community despite its informally reported abundance and relevance to human health. The objective of this research was to document the diversity of snakes within the Quebrada González sector of BCNP. We searched for snakes using visual encounter surveys along several trails, as well as in quadrants and transects within the forest interior. We captured 272 individual snakes across 28 species and five families. *Bothrops asper* (Fer-de-Lance) and *Bothriechis schlegelii* (Eyelash Viper), both Viperids, were the most abundant species encountered, most likely due to their generalist habits. Most other snake species were found in smaller numbers but with roughly equal frequency to each other. Snake species richness and relative abundance were similar between the sampled trails but did show temporal variation during the study period with higher values during the rainy season from April to August. Species composition between the sampled trails was similar, but we did detect some differences likely due to differing habitat characteristics. The species diversity identified here may have been positively affected by the location of the site along an elevational and habitat gradient with high temperatures and precipitation, but likely remains incomplete due to the preliminary nature of the survey and the difficulty of detecting many snake species. A species accumulation curve suggests that the inventory was approximately 81% complete; additional, less abundant species would likely be identified with increased sampling effort and additional survey techniques.**

Key Words.—Bothrops asper; conservation; dominance; inventory; management; rarity; richness

***Resumen*.—En el Parque Nacional Braulio Carrillo (PNBC) existe una carencia de datos cuantitativos de la comunidad de serpientes presentes, a pesar de su abundancia e importancia médica reportada informalmente. El objetivo de este estudio fue documentar la diversidad de serpientes en el sector Quebrada González del PNBC. Realizamos búsquedas mediante relevamiento por encuentro visual en los senderos del parque, así como en cuadrantes y transectos en áreas dentro del bosque. Capturamos 272 individuos, pertenecientes a 28 especies y cinco familias. *Bothrops asper* (Terciopelo) y *Bothriechis schlegelii* (Bocaracá), ambas de la familia Viperidae, fueron las especies más abundantes, probablemente debido a sus hábitos generalistas. Las otras especies fueron encontradas en una abundancia menor, pero equitativa entre sí. La riqueza y abundancia relativa de las serpientes fue similar entre los senderos, sin embargo varió temporalmente durante el período de estudio con los valores más altos en la época lluviosa entre abril y agosto. La composición de especies fue similar entre los senderos, sin embargo se detectaron algunas diferencias debido probablemente a que las características del hábitat en estos difieren entre sí. La diversidad observada podría estar afectada positivamente por la presencia del sitio de estudio en un gradiente altitudinal y de hábitat, con altas temperaturas y tasas de precipitación, sin embargo aún es incompleto debido a su naturaleza preliminar y a la dificultad de observar algunas especies de serpiente. La curva de acumulación de especies muestra que se completó el 81% del inventario; adicionalmente, podrían encontrarse especies menos abundantes si se aumentara el esfuerzo y se diversificaran las técnicas de muestreo.**

Palabras clave.—Bothrops asper; conservación; dominancia; inventario; manejo; rareza; riqueza

Introduction

Diversity surveys are important tools for the conservation and management of snake communities, especially considering the increasing loss of amphibians and reptiles around the world (Santos-Barrera et al. 2008; Morin 2011). These initial studies are important because they confirm the occurrence of species at a given site, document the range of distribution of a species in a country, and allow the identification of areas that feature rare, threatened, or protected species (Santos-Barrera et al. 2008). This serves as the basis for determining

Figure 1. Snakes found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica: (1) *Boa imperator* (Boa constrictor), (2) *Bothriechis schlegelii* (Eyelash Viper), (3) *Bothrops asper* (Fer-de-Lance), (4) *Chironius exoletus* (Green Keelback), (5) *Dendrophidion percarinatum* (Brown Forest Racer), (6) *Drymobius melanotropis* (Green Racer), (7) *Enuliophis sclateri* (White-headed Snake), (8) *Erythrolamprus mimus* (Ringed Snake), (9) *Hydromorphus concolor* (Tropical Seep Snake), (10) *Imantodes cenchoa* (Blunt-headed Tree Snake), (11) *Lachesis stenophrys* (Bushmaster) and (12) *Leptodeira septentrionalis* (Northern Cat-eyed Snake). (Photographed by Allan Artavia-León [2, 10 and 11], Daniel Ramírez-Arce [1, 3, 5, 6, 7, 8 and 9], and Alejandro Zúñiga-Ortiz [4 and 12]).

appropriate management strategies, the identification of priority sites for conservation, and the design of more-detailed studies (Magurran and McGill 2011).

Costa Rica is home to a rich diversity of snakes (Fig. 1 and 2), with more than 130 species from nine families found across the country (Bolaños et al. 2011). The availability of these data arose from many extensive herpetofaunal surveys carried out in the country, including those by Scott et al. (1983) and Hayes et al. (1989) in Monteverde, Guyer and Donnelly (1990) and Heinen (1992) in La Selva Biological Station, Sasa and Solorzano (1995) in Santa Rosa National Park, Santos-Barrera et al. (2008) in San Vito Coto Brus region, Laurencio and Malone (2009) in Carara National Park, and Morera-Chacón and Sánchez-Porras (2015) in Alberto Manuel Brenes Biological Reserve, among others. Many regions of the country, however, remain relatively unstudied and represent a priority for conservation efforts, including much of Braulio Carrillo National Park.

