Winter 2009

Ecology of Neotropical Arboreal Snakes and Behavior of New World Mollusk-Eating Snakes

Julie M. Ray
Old Dominion University

Recommended Citation

Ray, Julie M.. "Ecology of Neotropical Arboreal Snakes and Behavior of New World Mollusk-Eating Snakes" (2009). Doctor of Philosophy (PhD), dissertation, Biological Sciences, Old Dominion University, DOI: 10.25777/ysd1-2855
https://digitalcommons.odu.edu/biology_etds/84

ECOLOGY OF NEOTROPICAL ARBOREAL SNAKES AND BEHAVIOR OF NEW WORLD MOLLUSK-EATING SNAKES

by

Julie M. Ray
M.S. May 2004, Northern Illinois University
B.S. May 2000, University of Wisconsin – Stevens Point

A Dissertation Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirement for the Degree of

DOCTOR OF PHILOSOPHY

ECOLOGICAL SCIENCES

OLD DOMINION UNIVERSITY

December 2009

Approved by:

Alan H. Savitzky (Director)

Frank P. Day (Member)

Christopher A. Binckley
(Member)

ABSTRACT

ECOLOGY OF NEOTROPICAL ARBOREAL SNAKES AND BEHAVIOR OF NEW WORLD MOLLUSK-EATING SNAKES

Julie M. Ray
Old Dominion University, 2009
Director: Dr. Alan H. Savitzky

The Neotropics is a biologically diverse region that provides many opportunities for ecological and behavioral studies. I utilized the speciose ophidian fauna of central Panama to explore the general ecology of arboreal snakes, the defensive behaviors of the snake community, and the diet of mollusk-eating snakes. I studied arboreal species to understand interspecific relationships in several morphometric characters and to examine preferences in habitat. There were significant morphometric differences in relative length of jaw, mass, tail length, and size at midbody. The arboreal realm was partitioned among species by distance to ground, distance to water, and diameter of the perch. Correlations were found in some species between body mass or length and distance to the ground and leaf length. Additionally, many arboreal species have been documented to bridge gaps in vegetation, but few studies have investigated this behavior systematically. I tested average bridging ability of five Neotropical arboreal snakes and investigated morphological elements underlying differences in relative cantilevering ability. I found significant interspecific differences in average and maximum distances bridged. Species with the relative heaviest mass had the lowest cantilever ratios. Defensive behaviors, which are employed for protection from predators, also were evaluated. I document interspecific differences in these behaviors at the community level. With knowledge gained from the ophidian community in Panama, I further documented on the defensive behaviors of other New World mollusk-eating snakes. Finally, I studied the diet of selected mollusk-eating snakes. I evaluated fecal samples of *Dipsas* and *Sibon* and found that their diet is broader than mollusks alone. In fact, a majority of *Dipsas* in central Panama were feeding on oligochaetes. Some species of *Sibon* were feeding on mollusks, whereas others fed primarily on amphibian eggs and oligochaetes. The discovery of a broader diet in these taxa may have conservation implications as populations of amphibians and terrestrial mollusks decline worldwide. The expansion of our knowledge of the natural history, ecology, and behavior of Neotropical snakes has provided information that will be important for future studies of community- and ecosystem-level interactions and for the conservation of the biota of central Panama.

This dissertation is dedicated to Pablo Santana, Alexander Santana, and Aurelio Gonzalez and to my parents, John and Joanne Ray.

ACKNOWLEDGMENTS

As with many projects of this magnitude, especially those performed in extreme locations including lands where the language and culture are foreign, many persons deserve acknowledgement.

First, thank you to my committee and the people who helped me get to Panama: Alan Savitzky, Frank Day, Christopher Binckley, Roberto “Figa” Brenes, Karen Lips, Chad Montgomery, and Matt Whiles. Thank you to the part-time field help: Santana Arcia, Sarah Becker, Elicia Cano, Clint and Tammy Otto, Sandra Galeano, Scott Goetz, Edgardo Griffith, Andrew Hein, Melissa Miller, Heidi Ross, Amanda Rugenski, and Doug Woodhams. Thank you to the park staff: José Pérez (director of the park), Natalio Vargas, José Carmen, and Andres González. A very special thanks to Aurelio González, Alexander Santana, and Pablo Santana for extensive help in the field. Thank you for assistance with collections, analyses, or logistics to Mike Lane, Andy Mahon, Heidi Mahon, Greg Pauly, Richard B. King, Jace Robinson, Bud Rodi, and Jeremy Weisz. Thank you to all funding sources: American Society of Ichthyologists and Herpetologists, Chicago Herpetological Society, National Science Fund, North Carolina Herpetological Society, Sigma Xi, Society for the Study of Amphibians and Reptiles, Sophie Danforth Conservation Fund, and Wisconsin Division for Vocational Rehabilitation. Thank you to the Smithsonian Tropical Research Institute and ANAM, the Panamanian Environmental Authority, for logistical support while in Panama. Finally, to Lucy, mi chico, and Brett for making me believe.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

GENERAL INTRODUCTION

The Neotropics constitute a vast region of high biodiversity (e.g., Gentry, 1992; Kricher, 1999). Many threats exist for organisms residing within tropical forests (Kricher, 1999). Deforestation is destroying rainforests at astonishing rates (Laurance and Peres, 2006), and many populations of organisms are being lost or drastically reduced (e.g., Gibbons et al., 2000; Lydeard et al., 2004; Lips et al., 2006). The Neotropical biota must be studied to develop conservation-oriented management plans, and basic biological information is needed to protect species, communities, and ecosystems.

This study is intended to improve our understanding of a Neotropical snake community by focusing on the arboreal and mollusk-eating members of the fauna. Observations on temperate mollusk-eating snakes were included for comparative purposes in some analyses. Study sites were located in North America (USA), Central America (Panama), and South America (Peru).

STUDY SITES

The majority of my fieldwork was conducted in the Republic of Panama. Central America supports a highly diverse herpetofauna (Myers, 1982), and snakes, including arboreal species and mollusk-eating snakes of the genera *Dipsas* and *Sibon*, are abundant (C. E. Montgomery, pers. comm.; pers. obs.). Additional data on mollusk-eating snakes

---

The model journal is *Copeia*.

were collected in Peru and at various sites in the USA.

Parque Nacional General de División Omar Torrijos Herrera, Coclé Province, Republic of Panama.---Parque Nacional General de Divisiön Omar Torrijos Herrera (PNGDOTH; English translation: Omar Torrijos National Park; 8° 40' N, 80° 37' W) is 25,275 ha in total size and is situated along the Continental Divide. My study area is located in the mid-elevation (~800 m), pre-montane cloud forest on the Atlantic versant.

Trails in mature secondary forest (35+ years of age) and nearby mountain streams constituted the 3.5 km of terrestrial and riparian transects utilized for this study (Lips et al., 2006; Table 1.1; Fig. 1.1, 1.2). Transects were marked every 10 m with flagging to facilitate recording the movements of snakes and to allow snakes to be returned to the location of capture. Additional captures were made along the road within the boundary of the park and at a small pond within the forest.

Table 1.1. Study transects in Parque Nacional G. D. Omar Torrijos Herrera (PNGDOTH). Includes names of transect as used in this study and by PNGDOTH. The length of each transect is listed in meters. Numbers in parentheses refer to numbers on the map (Fig. 1.2).

Study Transect Name	PNGDOTH Transect Name	Length (m)
	Riparian	
Cascada (2)	-	200
Guabal (3)	Rió Guabal	200
Loop Stream (1)	Rió Ranita	200
Silenciosa (4)	Rió Silenciosa	200
	Terrestrial	
Loop Trail (5)	Sendero Los Helechos	430
Main Trail (7)	Sendero La Rana	400
Rocky Road (6)	La Salida	420
Verrugosa	Sendero Cuerpo de Paz	1800
	Other	
Pond	La Laguna	

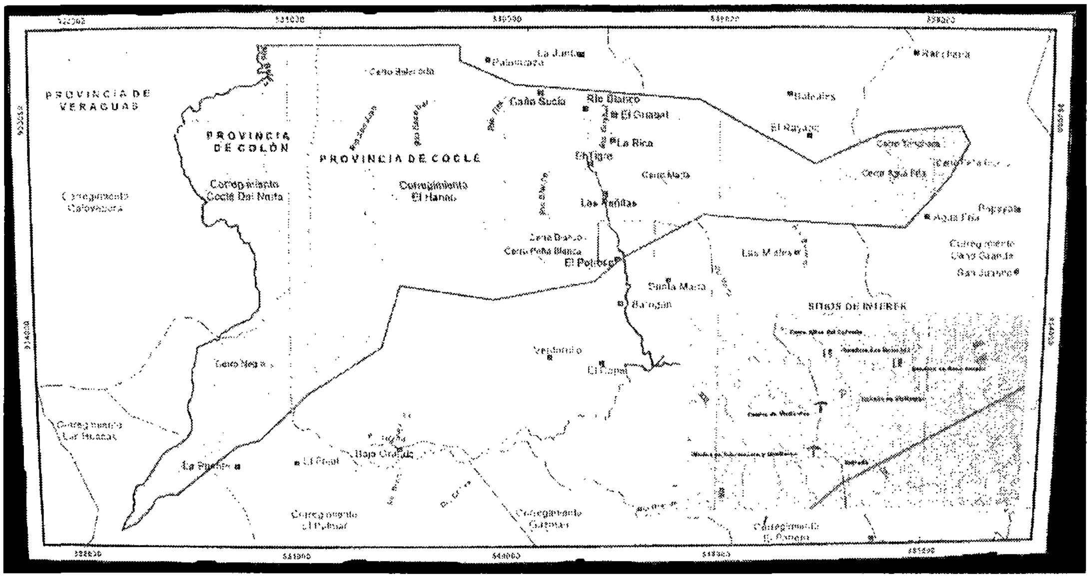

Fig. 1.1. Map of Parque Nacional G. D. Omar Torrijos Herrera. Inset in lower right includes buildings and area where the study transects were located.

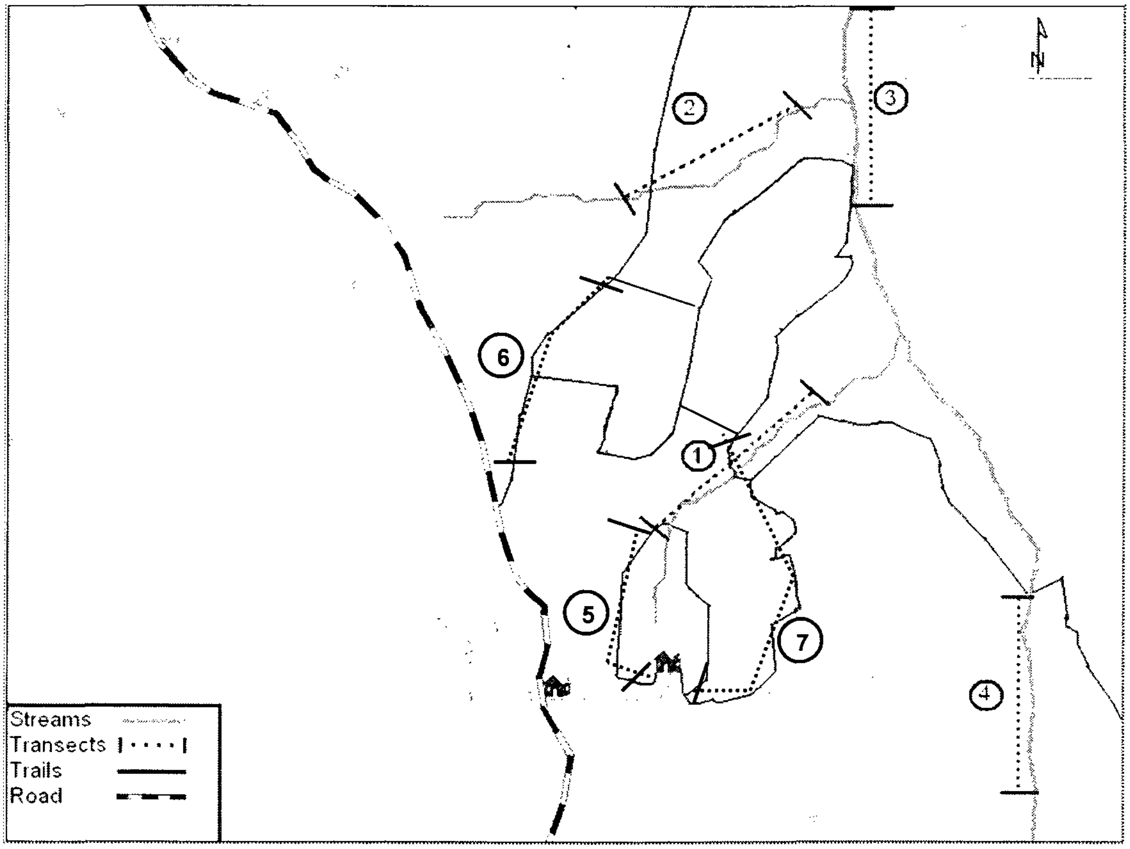

Fig. 1.2. Map of riparian and terrestrial transects in Parque Nacional G. D. Omar Torrijos Herrera. Verrugosa Trail begins at the northern point of transect 4 and is not shown in its entirety on this map. See Table 1.1 for details.

Chytridiomycosis, a disease spread by *Batrachochytrium dendrobatidis* and known to kill many species of amphibians (Lips et al., 2006), had already affected PNGDOTH prior to this study. The first frog that tested positive for chytridiomycosis, as determined by PCR (Brem, 2006; Brem et al., 2007), was found in September 2004 (Lips et al., 2006), and the first death attributed to chytridiomycosis occurred in October 2004. Fifty-seven percent of amphibians were lost in PNGDOTH between October 2004 and January 2005 (Lips et al., 2006), and amphibian populations have not recovered significantly (K. R. Lips, pers. comm.; pers. obs.).

Altos del Maria, Panama Province, Republic of Panama.---Altos del Maria (ADM) is located near El Valle de Antón in western Panamá Province (8^0 38' N, 80^0 4' W). The forest and streams included in this study had intact forest, but clearing of the forest was advancing toward the site and overtook one stream in July 2006. Riparian and terrestrial transects were located in primary forest at mid-elevation (500-1200 m) pre-montane habitat (Table 1.2) and were visually surveyed for snakes at night. ADM experienced a chytridiomycosis-induced decline of amphibians in early 2006. In conjunction with the decline, zoos began removing amphibians for the conservation-breeding center, El Valle Amphibian Conservation Center, located at El Nispero Zoo in El Valle de Antón. I abandoned ADM as a field site in July 2006.

Central Valley, California.---*Contia tenuis* was captured at various sites around the Central Valley of California by Gregory Pauly. Sites are listed below and coordinates are provided when available.

Table 1.2. Study transects in Altos del Maria. Includes name and length of riparian and terrestrial transects.

Study Transect Name	Length (m)
Riparian	
Rio Maria	200
Tributary 1	200
Terrestrial	
CAS/ADM2	200
Road	200

- Redding, located at the northern end of the Sacramento Valley, Shasta County, California (40°34'N, 122°22'W)
- Auburn, located in the Sierra Nevada foothills Placer County, California (38°53'N, 121°4'W)
- Quail Ridge Ecological Preserve, near the University of California, Davis in eastern Napa County, California (38°49'N, W122°15'W)
- Hwy 128 at Stebbins Cold Canyon, about 6 km from the Quail Ridge Ecological Reserve, Napa County, California
- Sacramento River, south of Sacramento, Yolo County, California (38°76'N, 121°96'W)
- South River Road (near Linden Road), in southwestern Sacramento, Yolo County, California (38°56'N, 121°16'W)
- Brannon Island State Recreation Area, Sacramento County, California

Lake Erie Islands, Ottawa and Erie Counties, Ohio.---*Storeria dekayi* (N = 95) was collected from South Bass, Middle Bass, and North Bass Islands, Ottawa County and from Kelleys Island, Erie County, in western Lake Erie, Ohio, USA (approximately 41°65'N, 82°82'W; see Ray and King, 2007 for map).

Potawatomi Woods Forest Preserve and Kishwaukee River State Fish and Wildlife Area, Kirkland, Illinois.---*Storeria dekayi* (n = 20) and *S. occipitomaculata* (n = 20) were collected from the Potawatomi Woods Forest Preserve and the Kishwaukee River State Fish and Wildlife Area near Kirkland, DeKalb County, Illinois, USA (42°06'N, 88°52'W). Snakes were collected from a grassy field with several old buildings; most snakes were captured under debris near the structures.

Beaver Island, Michigan.---*Storeria occipitomaculata* (n = 10)was collected from sites on Beaver Island, Charlevoix County, Michigan, USA (45°40'N, 85°32'W). Snakes were collected from a field where wood and tin cover sheets had been laid previously, near anthropogenic structures, and in debris piles at an old farm.

STUDY ORGANISMS

Neotropical snake communities.---The number of studies documenting the composition of Neotropical snake communities has increased in recent years (e.g., Guyer and Donnelly, 1990; Duellman and Salas, 1991; Ibáñez et al., 1995; Martins and Oliveira, 1998; Lee, 2000; Savage, 2002; Solórzano, 2004; Duellman, 2005; Wilson and Townsend, 2006). The diets of Neotropical snakes include invertebrates, amphibians, reptiles, birds, eggs of all latter prey items, and mammals. Habitats from fossorial to terrestrial, aquatic, and arboreal, and the activity period of particular species may be diurnal, nocturnal, or crepuscular (Savage, 2002; Solórzano, 2004; Duellman, 2005). Neotropical snakes range from about 25 cm to about 3 m in total length (Savage, 2002; Solórzano, 2004; Duellman, 2005).

Neotropical arboreal snakes.---An arboreal species is defined as one that spends at least 50% of its time in aboveground vegetation (Lillywhite and Henderson, 1993; Franca et al., 2008). Even the most highly arboreal species can be found occasionally on the ground (e.g., *Imantodes cenchoa* perched on rocks in the stream, pers. obs.) and terrestrial species occasionally are found moving or resting in trees (e.g., *Rhinobothryum bovallii*, Solórzano, 2004; pers. obs.).

Arboreal snakes may constitute a large proportion of the vertebrate biomass in some habitats (Duellman, 1978; Guyer and Donnelly, 1990; Duellman and Salas, 1991), suggesting they are important components of the community. Facultative or obligate arboreal snakes face several challenges while conducting routine activities (e.g., reproduction, locomotion, foraging) on an unstable substratum, which has led to evolution of morphological and behavioral specializations (e.g., Henderson and Nickerson, 1976; Myers, 1982; Lillywhite and Henderson, 1993). Morphological adaptations associated with arboreality include reduced body mass, laterally compressed body form, and eyes that can be directed downward (Lillywhite and Henderson, 1993), and behaviors include movements mimicking swaying branches, presumably to enhance crypsis (Lillywhite and Henderson, 1993). Furthermore, in an environment with highly variable microhabitats and environmental conditions (e.g., Allee, 1926; Allee et al., 1949;

Smith, 1973; Myers, 1969), resource partitioning may occur interspecifically and intraspecifically (between sexes, ages, or size/age classes, but see Tu et al. [2000], who found no differences in perch location between male and female *Trimeresurus stejnegeri*). What little information is available on the global arboreal snake assemblage has been deduced largely from a few species or genera (e.g., Henderson and Nickerson, 1976) and has not permitted conclusions to be drawn about an entire assemblage (Lillywhite and Henderson, 1993).

Furthermore, many studies focusing on arboreal snakes have not evaluated fully the environment higher than the limitations of human visibility from the ground (about 3 m; Lillywhite and Henderson, 1993). Until recently the canopy has been difficult to access (Barker and Pinard, 2001), so the vertical dimension rarely has been studied to its fullest potential. For example, Lillywhite and Henderson (1993) reviewed the literature on 19 species of snakes and found that 18 were frequently captured between 1.5 and 3 meters. However, with tens of meters of vertical habitat available, it is reasonable to assume that snakes visit higher sites, at least occasionally. This range of observations also was not logistically possible for this dissertation, due to the lack of a canopy access system and the relatively young age of the forests I studied, so trees were not large enough for single-tree climbing equipment.

Mollusk-eating snakes.---Morphological adaptations for the consumption of snails and slugs have evolved at least five times, with varying degrees of specialization (Gruz, 2002). Specialized skulls, cephalic musculature, and teeth (Dunn, 1951; Peters, 1960; Savitzky, 1983) have evolved among ophidian species specialized to consume mollusks.

Snakes exhibiting such modifications reside in Africa, Asia, and North America, as well as Central and South America, where the radiation is greatest. Four Neotropical genera are considered mollusk specialists: *Dipsas, Sibon, Sibynomorphus,* and *Tropododipsas,* belong to the colubrid subfamily Dipsadinae, which also includes predators on frogs and lizards, such as *Imantodes* and *Leptodeira* (Solórzano, 2004).

A diet of mollusks poses many challenges, especially considering that several ophidian predators on mollusks are arboreal and none are known to digest the calcified shell completely. Even without the shell, the consumption of slugs is complicated by a dynamic, hydrostatic body structure (Sazima, 1989; pers. obs.), production of copious mucous, and, at least in some species, defensive toxins (Schroeder *et al.,* 1999).

Several mollusk-eating snakes (including members that live in other areas of the New World) display interesting defensive behaviors, such as body pyramiding (e.g., Cadle and Myers, 2003), that have not been documented for other species of snakes. Furthermore, mimicry of vipers and coral snakes has been suggested for several taxa (e.g., Sazima, 1989; Greene, 1997; Solórzano, 2004). Understanding such behaviors may provide insights into potential predators on these species.

Tropical study species.---Fifty-six species of snakes, belonging to six families, have been reported from PNGDOTH (C. E. Montgomery, and K. R. Lips, unpublished data; pers. obs.; Table 1.3), and 23 species in three families have been reported from ADM (pers. obs.; Table 1.3). Snakes were studied at PNGDOTH in 1997-2007 (2006-2008 by me) and Altos de Maria in 2005-2006. *Dipsas* in central Panama may include as many as three cryptic species (Cadle and Myers, 2003; Myers et al., 2007; R. Ibáñez, pers.

comm.). For this study I treat the species of *Dipsas* encountered at my field sites, other than *D. nicholsi,* as one taxon, designated *Dipsas* sp.

To examine historical patterns in ecology and behavior I constructed a composite phylogeny of the Neotropical study species (Fig. 1.3) from multiple sources (Crother, 1999; Werman et al., 1999; Vidal et al., 2000; Taggart et al., 2002; Highton et al., 2002; Lawson et al., 2002; Castoe et al., 2005; Hollis, 2006, Mulcahy, 2007).

Table 1.3. Species documented in Parque Nacional G. D. Omar Torrijos Herrera (PNGDOTH) and in Altos del Maria (ADM). Snakes were studied at PNGDOTH in 1997-2008 and at ADM in 2005-2006. Numbers without parentheses indicate total captures; those in parentheses indicate numbers of individuals. X indicates species known from the site but not found during the study period of 2005-2007.

Family	Species	PNGDOTH	ADM
Anomalepididae	*Liotyphlops albirostris*	1	
Boidae	*Boa constrictor*	1	
	Corallus annulatus	1	
	Epicrates cenchria	1	
Ungaliophiidae	*Ungaliophis panamensis*	1	1
Colubridae: Colubrinae	*Chironius exoletus*	1	1
	Chironius grandisquamis	1	4 (4)
	Dendrophidion nucale	X	
	Dendrophidion percarinatum	X	
	Dendrophidion vinitor	X	1
	Dryadophis pleei	1	
	Drymobius rhombifer	X	
	Leptophis ahaetulla	X	
	Leptophis depressirostris	1	
	Leptophis nebulosus	4 (3)	
	Oxybelis aenus	1	
	Oxybelis brevirostris	132 (70)	
	Pseustes poecilonotus	4 (4)	
	Scaphiodontophis sp.	X	
	Spilotes pullatus	1	2
	Stenorrhina degenhardtii	1	
	Tantilla melanocephala	2 (2)	
Colubridae: Dipsadinae	*Atractus imperfectus*	X	
	Dipsas nicholsi	1	
	[1]*Dipsas* sp.	92 (71)	x
	Enulius flavitorques	2 (2)	

Table 1.3. Continued

Family	Species	PNGDOTH	ADM
	Geophis bellus	X	
	Geophis brachycephalus	4 (4)	1
	[2]*Geophis* sp.	1	
	Hydromorphus concolor	1	
	Imantodes cenchoa	66 (53)	6 (6)
	Imantodes inornatus	18 (12)	
	Leptodeira septentrionalis	27 (20)	3 (3)
	Ninia celata		1
	Ninia maculata	1	1
	[3]*Ninia* sp.	3	
	Rhadinaea decorata	2	
	Sibon annulatus	66 (53)	14 (13)
	Sibon argus	69 (39)	33 (25)
	Sibon longifrenis	8 (3)	14 (13)
	Sibon nebulatus	10 (10)	1
	Urotheca euryzona	1	5 (5)
Colubridae: Xenodontinae	*Amastridium veliferum*	2 (2)	
	Clelia clelia	2 (2)	
	Erythrolamprus mimus	1	
	Liophis epinephalus	1	1
	Nothopsis rugosus	1	1
	Oxyrhopus petolus	2 (2)	
	Rhinobothryum bovallii	1	
Elapidae	*Micrurus multifasciatus*	X	
	Micrurus mipartitus	1	
	Micrurus nigrocinctus	2 (2)	
Viperidae	*Atropoides nummifer*	1	
	Bothriechis lateralis		X
	Bothriechis schlegelii	34 (25)	3 (2)
	Bothrops asper	1	2 (2)
	Lachesis stenophrys	1	1
	Porthidium nasutum	X	X

1. Undescribed species (Myers et al., 2007)
2. Undescribed species (C. W. Myers, pers. comm.)
3. Undescribed species (R. Ibáñez, pers. comm.)

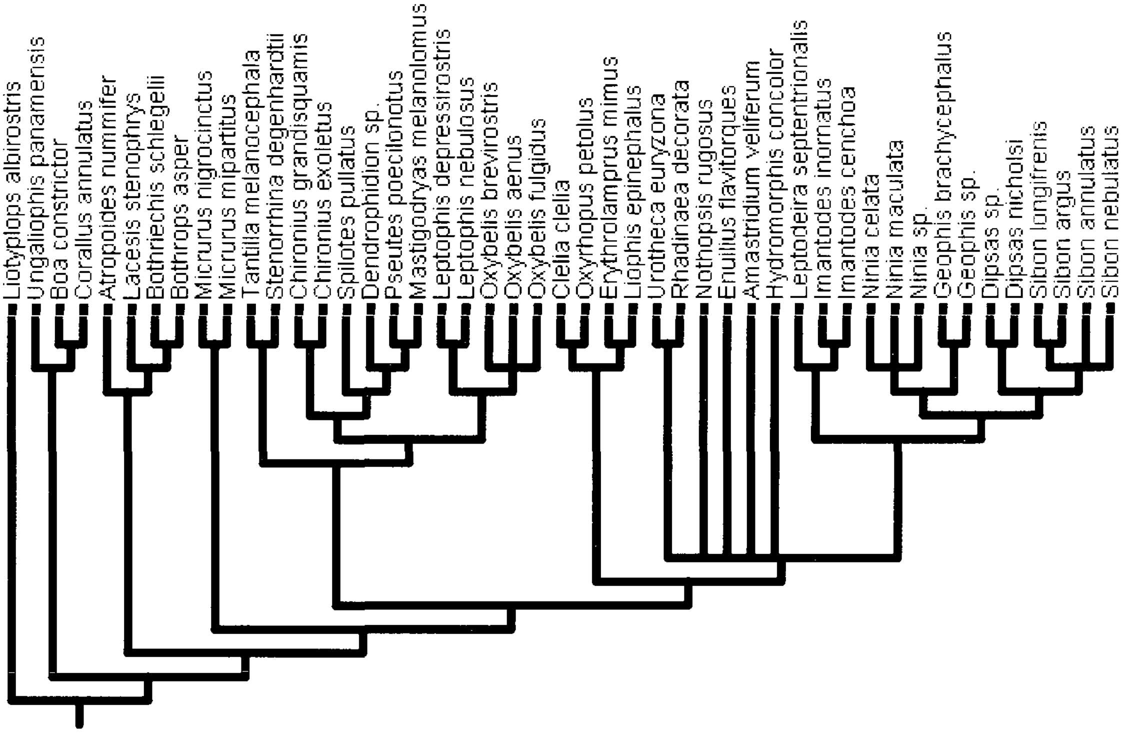

Fig. 1.3. Phylogeny of snakes captured in central Panama during this study. Tree constructed from phylogenies of Crother, 1999; Werman et al., 1999; Vidal et al., 2000; Taggart et al., 2002; Highton et al., 2002; Lawson et al., 2002; Castoe et al., 2005; Hollis, 2006, and Mulcahy, 2007.