Located along the Cordillera Central mountain range, Braulio Carrillo National Park (BCNP) is a large (47,683

Figure 2. Snakes found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica: (1) *Leptophis depressirostris* (Eastern Parrot Snake), (2) *Mastigodryas melanolomus* (Salmon-bellied Racer), (3) *Micrurus mosquitensis* (Costa Rican Coral Snake), (4) *Oxybelis brevirostris* (Short-nosed Vine Snake), (5) *Oxyrhopus petolarius* (Bush Racer), (6) *Phrynonax poecilonotus* (Bird-eating Snake), (7) *Rhadinaea decorata* (Pink-bellied Litter Snake), (8) *Rhinobothryum bovallii* (Costa Rican Tree Snake), (9) *Sibon annulatus* (Ringed Snail-eater), (10) *Sibon longifrenis* (Lichen-colored Snail-eater), (11) *Spilotes pullatus* (Tiger Rat Snake), (12) *Stenorrhina degenhardtii* (Brown Scorpion-eater), (13) *Tantilla reticulata* (Lined Crowned Snake), (14) *Pliocercus euryzonus* (Halloween Snake), (15) *Xenodon rabdocephalus* (False Fer-de-Lance) and (16) *Geophis hoffmanni* (Hoffman's Earth Snake). (Photographed by Allan Artavia-León [1, 4, 6 and 15], Daniel Ramírez-Arce [2, 7, 10, 11, 12, 13 and 16], Jonathan Vega-Coto [8], and Alejandro Zúñiga-Ortiz [3, 5, 9 and 14]).

ha) reserve, which, together with La Selva Biological Station, constitutes an elevational gradient from 30 m to 2,906 m and features a range of lowland through montane rainforests (Timm et al. 1989; Tenorio 1993). The park is divided into four sectors (Barva, Ceibo, Zurqui and Quebrada González) but often has difficult terrain and limited access. Thus, despite being one of the most diverse sites in the country, Quebrada González (QG) has seen relatively little formal study, largely restricted to two investigations with birds (Avalos-Rodríguez et al. 2002; Oviedo-Pérez and Fournier-Gutierrez 2008) and a mammal monitoring program by park officials (Roger Gómez, pers. comm.). The only studies addressing snakes have been carried out along an elevational transect through the park (Fauth et al. 1989; Federico Bolaños and Douglas Robinson, unpubl. report) and two natural history notes (Baaijen et al. 2015; Vega-Coto et al. 2015), resulting in an overall lack of information of the snake community within the sector.

Due to the lack of quantitative data for QG, rangers and park officials from the Ministerio de Ambiente y Energía (MINAE) often lack necessary information (Rodolfo Tenorio, pers. comm.), hindering their management of the snake community and conservation efforts. We therefore decided to conduct a snake community study in QG, allowing officials to make informed management decisions, to inform park visitors for educational and safety reasons, and as a basis for future studies. The objective of this study was to quantitatively describe the snake community at the Quebrada González sector of Braulio Carrillo National Park. Specifically, we identified all snakes observed over three years of field surveys and determined the relative abundance of each species. We also compared composition and relative abundance of different areas of the sector and across months, investigating spatial and temporal variation of the snake community.

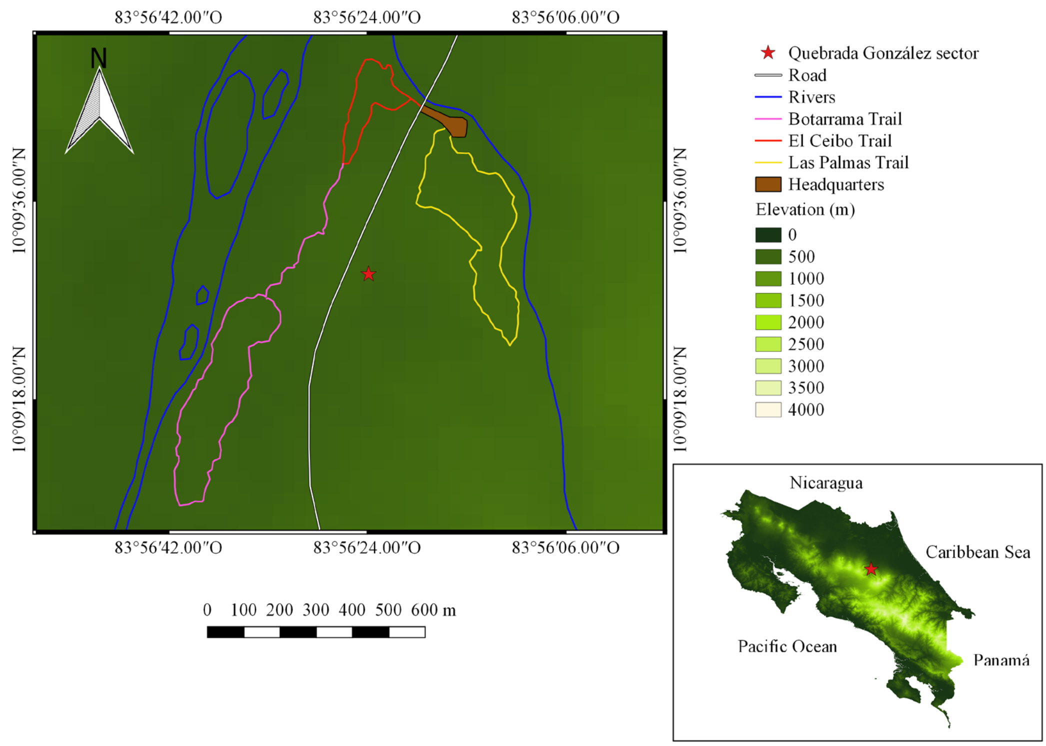

Figure 3. Map of Quebrada González sector, Braulio Carrillo National Park, Costa Rica. The location of the trails, headquarters, water bodies and roads are provided. See text for details. (Taken from ATLAS. 2014. Instituto Tecnológico Costarricense. Cartago, Costa Rica).

Materials and Methods

Study site.—The Quebrada González sector (10°09'39.88"N, 83°56'13.97"W) is a 42 ha region of BCNP in Pococí Cantón, Limón, Costa Rica (Fig. 3). The site consists primarily of tropical wet forest, with an average annual rainfall of 6,375 mm and an average temperature of 25° C. Elevation within the sector ranges from 433 to 595 m (Oviedo-Pérez and Fournier-Gutiérrez 2008). The study site consists mainly of three habitat types: mature forest, secondary forest, and pasture (Lücking 1999; Oviedo-Pérez and Fournier-Gutierrez 2008; Vásquez-Acosta 2009). It also contains important tributaries such as the Quebrada González, Río Sucio, and other small streams with a constant flow throughout the year, providing an abundant water source to plant and animal communities (Tenorio 1993; Schelhas and Sánchez-Azofeifa 2006).

Three unpaved trails are found within the sector: Las Palmas (LP), El Ceibo (EC) and Botarrama (BT; Oviedo-Pérez and Fournier-Gutiérrez 2008; Fig. 3). Las Palmas runs for 1.60 km, is characterized by steep slopes and mature forest, and is 172.48 ± (SD) 41 m (range, 131.48–213.48 m) apart from CE and 523.79 ± 117 m (range, 406.79–640.79 m) from BT. El Ceibo is 0.8 km, located within secondary forests and crossing several streams, and is connected to the BT trail. Botarrama is 2 km, crossing several forest gaps, secondary forests, and small swamps, and ending at the margin of the Río Sucio riverbed (Lücking 1999; Vásquez-Acosta 2009).

Field methods.—We collected field data from February 2012 to June 2015. We conducted 37 site visits, each consisting of a 3–5 d field trip, for 112 total days of fieldwork. In each field trip, we performed diurnal and nocturnal visual encounter surveys (VES; Solórzano 2004; Sutherland 2006; McDiarmid et al. 2012) along the LP, EC, and BT trails as well as along 25 permanent 50-m transects and within nine permanent 25 × 25 m quadrants located in the forest interior. We established transects and quadrants 200 m apart from each other and at least 20 m away from the trail. We determined locations of quadrants and transects randomly using the Quebrada González site map in Quantum 2.12.0 (QGIS Development Team. 2012. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from http://qgis.osgeo.org. [Accessed 12 February 2012]). We searched for snakes on the open forest floor, concealed beneath leaf litter, and above the ground on vegetation up to 2 m.

We performed 107 diurnal and 75 nocturnal surveys during our study period, which include all the surveys made in the three trails, transects and quadrants. Surveying each trail required an average of 4 ± (SD) 2 person-hours (range, 2–6 person-hours), while surveying each transect and quadrant required and average of 0.5 ± 0.15 person-hours (range, 0.35–0.65 person-hours). We spent a total of 444 person-hours on diurnal surveys and 282 person-hours on nocturnal surveys, for a total of 726 person-hours. Of the total sampling effort, we surveyed for 189 person-hours on the EC trail and surrounding transects/quadrants, 232 person-hours on LP and surrounding transects/quadrants, and 305 person-hours on BT and surrounding transects/quadrants. The time required to survey each trail varied with its length and difficulty of terrain, so the intensity of snake-searching efforts was equivalent along the three trails.

We captured every snake encountered by hand or with a snake hook or tongs, and we visually identified snakes to the species level following Savage (2002) and Solórzano (2004). We measured each captured individual for snout-vent length (SVL) and we determined its sex. We also marked each individual by ventral scale clipping, using a unique pattern to identify recaptures and determine the relative abundance for each species (Brown and Parker 1976). Finally, we recorded the date and time of capture, the trail along which it was observed, and the GPS point of capture using a Garmin 62s (Garmin International, Inc., Olathe, Kansas, USA).

Analysis of data.—We calculated a species accumulation curve to assess the quality of the inventory, estimating the likelihood of documenting additional species with further effort. We determined r^2 as an evaluation of the fit of the curve to the model, and calculated the quality of the inventory as $a/(1+b \cdot n)^2$ and the proportion of species found as $S_{obs}/(a/b)$, where a is the rate of increase of new species, b is a parameter related to the shape of the curve, n is the number of samples, and S is the number of species observed (Jiménez-Valverde and Hortal 2003). In addition, we calculated the Chao index as an estimate of overall species richness at the study site, considering that it gives a more accurate estimate in assemblages with rare species (Magurran and McGill 2011).

We plotted the relative abundance of each species found in Quebrada González with a column graph to determine the common and rare species. For each trail, we calculated the species richness, relative abundance, and the Shannon, Pielou, and Simpson diversity indices to evaluate the number of species, number of individuals, species diversity, species dominance, and species evenness, respectively. We also calculated the Bray-Curtis similarity index between the three trails and complemented it with analysis of similarity (ANOSIM) and similarity percentage (SIMPER) analyses to determine the similarity of the three trails' snake compositions as well as the species that most contributed to that similarity.

We plotted the relative abundance and species richness observed in each month to observe how those parameters varied across the year. If two visits were made in the same month, we used an average of those two visits for that month. Finally, we used a simple linear regression analysis to evaluate the relationship between relative abundance and species richness.