Temperate study species.---I conducted studies in the United States on *Contia tenuis*, *Storeria dekayi* and *S. occipitomaculata*. Gregory Pauly collected 50 *C. tenuis* from study sites in central California in April - May 2006. I collected seven *S. occipitomaculata* on Beaver Island in June 2005 and 25 *S. dekayi* on various islands in Lake Erie in June 2005. Richard B. King captured six *S. dekayi* and eight *S. occipitomaculata* at the Potawatomi Woods Forest Preserve and the Kishwaukee River State Fish and Wildlife Area in May 2005.

GENERAL METHODS

Methods for tropical research.---I conducted distance-constrained visual surveys by slowly walking established, metered transects, primarily at night using large lights. I captured nonvenomous snakes by hand when within reach. Venomous snakes and snakes out of reach were manipulated with a snake hook. I placed small snakes in plastic bags, to avoid dehydration, and large snakes in cloth pillowcases. I recorded only transect and distance, time, height, distance to water, defensive behavior at time of capture, and activity at time of first sighting in the field for the 94 captures from ADM. I returned snakes to the local laboratory, where I recorded morphological measurements and other data, including fecal samples, stomach contents, and observations of defensive behaviors and tested cantilevering abilities (Lillywhite and Henderson, 1993; Bernarde and Abe, 2006; Table 1.4).

I measured snout-vent length (SVL; from the rostral scale to the cloaca) and total length (TL; from the rostral to the tip of the tail) in a squeeze box (Quinn and Jones, 1974) to the nearest 0.1 cm, and mass to the nearest 0.1 grams on an electronic balance. I measured head and body dimensions (other than SVL and TL) with a digital caliper to the nearest 0.01 cm. Head dimensions and body circumferences were not measured for recaptures. I did not record head measurements for venomous snakes.

I maintained snakes in an air-conditioned or cool location in the house and typically returned snakes to the site of capture within 48 hours of capture to reduce stress and time away from normal activities, such as foraging and mate-searching.

Table 1.4. Data collected for snakes captured in Parque Nacional G. D. Omar Torrijos Herrera, 2006 - 2007. Units are listed when appropriate, and clarification of the type of data collected is included as needed.

Characteristic	Unit	Clarification
Data Collected in the Field		
Transect name		
Meter of transect	m	
Time of capture		00:00 – 23:59
Air temperature	°C	
Humidity	%	
Height from ground	cm	
Distance to end of branch/leaf	cm	
% vegetation density	%	measured at height of snake
Direction of head		stem or terminal end of leaf or branch
Direction moving		horizontal or vertical
Plant type		herb, tree, bromeliad, vine
Body position		elongate, loose coil, tight coil
Activity		moving, feeding, mating, sleeping
Diameter of perch	mm	measured at midbody (when applicable)
Length and width of leaf	mm	measured at midbody (when applicable)
Circumference of bromeliad	mm	measured at midbody (when applicable)
Data Collected in Laboratory		
Snout-vent length	cm	
Total length	cm	
Mass	g	
Sex		male or female
Individual identification		PIT tag or scale clip number
Height at mid-body	mm	
Width at mid-body	mm	
Head length	mm	snout to rear of quadrate
Head width	mm	widest point
Jaw length	mm	snout to last labial
Interoccular distance	mm	between eyes
Scars		presence, description of type, location
Stub		missing tail
Reproductive Status		female with enlarged follicles or eggs
Presence of prey item		palpation of stomach
Fecal sample		

Methods for temperate research.---I captured temperate snakes by hand and placed them in cloth pillowcases to return them to the local laboratory for measurement. I measured SVL (mm) and TL (mm) with a tape measure to the nearest 0.1 cm. Mass (g) was measured to the nearest 0.1 g with an electronic balance or spring scale.

Other individuals of several species were collected by other researchers and sent to Old Dominion University (ODU) in Norfolk, Virginia, USA. *Contia tenuis* were collected by G. Pauly and shipped from California. Some *Storeria dekayi* and *S. occipitomaculata* were captured by R. B. King in DeKalb County, Illinois, USA, and shipped to ODU. Snakes were measured and weighed upon arrival (1-2 days post-capture).

CHAPTER II

MOPHOMETRICS AND NICHE PARTITIONING IN A NEOTROPICAL ARBOREAL SNAKE ASSEMBLAGE

Many snake taxa (including boids, viperids, and colubrids) have adapted to arboreal environments (Lillywhite and Henderson, 1993). Even species considered terrestrial or aquatic and not arboreal (spending < 50% of their time in aboveground vegetation) often rest, perch, or forage in vegetation (e.g., Martins et al., 2008; pers. obs.). *Boa constrictor* (Boidae), for example, is known to take terrestrial prey, but also can be found perched in a sit-and-wait position in trees or shrubs (Solórzano, 2004). *Chironius grandisquamis* forages diurnally in the terrestrial environment, feeding on frogs, lizards, and small mammals (Solórzano, 2004). However, this species also searches for birds in the arboreal habitat and ascends trees at night, where it sleeps in a coiled position (pers. obs.). Other species of snakes have evolved to become essentially fully arboreal (e.g., *Corallus annulatus*; Solórzano, 2004).

Generally, highly arboreal snakes have a characteristic body form (Guyer and Donnelly, 1990; Lillywhite and Henderson, 1993). Lateral compression of the body, reduced mass-to-length ratio, rigid muscles, and eyes with the ability to be directed downward are several of the characteristics (Henderson and Nickerson, 1974; Lillywhite and Henderson, 1993). Furthermore, morphology may reflect microhabitat use (Guyer and Donnelly, 1990; Cadle and Greene, 1993; Martins et al., 2001; Franca et al., 2008) and habitat partitioning among species within an assemblage (i.e., smaller snakes utilize smaller branches; Lillywhite and Henderson, 1993).

Few communities of snakes have been studied comprehensively, especially in the tropics. Therefore, the composition of many ophidian communities has not been characterized. Obligate and facultative arboreal snakes can constitute a large proportion (up to 50%) of the vertebrate biomass (Guyer and Donnelly, 1990), and, as is the general case, species richness increases as latitude decreases (Lillywhite and Henderson, 1993). For example, an ophidian community of 12 species in temperate Kansas has one arboreal species (8.3%; Lillywhite and Henderson, 1993), whereas a community in Manaus, Brazil has 100 species, of which 52 (51.9%) are arboreal (Lillywhite and Henderson, 1993).

It is not known in what ways Neotropical arboreal snakes partition their environment (Lillywhite and Henderson, 1993). It is likely that members of the assemblage come into physical contact and may compete for food or space, so niche partitioning within the group is likely. To determine what environmental characteristics are preferred by each species, it is necessary to understand what habitat is available. Because of differences in rainfall throughout the year, surveys during both the wet and dry season are necessary to determine whether snakes are using all available habitats. However, studies of arboreal snakes often lack a fully three-dimensional approach that includes the canopy. Advancements in technology (e.g., mirror systems, bendable camera tubes, climbing gear) have improved, but have not yet served to perfect the study of arboreal organisms.

In this study I determined the proportion of arboreal species within the community of snakes at PNGDOTH and examined ecological and morphological variation within the arboreal assemblage. I also determined which environmental factors correlate with the occurrence of each species.

MATERIALS AND METHODS

Snakes were identified as arboreal if they spent at least 50% of their activity time in the aboveground vegetation (Lillywhite and Henderson, 1993). Categorization of each species was determined by data collected during this study and by consulting the literature (Henderson and Binder, 1976; Guyer and Donnelly, 1990; Myers, 1982; Savage, 2002; Solórzano, 2004). In some analyses data for *Sibon argus* and *S. longifrenis* were combined.

Morphometric data collection.---The arboreal snakes in Parque Nacional General de División Omar Torrijos Herrera (PNGDOTH), El Copé, Coclé Province, Republic of Panama (Chapter I) were studied in September 2006 – September 2007, November 2007, and May – November 2008. I measured snout-vent length (SVL) and total length (TL) to the nearest 0.1 cm using a squeeze box (Quinn and Jones, 1974). Mass was determined to the nearest 0.1 g using an electronic balance, and sex was determined with blunt-tipped probes. Other morphometric features (Fig. 2.1) were measured to the nearest 0.01 cm using digital calipers (King et al., 1999). I individually marked all snakes with a PIT tag (passive integrated transponder; Gibbons and Andrews, 2004) or a unique scale clip (Brown and Parker, 1976). I returned snakes to the exact location of capture within 48 hours to minimize disruption of their normal behavior.

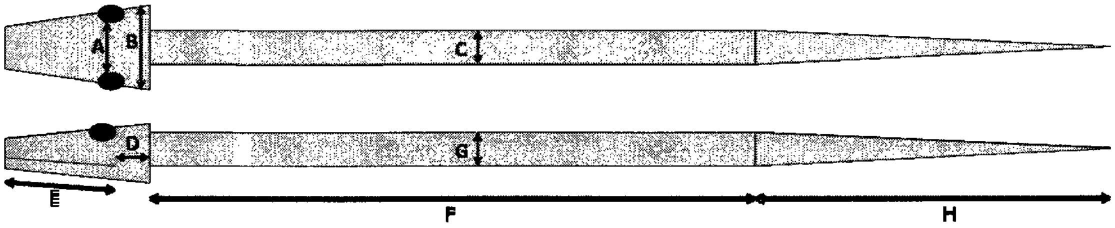

Fig. 2.1. Location of measurements in diagrammatic dorsal view (top) and lateral view (bottom). A = interocular distance, B = head width, C = width at midbody, D = temple length, E = jaw length, F = torso length, G = height at midbody, and H = tail length.

Morphometric measurements used in the MANOVA included jaw length, temple length (head length – jaw length), interocular distance, head width (measured at the widest place on the head), width at midbody, height at midbody, torso length (body length excluding head and tail), and tail length (Fig. 2.1).

Environmental data collection.---For each capture included in the analyses, I measured height, distance to water and distance to the end of the perch. Leaf width and length were measured to the nearest cm at the midbody of the snake using a tape measure. Branch width at midbody was measured to the nearest 0.1 cm with a dial caliper. Ambient temperature (°C) and humidity (%) were measured with an Oakton digital max/min thermohygrometer.

I also collected environmental data at random locations along 3.5 km of terrestrial and riparian transects in both the dry (March 2007) and rainy (May 2007) seasons, to provide information on habitat availability in PNGDOTH. Each data collection site was chosen using a random number table. An exact location for data collection (height, distance from water) was chosen by a field assistant who was unaware of the reason for measurement. Environmental data collected at each location included height from ground, distance from water (for riparian transects), leaf dimensions (length and width) or perch diameter, temperature and humidity.

General characteristics of the snake assemblage.---Comprehensive surveys of the snake community in PNGDOTH permitted analysis of the composition of species and of the proportion of arboreal species. I calculated the percentage of arboreal species in the community (as a percentage of individuals and a percentage of captures) and differences in the number of captures for each species between dry and wet seasons. Characteristics of the assemblage were determined from data collected in May 2006, September 2006-September 2007, and November 2007.

Statistics for morphometric analyses.---I used SAS for the MANOVA and SPSS (Version 13.0) for all other analyses. Alpha was maintained at 0.05 in all analyses (Zar, 1999). All data were log-transformed.

I tested for interspecific differences in relative tail length among *Bothriechis schlegelii, Dipsas* sp., *Imantodes cenchoa, Leptodeira septentrionalis, Oxybelis brevirostris, Sibon annulatus, S. argus/longifrenis*, and *S. nebulatus*. I calculated relative tail length by dividing the length of the complete tail (snakes with incomplete tails were omitted) by the total length of the snake and tested for intra- and interspecific differences using an ANOVA.

I tested for interspecific differences in relative mass among *Dipsas* sp., *Imantodes cenchoa, Leptodeira septentrionalis, Oxybelis brevirostris, Sibon annulatus*, and *S.*

argus/longifrenis. I used an analysis of covariance (ANCOVA) to test mass with SVL as a covariate.

I tested for differences in jaw length within and among *Dipsas* sp., *Imantodes cenchoa, Leptodeira septentrionalis, Oxybelis brevirostris, Sibon annulatus, S. argus/longifrenis*, and *S. nebulatus*. I used an ANCOVA to test for intraspecific differences between sexes and interspecific differences among species in log-transformed jaw length with head length as a covariate.

I tested for differences in size at midbody within and among *Dipsas* sp., *Imantodes cenchoa, Leptodeira septentrionalis, Oxybelis brevirostris, Sibon annulatus, S. argus/longifrenis*, and *S. nebulatus*. I used an ANOVA to test for intraspecific differences between sexes and interspecific differences among species in size at midbody, determined by measuring the dorsal and lateral widths and adding each twice to determine the distance around the snake. This type of measurement was used to capture the degree of lateral compression of the snake.

A MANOVA was used to test for interspecific differences in morphometric measurements among *Dipsas* sp., *Imantodes cenchoa, Imantodes inornatus, Leptodeira septentrionalis, Oxybelis brevirostris, Sibon annulatus, S. argus/longifrenis*, and *S. nebulatus* (Fig. 2.1). Morphological characteristics were averaged across captures for each individual, and characteristics were log-transformed for normality. Perch size is defined as the width of the perch regardless of whether it was a leaf or branch. I used descriptive discriminant function analyses to evaluate further any significant results of the MANOVA.

Statistics for environmental analyses.---I used SAS to conduct the MANOVA and SPSS (Version 13.0) for all other analyses. Alpha was maintained at 0.05 in all analyses (Zar, 1999).

I used a Pearson's bivariate correlation to test for correlations among the following environmental characteristics: temperature, humidity, distance to the ground, distance to water, distance to the end of the branch, perch diameter, leaf length, and leaf width.

Environmental characteristics were evaluated for eight taxa, including *Bothriechis schlegelii, Dipsas* sp., *Imantodes cenchoa, Leptodeira septentrionalis, Oxybelis brevirostris, Sibon annulatus, S. argus/longifrenis*, and *S. nebulatus*. All environmental variables were averaged across captures of an individual snake. Several environmental variables were evaluated for interspecific differences for species in which at least five captures were made.

I used an ANOVA to test for interspecific differences in distance from ground, distance from water, distance to the end of branch, and perch size. A post-hoc Student-Newman-Kuels Test was conducted when the ANOVA yielded significant results.

SAS was used to conduct a MANOVA to test for interspecific differences in the environmental variables.

Means were calculated for environmental characters including temperature, humidity, distance to ground, distance to water, distance to end of branch, perch diameter, leaf length, leaf width, and perch size for snakes and randomly selected sites along riparian and terrestrial transects in the wet and dry seasons. Wet season was defined as 01 April to 15 December, and dry season was 16 December to 31 March.

RESULTS

General characteristics of the snake assemblage.---The snake community in PNGDOTH consists of 56 species representing six families (K. R. Lips and C. E. Montgomery, unpublished data; pers. obs.; Table 1.3). Twenty-four species (42.9%) in four families spend at least 50% of their time in the aboveground vegetation (Savage, 2002; Solórzano, 2004; pers. obs.).

Between 2006 and 2007 I captured 16 species of arboreal snakes (Table 2.1). Half of the arboreal species were relatively abundant, whereas the others were represented by as few as one capture (Fig. 2.2). Captures in this study followed a distribution similar to that of total individuals (Fig. 2.3). Species were captured during both dry and rainy seasons, although some species, such as *Sibon annulatus* and *S. argus*, were represented by more captures during the rainy season (Fig. 2.4).

Morphometric analyses.---There was no significant intraspecific difference between sexes for log-transformed tail length ($P > 0.05$). There was a significant interspecific difference in log-transformed tail length ($F = 84.431$, $df = 7$, $P < 0.001$). *Bothriechis schlegelii* had the shortest relative tail length, whereas *Oxybelis brevirostris* had the longest.

S. annulatus did not show an intraspecific difference between sexes in mass ($F = 0.221$, $df = 1$, $P = 0.648$), but the other species did exhibit significant intraspecific differences between sexes ($P < 0.05$, Table 2.2). There was a significant interspecific

Table 2.1. **Relative abundance and general natural history information for arboreal snakes captured in 2006-2007 PNGDOTH.** Natural history information from Solórzano, 2004 and this study. Relative abundance based on capture number (Table 1.3, Chapter I). Species in bold were included in morphometric and environmental analyses.

Species	Relative Abundance	Reproductive Method	Period of Activity	Diet
Bothriechis schlegelii	**moderate**	**viviparous**	**crepuscular**	**frogs, rodents**
Chironius exoletus	rare	oviparous	diurnal	frogs, salamanders
Chironius grandisquamis	rare	oviparous	diurnal	frogs, salamanders
Corallus annulatus	rare	viviparous	nocturnal	rodents
Dipsas nicholsi	rare	oviparous	nocturnal	mollusks
***Dipsas* sp.**	**common**	**oviparous**	**nocturnal**	**mollusks, oligochaetes**
Imantodes cenchoa	**common**	**oviparous**	**nocturnal**	**amphibians, lizards**
Imantodes inornatus	rare	oviparous	nocturnal	amphibians, lizards
Leptodeira septentrionalis	**moderate**	**oviparous**	**nocturnal**	**amphibians, amphibian eggs**
Leptophis depressirostris	rare	oviparous	diurnal	lizards, frogs
Leptophis nebulosus	rare	oviparous	diurnal	lizards, frogs
Oxybelis brevirostris	**common**	**oviparous**	**diurnal**	**lizards, frogs**
Sibon annulatus	**common**	**oviparous**	**nocturnal**	**mollusks**
Sibon argus/longifrenis	**common**	**oviparous**	**nocturnal**	**mollusks, frog eggs, oligochaetes**
Sibon nebulatus	**moderate**	**oviparous**	**nocturnal**	**mollusks**

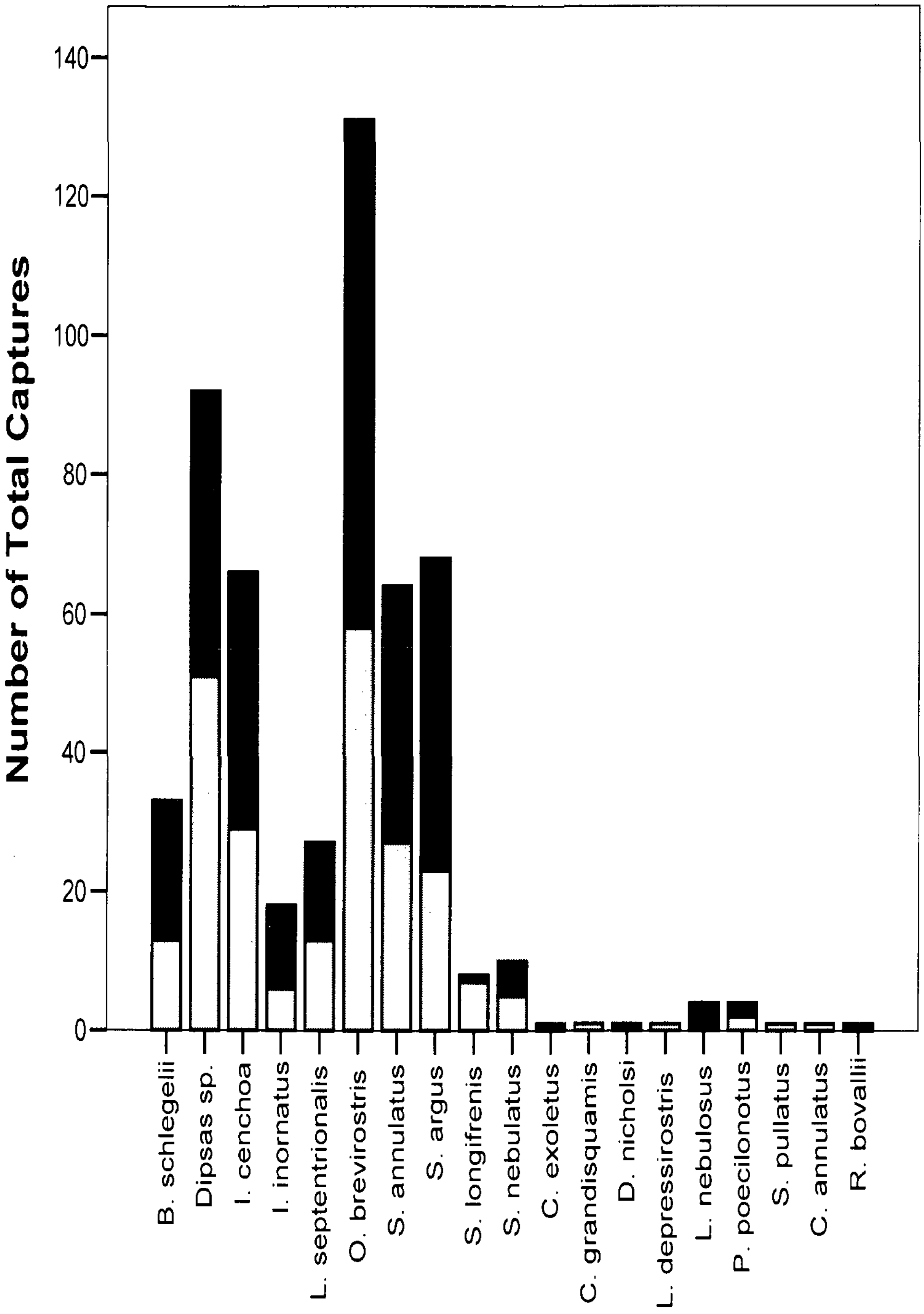

Fig. 2.2. Total number of captures of each arboreal species of snake captured during study periods between May 2006 and November 2007. Gray represents males and black represents females.

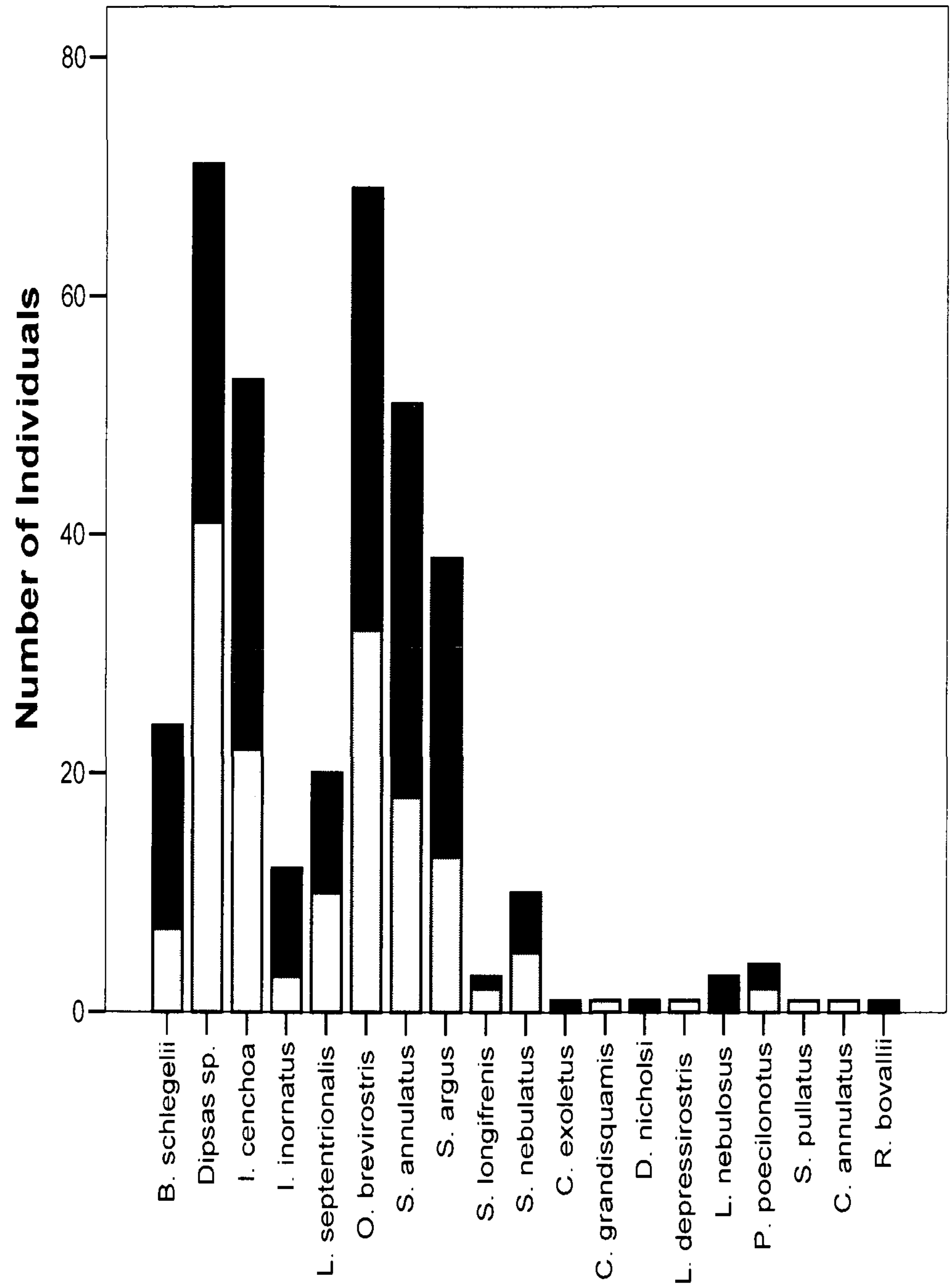

Fig. 2.3. Total number of individuals of each arboreal species of snake captured during study periods between May 2006 and November 2007. Gray represents males and black represents females.