We used R 3.3.2 and Tin R 5.1.2.0 (R Core Team 2016) to calculate diversity indices, the Chao index, and ANOSIM and SIMPER tests. We created the species accumulation curve, linear regression, column graph, and related line and scatterplots using EstimateS 9.1.0 (Colwell, R.K. 2013. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Software and User's Guide, Version 9.1.0. Freeware for Windows and Mac OS. Available from http://purl.oclc.org/estimates. [Accessed 23 August 2016]) and STATISTICA 8.0 (Weiß 2007). For all tests, $\alpha = 0.05$.

Results

We recorded 272 individual snakes from 28 species and five families during the study period (Table 1). Most species found belonged to the families Colubridae and Dipsadidae, with 11 and 12 species, respectively. The family Viperidae was represented by three species (Fer-de-Lance, *Bothrops asper*, Eyelash Viper, *Bothriechis schlegelii*, and Bushmaster, *Lachesis stenophrys*), but the former two of these were the most frequently encountered snakes at the study site. The families Elapidae and Boidae were each represented by a single species (Costa Rican Coral Snake, *Micrurus mosquitensis*, and Boa Constrictor, *Boa imperator*, respectively). All species are classified as Least Concern according to the International Union for Conservation of Nature (IUCN) Red List, with some species not evaluated, such as *B. imperator*, the Green Keelback (*Chironius exoletus*), the Tiger Rat Snake (*Spilotes pullatus*), *B. asper*, and *B. schlegelii*, among others (IUCN 2018).

The species accumulation curve indicates a reasonably comprehensive sampling effort, as the curve reached a shallow slope but did not quite asymptote (Fig. 4). The r^2 value was 0.99, indicating a good fit of the model to the data, and the slope reached a value of 0.03, indicating a good quality of the inventory. The Chao index, however, estimated a richness of 36.30 species and the proportion of species found was 0.81, indicating that the maximum number of species has not been reached and that we observed 81% of the species actually present at the study site.

Among all snake species, *B. asper* was the snake with the greatest relative abundance with 64 individuals (23.53% of total individuals), followed by *B. schlegelii* with 51 individuals (18.75% of total individuals), the Northern Cat-eyed Snake (*Leptodeira septentrionalis*) with 27 individuals (9.93% of total individuals), and the Lichen-colored Snaileater (*Sibon longifrenis*) with

Table 1. Taxon, common name and number of individuals on each trail of the snakes found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica.

	Trail		
Taxon	Botarrama	El Ceibo	Las Palmas
BOIDAE			
Boa imperator (Boa Constrictor)	1	0	0
COLUBRIDAE			
Chironius exoletus (Green Keelback)	0	0	2
Dendrophidion percarinatum (Brown Forest Racer)	1	0	0
Drymobius melanotropis (Green Racer)	0	0	1
Leptophis depressirostris (Eastern Parrot Snake)	5	0	0
Mastigodryas melanolomus (Salmon-bellied Racer)	0	2	0
Oxybelis brevirostris (Short-nosed Vine Snake)	5	8	3
Phrynonax poecilonotus (Bird-eating Snake)	1	3	1
Rhinobothryum bovallii (Costa Rican Tree Snake)	0	1	0
Spilotes pullatus (Tiger Rat Snake)	0	0	1
Stenorrhina degenhardtii (Brown Scorpion-eater)	0	0	1
Tantilla reticulata (Lined Crowned Snake)	0	0	1
DIPSADIDAE			
Enuliophis sclateri (White-headed Snake)	0	1	1
Erythrolamprus mimus (Ringed Snake)	1	0	0
Geophis hoffmanni (Hoffman's Earth Snake)	1	1	0
Hydromorphus concolor (Tropical Seep Snake)	0	2	2
Imantodes cenchoa (Blunt-headed Tree Snake)	5	6	4
Leptodeira septentrionalis (Northern Cat-eyed Snake)	11	9	7
Oxyrhopus petolarius (Bush Racer)	2	4	4
Pliocercus euryzonus (Halloween Snake)	1	0	0
Rhadinaea decorata (Pink-bellied Litter Snake)	4	2	1
Sibon annulatus (Ringed Snail-eater)	14	3	2
Sibon longifrenis (Lichen-colored Snail-eater)	7	12	7
Xenodon rabdocephalus (False Fer-de-Lance)	0	0	2
ELAPIDAE			
Micrurus mosquitensis (Costa Rican Coral Snake)	0	1	2
VIPERIDAE			
Bothrops asper (Fer-de-Lance)	32	21	11
Bothriechis schlegelii (Eyelash Viper)	7	10	34
Lachesis stenophrys (Bushmaster)	0	0	1

26 individuals (9.56% of total individuals; Fig. 5). Several species were represented by a single individual, including *B. imperator*, *L. stenophrys*, the Brown Forest Racer (*Dendrophidion percarinatum*), Costa Rican Tree Snake (*Rhinobothryum bovallii*) Lined Crowned Snake (*Tantilla reticulata*), Halloween Snake (*Pliocercus euryzonus*), *S. pullatus*, and Green Racer (*Drymobius melanotropis*) each one representing just 0.37% of total individuals (Fig. 5).

Las Palmas had the greatest number of species and BT the greatest number of individuals, but species richness and relative abundance were similar between the three trails of the sector (Table 2). Diversity index values were also similar, indicating evenness across the three trails. Each trail also presented similar Simpson index values close to 0.90, indicating dominance explained by the same species, mainly *B. asper*, *B. schlegelii*, *L. septentrionalis*, and *S. longifrenis*.

Analysis of similarity showed a great similarity between trails, indicating that their species compositions are similar ($r = 0.08$, $P = 0.002$). Similarity percentage revealed that the species most contributing to this

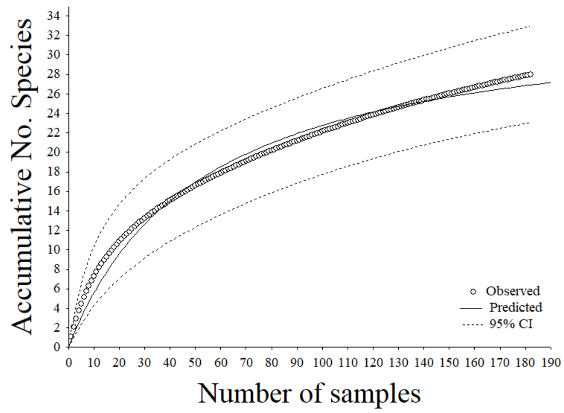

Figure 4. Species accumulation curve of snake species found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica. The observed, predicted values and 95% confidence intervals are shown.

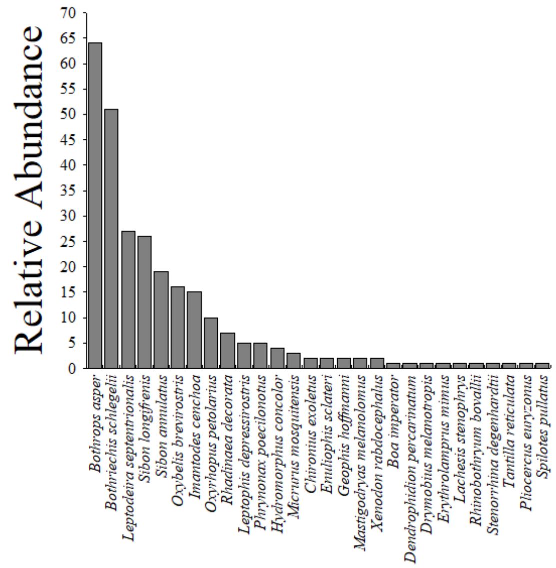

Figure 5. Relative abundance of snake species found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica.

similarity were *B. asper*, *B. schlegelii*, *L. septentrionalis*, and *S. longifrenis*, explaining almost 60% of the similarity. Bray-Curtis index showed that the trails with the highest values of similarity were the BT-EC trails and LP-EC, with lower values of similarity between LP and BT trails (Table 3).

Species richness and relative abundance varied throughout the study period (Fig. 6). Although an overall pattern was not obvious, peaks of high richness and abundance were between April and August, and in January and February. In addition, richness was significantly related to abundance ($F_{1,34}$ = 111.49, r^2 = 0.77, P < 0.001) because there were greater numbers of species identified when we observed greater numbers of individuals (Fig. 7).

Discussion

The snake diversity found during this study could be explained by the fact that QG is located along a transition from lowland to montane forest, both featuring the high temperatures and precipitation (Holdridge 1982; Oviedo-Pérez and Fournier-Gutierrez 2008) that are important factors for snake communities (Laurencio and Fitzgerald 2010). Laurencio and Malone (2009) mention that such transition zones could be expected to feature unusually high species richness, as organisms normally characteristic of each habitat could occur at the same transition site. The species accumulation curve shows that the inventory is fairly complete because we identified an estimated 81% of the species expected at the study site; however, it is very likely that additional rarer species would be identified with increased sampling effort, as the accumulation curve approached but did not reach an asymptote. Additional species could also be identified using additional sampling techniques such as drift fence arrays with pitfall and funnel traps or canopy ascents to survey highly arboreal species (Seigel and Collins 1993; Savage 2002; Solórzano 2004; Sutherland 2006), which we did not use here because we did not have enough funding and equipment. Also, more species can be added to the inventory if we use the museum specimens of Museum of Zoology of University of Costa Rica; nevertheless, we decided not to include them and to use only species with known relative abundance in the analysis.

The 28 species documented at QG in this study seems relatively low compared to surveys from other rainforest areas across Costa Rica, with 47 species reported at La Selva Biological Station (Guyer and Donnelly 1990), 48 at Rara Avis (Laurencio and Fitzgerald 2010), 37 in

Table 2. Number of individuals (N), number of species (S), Shannon index (H), Simpson index (D), and Pielou index (J) for each trail in Quebrada González sector, Braulio Carrillo National Park, Costa Rica.

	Botarrama	El Ceibo	Las Palmas
Number of individuals	98	86	88
Number of species	16	16	20
Shannon index	2.21	2.36	2.26
Simpson index	0.84	0.88	0.81
Pielou index	0.80	0.85	0.76

Table 3. Similarity matrix using the Bray-Curtis index between each trail in Quebrada González sector, Braulio Carrillo National Park, Costa Rica.

	Botarrama	El Ceibo	Las Palmas
Botarrama	1		
El Ceibo	0.69	1	
Las Palmas	0.48	0.62	1