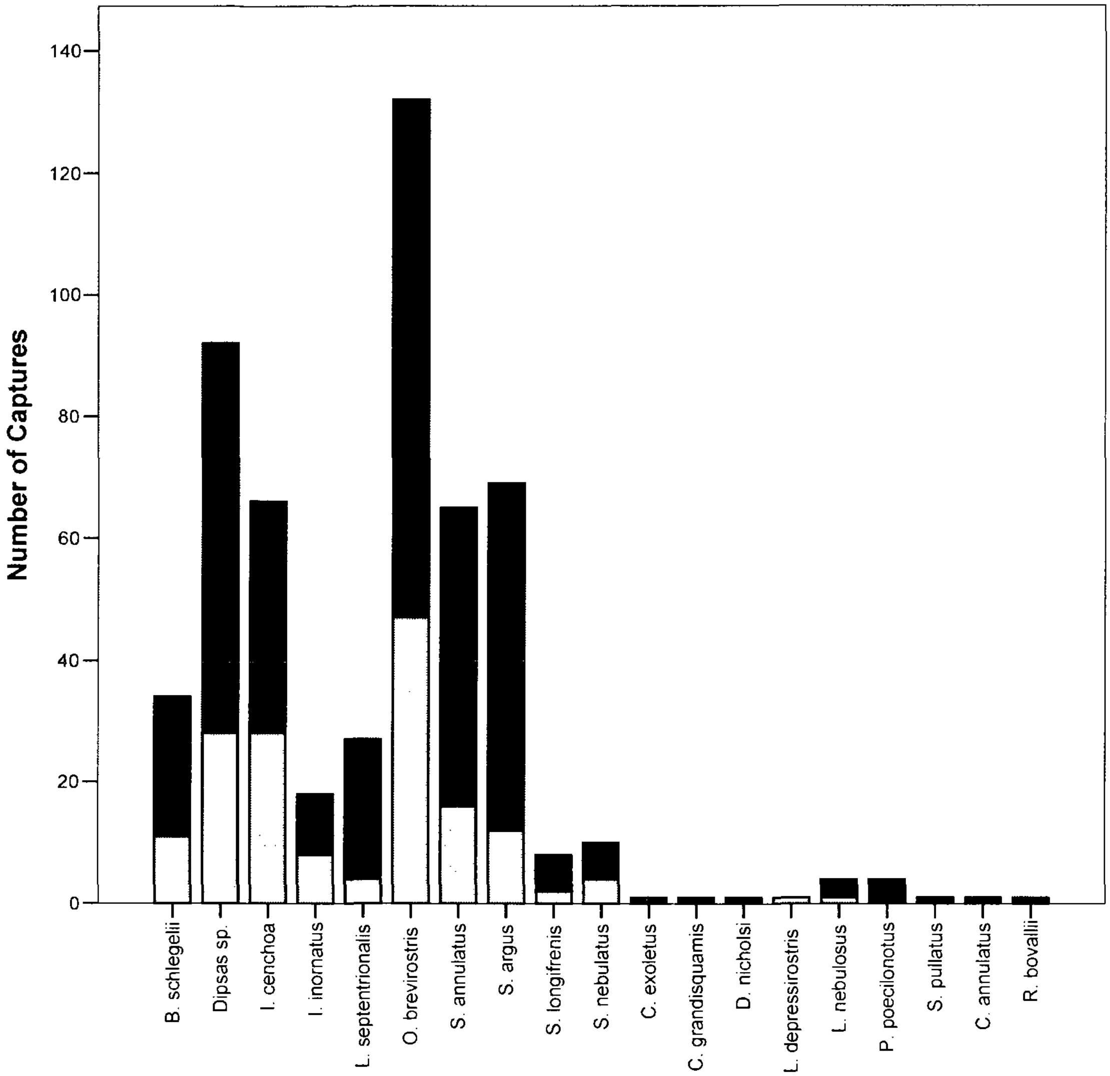

Fig. 2.4. Total number of captures of each arboreal species of snake captured during study periods between May 2006 and November 2007. Gray bars represent the dry season and black bars represent the wet season in PNGDOTH.

difference in mass when males and females were included separately in the ANCOVA (F = 50.518, df = 11, $P < 0.001$). *Bothriechis schlegelii* and *Sibon nebulatus* were excluded from the analysis because fewer than five individuals per sex were captured.

Bothriechis schlegelii was excluded from the analysis of relative jaw length because head measurements were not taken. There was no intraspecific difference between sexes ($P > 0.005$) in log-transformed jaw length (corrected for head length) except *Imantodes cenchoa* (F = 4.380, df = 1, P = 0.039) and *Sibon annulatus* (F = 17.373, df = 1, P < 0.001). There was a significant interspecific difference in log-transformed jaw length (corrected for head length) with *S. annulatus* and *I. cenchoa* sexes included separately (F = 20.354, df = 8, P < 0.001).

Table 2.2. Results of the ANCOVA testing for intraspecific differences in mass (corrected for SVL) for arboreal snakes in PNGDOTH. Significant results (α = 0.05) are in bold.

Species	n (male:female)	F	df	P
***Dipsas* sp.**	**48:36**	**53.882**	**1**	**< 0.001**
Imantodes cenchoa	**30:33**	**15.044**	**1**	**< 0.001**
Leptodeira septentrionalis	**11:14**	**9.166**	**1**	**0.006**
Oxybelis brevirostris	**32:43**	**4.512**	**1**	**0.037**
Sibon annulatus	18:38	0.211	1	0.648
Sibon argus/longifrenis	**14:25**	**10.598**	**1**	**0.002**

There was no intraspecific difference between sexes in size of snakes at midbody except in *Oxybelis brevirostris* (F = 5.959, df = 1, P = 0.016). There was a significant interspecific difference among species, with the sexes of *O. brevirostris* included separately (F = 48.461, df = 7, P < 0.001). A post-hoc Student-Newman-Kuels test showed five significantly different groups (Table 2.3).

Results of the MANOVA showed a significant difference between group centroids (Wilk's λ = 0.012; F = 22.8; P = 0.0001; Table 2.4). The first four descriptive discriminant functions (DDF) were significant (P < 0.05), and over 90% of variation was explained by DDF1 and DDF2 (Table 2.5, 2.6). Significant differences were found among all species (P < 0.0001) except *Sibon nebulatus* and *Leptodeira septentrionalis*, which did not differ significantly from each other (P = 0.5494; Table 2.4).

Table 2.3. Results of a Student-Newman-Kuels post-hoc analysis for interspecific differences in size at midbody (log-transformed) among arboreal snakes. Five significantly different groups were found.

Species	**n**	**1**	**2**	**3**	**4**	**5**
Sibon annulatus	71	1.3201				
Dipsas sp.	102		1.3842			
Imantodes cenchoa	81			1.4295		
Sibon argus/longifrenis	51			1.4581		
Oxybelis brevirostris male	41			1.4698		
Oxybelis brevirostris females	56				1.5226	
Leptodeira septentrionalis	33					1.6215
Sibon nebulatus	18					1.6582
P		1.000	1.000	0.172	1.000	0.102

Environmental analyses.---I found significant positive correlations between humidity and distance to ground, distance to ground and distance to the end of branch, distance to the end of branch and perch diameter, and leaf length and leaf width ($P < 0.05$; Table 2.7). There was a significant negative relationship between temperature and humidity ($P < 0.05$; Table 2.7).

The means for randomly collected environmental data for terrestrial and riparian transects in wet and dry seasons were calculated (Table 2.8). The greatest differences between snake and environmental data were observed along riparian transects in the rainy season.

I found significant interspecific differences in distance to ground ($f = 4.849$, $df = 7$, $p < 0.001$), distance to water ($f = 5.010$, $df = 7$, $p < 0.001$), branch diameter ($f = 2.767$, $df = 7$, $p = 0.012$), and humidity ($f = 2.465$, $df = 7$, $p = 0.019$) (Table 2.9). Temperature, distance to end of branch, perch width, leaf length, and leaf width did not differ

Table 2.4. Paired comparisons of between group centroids of unique morphometric measurements for eight arboreal snake species. Mahalanobis distance (top of cell), F statistic (middle), and P value (bottom) are provided for each comparison. All comparisons shown were significant at P --< 0.0001. Results in bold represent species that did not significantly differ from each other.

Species	***I. cenchoa***	***I. inornatus***	***L. septentrionalis***	***O. brevirostris***	***S. annulatus***	***S. argus***	***S. nebulatus***
***Dipsas* sp.**	19.06 33.39 <0.0001	14.68 7.68 <0.0001	15.52 20.15 <0.0001	54.43 130.37 <0.0001	4.59 8.54 <0.0001	2.37 4.78 <0.0001	16.52 14.08 <0.0001
I. cenchoa		6.79 3.43 0.001	33.81 40.34 <0.0001	39.32 81.04 <0.0001	20.59 34.01 <0.0001	19.76 35.07 <0.0001	42.25 34.04 <0.0001
I. inornatus			14.86 6.82 <0.0001	23.22 12.72 <0.0001	19.27 9.90 <0.0001	15.39 8.09 <0.0001	21.39 8.28 <0.0001
L. septentrionalis				28.03 40.94 <0.0001	25.29 31.42 <0.0001	17.55 23.01 <0.0001	**1.24** **0.86** **0.5494**
O. brevirostris					55.14 121.93 <0.0001	53.12 129.53 <0.0001	32.87 30.21 <0.0001
S. annulatus						2.31 4.36 <0.0001	24.71 20.45 <0.0001
S. argus							18.21413 15.61749 <0.0001

Table 2.5. Canonical correlations, eigenvalues, variance due to species of snake (proportion and cumulative) and tests of significance (Pr>F) for each descriptive discriminant function (DDF).

Discriminant Function	Canonical Correlation	Eigenvalue	Proportion	Cumulative	Approx. F Value	Num DF	Den DF	Pr>F
DDF1	0.949	9.056	0.718	0.718	22.8	56	1012	.0001
DDF2	0.844	2.485	0.197	0.915	11.8	42	885	<0.0001
DDF3	0.672	0.822	0.065	0.980	5.88	30	758	<0.0001
DDF4	0.363	0.152	0.012	0.992	2.34	20	631	0.0009
DDF5	0.240	0.061	0.005	0.997	1.56	12	506	0.1011
DDF6	0.181	0.034	0.003	1.000	1.18	6	384	0.3137
DDF7	0.059	0.004	0.000	1.000	0.34	2	193	0.7151

Table 2.6. Variables considered important contributors to species separation along DDF1 and DDF2. Provided are the between-group structure R value and potency index and the P value for an F-test of a significant difference between species for each morphometric measure.

	DDF1		DDF2		Univariate Comparisons		
Variable	R Value	Potency	R Value	Potency	R-Square	F Value	Pr>F
Head width (mm)	0.496	0.178	0.221	0.010	0.507	28.53	<0.0001
Temple size (mm)	0.594	0.255	0.449	0.040	0.221	7.87	<0.0001
Dorsal height (mm)	0.595	0.256	0.462	0.042	0.459	23.49	<0.0001
Torso length	0.624	0.282	-0.714	0.101	0.672	56.8	<0.0001
Lateral width (mm)	0.673	0.328	0.422	0.035	0.376	16.68	<0.0001
Interocular length (mm)	0.821	0.488	0.201	0.008	0.504	28.17	<0.0001
Mass (g)	0.824	0.492	0.064	0.001	0.576	37.58	<0.0001
Jaw length (mm)	0.964	0.672	0.139	0.004	0.843	149.2	<0.0001

Table 2.7. Results of Pearson's Bivariate correlation of environmental variables in PNGDOTH. Bold type designates a significant correlation ($P < 0.05$).

		Temperature	Distance to ground	Distance to water	Distance to end of branch	Perch diameter	Leaf length	Leaf Width
Humidity	r	**-.356**	**.151**	-.141	.013	-.021	-.050	-.054
	P	**.000**	**.019**	.093	.871	.836	.596	.569
	n	**244**	**241**	144	157	96	114	114
Temperature	r		-.060	-.032	-.123	.007	-.016	-.033
	P		.346	.701	.122	.948	.867	.728
	n		253	149	160	98	112	112
Distance to ground	r			-.093	**.423**	-.082	-.092	-.049
	P			.188	**.000**	.409	.334	.612
	n			204	**160**	104	113	112
Distance to water	r				-.108	.004	.016	.188
	P				.288	.979	.895	.127
	n				99	59	69	67
Distance to end of branch	r					**.487**	-.043	-.062
	P					**.000**	.720	.605
	n					**89**	72	72
Perch diameter	r						.028	-.218
	P						.900	.330
	n						23	22
Leaf length	r							**.623**
	P							**.000**
	n							**114**

Table 2.8. Means of environmental characteristics for random sites along terrestrial and riparian transects and in wet and dry seasons.

	Terrestrial, Dry	Terrestrial, Wet	Riparian, Dry	Riparian, Wet
Variable	**Random**	**Random**	**Random**	**Random**
Temperature (C)	23.46 ±2.1 (18)	23.55±1.8 (28)	22.71±1.8 (19)	23.22±1.4 (40)
Humidity (%)	70.67±8.8 (18)	76.11±9.6 (27)	72.60±19.5 (18)	84.03±5.5 (35)
Distance to ground (cm)	152.91±87.6 (22)	148.63±82.1 (38)	136.41±68.5 (27)	205.50±201.9 (62)
Distance to water (cm)	580.00±356.3 (5)	560.00±1143.2 (10)	147.56±141.0 (27)	87.24±118.4 (61)
Distance to end of branch (cm)	27.88±20.5 (8)	38.95±32.4 (20)	57.64±51.6 (11)	57.304±55.1 (27)
Perch diameter (cm)	0.68±0.2 (3)	16.86±32.0 (11)	70.23±83.4 (5)	17.28±31.7 (20)
Leaf length (cm)	28.11±26.2 (9)	22.14±29.7 (21)	11.43±17.6 (14)	17.75±27.1 (32)
Leaf width (cm)	9.25±12.2 (8)	10.67±14.1 (21)	7.40±11.7 (14)	8.78±15.7 (32)
Width of Surface (cm)	9.63±11.9 (8)	20.45±24.4 (20)	45.70±61.6 (10)	19.35±27.8 (31)

significantly ($p > 0.05$) among species (Table 2.9). Post-hoc Student-Newman-Kuels analyses conducted for variables with significant interspecific differences found two significantly different groups in each analysis (Table 2.10-2.13).

I found significant correlations between SVL and mass and several environmental variables ($P < 0.05$; Table 2.14). Size of snake at midbody was correlated with leaf length ($r = 0.459$, $df = 22$, $P = 0.032$) for *Dipsas* sp.

Table 2.9. Results of ANOVA testing for interspecific differences in environmental variables for the arboreal snake assemblage. Significant results are in bold.

Environmental Variable	df	F	P
Temperature	7	0.783	0.602
Humidity	**7**	**2.465**	**0.019**
Distance to ground	**7**	**4.849**	**0.000**
Distance to water	**7**	**5.010**	**0.000**
Distance to end of branch	7	1.862	0.079
Branch diameter	**7**	**2.767**	**0.012**
Perch width	7	1.987	0.059
Leaf length	7	1.057	0.396
Leaf width	7	0.930	0.487

Table 2.10. Results of a Student-Newman-Kuels post-hoc analysis for interspecific differences in humidity among arboreal snakes. Two significantly different groups were found.

Species	n	1	2
Bothriechis schlegelii	11	68.245	
Sibon nebulatus	8	73.063	73.063
Oxybelis brevirostris	56		75.589
Imantodes cenchoa	36		75.944
Dipsas sp.	53		76.547
Sibon annulatus	40		77.460
Leptodeira septentrionalis	13		77.877
Sibon argus/longifrenis	29		80.524
P		0.103	0.151

Table 2.11. Results of Student-Newman-Kuels post-hoc analysis for interspecific differences in distance to ground at time of capture among arboreal snakes. Two significantly different groups were found.

Species	n	1	2
Sibon nebulatus	10	84.50	
Imantodes cenchoa	62	109.63	
Dipsas sp.	84	118.35	
Bothriechis schlegelii	21	137.00	
Sibon annulatus	56	140.09	
Leptodeira septentrionalis	24	162.61	162.61
Oxybelis brevirostris	70	171.50	171.50
Sibon argus/longifrenis	36		232.79
P		0.103	0.077

Table 2.12. Results of Student-Newman-Kuels post-hoc analysis for interspecific differences in distance to water at time of capture among arboreal snakes. Two significantly different groups were found.

Species	n	1	2
Sibon argus/longifrenis	36	109.231	
Bothriechis schlegelii	15	153.793	
Sibon annulatus	35	167.911	
Sibon nebulatus	7	183.714	
Leptodeira septentrionalis	16	186.000	
Imantodes cenchoa	31	233.055	
Oxybelis brevirostris	35	466.280	466.280
Dipsas sp.	35		855.086
P		0.593	0.060

Table 2.13. Results of Student-Newman-Kuels post-hoc analysis for interspecific differences in the width of the surface at time of capture among arboreal snakes. Two significantly different groups were found.

Species	n	1	2
Leptodeira septentrionalis	9	12.389	
Dipsas sp.	47	13.611	
Imantodes cenchoa	29	14.914	
Bothriechis schlegelii	11	15.036	
Sibon argus/longifrenis	24	20.929	
Oxybelis brevirostris	39	23.208	
Sibon annulatus	31	33.226	33.226
Sibon nebulatus	6		53.500
P		0.614	0.099

Results of the MANOVA for environmental characteristics showed no significant difference among group centroids ($P < 0.05$). A Pearson's Correlation tested for correlations between SVL and mass with environmental characteristics for eight common species (Table 2.14).

Table 2.14: Pearson's Bivariate correlation of SVL and mass to environmental variables for eight common species of arboreal snakes in PNGDOTH. Cells in bold designate significant correlation ($P < 0.05$).

Variable		*B schlegelii*		*Dipsas sp.*		*I. cenchoa*	
		SVL	**mass**	**SVL**	**mass**	**SVL**	**mass**
Temperature	r	0.427	0.516	0.014	-0.067	-0.044	-0.120
	P	0.166	0.104	0.920	0.626	0.787	0.459
	n	12	11	55	55	40	40
Humidity	r	0.378	0.490	0.063	0.138	-0.124	-0.037
	P	0.252	0.151	0.656	0.323	0.471	0.829
	n	11	10	53	53	36	36
Distance to ground	r	0.002	-0.098	0.086	0.095	0.187	**0.286**
	P	0.994	0.691	0.439	0.389	0.145	**0.024**
	n	21	19	84	84	62	**62**
Distance to water	r	-0.065	0.123	0.095	0.110	-0.125	-0.136
	P	0.818	0.689	0.586	0.528	0.502	0.467
	n	15	13	35	35	31	31
Distance to end of branch	r	0.000	0.059	-0.023	-0.110	0.122	0.086
	P	0.999	0.890	0.900	0.557	0.587	0.703
	n	8	8	31	31	22	22
Perch diameter	r	0.139	0.141	0.060	0.159	-0.051	-0.101
	P	0.766	0.763	0.806	0.515	0.835	0.680
	n	7	7	19	19	19	19
Leaf length	r	0.462	0.396	0.308	0.260	0.445	**0.558**
	P	0.297	0.436	0.092	0.157	0.111	**0.038**
	n	7	6	31	31	14	**14**
Leaf width	r	**0.789**	0.773	0.136	0.033	**0.575**	**0.633**
	P	**0.035**	0.071	0.467	0.861	**0.040**	**0.020**
	n	7	6	31	31	**13**	**13**

Table 2.14. Continued

Variable		*L. septentrionalis*		*O. brevirostris*	
		SVL	mass	SVL	mass
Temperature	r	0.142	-0.063	-0.198	-0.181
	P	0.628	0.831	0.132	0.173
	n	14	14	59	58
Humidity	r	0.179	0.402	0.151	0.130
	P	0.558	0.174	0.268	0.343
	n	13	13	56	55
Distance to ground	r	0.130	0.035	**0.253**	**0.315**
	P	0.544	0.872	**0.034**	**0.008**
	n	24	24	**70**	**69**
Distance to water	r	-0.208	-0.179	0.032	0.004
	P	0.440	0.506	0.856	0.983
	n	16	16	35	35
Distance to end of branch	r	0.178	0.048	0.124	0.109
	P	0.673	0.910	0.452	0.516
	n	8	8	39	38
Perch diameter	r	0.243	-0.558	-0.136	-0.057
	P	0.694	0.329	0.568	0.810
	n	5	5	20	20
Leaf length	r	0.731	0.655	0.340	-0.032
	P	0.269	0.345	0.083	0.877
	n	4	4	27	26
Leaf width	r	-0.010	-0.073	0.282	0.238
	P	0.990	0.927	0.154	0.242
	n	4	4	27	26

Table 2.14. Continued

Variable		*S. annulatus*		*S. argus/ longifrenis*		*S. nebulatus*	
		SVL	mass	SVL	mass	SVL	mass
Temperature	r	0.296	0.299	0.309	0.208	0.140	0.202
	P	0.057	0.061	0.103	0.278	0.741	0.631
	n	42	40	29	29	8	8
Humidity	r	-0.158	-0.199	-0.147	-0.172	-0.370	-0.374
	P	0.329	0.232	0.448	0.373	0.366	0.362
	n	40	38	29	29	8	8
Distance to ground	r	-0.173	-0.085	-0.024	0.054	0.233	0.256
	P	0.202	.543	0.890	0.753	0.517	0.476
	n	56	54	36	36	10	10
Distance to water	r	0.010	0.246	0.267	0.278	0.244	0.250
	P	0.954	0.154	0.115	0.100	0.597	0.588
	n	35	35	36	36	7	7
Distance to end of branch	r	0.132	0.257	0.301	0.348	0.230	0.277
	P	0.512	0.205	0.153	0.096	0.661	0.596
	n	27	26	24	24	6	6
Perch diameter	r	0.251	0.293	0.220	-0.039	-0.261	-0.112
	P	0.457	0.382	0.381	0.877	0.672	0.858
	n	11	11	18	18	5	5
Leaf length	r	0.374	0.227	0.100	0.035		
	P	0.079	0.322	0.784	0.924		
	n	23	21	10	10		
Leaf width	r	0.276	0.033	0.087	-0.045		
	P	0.203	0.887	0.811	0.902		
	n	23	21	10	10		

DISCUSSION

The speciose arboreal snake assemblage at PNGDOTH represents 42.9% of the ophidian community. Based on information collected from other tropical snake communities, the arboreal snake assemblage in PNGDOTH is similar in proportion to the entire ophidian community. For example, the snake community at La Selva Biological Station in Costa Rica includes 36.5% arboreal species, whereas Manaus, Brazil has 51.9% arboreal species (Lillywhite and Henderson, 1993). In contrast, a temperate snake community in Kansas includes only one arboreal species (Lillywhite and Henderson, 1993).

In general arboreal snakes have evolved morphological characteristics to aid them in their life in aboveground vegetation (Henderson and Binder, 19801 Lillywhite and Henderson, 1993). However, some species of arboreal snakes are more highly specialized than others. Differences in morphology were found in relative body mass (Table 2.2), relative tail length, relative jaw length, and relative size at midbody (Table 2.3). Guyer and Donnelly (1990) evaluate the snake community at La Selva Biological Station in Costa Rica, including the terrestrial members, and find that arboreal snakes were lighter in relative body mass and had relatively elongated tails. Vitt and Vangilder (1983) also report reductions in relative body mass in arboreal species in the Caatinga region of Brazil.

Differences in morphology within the arboreal assemblage may have evolved for a number of reasons. First, some snakes are more active (e.g., *Oxybelis brevirostris*), moving through the branches in search of prey, whereas other species are sit-and-wait predators (e.g., *Bothriechis schlegelii*). *O. brevirostris* is diurnal and feeds on fast-moving diurnal anoline lizards. Snakes that forage actively and stalk prey presumably require agility. Increased tail length and reduction in body mass may reflect adaptations for moving easily across branches.

Other differences may be related to the diverse prey base available in the tropics (Guyer and Donnelly, 1990), including in the aboveground vegetation. Differences in jaw length likely are attributable to differences in prey type and size; species with larger relative jaw lengths (e.g., *Oxybelis brevirostris*) feed on larger prey items, such as lizards, whereas species with smaller jaws feed on soft-bodied invertebrates (e.g., *Dipsas* sp., *Sibon* spp.).

Differences in the morphology of snakes have been attributed to differences in the habitat commonly utilized by the species (e.g., Guyer and Donnelly, 1990; Franca et al., 2008). Habitat partitioning occurs within the arboreal snake assemblage in PNGDOTH. Variation in the height where snakes were captured (Table 2.9, 2.11) can be explained by a couple of factors. First, as height increases, branch diameter presumably tends to decrease (although a significant correlation was not found in the lower vegetation that was measured in this study; Table 2.14), with the top of the tree having finer branches. Snakes of large body size cannot be supported by very small branches and were not found on such perches. Perch or foraging height also may be influenced by the prey consumed by the species of snakes. Many anoles, a group of lizards commonly consumed by *Imantodes* spp. and *Oxybelis* spp., partition the vertical environment (Reagan, 1992; Buckley and Roughgarden, 2005), and snakes feeding on particular species of lizards (perhaps due to gape limitation) may remain near the prey source. The same argument can be applied to snakes that prey on frogs; snakes feeding on leaf litter frogs remain lower to the ground.

Distance to water (Table 2.9, 2.11) and humidity (Table 2.9, 2.10) were correlated and were significant factors determining where a species was captured (Table 2.7). Such factors may be related to moisture requirements of each species of snake. Small snakes may experience dehydration or water loss more quickly than larger snakes and may be limited to microenvironments of higher humidity (near streams or tank bromeliads that hold water). However, the distance a snake travels from water also may be correlated with their dietary requirements. Taxa feeding on frog eggs (*Sibon argus/longifrenis*) likely remain near streams, where they were encountered feeding on anuran eggs laid on leaves overhanging the streams.

Cody (1966) suggests that there are three main factors separating species within grassland bird communities. The factors include placement in the vertical habitat, placement in the horizontal habitat, and prey type. These factors also were important in the partitioning of the arboreal snake assemblage in PNGDOTH. Temporal separation is noted by Schoener (1974) as an additional factor. Differences in diel activity pattern (only one species was diurnal) or seasonal separation were not tested in this study. Differences may occur between rainy and dry seasons, but further investigation is needed to confirm this.

It is important to understand what potential habitat is available to the snakes when assessing habitat selection and partitioning. Despite large sample sizes of captures of snakes for this study, many individuals were recaptured and those often demonstrated small activity ranges. \Snakes frequently were captured within the same 10-20 meters straightline distance along a transect, and at times, on the same plant as previous captures (J. M. Ray, C. E. Montgomery, and K. R. Lips, unpublished data). These frequent recaptures reduce the indepence of the data and limit analysis. Vegetation grows quickly during the rainy season, expanding the size of the plant and often producing many small and/or tender new leaves that may not immediately be utilized by snakes, especially those of relatively heavy body mass. Nonetheless, this study demonstrates that species of snakes differ in capture site according to certain environmental factors and continued study of the community will allow for more detailed analyses in the future.

Limitations in the analysis were unavoidable because of restrictions in the methods used during data collection. When studying an arboreal assemblage it is desirable to access the entire vertical realm, but that was not possible for this study. First, this project was conducted in the secondary forest of PNGDOTH. Although the trees are over 30 years old, most are relatively small and are not sturdy enough to support single-tree climbing gear. Larger trees spared during the clear-cut were not appropriate for climbing (e.g., strangler figs) or were decaying and unsafe for climbing.

Other limitations were associated with the equipment used for recording measurements. Ideally, temperature would have been measured with a cloacal probe, but attempts to use one such device failed due to high humidity. Humidity itself was not recorded to a high degree of accuracy due to a lack of equipment that could withstand the extreme conditions at PNGDOTH. Furthermore, data from a weather station is not available for the mid-elevation forests of central Panama. Attempts to collect regular rainfall data and employ temperature loggers were foiled by the destruction of equipment by people or animals.