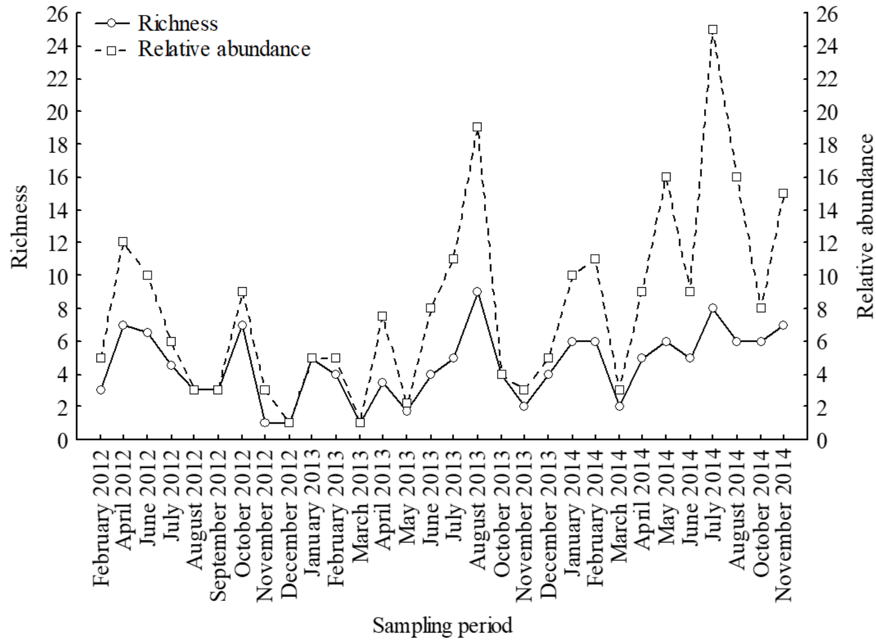

Figure 6. Richness and relative abundance of the snakes found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica, during the study period.

Alberto Manuel Brenes Biological Reserve (Morera-Chacón and Sánchez-Porras 2015) and 36 in Carara National Park (Laurencio and Malone 2009). This apparent disparity may be due to actual differences between sites, to varied sampling methods, or just to the preliminary nature of the current study. La Selva and Alberto Manuel Brenes both feature a greater heterogeneity of habitats than QG, further suggesting its importance to snake species diversity (Fauth et al. 1989; Laurencio and Fitzgerald 2010; Wasko and Sasa 2010). More comprehensive survey methods were used for Rara Avis (Laurencio and Fitzgerald 2010), which included historical literature and museum specimens, and at Carara (Laurencio and Malone 2009), drift fences with pitfall and funnel traps, more extensive leaf-litter plot sampling, and canopy ascents. Considering our species accumulation curve, we expect that additional sampling effort, use of supplementary techniques, and/or surveying a greater range of microhabitats would result in the identification of additional species, similar to these other sites.

We observed a snake community highly dominated by the terrestrial *B. asper* and arboreal *B. schlegelii*, both pitvipers that are fairly generalist in feeding and spatial habits (Savage 2002; Morrison et al. 2006). *Bothrops asper* is also particularly fecund with a mean of 41.1 ± 2.0 (SD) offspring per clutch (Solórzano and Cerdas 1989), and is widely considered one of the most prolific snake species in the Neotropics (Campbell and Lamar 2004). Both species forage primarily at night and are capable of feeding on a wide variety of mammals, amphibians, reptiles, birds, and arthropods, and seem capable of adapting foraging habits based on shifting environmental conditions (Solórzano 2004; Sasa et al. 2009; Sorrell 2009; Meza-Ramos et al. 2010; Wasko and Sasa 2010). Neotropical snake communities are commonly characterized by a few highly abundant generalist species, with others increasingly rare with greater specialization (Fauth et al. 1989; Heinen 1992; Laurencio and Fitzgerald 2010).

Other snakes, even if not typically considered especially rare, may be underrepresented in our data due to detection bias. Some species are small and usually

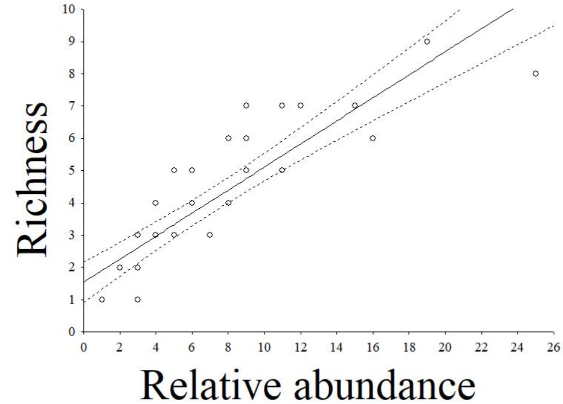

Figure 7. Simple linear regression between the richness and relative abundance of snakes found in Quebrada González sector, Braulio Carrillo National Park, Costa Rica. The regression line (—), r^2 value (0.76) and 95% confidence intervals (---) are shown.

found under leaf litter (e.g., Hoffman's Earth Snake, *Geophis hoffmanni*, *T. reticulata*, Pink-bellied Litter Snake, *Rhadinaea decorata*), making them much more likely to avoid detection than a large surface-dwelling pitviper (Solórzano 2004). Others are highly arboreal (e.g., Bird-eating Snake, *Phrynonax poecilonotus*, *S. pullatus*) and may spend a great deal of time outside of the detection zone (Solórzano 2004). In addition, some species, such as *L. stenophrys*, normally occur in low densities and require areas of extensive mature forest with minimal human interruption, thus may rarely be observed (Zamudio and Greene 1997; Solórzano 2004).

Quebrada González is a relatively small area without dramatic habitat differences, so we did not expect and did not find radically differing snake compositions across the site; snake richness, relative abundance, and alpha diversity were fairly similar across the three trails. The greatest richness was observed along the LP trail, however, which consists mostly of mature forest and so may be suitable for species that do not inhabit the secondary forests characteristic of the EC and BT trails (Lücking 1999; Vásquez-Acosta 2009; Luja et al. 2008). Botarrama trail resulted in the greatest number of individual snake captures, which may also be affected by relatively greater sampling effort or by greater detectability of snakes in the area.

Similarity indices indicated that the LP and BT trails were least similar to each other in species composition but differed less from the EC trail. Las Palmas is an area of mature forest with steep slopes, while BT is a flatter area of secondary forest with flooded regions and forest gaps (Lücking 1999; Vásquez-Acosta 2009). El Ceibo trail is similar to the BT in terms of secondary growth but is situated between the other two trails and so may represent a small-scale transitional zone. These results reinforce the importance of habitat structure in determining snake diversity, with the communities of the LP and BT trails differing from each other, but neither differing substantially from the intermediate EC trail.

The richness and relative abundance of snakes varied temporally with season. The highest values were from April-August, coinciding with the rainy season in the Caribbean, and the lowest values from October-December, coinciding with the dry seasons (Solórzano 2004). This observation was not unexpected, as precipitation is an important factor for the establishment of amphibians and reptiles (Laurencio and Fitzgerald 2010) and the highest values of richness and abundance are typically observed during the rainy season across several parts of Costa Rica (Savage 2002). As precipitation increase during the rainy season, prey availability (amphibians, insects, other reptiles, etc.) increases as well, which promote a higher abundance and activity of snakes (Savage 2002).

Richness and abundance also varied between years, with the greatest values observed in 2014 and the lowest in 2012. This could be due to the El Niño Southern Oscillation (ENSO) conditions affecting Costa Rica during those years, with its associated bands of ocean surface temperature and atmospheric pressure. Costa Rica was strongly affected by this phenomenon in 2012, with Caribbean parts of the country receiving much lower-than-average rainfall. The area in 2013 was largely unaffected and had average rainfall, where 2014 saw a cooling in the Atlantic and the area received higher than average rainfall along the Caribbean slope (Instituto Meteorológico Nacional 2017). Thus, the observed annual variation may again emphasize the importance of precipitation in determining overall reptile diversity and abundance. We considered this study an important first step in understanding the herpetofaunal diversity of Quebrada González sector within BCNP and may serve as a necessary first step for additional studies. These data may also help park officials in making informed management decisions, considering for example the extreme dominance of *B. asper* from a visitor-safety perspective, and the limited presence of threatened species like *L. stenophrys* that are highly sensitive to human disturbance.

Acknowledgments.—The authors would like to thanks the Quebrada González officials for all the help and use of facilities they gave us during the study period. We thank Rodolfo Tenorio and Jorge Hernández for giving us permission to perform the research, Oscar Ramírez for providing us equipment, and Arnoldo Ramírez for reviewing drafts of this manuscript. We thank Jorge De la O, Katherine González, Jairo Hidalgo, and German Vargas, for contributing to sampling efforts. Finally, we thank Federico Bolaños for the special help provided in reviewing the final version of this manuscript and assisting with statistical analysis.

Literature Cited

Avalos-Rodríguez, G.M., A. Soto, J. Veenstra, C. Keller, K. Saturley, J. Schreiber, T. Smith, and S. Zisa. 2002. Effects of a major highway on bird distributions in Braulio Carrillo National Park. Editorial Panamá City, The Association for Tropical Biology, Panama City, Panamá. 4 p.

Baaijen, W., D. Ramírez-Arce, J. Vega-Coto, A. Zúñiga, K. González, and J.M. De La O. 2015. *Sibon longifrenis* (Drab Snail-eater). Aggregation. Herpetological Review 46:649–650.

Bolaños, F., J.M. Savage, and G. Chaves. 2011. Anfibios y Reptiles de Costa Rica. Listas Zoológicas Actualizadas, Universidad de Costa Rica, San Pedro, San José, Costa Rica. 19 p.

Brown, W.S., and W.S. Parker. 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). Journal of Herpetology 10:247–249.

Campbell, J.A., and W.W. Lamar. 2004. The Venomous Reptiles of the Western Hemisphere. Cornell University Press, Ithaca, New York, USA.

Fauth, J.E., B.I Crother, and J.B Slowinski. 1989. Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. Biotropica 21:178–185.

Guyer, C., and M.A. Donnelly. 1990. Length-mass relationships among an assemblage of tropical snakes in Costa Rica. Journal of Tropical Ecology 6:65–76.

Hayes, M.P., J.P. Pounds, and W.W. Timmerman. 1989. An annotated list and guide to the amphibians and reptiles of Monteverde, Costa Rica. Society for the Study of Amphibians and Reptiles, Herpetological Circulars 17:70.

Heinen, J.T. 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. Biotropica 24:431–439.

Holdridge, L. 1982. Ecología Basada en Zonas de Vida. Instituto Interamericano de Cooperación para la Agricultura, San José, Costa Rica. 216 p.

Instituto Meteorológico Nacional. 2017. Boletín del ENOS 2012, 2013 y 2014. Instituto Meteorológico Nacional, San José, Costa Rica. 151 p.

Jiménez-Valverde, A., and J. Hortal. 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. Revista Ibérica de Aracnología 8:51–61.

Laurencio, D., and L.A. Fitzgerald. 2010. Environmental correlates of herpetofaunal diversity in Costa Rica. Journal of Tropical Ecology 26:521–531.

Laurencio, D., and J.H. Malone. 2009. The amphibians and reptiles of Parque Nacional Carara, a Transitional herpetofaunal assemblage in Costa Rica. Herpetological Conservation and Biology 4:120–131.

Lücking, R. 1999. Ecology of foliicolous lichens at the "Botarrama" Trail (Costa Rica), a Neotropical Rain Forest. I. Species composition and its ecogeographical implications. Biotropica 31:553–564.

Luja, V.H., S. Herrando-Pérez, D. González-Solís, and L. Luiselli. 2008. Secondary rain forests are not havens for reptile species in tropical México. Biotropica 40:747–757.

Magurran, A.E., and B.J. McGill. 2011. Biological Diversity. Oxford University Press, New York, New York, USA.