This study has provided information on interspecific differences among the community of Neotropical arboreal snakes in both morphology and preferred environmental characteristics. If the limitations described above can be overcome, a more detailed analysis of interspecific resource partitioning by this community can be explored.

CHAPTER III

BRIDGING THE GAP: INTERSPECIFIC DIFFERENCES IN CANTILEVERING ABILITY IN A NEOTROPICAL ARBOREAL SNAKE ASSEMBLAGE

Arboreal snakes face many challenges during routine activities, such as courtship and reproduction, feeding, and escape from predators, which must occur in the unstable substrate on the aboveground vegetation (Lillywhite and Henderson, 1993; Jayne and Riley, 2007). Several morphological adaptations facilitate an arboreal existence, including lateral compression of the body, elongation of the tail, widening of ventral scales, forward-facing eyes that also can be aimed downward, and reduction in relative mass (Henderson and Nickerson, 1976; Lillywhite and Henderson, 1993). The most nimble of the arboreal snakes have rigid muscles and tight skin, allowing more controlled movements and free extension (cantilevering) of the body (Lillywhite and Henderson, 1993). Behavioral modifications also play an adaptive role, but have been less studied because of the logistic difficulties of accessing and working in the trees (e.g., Lowman and Moffett, 1993). Behavioral differences include species-specific habitat preference (e.g., vine snakes occur in foliage [Henderson and Binder, 1980], whereas some *Dipsas* spp. hide in bromeliads [Duellman, 2005; pers. obs.]) and foraging tactics (e.g., feeding on arboreal prey versus foraging on terrestrial prey from an elevated position; Shine et al., 1996, Fitzgerald et al., 2002).

Many of the morphological adaptations cited above enable the body to bridge gaps in the aboveground vegetation (Henderson and Nickerson, 1976; Lillywhite et al., 2000). The ability of arboreal species to move between points in three dimensions may not only play a role in escaping from predators and assisting active foragers in prey acquisition, but may also function to conserve energy by reducing the need to crawl to the ground and then back up an adjacent plant.

Previous work on cantilevering ability in arboreal snakes suggested that they can freely extend their bodies up to 50% of their length to bridge a gap under laboratory conditions (Lillywhite and Henderson, 1993; Lillywhite et al., 2000; Lin et al., 2003; Jayne and Riley, 2007). Lillywhite et al. (2000) tested captive individuals of several species of terrestrial, aquatic, and arboreal snakes for differences in cantilever distances between terrestrial, aquatic, and arboreal snakes and demonstrated that arboreal species can bridge significantly further than aquatic and terrestrial snakes.

This study provided experimental data and field observations on gap bridging for five Neotropical arboreal species that have not previously been evaluated. I predicted that species with lower relative body mass bridge further than heavy-bodied snakes.

MATERIALS AND METHODS

Study site and species.---I conducted this study using freshly captured snakes from Parque Nacional G. D. Omar Torrijos Herrera (PNGDOTH), near El Copé, Coclé Province, Republic of Panama (8° 40’ N, 80° 37’ W). Cloud forest at the site ranges in temperature from 19-30° C, and annual rainfall is about 3500 mm (Lips et al., 2006). Snakes were individually marked with PIT tags (Gibbons and Andrews, 2004) or scale clipped (Brown and Parker, 1976), and recaptured individuals were not retested for their gap-bridging ability. Other snakes had their tails clipped as part of a stable-isotope study

(C. E. Montgomery and K. R. Lips, unpublished data), and their total length was measured to the end of the stubbed tail. Five species of arboreal snakes were selected for laboratory experiments: *Dipsas* sp. (an undescribed species [Myers et al., 2007]), *Imantodes cenchoa*, *Oxybelis brevirostris*, *Sibon argus*, and *S. annulatus*. These species were relatively abundant at the site and exhibited a range of snout-vent lengths from about 500 cm to over 1 m in length. Several less abundant species were tested opportunistically, but sample sizes were not large enough to include in most analyses. The latter species included *I. inornatus, Leptodeira septentrionalis, Leptophis depressirostris, O. aenus*, and *S. nebulatus*.

Experimental design.---To test cantilevering experimentally, an apparatus modeled after that of Lillywhite et al. (2000) was constructed. The apparatus provided one stationary perch and one sliding perch, both at a height of 1 m (Fig. 3.1). Both perches were dressed with artificial (plastic) plants to provide visual complexity, which was presumed to enhance motivation of the snakes to gap-bridge. To estimate the distance between perches, a weight was attached by a string, as a plumb bob, to the end of the sliding perch and a tape measure was placed on the floor below. As the perches were separated, the distances were measured based on the location of the plumb.

Snakes were transported 7.5 km to the laboratory located in El Copé (700 m) for measurement, and all were tested indoors under ambient temperature and humidity conditions, with no wind to influence movement of the experimental perches. For logistic reasons, both diurnal and nocturnal species were tested during daylight hours; all snakes were placed on the apparatus for testing and thus were awake. Each snake was placed on the stationary perch and encouraged to move forward by gently tapping it on the tail. Once movement began, most snakes continued forward toward the sliding perch without further encouragement. The sliding perch was withdrawn in a slow, steady fashion as the snake approached, and nearly every snake followed the perch, attempting to reach it. The distance bridged was measured from the tip of the stationary branch to the point where the snake either withdrew or could no longer move forward without the anterior portion of the body falling due to lack of support (Lillywhite et al., 2000). Each snake was tested three times; both maximum and mean bridging distances were analyzed.

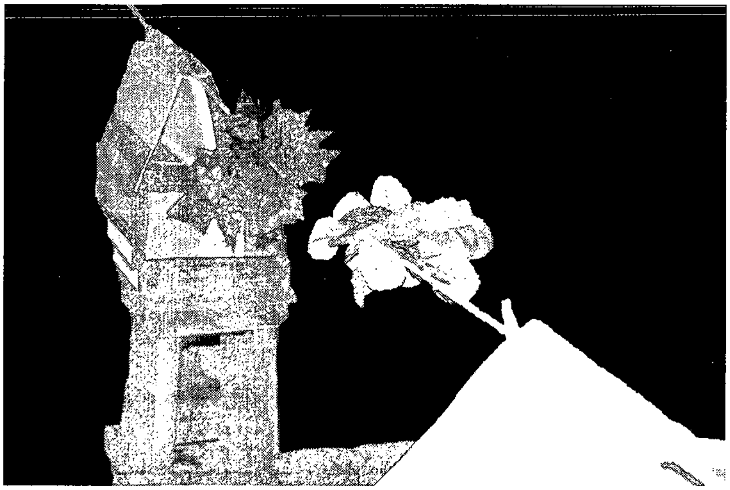

Fig. 3.1. Photograph of experimental apparatus used to test cantilever distance of Neotropical arboreal snakes. Stationary perch on right (in foreground), sliding perch on left (in background). Photo by A. H. Savitzky.

Field observations.---Observations of gap-bridging events were recorded in the wild whenever a snake was found extending from one perch toward another. The snake was left undisturbed until it was able to bridge the distance or withdrew. The snake was then captured, and the distance of the gap the snake bridged was measured.

Statistics.---The cantilever ratio was calculated by dividing the distance bridged by the total length of the snake (Lillywhite et al., 2000). A one-way ANOVA (SPSS Version 13.0) was used to calculate intraspecific differences (between snakes with and without a stub tail; and between sexes) and interspecific differences in the mean and maximum distances bridged (Zar, 1999). Post-hoc Tukey tests were performed to test for similarities among species. Pearson's Partial Correlations were used to test for correlations between mass relative to total length and distance bridged (mean and maximum). Alpha level was maintained at 0.05 unless otherwise noted (Zar, 1999).

RESULTS

There were no significant intraspecific differences (following Bonferroni adjustment; Zar, 1999) in the mean or maximum cantilever ratios between sexes ($P > 0.025$; Table 3.1). There also was no significant intraspecific difference between snakes with and without damaged tails in mean cantilever ratio ($P > 0.025$, Table 3.1), and only *I. cenchoa* exhibited a significant difference in maximum cantilever ratio between snakes with or without a stub tail ($F = 6.515$, $P = 0.020$). Because sample sizes were small for the latter analysis and because all *I. cenchoa* with a stub tail were small individuals, all snakes within a species were grouped for further analysis regardless of tail condition.

There was a significant difference in the mean and maximum cantilever ratios between different species (mean: $F = 8.500$, $df = 4$, $P < 0.001$; maximum: $F = 8.505$, $df = 4$, $P < 0.001$). Post-hoc Tukey Tests were performed for mean (Table 3.2) and maximum bridged distances (Table 3.3).

Table 3.1. Results of one-way ANOVAs to test for intraspecific differences in cantilevering ability. Results included for mean and maximum cantilever ration by sex and between snakes with or without a stub tail. M=males, F=females. Alpha level = 0.025 following Bonferroni adjustment. Significant values shown in bold.

	Sex			Tail Incomplete		
Species	**M: F**	**Mean**	**Maximum**	**No:Yes**	**Mean**	**Maximum**
Sibon argus	5:8	F=0.544 P=0.476	F=0.481 P=0.502	8:5	F=1.724 P=0.216	F=2.547 P=0.139
Sibon annulatus	4:6	F=0.030; P=0.867	F=0.188 P=0.676	9:1	**F=7.468** **P=0.026**	**F=5.600** **P=0.046**
Oxybelis brevirostris	7:14	F=0.077 P=0.785	F=0.461 P=0.505	14:7	F=1.504 P=0.235	F=1.583 P=0.224
Dipsas sp.	7:6	F=3.396 P=0.092	F=3.099 P=0.106	11:2	F=0.083 P=0.779	F=0.005 P=0.945
Imantodes cenchoa	9:11	F=0.046 P=0.833	F=0.001 P=0.978	17:3	**F=5.864** **P=0.026**	**F=6.515** **P=0.020**

Table 3.2. Results of the Tukey post-hoc analysis for mean cantilever ratio, showing groups based on similar values. Alpha = 0.05.

Species	n	2	3	1
Dipsas sp.	13	0.3565		
Oxybelis brevirostris	21	0.3808	0.3808	
Sibon annulatus	10		0.4284	0.4284
Imantodes cenchoa	20			0.4411
Sibon argus	13			0.4452
Significance		**0.729**	**0.123**	**0.913**

Table 3.3. Results of the Tukey post-hoc analysis for maximum cantilever ratio, showing groups based on similar values. Alpha = 0.05.

Species	n	2	3	1
Dipsas sp.	13	0.3710		
Oxybelis brevirostris	21	0.3985	0.3985	
Sibon annulatus	10		0.4491	0.4491
Imantodes cenchoa	20		0.4548	0.4548
Sibon argus	13			0.4675
Significance		**0.658**	**0.053**	**0.893**

Pearson's partial correlation analysis was used to test for interspecific correlations between mass (relative to SVL) and mean and maximum distances bridged by each species (Table 3.4). Mass was significantly correlated with mean and maximum bridging ratio for *Oxybelis brevirostris* and with mean bridging distance for *Dipsas* sp. These species had the lowest values for both mean and maximum cantilever ratio. Significant correlations between mass and mean or maximum bridging distances were not found for the other species (Table 3.4).

Ten observations of bridging in the wild were collected for the target species (Table 3.5). Wild observations for *Imantodes cenchoa* and *Oxybelis brevirostris* were within the range observed in the laboratory, but observations of *Dipsas* sp. and *Sibon argus* exceeded the maximum cantilever ratio for those species in the laboratory.

Table 3.4. Pearson's partial correlations for mass (relative to SVL) to mean and maximum distances bridged. Significant relationships are shown in bold type.

Species	df	Mean cantilever ratio	Mean bridged distance	Maximum cantilever ratio	Maximum bridged distance
Sibon argus	10	0.44	r=0.117 P=0.718	0.47	r=0.000 P=0.853
Sibon annulatus	7	0.43	r=0.508 P=0.162	0.45	r=0.459 P=0.214
Oxybelis brevirostris	18	0.38	**r=0.576** **P=0.008**	0.40	**r=0.631** **P=0.003**
Dipsas sp.	10	0.36	**r=-0.586** **P=0.045**	0.37	r=-0.552 P=0.063
Imantodes cenchoa	17	0.44	r=-0.059 P=0.810	0.45	r=0.-.035 P=0.886

Less abundant species also were tested for bridging ability in the laboratory and observed in the field as available. Two *Sibon nebulatus* bridged a mean of 51% of their total length in the laboratory, and one observation was made in the wild of a snake bridging 49% of its total length. Three individuals of *Leptodeira septentrionalis* exhibited a mean cantilever ratio of 38.7, and one individual in the wild bridged 21% its total length. Two individuals of *Imantodes inornatus* had a cantilever ratio of 38, and one individual in the wild bridged 59% of its total length. One *Leptophis depressirostris* had a cantilever ratio of 43, and one *Oxybelis aenus* had a cantilever ratio of 40 in the laboratory.

Table 3.5. Mean bridging distance, range of distances bridged, and cantilever ratio (mean percentage of total length bridged) for each species in the laboratory and for observations in the wild. Sample sizes (n) are noted. Species below the line were not included in ANOVAs.

	Laboratory				Wild			
Species	**n**	**Mean bridge (cm)**	**Range**	**Cantilever Ratio**	**n**	**Mean bridge (cm)**	**Range**	**Cantilever Ratio**
Dipsas sp.	13	16.2 + 5.10	10.3-28.0	35.7 + .07	3	38.7 + 8.08	30.0-46.0	55.3 +0.09
Imantodes cenchoa	20	37.5 + 11.10	19.7-53.5	44.1 + 0.06	5	45.4 + 12.64	30.0-64.0	45.9+0.10
Oxybelis brevirostris	21	40.7 + 5.39	27.8-49.2	38.1 + 0.03	1	49.0	-	54.0
Sibon annulatus	10	23.6 + 6.54	10.8-30.0	42.8 + 0.06	0	-	-	-
Sibon argus	13	24.4+4.86	14.8-30.8	44.5+.05	1	40.0	-	65.0
Imantodes inornatus	2	34.83+5.42	31.0-38.4	37.9+0.05	1	54.0	-	58.6
Leptodeira septentrionalis	3	22.78+4.23	20.3-27.7	38.8+0.12	1	12.0	-	20.9
Sibon nebulatus	2	26.52 +1.06	25.7-27.2	51.1+.15	1	30.0	-	49.0

DISCUSSION

The ability of Neotropical arboreal snakes to bridge gaps in vegetation is well documented (e.g., Henderson and Nickerson, 1976; Lillywhite and Henderson, 1993; Lillywhite et al., 2000; Jayne and Riley, 2007), but few studies have quantified their average or maximum achievable cantilever distance (Lillywhite et al., 2000). This study provided quantitative cantilever distances under standardized conditions for five species not previously tested, employing specimens freshly collected in the field. This study also related those experimental cantilevering distances to observations made in the field under natural conditions.

Behavioral differences in arboreal species' preferred habitat have been noted (Henderson and Binder, 1980; Shine et al., 1996) and have been associated with differences in crypsis (Fitzgerald et al., 2003). However, some differences likely are related to body mass, reflecting the abilities of different perches to support the mass of a snake. Boas and pythons presumably are limited to occupying thicker branches because the smaller branches may not support their weight. Conversely, smaller snakes such as *Imantodes* and *Sibon* can move on the smaller twigs (pers. obs.).

Both *Oxybelis brevirostris* and *Dipsas* sp. showed significant correlations between body mass and the average distance bridged (Table 3.4). These two species had the lowest cantilever ratios. Such species likely cannot access the smallest of branches because their mass is too great (Henderson and Nickerson, 1976). In the present laboratory experiment, the relatively thick perch provided strength sufficient to support any individual of *O. brevirostris* or *Dipsas* sp. However, individuals of these species were quick to drop to the ground when placed on the perch, and the initial flight behavior was considered a defensive response to handling, as observed in most ophidian species. *Dipsas* sp. launched itself from the branch, flipping laterally as it landed, and then remained motionless. Individuals of that species typically acclimated and bridged after one or two attempts to place it on the apparatus. Alternatively, *O. brevirostris* repeatedly dropped to the ground, even after extensive handling, often climbing another nearby object (e.g., chair or table leg). Henderson and Nickerson (1976) suggest that a great deal of energy is consumed when *Oxybelis* spp. attempt to bridge gaps because of their relatively heavy bodies, and therefore less energy may be expended if the snakes descend to the ground and ascend the adjacent structure, as opposed to bridging gaps. Moreover, when *O. brevirostris* did attempt to bridge, they would reach forward until about 40% of the body was extended, and then would turn the tail forward in front of the body until it served as a brace. This behavior appeared to add support, allowing the snake to bridge more effectively.

Species of *Imantodes* and *Sibon* did not exhibit a significant correlation between body mass and the distance bridged (Table 3.4). Individuals of these species typically did not perform an active defensive behavior during testing of gap-bridging and remained on the perch without attempting to flee. These species exhibited the greatest bridging distances in these experiments (Table 3.1, 3.5). Furthermore, these species are more highly adapted morphologically for arboreal habits (Henderson and Nickerson, 1976) and are able to exploit smaller twigs, which would facilitate movement between the ends of branches and subsequent cantilevering.

Ten observations of voluntary bridging in the field, under natural conditions, were observed for the five target species (Table 3.5). The mean bridging of *Dipsas* sp. in the field exceeded that observed in the laboratory and also was greater than the maximum bridging distance. The distance for *Sibon argus* in the field also exceeded the maximum distance observed in the laboratory, and the species was observed bridging the greatest relative distance of any of the focal species in the field.

This study has expanded our knowledge of cantilevering in Neotropical arboreal snakes, providing data on species that had not been investigated previously. Further investigations are needed to determine how arboreal species partition among the available arboreal habitat, an aspect of their biology that is not yet well understood (Lillywhite and Henderson, 1993). In particular, the ability to cantilever and access the terminal branches may be an important element of behaviors such as foraging, predator escape, and courtship.

CHAPTER IV

DEFENSIVE BEHAVIORS OF A NEOTROPICAL SNAKE COMMUNITY

Animals employ diverse defensive behaviors to protect themselves from potential predators or from conspecifics during competitive interactions for mates, territories, or food. Endler (1986) defines five stages of attack by a predator, during which defensive tactics may be employed as an attempt to avoid death or serious injury: detection, identification, approach, subjugation, and consumption (Endler, 1986; Martins, 1996).

Defenses vary widely across taxa. Many plants have modified stems (thorns) or leaves (spines). Others possess defensive toxins (e.g., Rhoades, 1979; Coley and Barone, 1996). Animals use many different tactics, including locomotor escape, biting, stinging, scratching, and tail-thrashing (e.g., Evans and Schmidt, 1990; Greene, 1988). Many utilize color patterning for protection (Endler, 1981), including crypsis to blend in with their background (e.g., Merilaita et al., 1999; Ruxton et al., 2004) or mimicry of venomous or poisonous taxa (e.g., Ruxton et al., 2004).

Snakes present interesting subjects for study because they lack the appendages that are often utilized by other vertebrates for protection (Coates and Ruta, 2000). Despite this apparent disadvantage, snakes employ a wide array of defensive behaviors (Greene, 1988; Table 4.1), from simple tactics such as locomotion and crypsis to complex behavioral repertoires, including flaring the quadrate bones, raising the anterior body, hissing, and false striking (Martins, 1996).

Few studies have consistently and comprehensively looked at the defensive behaviors of a community of snakes (Martins, 1996; Martins and Oliveira, 1998). Greene

(1988) reviews the defensive behaviors of reptiles and suggests that some observations may have been confused with feeding or other behaviors (i.e., a strike may be in response to the presence of potential prey or in defense). The designing of consistent documentation or laboratory trials are suggested as methods to expand the available data on ophidian defensive behaviors (Green, 1988; Martins, 1996).

Martins (1996) reviews ophidian defensive behaviors and suggests which behaviors may be employed at each stage of predatory attack (Endler, 1986). Initial stages are defended with inaccessibility, concealing coloration, and immobility. Later stages are defended using noxious discharges, body thrashing, and biting.

Martins (1996) states that defensive behaviors have evolved in one of two ways: rooted within the phylogeny of snakes, with closely related species exhibiting similar behaviors, or evolved more recently in response to ecological conditions. However, many closely related species occupy similar ecological niches, and defensive behaviors may appear to vary ecologically despite having a deeper phylogenetic origin.

Identifying potential predators in the local community is important for understanding defensive behaviors. Potential ophidian predators native to central Panama include other snakes (Savage, 2002; Solórzano, 2004, Martins, 1996), the large frog *Leptodactylus pentadactylus* (K. R. Lips, pers. comm.), birds (e.g., Pough, 1964; Smith, 1969; Greene, 1988; Stiles and Skutch, 1989; Ridgely and Gwynne, 1992; Robinson, 1994; DuVal et al., 2006), especially raptors (Sazima, 1992; Martins, 1996), and mammals (e.g., Emmons, 1987; Eisenberg, 1989). Other potential predators include some large invertebrates, such as crabs (Maitland, 2003), spiders, centipedes, scorpions (McCormick and Polis, 1982; Martins, 1996), tarantulas, and ants (Martins, 1996).

Table 4.1. Description of morphological attributes and behaviors used in defense by snakes.

Behavior	Description
	Morphological Attributes
Aposematic coloration	possess color pattern that is marked with bright colors including yellows and reds
Concealing coloration	possess color pattern that is cryptic against substrate or local environment where snake spends most of time
Mimicry	possess a color pattern that closely resembles a sympatric venomous snake or other toxic or dangerous organism
Scale adaptation	scales are rough or inflict injury when seized
	Locomotion
Same substrate	flees through same environment where first encountered
To water	flees directly into water
To ground	falls from tree/cliff to ground and makes movement to escape on the ground
To cover	moves rapidly toward cover
Immobility	freezes in place and does not move
Death feigning	acts as if dead: body is limp and unresponsive when initially touched
Wind movements	moves back and forth to resemble a leaf in the wind
Lateral flip	flips to side when fleeing to expose ventral surface momentarily
Non-defensive	does not respond in any obvious manner
	Nonlocomotor Behaviors
Head enlargement	flares quadrate bones giving head a triangular appearance
Lateral neck compression	neck is compressed side to side so region appears wider in lateral view
Lateral body compression	body is compressed side to side so regions appears wider in lateral view
Dorso-ventral neck compression	neck is compressed from top to bottom to appear larger from above or below
Dorso-ventral body compression	body is compressed from top to bottom to appears larger from above or below
Elevate head and neck	elevation of head and neck from substrate
Body elevation	anterior portion of body, including head and neck is raised from substrate
Hide head in own body	place head under one or more coils of body
Hide head in substrate	place head under substrate

Table 4.1. Continued

Behavior	Description
	Nonlocomotor Behaviors continued
Body coil	coils the body into flat concentric circles
Body pyramid	coils body into vertical pyramid with head inside or outside of top loop
Body ball	coils body into ball
Body thrash	violently thrashes unrestricted regions of body
Gape	mouth is opened wide
Flare labials	supralabial scales are raised away from dentition
False strike	moves head and neck forward with closed mouth, not as part of feeding response
Strike	moves head and neck forward with open mouth in an attempt to bite
Bite	makes contact with fangs, but not as part of feeding response
Cloacal discharge	releases urates and/or musk from cloaca
Tail breakage	tail breaks completely off
Rattling	vibration of specialized caudal scales that produce a sound
Tail vibration	vibration of tail; no special caudal scales are present
Tail display	movement of tail
Head-tail display	tail and head are moved in similar fashion
Spit venom	venom is forced from fangs in direction of predator
Constriction	tightening of coil in defense not as a feeding response
Disgorge meal	disgorges meal in response to seizure or harassment by predator or before flight
Hemipenal eversion	extend one or both hemipenes from inverted (retracted) position

The indirect documentation of attacks can lend insight into which predators influence the behavior of snakes. Clay models have been used to record claw, tooth, or bill marks, to understand the role of aposematic coloration in coral snakes (*Micrurus* spp.) and their mimics (Brodier, 1995; Brodie and Janzen, 1995). Clay models are most useful when snakes have simple or uniform color patterns that can be easily replicated. However, models are more difficult to construct for snakes with complicated patterns (e.g., *Sibon argus, Bothriechis schlegelii*). An alternative method involves documenting the presence and location of scars and can be accomplished in conjunction with a capture-mark-recapture study at a site where individuals are abundant. Although snakes that were unsuccessful in escaping a predation event cannot be included in this method, it provides some insight into the types of predators that influence the defensive behaviors of the ophidian fauna.

The speciose community of snakes in central Panama provides an opportunity to document the defensive behaviors among diverse Neotropical snakes. I tested abundant species for defensive behaviors, evaluated the presence of scars on various species of snakes within the community, and obtained lists of potential ophidian predators in at a site in central Panama.

MATERIALS AND METHODS

Study Site.---Snakes were evaluated at two sites in the central region of the Republic of Panama. Both sites are pre-montane cloud forest with mature secondary forest and numerous streams (Chapter I). Snakes at Parque Nacional General de División Omar

Torrijos Herrera (PNGDOTH; Chapter I) were evaluated in October 2005, May 2006, September 2006 - August 2007, and November 2007. Snakes were evaluated at Altos del Maria (ADM; Chapter I) in October 2005 and May - July 2006.

Study species.---I documented the defensive behaviors of 45 species representing six families of snakes in central Panama (Table 4.2).

Behavioral trials and analyses.---Defensive behaviors for all snakes found in the field were evaluated at the time of initial capture. Once the investigator was in position, the snake was poked with the tip of a snake hook to gain the attention of the snake and to initiate any immediate responses that may occur on the vegetation (arboreal snakes) or on the ground (terrestrial snakes). After the initial behavior was noted, nonvenomous snakes were grasped by a single hand at midbody and their behaviors were recorded. Venomous snakes were handled with a snake hook at all times. Behaviors were recorded for up to one minute or until the snake ceased responding with any obvious defensive behaviors. Behaviors were classified based on descriptions from Greene (1988) and modifications that I made to his list (Table 4.1).

Quantitative analysis of defensive behaviors.---Four defensive behaviors were evaluated quantitatively. The behaviors included three apparently common behaviors, head enlargement, body thrashing, and cloacal discharge, and one apparently rare behavior, hemipenal extension. Each behavior was scored as present or absent for each individual of four commonly occurring ophidian taxa (*Dipsas* sp., *Imantodes cenchoa*, *Oxybelis brevirostris*, and *Sibon argus/longifrenis*).

Table 4.2. Species of snakes from central Panama included in defensive analyses. Natural history information from Savage (2002) and Solórzano (2004).