McDiarmid, R.W., M.S. Foster, C. Guyer, J.W. Gibbons, and N. Chernoff. 2012. Reptile Biodiversity: Standard Methods for Inventory and Monitoring. University of California Press, Berkeley, California, USA.

Meza-Ramos, P.A., L. Almendáriz, and M.H. Yánez-Muñoz. 2010. Datos sobre la dieta de *Bothriechis schlegelii* (Berthold, 1846) (Serpentes-Viperidae) en el Occidente del Ecuador. Boletín Técnico 9 Serie Zoológica 6:15–18.

Morera-Chacón, B.H., and R. Sánchez-Porras. 2015. Anfibios y reptiles de la Reserva Biológica Alberto Manuel Brenes. Revista Pensamiento Actual 15:39–59.

Morin, P.J. 2011. Community Ecology. Blackwell Science, Hoboken, New Jersey, USA.

Morrison, M.L, B.G. Marcot, and R.W. Mannan. 2006. Wildlife–Habitat Relationships: Concepts and Applications. Island Press, Washington D.C., USA.

Oviedo-Pérez, P.E., and L. Fournier-Gutiérrez. 2008. Caracterización de la avifauna del sector Quebrada González, Parque Nacional Braulio Carrillo, Costa Rica. Brenesia 69:25–33.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Santos-Barrera, G., J. Pacheco, F. Mendoza-Quijano, F. Bolaños, G. Cháves, G.C. Daily, P.R. Ehrlich, and G. Ceballos. 2008. Diversity, natural history and conservation of amphibians and reptiles from the San Vito Region, southwestern Costa Rica. Revista de Biología Tropical 56:755–778.

Sasa, M., and A. Solórzano. 1995. The reptiles and amphibians of Santa Rosa National Park, Costa Rica, with comments about the herpetofauna of xerophytic areas. Herpetological Natural History 3:113–126.

Sasa, M., D.K. Wasko, and W.W. Lamar. 2009. Natural history of the Terciopelo *Bothrops asper* (Serpentes: Viperidae) in Costa Rica. Toxicon 54:904–922.

Savage, J. 2002. The Amphibians and Reptiles of Costa Rica. The University of Chicago Press, Chicago, Illinois, USA.

Schelhas, J., and G.A. Sánchez-Azofeifa. 2006. Post-frontier forest change adjacent to Braulio Carrillo National Park, Costa Rica. Human Ecology 34:407–431.

Scott, N.J., J.M. Savage, and D.C. Robinson. 1983. Amphibians and reptiles list. Pp. 372–379 *In* Natural History of Costa Rica. Janzen, D.H. (Ed.). Editorial de la Universidad de Costa Rica, San José, Costa Rica.

Seigel, R.A., and J.T. Collins. 1993. Snakes: Ecology and Behavior. McGraw-Hill, Inc., New York, New York, USA.

Solórzano, A. 2004. Serpientes de Costa Rica: Distribución, Taxonomía e Historia Natural. Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica.

Solórzano, A., and L. Cerdas. 1989. Reproductive biology and distribution of the Terciopelo, *Bothrops* *asper* Garman (Serpentes: Viperidae), in Costa Rica. Herpetologica 45:444–450.

Sorrell, G.G. 2009. Diel movement and predation activity patterns of the Eyelash Palm-pitviper (*Bothriechis schlegelii*). Copeia 2009:105–109.

Sutherland, W. 2006. Ecological Census Techniques. Cambridge University Press, New York, New York, USA.

Tenorio, R. 1993. Parque Nacional Braulio Carrillo, un viaje a la Biodiversidad. Ministerio del Ambiente y Energía, Sistema Nacional de Áreas de Conservación, Área de Conservación Cordillera Volcánica Central, San Isidro, Heredia, Costa Rica. 13 p.

Timm, R.M., D.E. Wilson, B.L. Clauson, R.K. La Val, and C.S. Vaughan. 1989. Mammals of the La Selva-Braulio Carrillo Complex, Costa Rica. North American Fauna 75:1–162.

International Union for Conservation of Nature (IUCN). 2018. The IUCN Red List of Threatened Species. Version 2018–2. www.iucnredlist.org.

Vásquez-Acosta, D. 2009. Historia de vida de cinco especies de Baétidos (Ephemeroptera: Baetidae) en la Quebrada González, Parque Nacional Braulio Carrillo. Licenciatura Thesis, Universidad de Costa Rica, San José, Costa Rica. 71 p.

Vega-Coto, J., D. Ramírez-Arce, W. Baaijen, A. Artavia-León, and A. Zúñiga. 2015. *Bothrops asper*. Arboreal behavior. Mesoamerican Herpetology 2:199–201.

Wasko, D.K., and M. Sasa. 2010. Habitat selection of the Terciopelo (Serpentes: Viperidae: *Bothrops asper*) in a lowland rainforest in Costa Rica. Herpetologica 66:148–158.

Weiß, C.H. 2007. StatSoft Inc, Tulsa, OK.: STATISTICA, Version 8. AStA. Advances in Statistical Analysis 91 (3):339–341. doi:10.1007/s10182-007-0038-x.

Zamudio, K.R., and H.W. Greene. 1997. Phylogeography of the Bushmaster (*Lachesis muta*: Viperidae): Implications for Neotropical biogeography, systematics, and conservation. Biological Journal of the Linnean Society 62:421–442.

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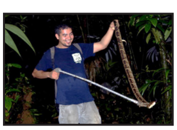

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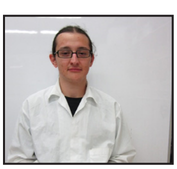

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