Species	Activity Time	Activity Area
Anomalepididae		
Liotyphlops albirostris	unknown	fossorial
Boidae		
Boa constrictor	diurnal	scansorial
Corallus annulatus	nocturnal	arboreal
Ungaliophiidae		
Ungaliophis panamensis	nocturnal	arboreal
Colubridae		
Amastridium veliferum	diurnal	terrestrial
Chironius exoletus	diurnal	scansorial
Chironius grandisquamis	diurnal	scansorial
Clelia clelia	diurnal	terrestrial
Dipsas nicholsi	nocturnal	arboreal
[1]*Dipsas* sp.	nocturnal	arboreal
Enuilius flavitorques	diurnal	terrestrial
Erythrolamprus mimus	diurnal	terrestrial
Geophis brachycephalus	nocturnal	terrestrial
Hydromorphus concolor	nocturnal	aquatic
Imantodes cenchoa	nocturnal	arboreal
Imantodes inornatus	nocturnal	arboreal
Leptodeira septentrionalis	nocturnal	arboreal
Leptophis depressirostris	diurnal	arboreal
Leptophis nebulosus	diurnal	arboreal
Liophis epinephalus	diurnal	terrestrial
Ninia celata	diurnal	terrestrial
Ninia maculata	diurnal	terrestrial
[2]*Ninia* sp.	nocturnal	terrestrial
Nothopsis rugosus	nocturnal	terrestrial
Oxybelis aenus	diurnal	arboreal
Oxybelis brevirostris	diurnal	arboreal
Oxybelis fulgidus	diurnal	arboreal
Oxyrhopus petolus	diurnal	terrestrial
Pseustes poecilonotus	diurnal	scansorial
Rhadinaea decorata	diurnal	terrestrial
Rhinobothryum bovallii	nocturnal	arboreal
Sibon annulatus	nocturnal	arboreal
Sibon argus	nocturnal	arboreal
Sibon longifrenis	nocturnal	arboreal
Sibon nebulatus	nocturnal	arboreal
Spilotes pullatus	diurnal	scansorial
Stenorrhina degenhardtii	diurnal	terrestrial
Tantilla melanocephala	diurnal	terrestrial
Urotheca euryzona	nocturnal	terrestrial

Table 4.2 continued.

Elapidae		
Micrurus mipartitus	diurnal	terrestrial
Micrurus nigrocinctus	diurnal	terrestrial
Viperidae		
Atropoides nummifer	nocturnal	terrestrial
Bothrieches schlegelii	nocturnal	arboreal
Bothrops asper	nocturnal	terrestrial
Lachesis stenophrys	diurnal	terrestrial

[1] Undescribed species (Myers et al., 2007)
[2] Undescribed species (R. Ibáñez, pers. comm.)

A χ^2 analysis was conducted for each behavior for each species, to test whether the frequency of behaviors differed from the expectation that 50% of individuals would demonstrate the behavior. *Oxybelis brevirostris* was excluded from the analysis of head enlargement because no individuals demonstrated this behavior (see Results).

I used an ANOVA to test for interspecific differences for the frequency with which each behavior was displayed. A post-hoc Tukey test was conducted when a significant result was reported. Alpha was maintained at 0.05 for all analyses (Zar, 1999).

Phylogenetic basis of behaviors.---I used MacClade (Version 4.08 OS X) to map selected defensive behaviors by mapping the presence/absence of each behavior for each species on a previously constructed tree (Chapter I). Selected defensive behaviors included: head enlargement, body thrashing, cloacal discharge, hemipenal eversion, body coiling, and head elevation. I also compared snakes of difference color patterns (no obvious patterning, concealing coloration, aposematic coloration, and mimetic coloration).

Analysis of scars.---All snakes captured at PNGDOTH were returned to the laboratory for measurement. Scars on snakes were documented by a written description and digital photograph. I recorded the body region (anterior, posterior, or midbody) and position (dorsum, lateral surface, venter, or tail) of each scar.

A Kruskal-Wallis Test was used to test for interspecific differences in the presence of scars. Nonvenomous snakes presumed to exhibit mimicry (*Dipsas* sp., *Sibon annulatus, S. argus, S. nebulatus*; Sazima, 1989; Green, 1997; Solórzano, 2004) were compared to other nonvenomous snakes (*Oxybelis brevirostris, Leptophis nebulosus, Leptodeira septentrionalis, Imantodes cenchoa*, and *I. inornatus*) and to *Bothriechis schlegelii*. A Kruskal-Wallis Test analyzed interspecific differences in the body region and position of scars. Alpha was maintained at 0.05 for all analyses (Zar, 1999).

Potential ophidian predators.---Local people with knowledge of the forest were asked to compile a list of birds (S. Arcia and A. González, local guides) and mammals (J. del Carmen, park ranger; A. Gonzalez, local guide; and J. A. Santana, local resident) that occur within the boundaries of PNGDOTH. Additional data were gathered from the Rapid Ecological Assessment conducted following the establishment of PNGDOTH (Alvarado, 2000) and notes from other investigators (K. R. Lips, R. Brenes, F. Brem, C. E. Montgomery). Potential ophidian predators were identified based on published reports of diet or predatory events and personal observations of predation or gut contents.

RESULTS

Behavioral diversity.---Among members of the Panamanian snake assemblage defensive behaviors ranged from crypsis and mimicry to displays such as dorsoventral compression of the neck and coiling of the body into a raised pyramid (Table 4.3).

All species exhibited locomotion when manipulated. Twenty species (44.4%) possess concealing coloration, and eight species (17.8%) possess coloration that presumably mimics an allopatric species of venomous snake. Four of the mimetic species (*Urotheca euryzona, Erythrolamprus mimus, Oxyrhopus petolus*, and *Rhinobothryum bovallii*) possess ringed patterns that presumably mimic coral snakes (*Micrurus* spp.). Two species (*Sibon argus* and *S. longifrenis*) possess mottled color patterns that presumably mimic *Bothriechis schlegelii.*

Fifteen species (33.3%) of snakes struck and bit during defensive trials. False strikes were documented for seven species (15.6%), including the two coral snakes (*Micrurus* spp.), three species with ringed patterning (*Urotheca euryzona, Oxyrhopus petolus, Rhinobothryum bovallii*), *Liophis epinephalus* and *Dipsas nicholsi*. Eighteen species (40%) exhibited head enlargement by flaring the quadrate bones to form a triangular shape to the head.

Quantitative Data.---Four species of snakes were evaluated for the number of captures in which they performed each of four defensive behaviors (Table 4.4). Of three commonly observed behaviors, cloacal discharge (72.73%-82.35%), was observed in the highest frequencies among all species, but was not ubiquitous. Head enlargement was not

Table 4.3. Defensive behaviors performed by each species of snake. Includes total number of captures by site. ADM = Altos de Maria and PNGDOTH = Parque Nacional General de División Omar Torrijos Herrera.

Species	Site		Behaviors
	ADM	PNGDOTH	
Anomalepididae			
Liotyphlops albirostris	0	3	locomotion on same substrate, locomotion to cover, body thrash
Boidae			
Boa constrictor	0	1	concealing coloration, locomotion on same substrate, head enlargement, strike, bite, constrict
Corallus annulatus	0	1	concealing coloration, locomotion on same substrate, head enlargement, body coil, strike, bite, constrict
Ungaliophiidae			
Ungaliophis panamensis	0	1	concealing coloration, locomotion on same substrate, locomotion to cover, body coil, body thrash, cloacal discharge, constrict
Colubridae			
Chironius exoletus	1	1	concealing coloration, locomotion to ground, hide head in own body, strike, bite, constrict
Chironius grandisquamis	4	3	scale adaptation, other morphological attribute, locomotion to ground, head enlargement, elevate head and body, strike, bite, constrict
Leptophis depressirostris	0	1	concealing coloration, locomotion on same substrate, head enlargement, elevate head and neck, strike, bite, gape
Leptophis nebulosus	0	4	concealing coloration, locomotion on same substrate, head enlargement, elevate head and neck, strike, bite, gape
Oxybelis aeneus	0	1	concealing coloration, locomotion on same substrate, locomotion to ground, locomotion on same substrate, wind movement, head enlargement, elevate head and neck, strike, bite, cloacal discharge
Oxybelis brevirostris	0	132	concealing coloration, locomotion on same substrate, locomotion to ground, wind movement, head enlargement, elevate head and neck, strike, bite, cloacal discharge, hemipenal extraction

Table 4.3. Continued

Species	Site		Behaviors
	ADM	PNGDOTH	
Oxybelis fulgidus	0	1	concealing coloration, locomotion on same substrate, locomotion to ground, locomotion to cover, immobility, wind movement, elevate head and neck, body thrash, strike, bite, cloacal discharge
Pseustes poecilonotus	0	6	locomotion on same substrate, locomotion to ground, lateral neck compression, elevate head and neck strike, bite, tail vibration, gape, constrict, hemipenal extraction
Spilotes pullatus	2	1	locomotion on same substrate, locomotion to ground, head enlargement, lateral neck compression, elevate head and neck, strike, bite, cloacal discharge, tail vibration, gape, constrict,
Stenorrhina degenhardtii	0	3	locomotion on same substrate, hide head in substrate, cloacal discharge
Tantilla melanocephala	0	3	concealing coloration, locomotion on same substrate, locomotion to cover, hide head in substrate
Dipsas nicholsi	0	1	locomotion on same substrate, head enlargement, hide head in own body, body pyramid, body thrash, false strike
Dipsas sp.	0	95	concealing coloration, locomotion on same substrate, locomotion to ground, lateral flip, head enlargement, cloacal discharge
Enulius flavitorques	0	2	locomotion on same substrate, locomotion to cover, hide head in substrate, cloacal discharge, tail breakage
Geophis brachycephalus	0	3	concealing coloration, locomotion on same substrate, locomotion to cover, hide head in substrate, tail breakage
Geophis sp	0	2	concealing coloration, locomotion on same substrate, locomotion to cover, hide head in substrate
Hydromorphus concolor	0	1	locomotion on same substrate, locomotion to water, locomotion to cover, hide head in substrate, body thrash
Imantodes cenchoa	6	66	concealing coloration, locomotion on same substrate, head enlargement, body coil, cloacal discharge
Imantodes inornatus	0	18	scale adaptation, other morphological attribute, locomotion on same substrate, head enlargement, body coil cloacal discharge

Table 4.3. Continued

Species	Site ADM	 PNGDOTH	Behaviors
Leptodeira septentrionalis	3	27	concealing coloration, locomotion on same substrate, head enlargement, elevate head and neck, strike, bite, cloacal discharge
Ninia celata	1	0	concealing coloration, locomotion on same substrate, locomotion to covere, head enlargement, hide head in substrate, body thrash
Ninia maculata	1	0	locomotion on same substrate, locomotion to cover, immobility, head enlargement, hide head in substrate
Ninia sp.			locomotion on same substrate, immobility, head enlargement, dorso-ventral neck compression, elevate head and neck, body elevation, hide head in substrate
Nothopsis rugosus	1	1	concealing coloration, scale adaptation, other morphological attribute, locomotion on same substrate, locomotion to cover, hide head in substrate
Rhadinaea decorata	0	2	locomotion on same substrate, locomotion to cover, hide head in own body, hide head in substrate, body coil, cloacal discharge
Sibon annulatus	14	64	locomotion on same substrate, cloacal discharge
Sibon argus	33	68	mimicry, locomotion on same substrate, head enlargement, hide head in own body, body pyramid, cloacal discharge
Sibon longifrenis	14	10	mimicry, locomotion on same substrate, head enlargement, cloacal discharge, hemipenal extraction
Sibon nebulatus	1	12	locomotion on same substrate, head enlargement, hide head in own body, body pyramid, strike, bite, cloacal discharge
Urotheca euryzona	5	1	mimicry, locomotion on same substrate, hide head in substrate, body coil, body thrash, false strike, cloacal discharge, tail breakage, trail vibrate, tail display, head-tail display
Amastridium veliferum	0	2	concealing coloration, locomotion on same substrate locomotion to cover, hide head in substrate
Clelia clelia	0	3	mimicry, locomotion on same substrate, constrict, disgorge meal
Erythrolamprus mimus	0	1	mimicry, locomotion on same substrate, locomotion to cover, elevate head and neck, body thrash, false strike, head-tail display

Table 4.3. Continued

Species	Site		Behaviors
	ADM	PNGDOTH	
Liophis epinephalus	1	0	mimicry, locomotion on same substrate, head enlargement, dorso-ventral neck compression, elevate head and neck, false strike, strike, bite, gape
Oxyrhopus petolus	0	2	mimicry, locomotion on same substrate, elevate head and neck, false strike, cloacal discharge, tail vibration, tail display, head-tail display
Rhinobothryum bovallii	0	1	mimicry, locomotion on same substrate, locomotion to cover, elevate head and neck, body thrash, false strike, strike, bite, cloacal discharge, tail vibration
Elapidae			
Micrurus mipartitus	0	1	aposematic coloration, locomotion on same substrate, locomotion to cover, elevate head and body, body elevation, body thrash, false strike, tail display, head-tail display
Micrurus nigrocinctus	0	1	aposematic coloration, locomotion on same substrate, locomotion to cover, elevate head and neck, body elevation, body thrash, false strike, tail display, head-tail display
Viperidae			
Atropoides nummifer	0	1	concealing coloration, locomotion on same substrate, locomotion to cover, elevate head and neck, body thrash, strike, bite
Bothriechis schlegelii	3	34	aposematic coloration, locomotion on same substrate, head enlargement, strike, bite
Bothrops asper	2	7	concealing coloration, locomotion on same substrate, locomotion to water, head enlargement, elevate head and neck, strike, bite, constrict
Lachesis stenophrys	0	1	concealing coloration, locomotion on same substrate, immobility, hide head in own body, body coil

observed for *Oxybelis brevirostris* (Table 4.4). Hemipenal eversion was most commonly observed in males of *Dipsas* sp. (28.57%).

Table 4.4. Selected defensive behaviors for four common species of snakes in central Panama. Ratios indicate absence:presence of each defensive behavior. Data for hemipenial eversion include only male individuals.

Species	sex (m:f)	Head Enlargement	Body Thrash	Cloacal Discharge	Hemipenial Eversion
Dipsas sp.	14:8	8:14	9:13	6:16	10:4
		63.63%	59.09%	72.73%	28.57%
Imantodes cenchoa	8:9	14:3	5:12	3:14	7:1
		17.65%	70.59%	82.35%	12.50%
Oxybelis brevirostris	10:10	20:0	7:13	4:16	9:1
		0%	65.00%	80.00%	10.00%
Sibon argus	6:8	4:10	5:9	3:11	5:1
		71.43%	69.29%	78.57%	16.70%

Results from χ^2 analyses showed that *Imantodes cenchoa* differed significantly from expected in head enlargement, all species differed significantly for cloacal discharge, and *I. cenchoa* and *Oxybelis brevirostris* differed significantly for hemipenal eversion (Table 4.5).

Table 4.5. Results of χ^2 testing for differences from expected frequency of each of four defensive behaviors for four common species of snakes in PNGDOTH. Significant results are in bold.

Species	Head Enlargement	Body Thrash	Cloacal Discharge	Hemipenal Eversion
Dipsas sp.	$\chi^2 = 1.636$	$\chi^2 = 0.727$	**$\chi^2 = 4.545$**	$\chi^2 = 2.571$
	P = 0.201	P = 0.394	**P = 0.033**	P = 0.109
Imantodes cenchoa	**$\chi^2 = 7.118$**	$\chi^2 = 0.059$	**$\chi^2 = 7.118$**	**$\chi^2 = 4.500$**
	P = 0.008	P = 0.808	**P = 0.008**	**P = 0.034**
Oxybelis brevirostris	-	$\chi^2 = 1.800$	**$\chi^2 = 7.200$**	**$\chi^2 = 6.400$**
		P = 0.180	**P = 0.007**	**P = 0.011**
Sibon argus	$\chi^2 = 2.571$	$\chi^2 = 1.143$	**$\chi^2 = 4.571$**	$\chi^2 = 2.667$
	P = 0.109	P = 0.285	**P = 0.033**	P = 0.102

No significant interspecific differences (P > 0.005) were found in the ANOVA of defensive behaviors, except that head enlargement differed interspecifically (F = 14.559, P < 0.001; Table 4.6). A post-hoc Tukey Test for head enlargement revealed two significantly different groups (Table 4.7).

Table 4.6. Results of ANOVA testing for interspecific differences in each of four defensive behaviors. Significant results are in bold.

Defensive Behavior	df	F	P
Head enlargement	**3**	**14.559**	**< 0.001**
Body thrashing	3	0.469	0.705
Cloacal discharge	3	0.189	0.904
Hemipenial Eversion	3	0.508	0.679

Table 4.7. Results of a Tukey post-hoc analysis for interspecific differences in head enlargement among four arboreal snakes. Two significantly different groups were found.

Species	n	1	2
Oxybelis brevirostris	20	0.00	
Imantodes cenchoa	17	0.176	
Dipsas sp.	22		0.636
Sibon argus	14		0.714
P		0.534	0.933

Phylogenetic basis of behaviors.---Dendrograms were constructed for the presence/absence of each of 10 defensive behaviors for species of snakes in central Panama (Fig. 4.1–4.7).

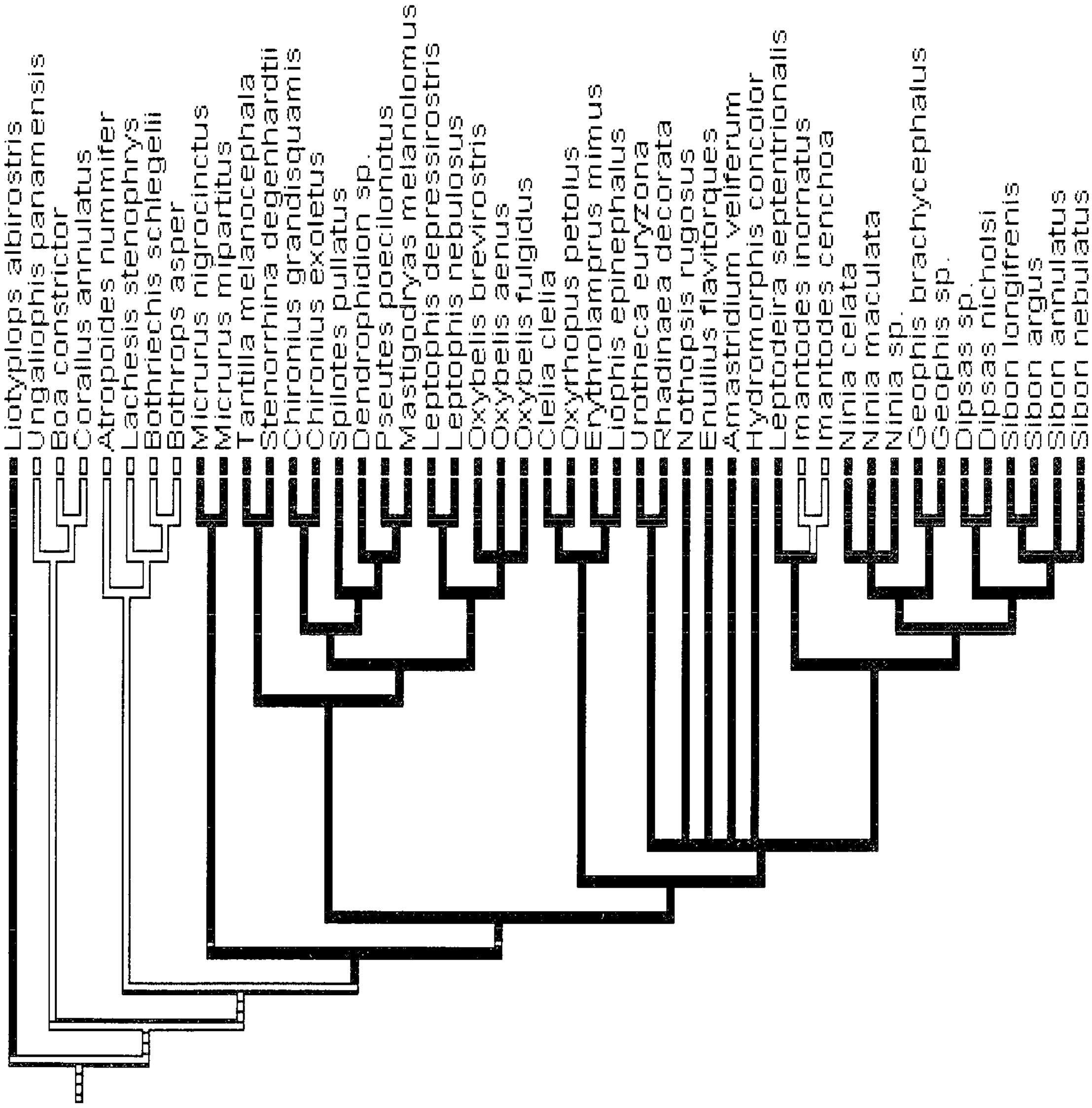

Fig. 4.1. Cladogram showing presence of body thrashing among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

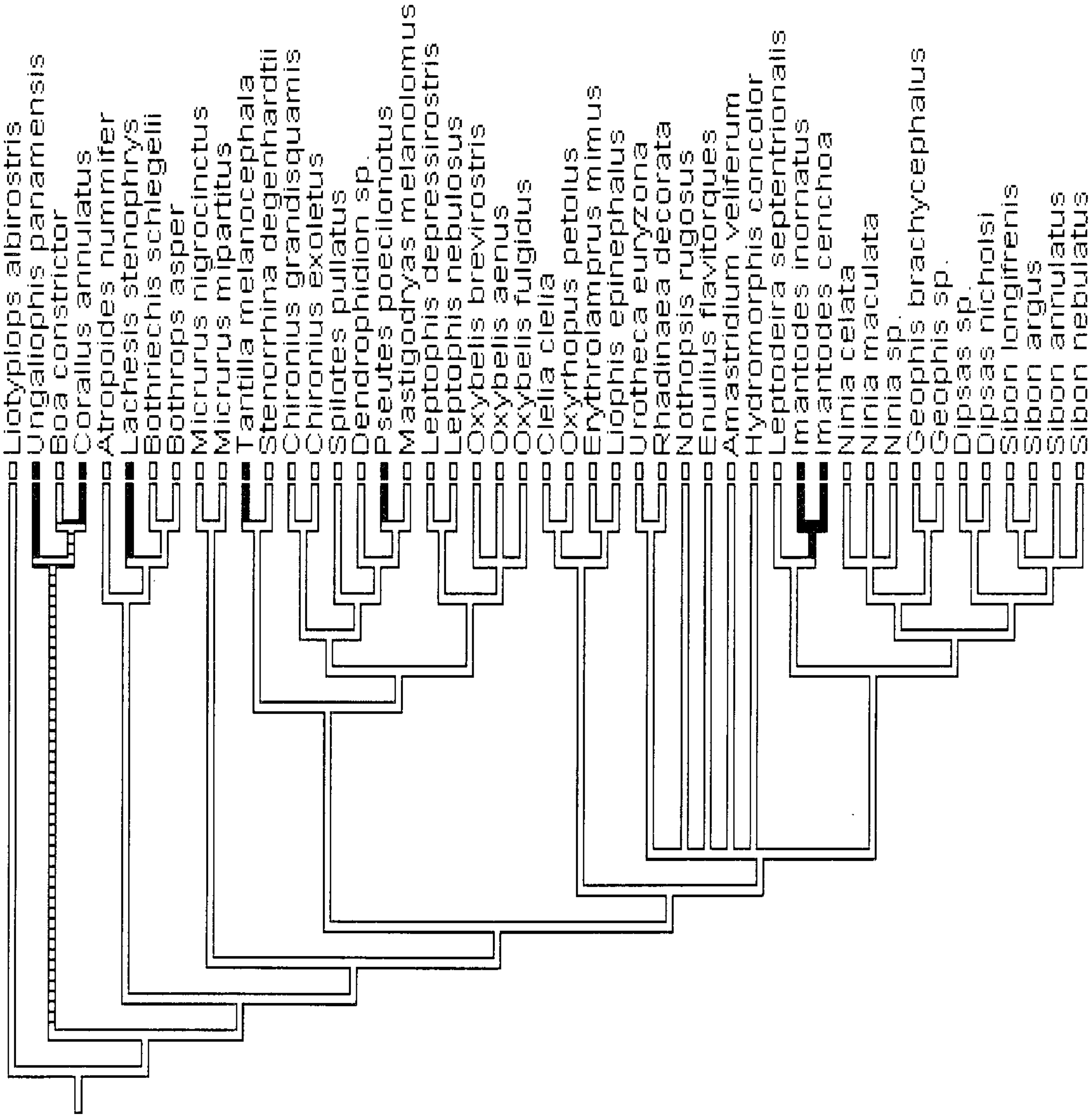

Fig. 4.2. Cladogram showing presence of body coiling among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior. Hatched lines represent unresolved condition for the branch.

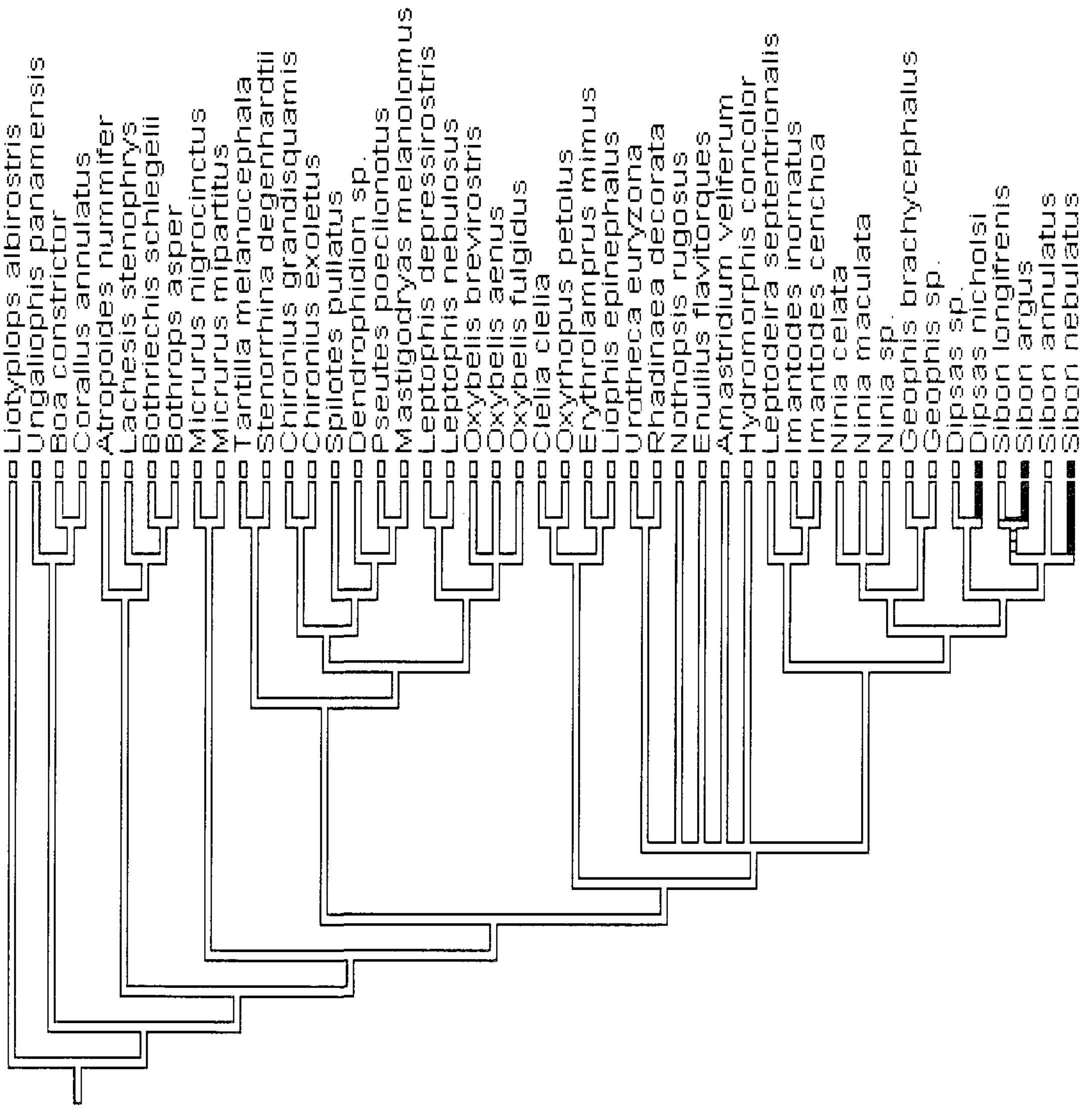

Fig. 4.3. Dendrogram of presence of body pyramiding among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior. Hatched lines represent unresolved condition for the branch.

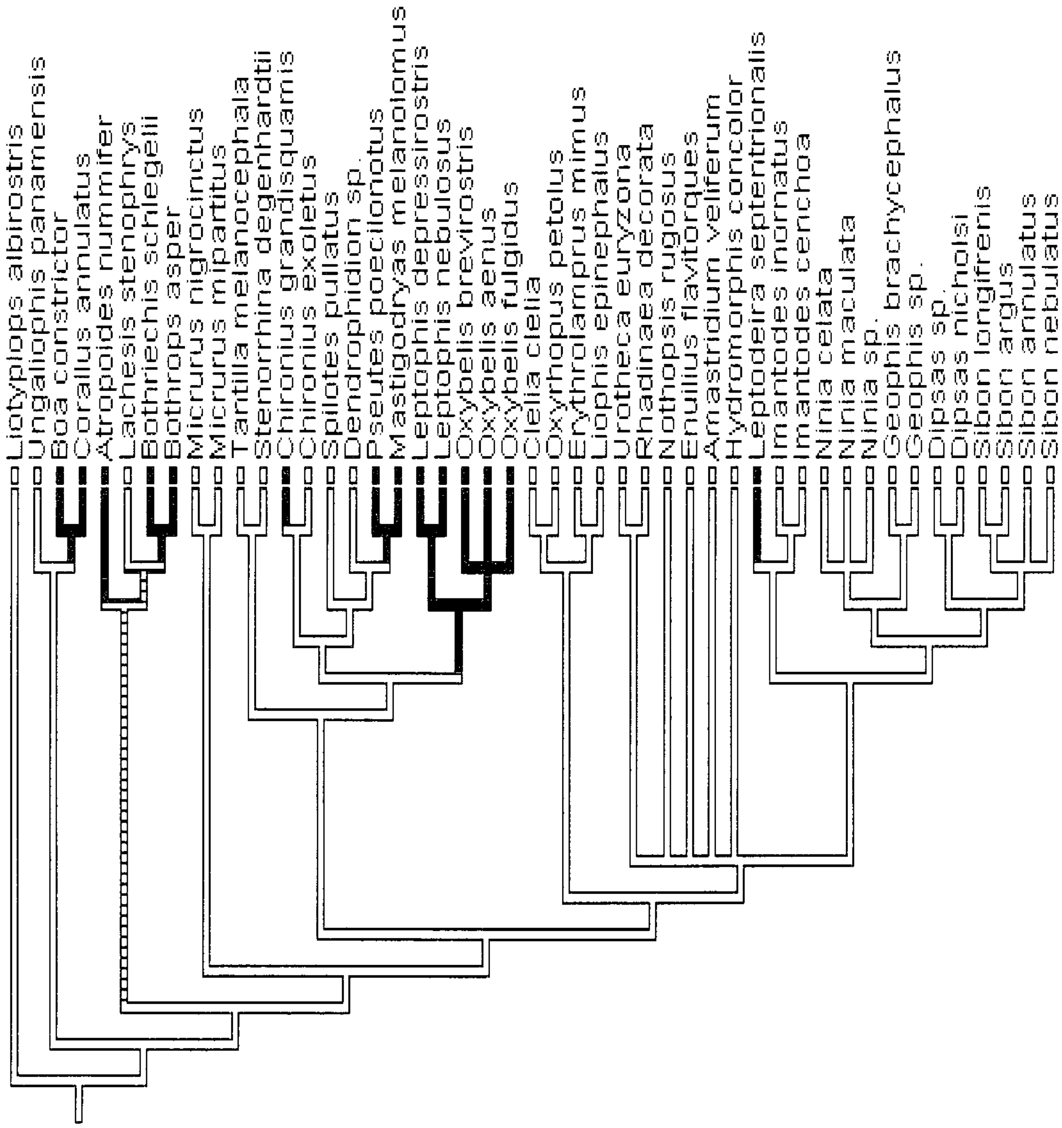

Fig. 4.4. Cladogram showing presence of striking among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior. Hatched lines represent unresolved condition for the branch.

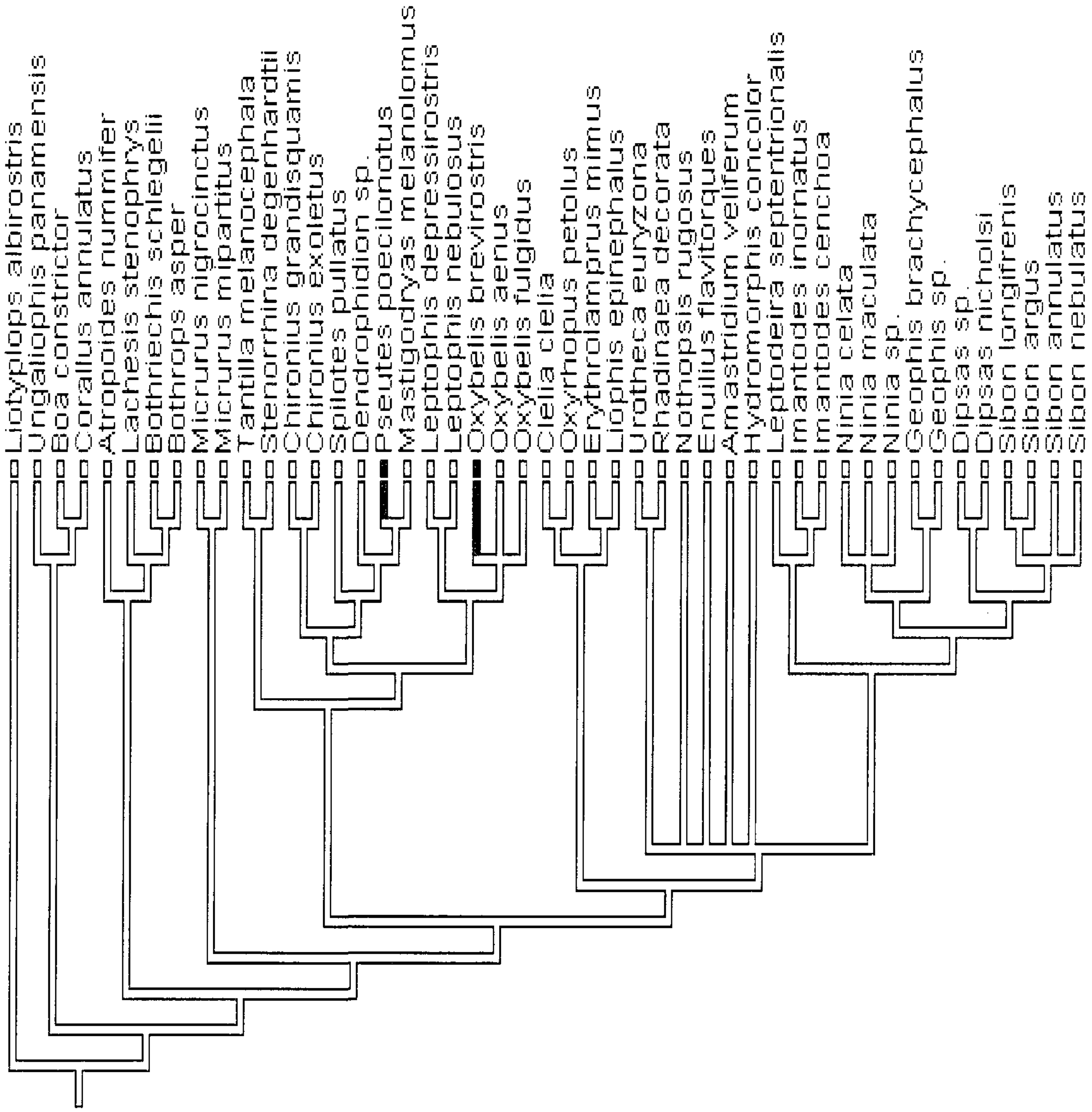

Fig. 4.5. Cladogram showing presence of hemipenial eversion among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior. Hatched lines represent unresolved condition for the branch.

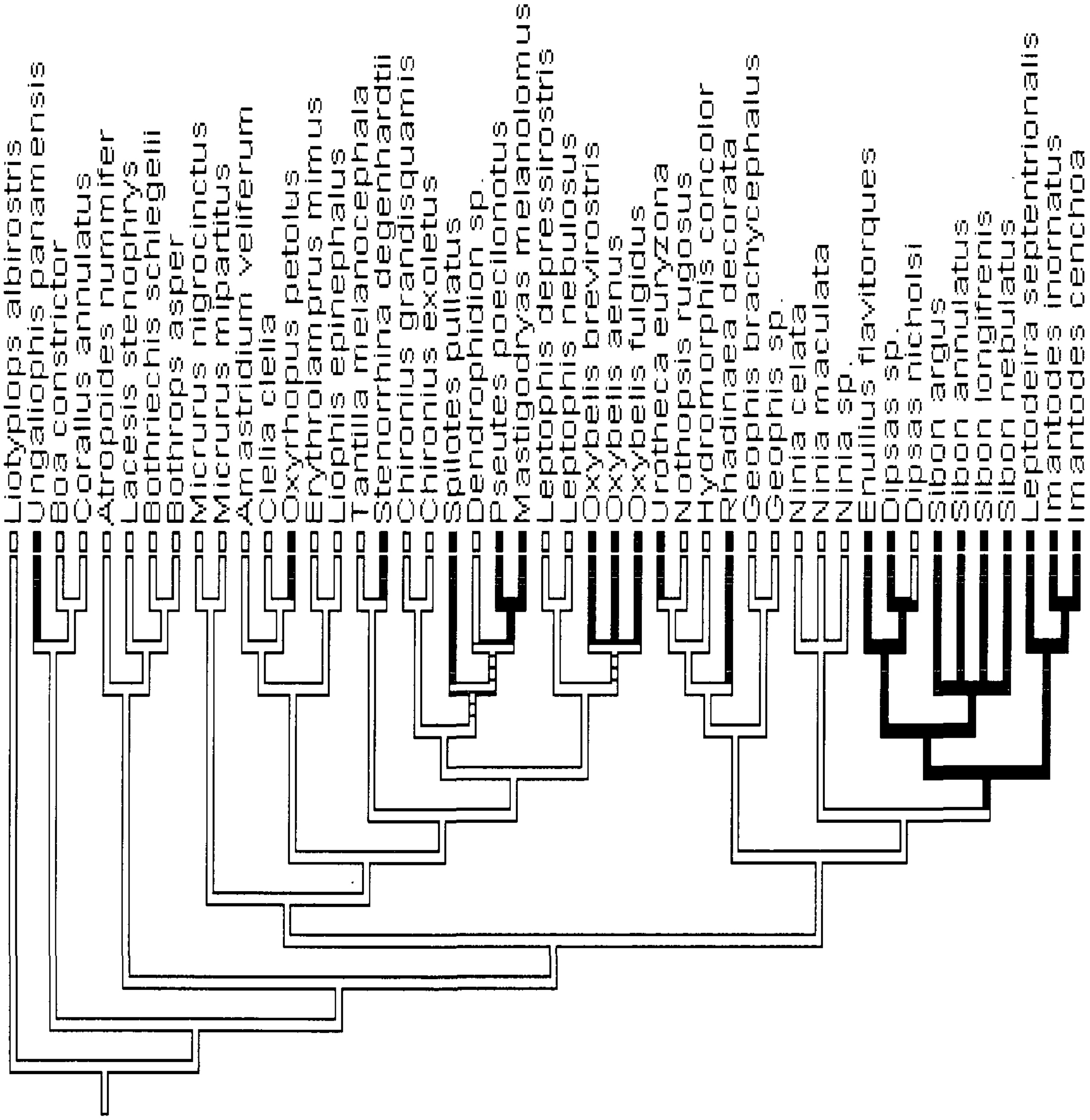

Fig. 4.6. Cladogram showing presence of cloacal discharge among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior. Hatched lines represent unresolved condition for the branch.

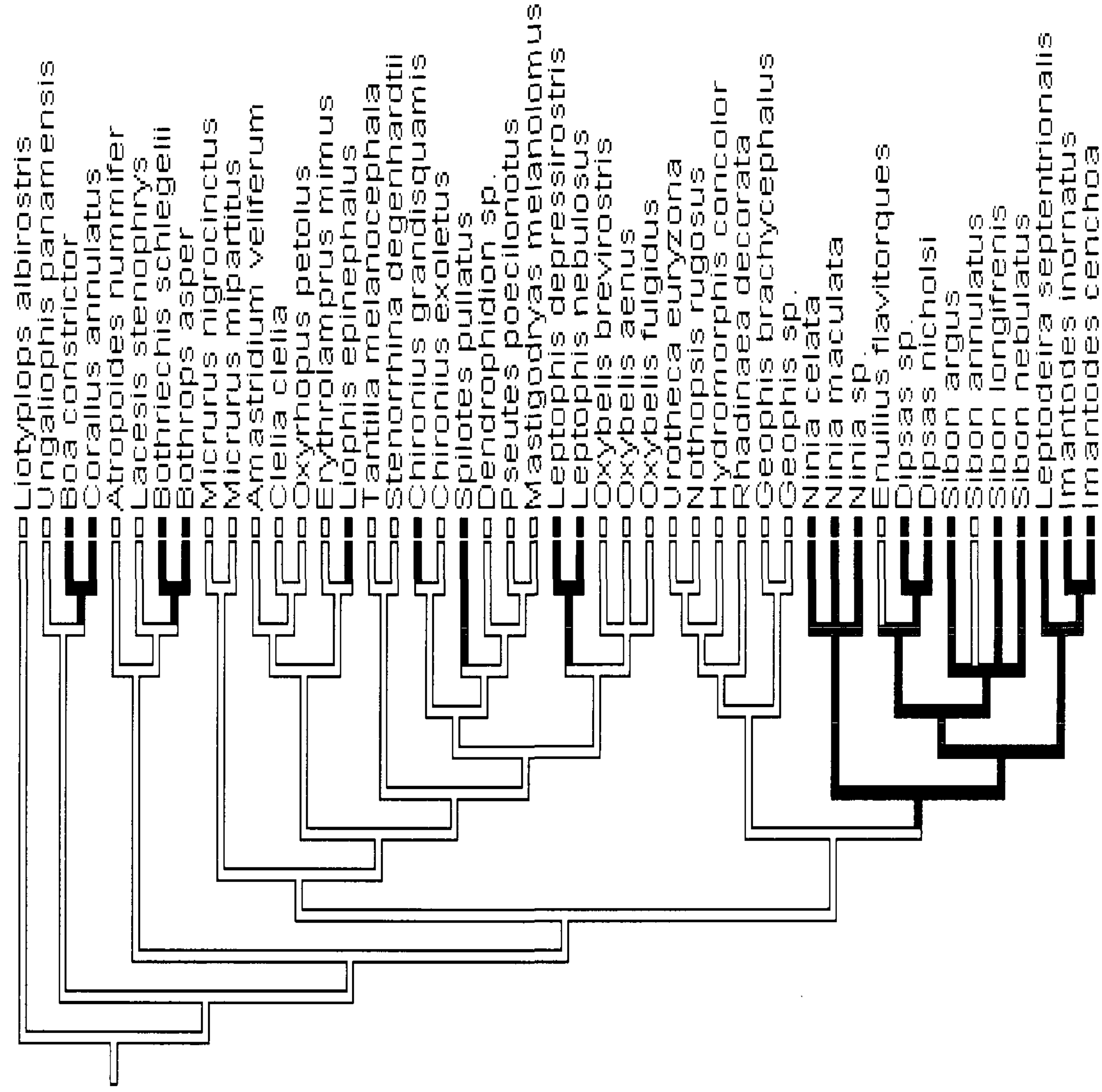

Fig. 4.7. Cladogram showing presence of head enlargement among snakes from central Panama evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior. Hatched lines represent unresolved condition for the branch.

Analysis of scars.---Scars were documented on only six species of snakes at PNGDOTH: *Imantodes cenchoa* (3 of 43 individuals, or 7.0%), *Leptodeira septentrionalis* (4 of 18, 22.2%), *Leptophis nebulosus* (1 of 3, 33%), *Oxybelis brevirostris* (12 of 60, 20.0%), *Sibon annulatus* (1 of 41, 2.4%), and *S. argus* (1 of 31, 3.2%). Scars ranged in size and shape from elongate wounds (most common in the diurnal *O. brevirostris*; Fig. 4.8) to small areas were scales were missing. In all of the scarred snakes except one, scars were limited to one area of the body, typically on the dorsal or lateral surface. One *L. septentrionalis* had several wounds along its body (Fig. 4.9). No scars were documented on the venomous snake *Bothriechis schlegelii* (n = 25) or on the nonvenomous *Dipsas* sp. (n = 57) or *Sibon nebulatus* (n = 10), species for which sample sizes were sufficient to have expected such evidence of predation.

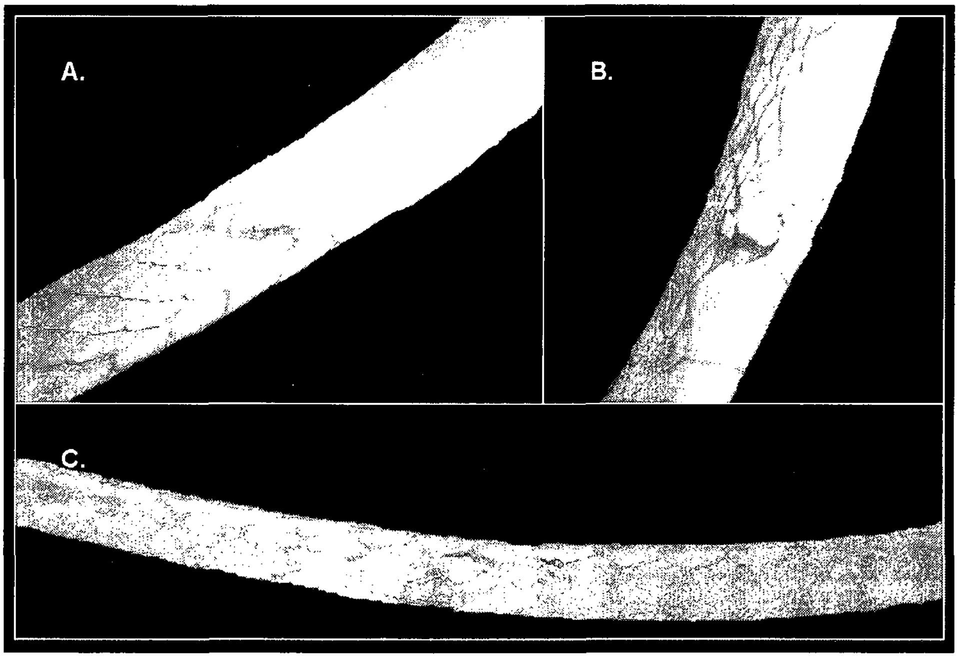

Fig. 4.8. Wounds and scars on individuals of *Oxybelis brevirostris*. A. Female, SVL = 65.8 cm, mass = 19.6 g. B. Male, SVL = 67.8 cm, mass = 20.3 g. C. Male, SVL = 62.6 cm, mass = 21.9 g.

There was a significant difference between the presence of scars among the four focal species ($\chi^2 = 34.820$, df = 9, $P > 0.001$), but not in the region where the scar was located (anterior, posterior, midbody; $\chi^2 = 7.653$, df = 5, $P = 0.177$) or position (dorsum, lateral, venter, tail; $\chi^2 = 4.476$, df = 5, $P = 0.483$) (Table 4.8).

There was a significant difference between nonvenomous snakes with mimetic coloration (*Dipsas* sp., *Sibon* spp.) and those without such coloration (*Imantodes cenchoa*, *Leptodeira septentrionalis*; *Leptophis nebulosus*, *Oxybelis brevirostris*; χ^2 = 18.358, P < 0.001; Table 4.8). However, there was no difference in region of the scar (χ^2 = 0.024, P = 0.876; Table 4.8) or position of the scar (χ^2 = 0.033, P = 0.857; Table 4.8) in these taxa.

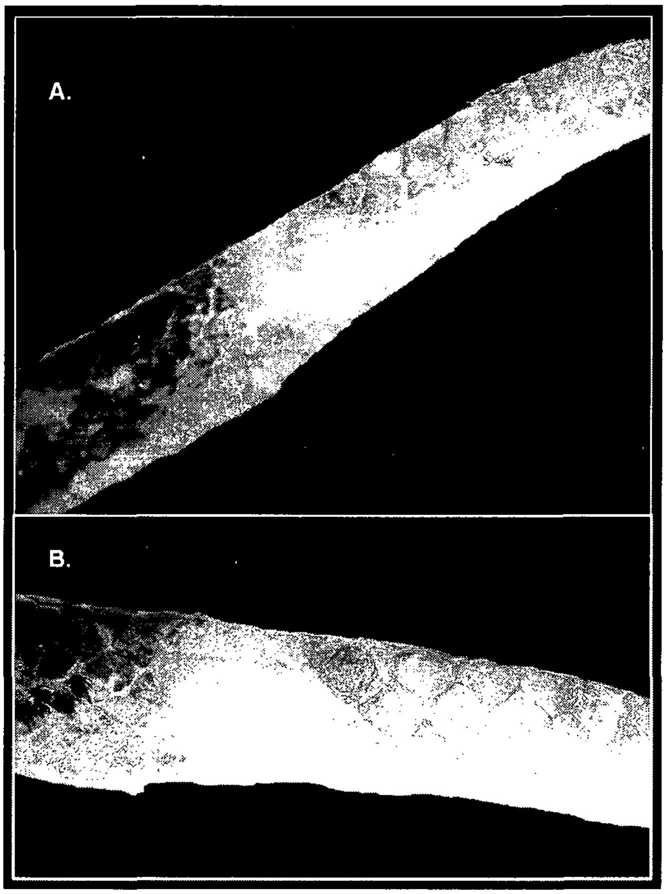

Fig. 4.9. Scars found on an individual of *Leptodeira septentrionalis*. A - B: Male, SVL = 50.0 cm, mass = 2.0 g.

There was no difference in the presence of scars between nonvenomous snakes with mimetic coloration (*Dipsas* sp. and *Sibon* spp.) and *Bothriechis schlegelii* (F = 0.361, df = 1, P = 0.549; Table 4.8).

Table 4.8. Results for a Kruskal-Wallis Test for interspecific differences in the presence and location of scars. Alpha = 0.05.

Test Snakes	Presence of Scar	Position	Scar
All species	34.820 (P<0.001)	4.476 (P=0.483)	7.652 (P=0.177)
Nonvenomous snakes: mimetic vs. nonmimetic coloration	18.358 (P<0.001)	0.024 (P=0.876)	0.033 (P=0.857)
Mimetic snakes vs. *Bothriechis schlegelii*	0.362 (P=0.547)	-	-

Potential predators of snakes.---The avian fauna of PNGDOTH includes at least 360 species in 45 families (S. Arcia, unpublished data). Species in eight families have been documented to feed on snakes (Ridgely and Gwynne, 1989, Stiles and Skutch, 1989; Table 4.9).

The mammalian fauna includes at least 41 species in nine orders and 19 families (Alvarado, 2000; J. Del Carmen, pers. comm.; unpublished data). Fourteen species in three orders (Didelphimorphia, Carnivora, and Artiodactyla) are potential predators of snakes (Goldman, 1920; Handley, 1966; Eisenberg, 1989) (Table 4.10). The bats and rodents have been poorly studied at PNGDOTH, and species within these two orders also

Table 4.9. Families that include potential avian predators of the snake fauna in PNGDOTH.

Family	Common Name
Ardeidae	herons
Accipitridae	hawks, eagles, kites
Falconidae	falcons, caracaras
Strigidae	owls
Momotidae	motmots
Bucconidae	puffbirds
Corvidae	jays, magpies, crows
Icteridae	orioles, blackbirds

may consume snakes (Goldman, 1920; Handley, 1966; Eisenberg, 1989).

Table 4.10. Potential mammalian predators of the snake fauna in PNGDOTH.

Order	Family	Species
Didelphimorphia	Didelphidae	*Didelphis marsupialis*
		Chironectes minimus
		Philander opossum
Carnivora	Procyonidae	*Nasua narica*
		Procyon lotor
	Mustelidae	*Conepatus semistriatus*
		Eira barbara
	Felidae	*Herpailurus yaguarundi*
		Leopardus pardalis
		Leopardus wiedii
		Panthera onca
		Puma concolor
Artiodactyla	Tayassuidae	*Tayassu pecari*
		Tayassu tajacu

Several species of snakes feed exclusively or opportunistically on other snakes. Ophiophagous snakes (Solórzano, 2004) from three families have been reported from PNGDOTH (Table 4.11).

Table 4.11. Potential ophidian predators on snakes reported from PNGDOTH and surrounding communities. Information on diet from Solórzano, 2004.

Family	Species
Colubridae	*Clelia clelia*
	Erythrolampris spp.
	Masticodryas melanolomus
	Drymobius margaritiferus
	Oxyrhopus petolus
	Rhinobothryum bovallii
Viperidae	*Bothrops asper*
	Porthidium nasutum
Elapidae	*Micrurus multifasciatus*
	Micrurus mipartitus
	Micrurus nigrocinctus

DISCUSSION

I performed a comprehensive study of snakes at two mid-elevation, pre-montane sites in central Panama, which revealed previously unreported ophidian defensive behaviors. Furthermore, through evaluation of scars on snakes and documentation of the vertebrate community, I was able to predict some potential predators of the snake community.

At least some individuals of all species evaluated in my study exhibited an initial attempt to flee (Table 4.3). Many species possessed either concealing coloration or mimetic coloration of a venomous snake. Other behaviors, such as cloacal discharge (Fig. 4.6), striking (Fig. 4.4), and biting, which are considered reactions to later stages of attack (Endler, 1986, Martins, 1996), were observed in fewer species, typically following initial attempts to escape by locomotion (Table 4.3). The rarest observations included behaviors such as hemipenial eversion, head-tail displays, and lateral neck compression and were observed in only one to a few species (Table 4.3).

Quantitative analyses of three commonly observed behaviors and one relatively rare behavior yielded important results. Of the three common behaviors, none were observed in all individuals for any of the four species of snakes included in the analysis (Table 4.4). This suggests that care must be taken when assigning terms such as "common" or "rare" to defensive behaviors for a given species until a relatively large sample has been tested. In species with low capture rates a behavior that is quite rare may be exhibited by one individual, but appear proportionally common. Alternatively, common behaviors are not always exhibited and may be overlooked or underrepresented in species represented by small sample sizes. Hemipenal eversion, which was relatively rarely observed (Fig. 4.8), was most common in *Dipsas* sp. and *Sibon argus* (Table 4.4), two relatively closely related species, although there was no significant difference in frequency among species (Table 4.6). Greene (1988) included hemipenal eversion as a potential defensive behavior performed by reptiles, but little work as been conducted to understand the function of the behavior or the range of taxa that exhibit it (Greene, 1988).

Phylogenetic mapping of several behavioral characters using MacClade (Fig. 4.1-4.7) further emphasizes that behaviors thought to be widespread may not be. Many behaviors were found to be limited to smaller numbers of closely related snakes, suggesting that the behavior evolved in a recent common ancestor. However, some taxa within a lineage did not perform a behavior found in related species, suggesting that the behavior was either lost or simply not observed during this study.

Interactions between tropical snakes and their predators are poorly understood because of a lack of direct observations. I applied the alternative method of evaluating snakes for scars in an attempt to understand such interactions. I observed few scars, especially among the nocturnal species, suggesting several possibilities. First, nocturnal species may be exposed to fewer predators than diurnal snakes, thus incurring fewer scars from attacks. Several individuals of *Oxybelis brevirostris* and *Leptophis nebulosus*, both diurnal species, had elongate scars on their dorsal and/or lateral surfaces (Fig. 4.8) that likely were inflicted by an avian predator. One *Leptodeira septentrionalis*, a nocturnal species, had round scars (Fig. 4.9) on the dorsal and lateral surfaces, but most nocturnal species were unmarked. Alternatively, nocturnal snakes may not be successful in escaping from predatory attacks, and thus nocturnal snakes with scars may not be found.

Third, color pattern may play a role in preventing attacks from predators. Some of the nocturnal species I evaluated with few or no scars (*Sibon argus, S. longifrenis*) are suspected to mimic venomous snakes (*Bothriechis schlegelii*) and may be thus protected from predatory attack. *Imantodes cenchoa*, a nocturnal species with cryptic coloration, and *O. brevirostris* and *L. nebulosus*, diurnal species, exhibited scars, suggesting that cryptic color patterning is not as effective against predators. *S. argus* and *S. longifrenis* exhibited head enlargement, a behavior that presumably mimics the head shape of vipers (Greene, 1997) and thus may be protected by a combination of color pattern and behavior. The diurnal species (*O. brevirostris* [Table 4.1, 4.4] and *L. nebulosus* [Table 4.1]) did not show head enlargement (perhaps due to morphological constraints that have evolved in associated with narrowness of the head for crypsis, but did exhibit several behaviors typically associated with later stages of attack (cloacal discharge, body thrashing, striking and biting).

People who live near or in PNGDOTH provided data on the avian and mammalian fauna. By compiling lists of all known local species, I was able to survey the literature on diet and suggest potential predators on the ophidian community (Table 4.9 - 4.11). The most likely predators include certain birds, mammals, and other snakes. Birds are primarily visual predators, whereas many species of mammals and snakes feeding on other snakes likely utilize olfactory senses to find their prey. Different defensive behaviors presumably have evolved for protection from different predators. Crypsis (e.g., *Oxybelis* spp., *Leptophis* spp., Table 4.3) and mimicry (*Sibon argus, S. longifrenis, Urotheca euryzona, Oxyrhopus petolus*, etc.; Table 4.3) are likely used to protect snakes from visual predators. Other behaviors, such as biting, body thrashing, and cloacal discharge, can be employed against any predator, regardless of sensory modality.

Martins (1996) suggests that interspecific similarities in defensive behaviors are attributable to phylogeny or ecological similarity. Unfortunately, a robust phylogeny does not exist for the snakes of central Panama, and many relationships are still not well understood. Some predictions can be made in terms of the evolution of behaviors. Widely distributed behaviors, such as cloacal discharge, likely evolved in a common ancestor of the snakes evaluated during this study (Fig. 4.6). However, other behaviors, such as mimicry, hemipenal eversion, and biting and striking are limited to specific ophidian lineages, in some cases apparently having evolved more than once. Many closely related species reside in similar environments, and some behaviors may be more common under certain environmental conditions. For example, complex behaviors such as head and tail displays or body coiling likely can be performed only on the ground or on a broad branch, large leaf, or bromeliad.

Another limitation of this analysis is the lack of documented predator-prey encounters for most species. Such events are difficult to observe in the tropics, especially during a limited study period. Researchers in Costa Rica have used clay models to test for differences in predation rates on venomous and mimetic color patterns (e.g., Brodie, 1993; Brodie and Janzen, 1995). However, color patterns of many species of snakes are complex and not easily replicated with models. A new method utilizes printable fabric to make an exact replica of the snake's pattern (M. F. Westphal, pers. comm.). The fabric is wrapped around clay and placed in the natural environment. However, the fabric restricts access to the clay, and thus impressions from predators' claws, teeth, or bills are not clearly defined (M. F. Westphal, pers. comm.). Such models could be used in conjunction with motion-sensitive cameras that would take a picture of the event, allowing easier identification of the predator.

Much remains unknown about the interactions between snakes and their predators, but this study provides new data about the defensive behaviors of Neotropical snakes.

CHAPTER V

DEFENSIVE BEHAVIORS OF NEW WORLD MOLLUSK-EATING SNAKES

Mollusk-eating snakes are a polyphyletic group consisting of species believed to feed exclusively or primarily on molluscan prey (Dunn, 1951; Peters, 1960; Savitzky, 1983; but see Chapter 6). Molluscivory has evolved at least five times among colubrid snakes (Gruz, 2002), and representatives can be found in Asia (*Aplopeltura*, *Pareas*), Africa (*Duberia lutrix*), and the Americas (*Contia*, *Dipsas*, *Ninia*, *Sibon*, *Sibynomorphus*, *Storeria*, *Tomodon*, and *Tropidodipsas*), with the largest radiation in Central and South America (Peters, 1960; Gruz, 2002; Savage, 2002). There are similarities among many of the constituent taxa in morphology (Dunn, 1951; Peters, 1960; Savitzky, 1983; Greene, 1997), color pattern, and behavior (Cadle and Myers, 2003). Head enlargement caused by spreading the quadrate bones (Cadle and Myers, 2003), mimicry (Gallardo, 1972; Campbell and Lamar, 1989; Sazima, 1989, Cei, 1993, Greene, 1997; Leonard and Stebbins, 1999; Harvey and Muñoz, 2004; Solórzano, 2004) and various forms of body coiling (Ovaska and Engelstoft, 1999; Cadle and Myers, 2003, Mitchell, 2008) are commonly observed. However, no comprehensive study has evaluated the defensive behaviors of the New World mollusk-eating snakes. A review of the available data on defensive behaviors of New World mollusk-eating snakes, including *Tomodon* spp. and *Sibynomorphus* spp., which were not included in this study, is provided below.

Storeria.---Three species of *Storeria* are found in North America, two of which occur in the United States. The Brown Snake (*Storeria dekayi*) is a small colubrid that ranges from southern Canada to Mexico (Trapido, 1944). *S. dekayi* is viviparous, diurnal, and cryptozoic. Individuals are often found under logs or other cover objects (Willson and Dorcas, 2004; pers. obs.). Concealing coloration (Taylor, 1892) and locomotion away from the threat or toward a cover object are the defensive behaviors most commonly observed (Harwood, 1945).

The Redbelly Snake (*Storeria occipitomaculata*) is a small colubrid that ranges from North Dakota and Texas to Nova Scotia and south to Florida (Trapido, 1944). *S. occipitomaculata* is viviparous, diurnal, and fossorial (Blanchard, 1937; Willson and Dorcas, 2004). Individuals are often found under logs or other cover objects (Willson and Dorcas, 2004; pers. obs.).

The most common defensive behavior of *Storeria occipitomaculata* is locomotion. Flaring of the labials has been suggested to serve a defensive function (Gosner, 1942; Sousa do Amaral, 1999), although other authors suggest that this behavior is used primarily to aid in the removal mollusk or oligochaete mucous from the labials after feeding (de Queiroz, 1997; Cummingham and Burghardt, 1999). Death-feigning also has been documented for this species (Jordon, 1970).

Contia tenuis.---The Sharp-Tailed Snake (*Contia tenuis*) is native to northern California, Oregon, and Washington in the United States and British Columbia in Canada (Leonard and Ovaska, 1998). The northern populations are disjunct and individuals are uncommon there (Shaw and Campbell, 1974). In contrast, *C. tenuis* appears to be expanding its range in the south, through the Central Valley of California (G. Pauly, pers. comm.). Individuals can be found active in all months of the year, especially in the southern portion of the range, and occur at high elevations (2000 m), suggesting that they are relatively tolerant of cold conditions (individuals have been observed active at 10°C in February [Shaw and Campbell, 1974; Cunningham, 1962]). *C. tenuis* is a secretive snake typically found beneath logs. It also appears to be fairly common in human settlements, living under landscaping fabric, among mulched flowerbeds, or under anthropogenic cover objects (Shaw and Campbell, 1974; G. Pauly, pers. comm.).

Contia tenuis is a small (<400 mm) snake with a dark dorsum and contrasting black and white lines on the ventral scales (Cook, 1960; Shaw and Campbell, 1974; Leonard and Ovaska, 1998). A relatively sharp spine is present at the tip of the tail. *C. tenuis* lays 2-9 eggs in the summer, which hatch in the fall (Shaw and Campbell, 1974). *C. tenuis* has long, recurved teeth, which presumably aid in the consumption of slugs (Zweifel, 1954; Shaw and Campbell, 1974).

Reported defensive behaviors of *Contia tenuis* include locomotion, elevation of the anterior portion of the body, and coiling (Ovaska and Engelstoft, 1999). Body coiling, in association with the contrasting ventral coloration, may have evolved to mimic sympatric millipedes (Leonard and Stebbins, 1999). The function of the spine at the tip of the tail has not been determined (Cook, 1960), but may be involved in defense (Nussbaum et al., 1983; but see Carl, 1949, 1968; Darda, 1995 [locomotion], or Stebbins, 1972 [prey capture]). Predators of *C. tenuis* may include birds and Ringneck Snakes (*Diadophis punctatus;* [Shaw and Campbell, 1974; Leonard and Ovaska, 1998]).

Dipsas.---Approximately 30 species of "snail suckers" of the genus *Dipsas* are found in southern Mexico, Central America, and northern South America (Peters and Orejas-

Miranda, 1970; Solórzano, 2004). Species of *Dipsas* are presumed to be arboreal (Savage, 2002; Solórzano, 2004; but see Kofron [1982] for a contrary interpretation), and are nocturnal and oviparous. Clutch sizes range from 1-4 eggs (Hartmann et al., 2002; Savage, 2002; Pizzatto et al., 2008; pers. obs.). *Dipsas* in central Panama may include as many as three cryptic species (Cadle and Myers, 2003; Myers et al., 2007; R. Ibáñez, pers. comm.). For this study I treat the *Dipsas* encountered at my field sites, other than *D. nicholsi,* as one taxon, *Dipsas* sp.

A wide range of defensive tactics has been observed in this genus, including head flaring, body thrashing, and cloacal discharge (*Dipsas indica* and *D. pavonina* [Martins and Oliveira 1998]; *D. catesbyi* and *Dipsas* sp. [pers. obs.]). *D. pavonina* also smears cloacal discharge while wrapping its tail around the handler, then flattens its body dorsoventrally and hides its head among coils of the body (Martins and Oliveira 1998). *D. nicholsi* coils the body into a conical pyramid (Cadle and Myers, 2003; pers. obs.).

Sazima (1989) suggests that *Dipsas indica* mimics the sympatric pitviper *Bothrops jararaca* in color pattern and certain defensive behaviors (Greene, 1988; Sazima, 1988). Others suggest that some species of *Dipsas* mimic sympatric coral snakes (Kofron, 1982; Pough, 1988; Sazima, 1989).

Sibon.---The 12 or more species of "snail suckers" in the genus *Sibon* are small to medium-sized snakes that range from Mexico to the Amazon basin (Peters, 1960; Wallach, 1995; Savage, 2002; McCranie et al., 2003; Solórzano, 2004). Species are oviparous, nocturnal, and arboreal (Savage, 2002; Solórzano, 2004; Pizzatto et al., 2008).

Cadle and Myers (2003) note that *Sibon nebulatus*, a wide-ranging and relative large species, exhibits pyramidal body coiling similar to some species of *Dipsas*, and report that *S. nebulatus* does not bite. *S. argus* coils the body into a conical pyramid (Cadle and Myers, 2003). *S. argus* and *S. longifrenis* may mimic *Bothriechis schlegelii* in color pattern (Greene, 1997; Solórzano, 2004).

Ninia.---The nine species of Coffee Snakes (*Ninia*) are small, terrestrial or semi-fossorial colubrids that occur from Oaxaca, Mexico to northern South America (Peters and Oreja-Miranda, 1970; Savage, 2002; Solórzano, 2003). *Ninia* spp. are oviparous and diurnal (Dunn, 1935; Greene, 1975; Savage, 2002; Solórzano, 2004; Pizzatto et al., 2008).

Greene (1975) describes coral snake mimicry, head flaring, and elevation of the anterior body and tail as defensive strategies of *Ninia sebae*. *N. sebae* also displays dorsoventral compression of the body, as do *N. diademata*, *N. maculata*, and *N. psephota* (Dunn, 1935; Lee, 1996).

Tomodon.---The two or three species of Pampas Snakes (*Tomodon* spp.) are small to medium-sized South American snakes. *Tomodon ocellatus* flares its head, inflates the body, and coils the tail in defense, and *T. orestes* is suspected to act in the same manner (Harvey and Muñoz, 2004). *T. orestes* resembles the sympatric pitviper *Bothrops jonathani* in color pattern and some behaviors (Harvey and Muñoz, 2004), and researchers have noted the similarity in color pattern between *T. ocellatus* and *Bothrops* spp. (Gallardo, 1972; Campbell and Lamar, 1989; Cei, 1993).

Sibynomorphus.---The South American snakes of the genus *Sibynomorphus* consist of about 12 species of small to medium-sized snakes (Cadle, 2007; Pizzatto et al., 2008). Species are found in southwestern Ecuador and northern Peru and south of the Amazon Basin in Brazil through Argentina (Cadle, 2007). *Sibynomorphus* spp. are oviparous and primarily terrestrial (Pizzatto et al., 2008). Cadle and Myers (2003) report that *Sibynomorphus mikanii* raises and flattens the head, inflates the neck, and curls the tail into a flattened coil. The snake may continue to coil into "an irregular ball" or twisted coil, with the head inside or under the ball. *Sibynomorphus* spp. are not reported to strike or bite.

MATERIALS AND METHODS

Study species and sites.---This study focused on the defensive behaviors of putative mollusk-eating snakes, including the New World genera *Contia, Dipsas, Ninia, Sibon,* and *Storeria.* Individuals were studied in, or collected from, North, Central, and South America (Chapter I).

Documentation of defensive behaviors.---I studied 13 species from five genera of New World mollusk-eating snakes in the field or laboratory. Observations of defensive behaviors were made in the field upon first capturing a snake, following methods outlined in Chapter IV. Reactions to a tactile stimulus were noted according to Table 4.1. Recaptured individuals were retested.

Laboratory tests were performed in arenas that resembled the natural habitat of the snakes. The arenas used for *Contia tenuis*, *Storeria dekayi*, *S. occipitomaculata*, and *Ninia* were dressed with a mulch substrate and a log for cover, inside a rectangular plastic tub measuring 58 cm x 40 cm. The arena for *Dipsas* and *Sibon* was dressed with a substrate of leaves and a vertical branch, within a round plastic tub measuring 1 m in diameter. Snakes were given 30 seconds to acclimate and then were gently tapped with a small snake hook for 120 seconds, alternating between posterior and anterior regions of the body. Defensive behaviors were classified according to modifications made to the list of behaviors described by Greene (1988) (Table 4.1).

Presence or absence of each of 15 behaviors (Table 5.1) was documented for *Contia tenuis* in two trials. Comparisons were made between trials to test for a change in the presence of a given behavior.

Table 5.1. Description of morphological attributes and behaviors used in defense by *Contia tenuis*.

Behavior	Description
Immobile	freezes in place and does not move
Stiff	body becomes rigid
Locomotion – slow	locomotes slowly within the arena
Locomotion – fast	locomotes quickly within the arena
Locomotion to cover	moves rapidly toward cover
Locomotion over the edge	moves rapidly over the end of the microcosm
Elevate head	elevation of head and neck from substrate
Bury head in substrate	head is pushed into substrate
Bury body in substrate	body is pushed under substrate, typically following the head
Body thrash	violently thrashes unrestricted regions of body
Coil	coils the body into flat concentric circles
Lateral flip	flips to side when fleeing to expose ventral surface momentarily
Tail flip	tail is flipped to the side one time
Tail wag	tail is lifted and moved from side to side quickly
Cloacal discharge	releases urates and/or musk from cloaca

Phylogenetic basis of behaviors.---Defensive behaviors found in multiple species were compared to the phylogenetic tree constructed for the New World mollusk-eating snakes (Highton et al., 2002; Pinou et al., 2004; Fig. 5.1). I used MacClade (Version 4.08 OS X) to map selected defensive behaviors by importing the presence/absence of each behavior for each species and then adjusting the tree to match that I constructed. Selected defensive behaviors included: body coiling, body pyramiding, body thrashing, head enlargement, cloacal discharge, and hemipenal eversion.

Fig. 5.1. Phylogeny of New World mollusk-eating snakes evaluated in this study. Tree constructed from Highton et al., 2002 and Pinou et al., 2004.

RESULTS

Defensive behaviors.---Three temperate species (Table 5.2) and eight tropical species (Table 5.3) of mollusk-eating snakes were tested. The defensive behaviors of Dipsas catesbyi, Dipsas sp., Ninia sp., and Sibon annulatus were documented for the first time in this study. In other cases my observations elaborated upon previously published accounts (S. longifrenis and S. nebulatus). The defensive tactics of New World mollusk-eating snakes captured during this study are described below.

Table 5.2. Sample sizes of temperate mollusk-eating snakes included in defensive behavior trials. See Chapter I for descriptions of study sites.

	Site				
Species	**California**	**Kishwaukee**	**Lake Erie**	**Beaver Island**	**Total**
Contia tenuis	50	0	0	0	50
Storeria dekayi	0	20	95	0	115
Storeria occipitomaculata	0	20	0	10	30

Table 5.3. Sample sizes of Neotropical species of mollusk-eating snakes included in defensive behavior trials. ADM: Altos del Maria, PNGDOTH: Parque Nacional General de División Omar Torrijos Herrera, RA: Reserva Amazónica. See Chapter I for descriptions of study sites.

	Site			
Species	**ADM**	**PNGDOTH**	**RA**	**Total**
Dipsas catesbyi	0	0	2	2
Dipsas nicholsi	0	1	0	1
Dipsas sp.	0	95	0	95
Ninia celata	1	0	0	1
Ninia maculata	1	0	0	1
Ninia sp.	0	3	0	3
Sibon annulatus	14	64	0	78
Sibon argus	33	68	0	101
Sibon longifrenis	14	10	0	24
Sibon nebulatus	1	12	0	13

Contia tenuis.---Several accounts (see Leonard and Ovaska, 1998 for review) have documented defensive displays and have suggested the existence of other behaviors (e.g., use of the tail spine). In my study individuals performed a lateral flip, in which the snake quickly revealed part of the horizontally marked ventral surface. The tail spine was not used in any obvious defensive behavior. At times the tail was planted into the substrate of the arena, appearing to aid the snake in changing direction quickly or anchoring the snake as it flipped laterally.

During testing, one individual of *Contia tenuis* escaped to the floor near a golden retriever (*Canis familiaris*). The snake raised the anterior portion of its body off the ground (Fig. 5.2A) and maintained this position even after being moved away from the dog. This behavior was not observed in any snake without the presence of the dog (n = 50), and two other snakes placed in front of the dog did not assume the elevated posture. The same snake that reacted to the dog revealed its ventral surface (Fig. 5.2B) when placed on a table shortly afterward and gently tapped with a snake hook. The elevated posture has been reported previously (Collins, 2003), but the association of the behavior only with a large canid in this study suggests that this may be a high-intensity display.

Quantitative analyses of Contia tenuis.---I determined the frequency of each of 15 defensive behaviors for individual *Contia tenuis* tested during two trials (Table 5.4). Results of ANOVAs to test for differences between trials showed no significant differences ($P > 0.05$) for any behavior (Table 5.5).

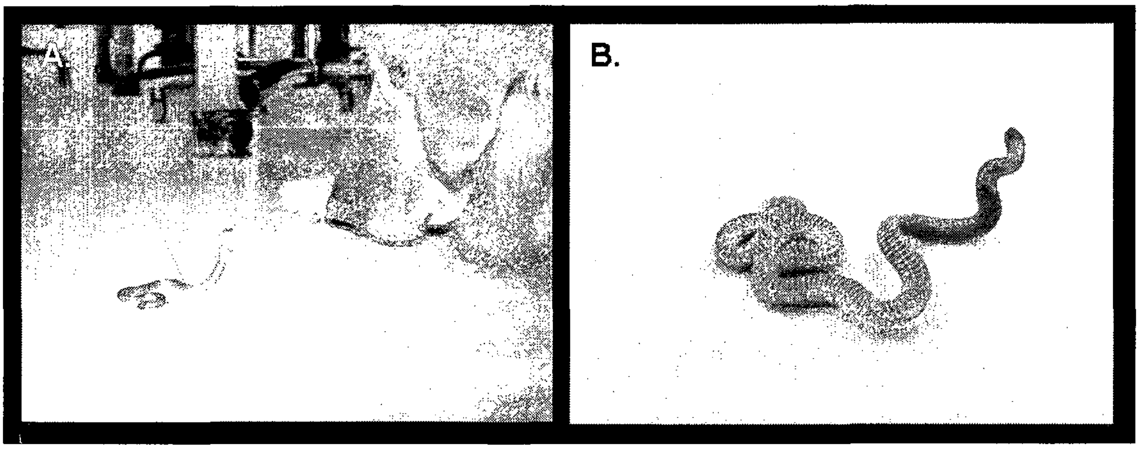

Fig. 5.2. Defensive behaviors of *Contia tenuis*. A) *C. tenuis* responding to a golden retriever by raising anterior portion of the body; the position was maintained for several minutes. B) *C. tenuis* placed so as to reveal its contrasting ventral pattern.

Table 5.4. Number of and percentage of *Contia tenuis* individuals performing each defensive behavior in two trials. Trial 1 (T1) consisted of 46 individuals. Trial 2 (T2) consisted of 25 individuals.

	Immobile	Stiff	Locomotion (slow)	Locomotion (fast)	Locomotion to cover	Locomotion to edge
T1	19	12	9	38	34	15
%	41.30	26.09	19.57	82.61	73.91	32.61
T2	10	4	3	19	17	7
%	40	16	12.00	76	68	28

Table 5.4. continued

	Elevate head	Bury head	Bury body	Body thrash	Coil
T 1	4	40	20	14	15
%	8.70	87.00	43.78	30.43	32.61
T2	3	23	10	7	7
%	10	92	40	28	28

Table 5.4. continued

	Lateral flip	Tail flip	Tail wag	Cloacal discharge
T 1	17	4	33	20
%	36.96	8.70	71.74	43.48
T2	9	2	17	12
%	36	8	70	50

Table 5.5: Results of ANOVA to test for differences in presence of each defensive behavior between Trial 1 and Trial 2 for *Contia tenuis*.

Defensive Behavior	F	P
Immobile	0.041	0.840
Stiff	0.780	0.380
Locomotion – slow	0.543	0.464
Locomotion - fast	0.120	0.730
Locomotion to cover	0.074	0.787
Locomotion over the edge	0.084	0.772
Elevate head	0.247	0.621
Bury head in substrate	0.337	0.563
Bury body in substrate	0.021	0.886
Body thrash	0.012	0.914
Coil	0.084	0.772
Lateral Flip	0.002	0.965
Tail flip	0.003	0.960
Tail wag	0.006	0.938
Cloacal discharge	0.264	0.609

Storeria occipitomaculata.---Body thrashing and cloacal discharge were observed. Snakes from the Kishwaukee River State Fish and Wildlife Area and Potawatoni Woods Forest Preserve (Illinois) did not flare their labials or death feign. Five snakes (50%) tested on Beaver Island (Michigan) did flare their labials, and a researcher working on the island reported that three individuals exhibited death-feigning after being captured and handled (M. Cross, pers. comm.).

Storeria dekayi.---Individuals of *Storeria dekayi* attempted locomotor escape and cloacal discharge.

Dipsas catesbyi.---Two individuals of *Dipsas catesbyi* exhibited body thrashing, head enlargement, and cloacal discharge. Neither individual showed signs of forming flat or pyramidal body coils, as have been observed in other species of *Dipsas* (Cadle and Myers, 2003).

***Dipsas* sp.**.---Individuals readily exhibited head enlargement resulting from flaring of the quadrate bones (Fig. 5.3), body thrashing, and cloacal discharge. I did not observe pyramiding or body coiling in any individual (n = 92).

Fig. 5.3. Head enlargement observed in *Dipsas* sp.

Additional observations (n = 13) were made of *Dipsas* sp. performing defensive behaviors in trees or on an artificial apparatus built to resemble a branch. Snakes launched themselves from the branch or artificial perch to the ground, flipping laterally as they landed, and then remained motionless.

Dipsas nicholsi.---One adult female *Dipsas nicholsi* was captured at PNGDOTH and represented the first capture of this rare species west of the Panama Canal (Myers et al., 2007). When gently prodded with a snake hook, the snake exhibited jerking movements, flinging the head and tail toward each other in reversing directions, often halting in one position before flipping in the opposite direction (Fig. 5.4). After 3-4 such jerking movements the snake formed a raised coil (Fig. 5.4) and eventually assumed a raised pyramidal posture as reported for the species by Cadle and Myers (2003). After three days the behavior was reduced in intensity and could not readily be elicited.

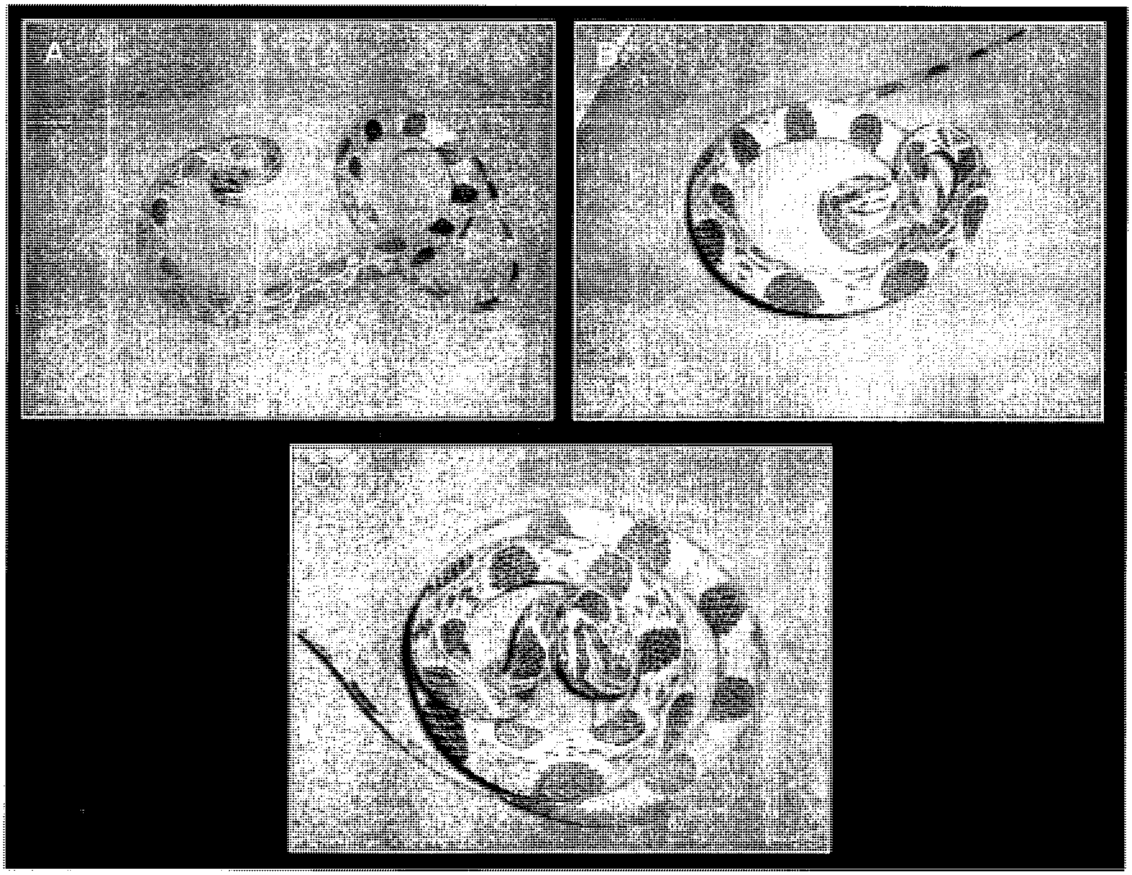

Fig. 5.4. Defensive behaviors of *Dipsas nicholsi*. A-B) Positions assumed by body between jerking movements. C) Snake beginning to form raised coil, with head in the center.

Sibon argus.---Individuals of *Sibon argus* collected during this study performed the characteristic coiling behavior described by Cadle and Myers (2003) (Fig. 5.5). *S. argus* exhibited a similar escape response to that of *Dipsas* sp. when tested in an arboreal location: snakes launched themselves to the ground, although they did not flip laterally as they landed. When *S. argus* remained motionless on the ground in the wild, it was difficult to distinguish the cryptically-colored snake against the substrate; one individual was lost after it dropped from a branch.

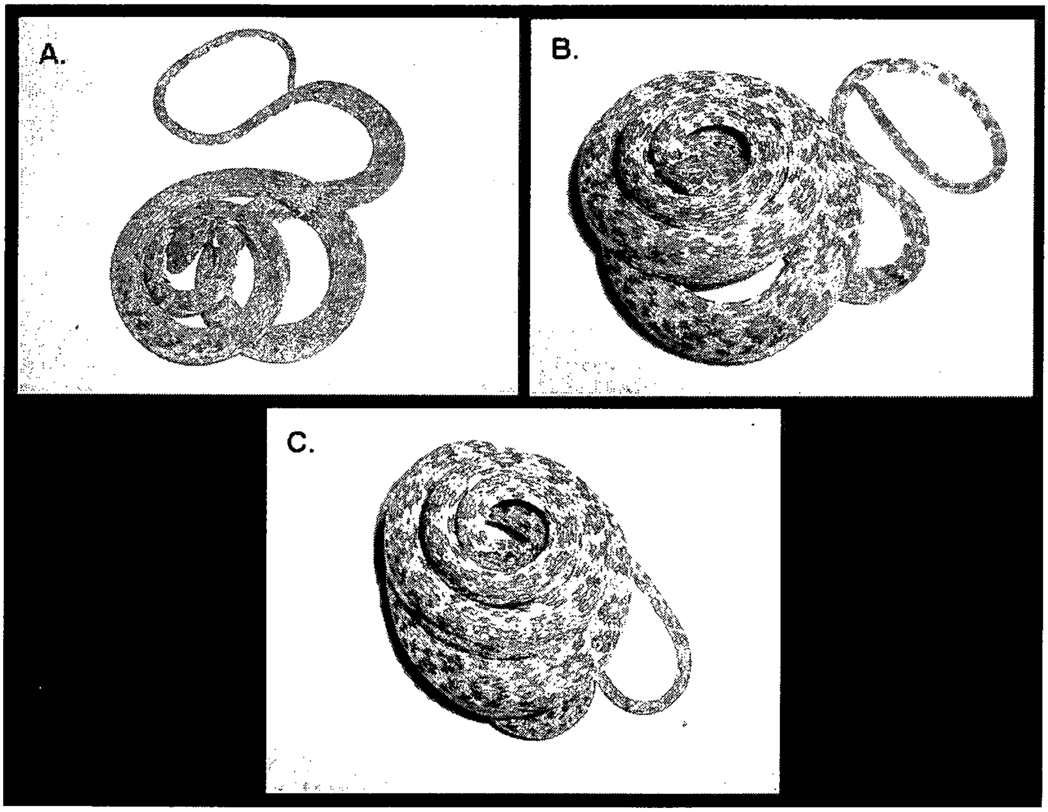

Fig. 5.5. Body coiling behavior of *S. argus*. Note that the head is tucked inside of the coils.

Sibon longifrenis.---Despite its morphological similarity to *Sibon argus* (Savage and McDiarmid, 1992), *S. longifrenis* did not coil the body when threatened (n = 24), as did

S. argus (Cadle and Myers, 2003; pers. obs.). *S. longifrenis* exhibited locomotor escape, body thrashing, and cloacal discharge.

Sibon nebulatus.---The defensive tactics observed for *Sibon nebulatus* (n = 12) were similar to those observed during previous studies (Cadle and Myers, 2003). Individuals exhibited jerky movements (Fig. 5.6A-C) and assumed the posture of an elevated pyramid (Cadle and Myers, 2003; Fig. 5.6D). When coiled, the head either was tucked inside of the body coils (Fig. 5.6D) or rested on top of the coils (Cadle and Myers, 2003). Furthermore, two individuals bit me during handling, contrary to the experience of Cadle and Myers (2003).

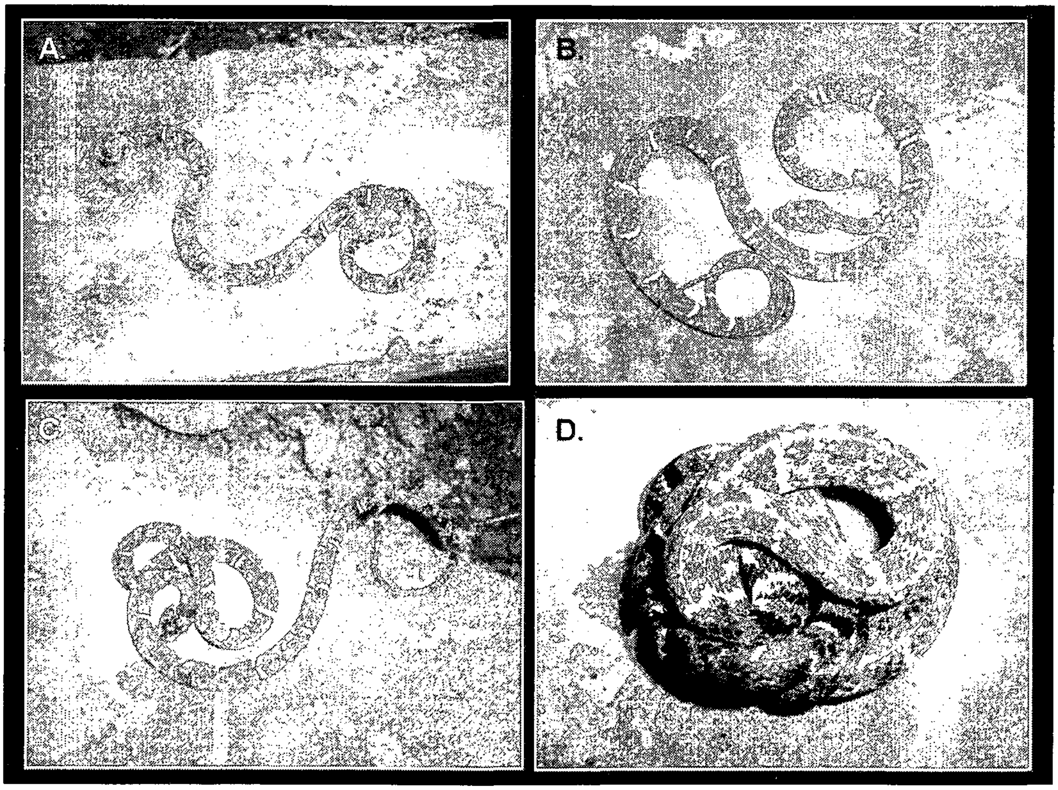

Fig. 5.6. Defensive behaviors performed by *Sibon nebulatus* while forming a raised pyramid. A-C) Jerky movements displayed as snake flipped in various directions. D) Raised pyramid with head tucked inside coil.

Sibon annulatus.---*Sibon annulatus* exhibited locomotor escape, body thrashing, and cloacal discharge as defensive behaviors. *S. annulatus* never attempted to strike or bite (n = 78).

***Ninia* sp.**.---All three individuals of an undescribed species of *Ninia* (R. Ibáñez, pers. comm.) exhibited locomotor escape and body thrashing. One individual conspicuously enlarged its head laterally (Fig. 5.7A), then elevated the anterior portion of the body and conducted a series of false strikes, with no attempt to open the mouth or bite (Fig. 5.7B-C).

Ninia celata.---*Ninia celata* (n = 1) attempted locomotor escape before exhibiting body thrashing, head enlargement, and cloacal discharge. When placed on the ground, the snake attempted to bury its head in the substrate.

Ninia maculata.---*Ninia maculata* (n = 1) attempted locomotor escape and then exhibited body thrashing, head enlargement, and cloacal discharge. When placed on the ground, the snake attempted to bury its head in the substrate.

Phylogenetic basis of behaviors.---The presence or absence of each of six defensive behaviors was mapped on a cladogram for 13 species of mollusk-eating snakes (Fig. 5.8 – 5.13).

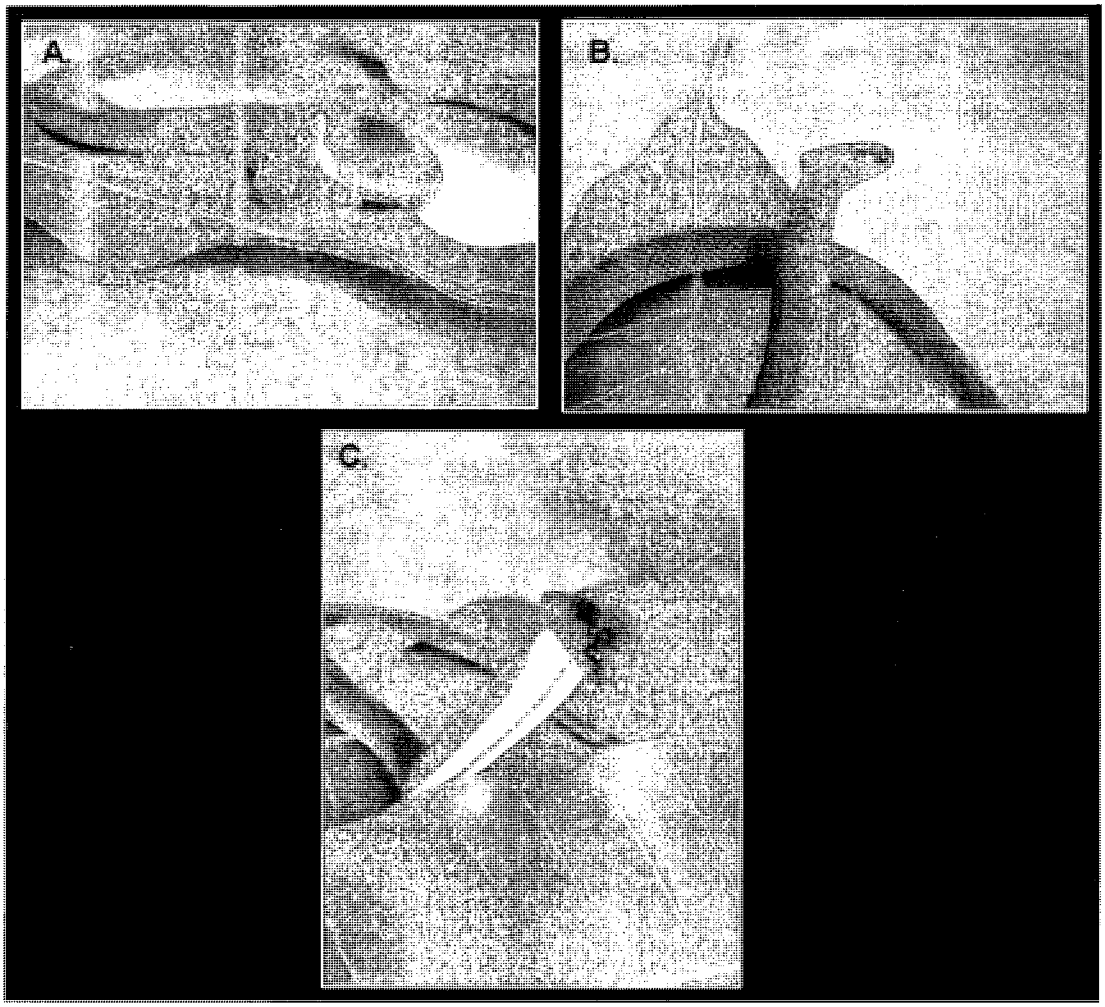

Fig. 5.7. Defensive display of *Ninia* sp. A-B) showing head enlargement and dorso-ventral body compression. c) The flattened anterior elevated, revealing a series of small ventral triangles of pigmentation.

DISCUSSION

The assemblage of mollusk-eating snakes evaluated in this study was examined because members were believed to consume primarily or exclusively mollusks and therefore might be expected to share other aspects of their ecology and behavior. However, several recent accounts have found that some of these species have broader diets (Ryan and Lips, 2004; Montgomery et al., 2007; Ray et al, in review), suggesting

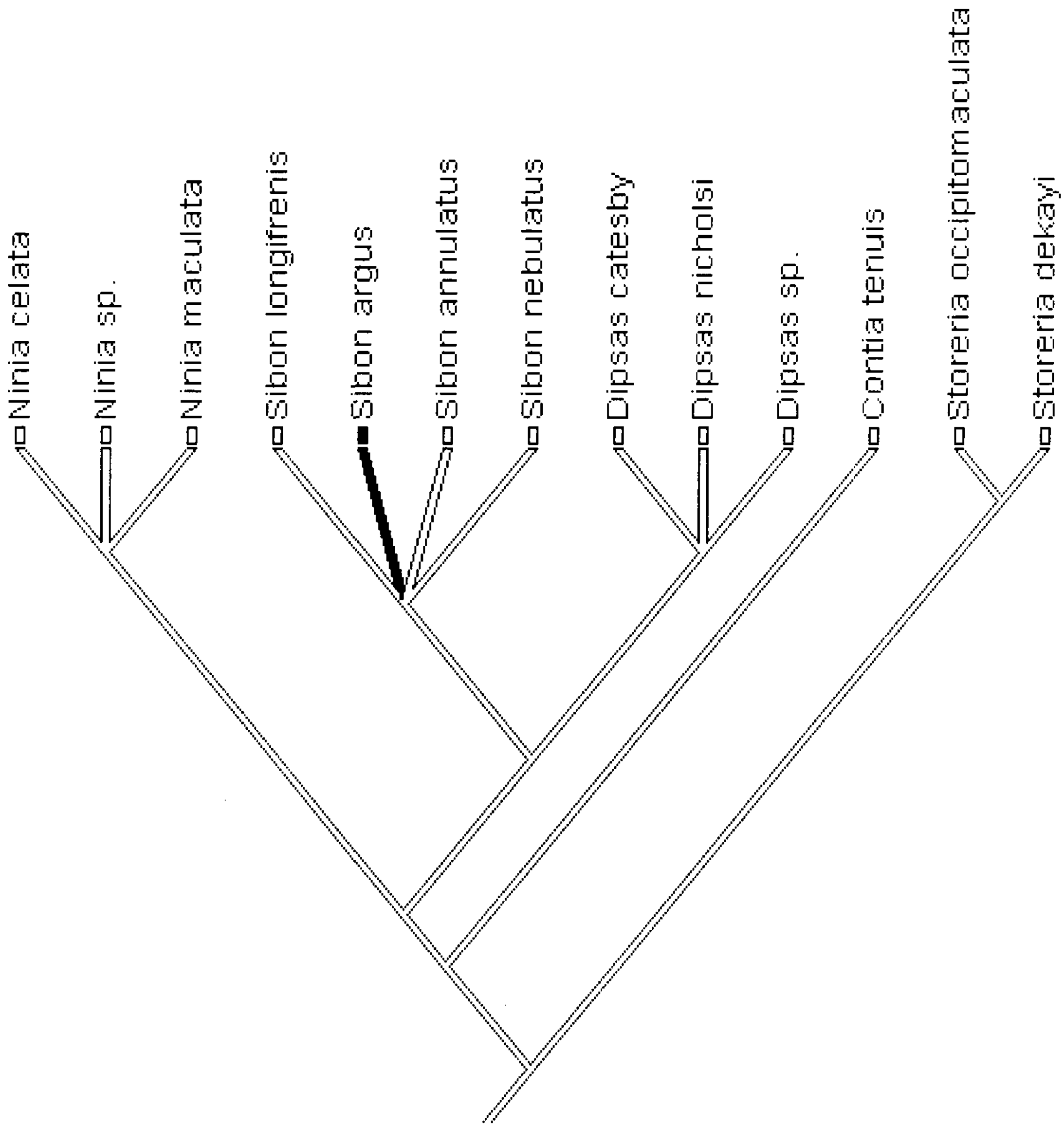

Fig. 5.8. Cladogram showing presence of body coiling among mollusk-eating snakes evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

Fig. 5.9. Cladogram showing presence of body pyramiding among mollusk-eating snakes evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

Fig. 5.10. Cladogram showing presence of body thrashing among mollusk-eating snakes evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

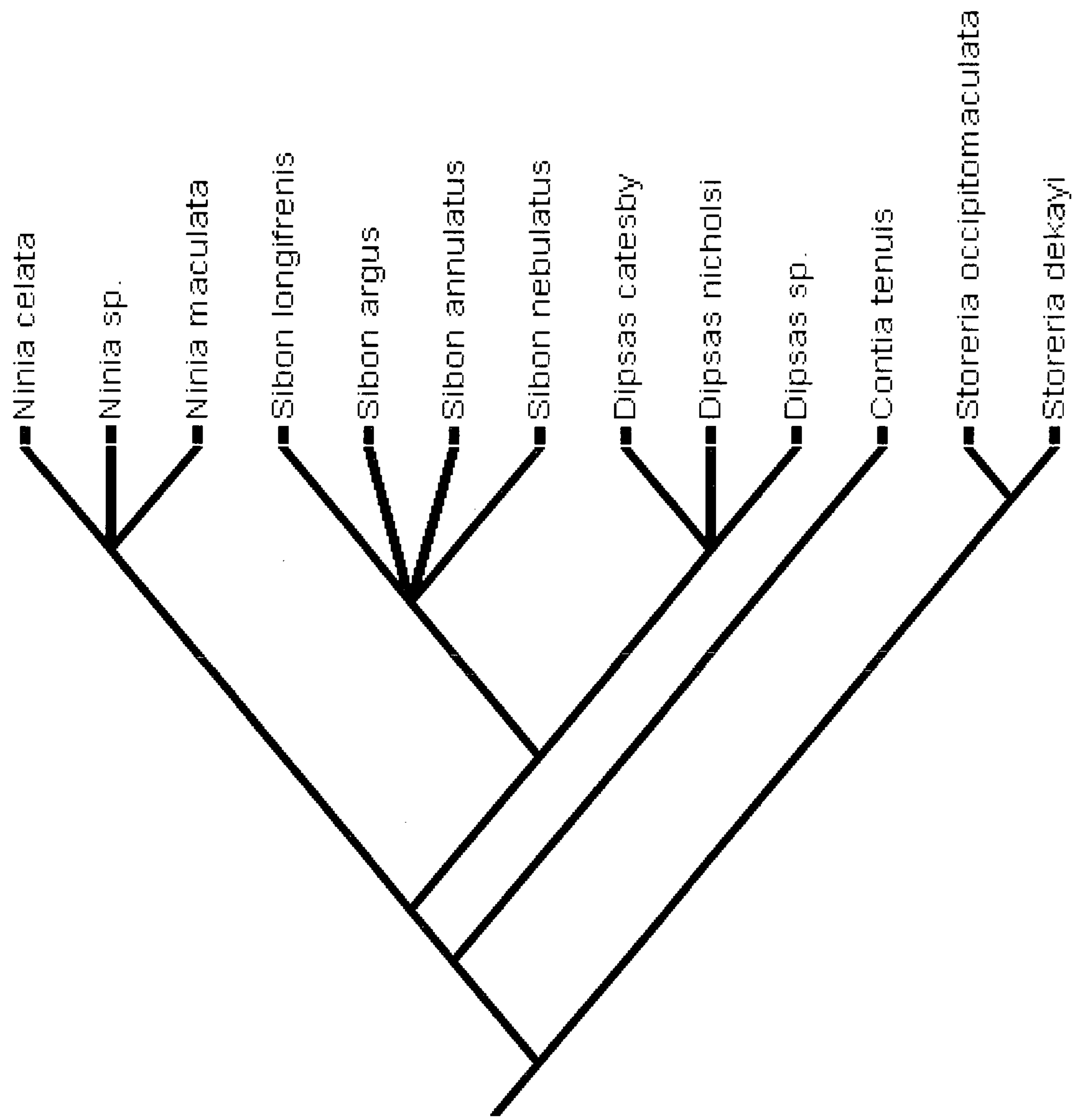

Fig. 5.11. Cladogram showing presence of cloacal discharge among mollusk-eating snakes evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

Fig. 5.12. Cladogram showing presence of head enlargement among mollusk-eating snakes evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

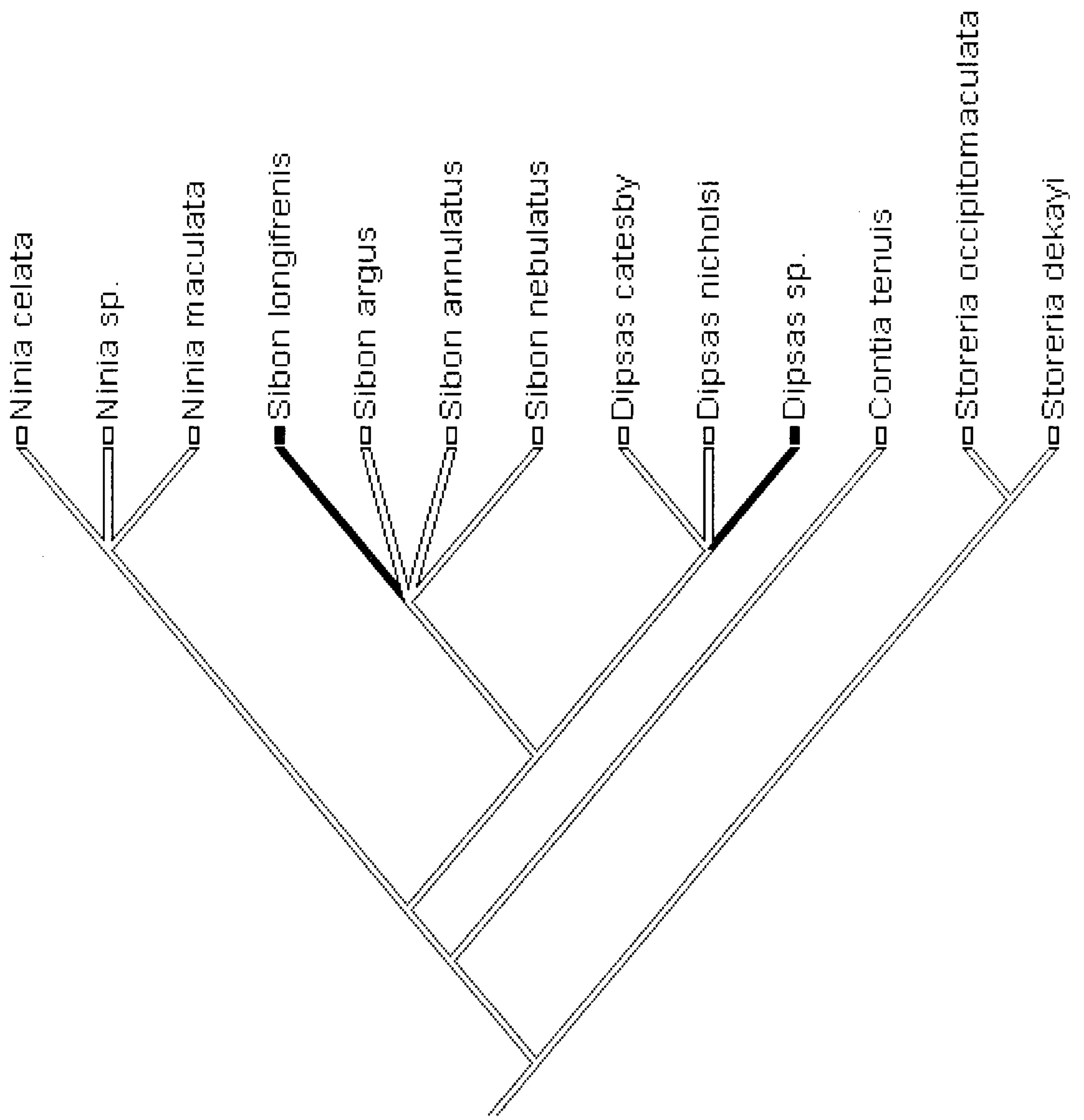

Fig. 5.13. Cladogram showing presence of hemipenial eversion among mollusk-eating snakes evaluated during this study. Black represents the presence of the behavior and white represents absence of the behavior.

that the group may be less distinctive in regard to prey than previously believed. Nonetheless, some defensive behaviors (e.g., head flaring, coiling the body into a raised pyramid) are observed among several taxa in this assemblage, and the raised pyramidal posture has been documented only among Dipsadini. Some other snakes coil their body (Greene, 1988), but do not form a tight, raised pyramid as observed in several of the New World mollusk-eaters (Cadle and Myers, 2003; pers. obs.). Under laboratory conditions pyramiding was performed when the snake was on a flat, broad surface, suggesting that these arboreal species spend time on the ground, are regularly displaced to the ground during predatory events, or perform such displays on large branches, leaves, or epiphytes that provide a stable platform for such a display. Further investigations are needed to understand how these species defend themselves above the forest floor or to document their regular presence on the ground.

Dendrograms were made for each of six behaviors for the 13 species of mollusk-eating snakes included in the study. Cloacal discharge was documented for all species and likely evolved in a distant common ancestor (Fig. 5.11). Other behaviors were found only in some species. Body thrashing likely evolved in a relatively distant common ancestor and subsequently was lost in the *Storeria* (Fig. 5.10). Head enlargement was not observed in either *Storeria* or in *Contia*, so presumably it evolved after the Dipsadini diverged from the later taxa (Fig. 5.12). The behavior may subsequently have been lost in *Sibon annulatus* (Fig. 5.12). Body coiling (Fig. 5.8) likely evolved in *S. argus*, and body pyramiding likely evolved in *S. nebulatus* and *Dipsas* sp. (it also has been reported in species of *Dipsas* that were not included in this analysis) (Fig. 5.9). Finally, hemipenial eversion likely evolved independently in *S. longifrenis* and *Dipsas* sp. (Fig. 5.13). It is interesting that this behavior was not observed in *S. argus*, a species that is morphologically very similar to *S. longifrenis* (Savage and McDiarmid), although the species seem to differ behaviorial (i.e. *S. argus* exhibited body coiling, which was not observed in *S. longifrenis*).

In considering the phylogenetic analyses, it is important to note that a behavior simply may not have been observed. For example, head enlargement appears to have been lost in *Sibon annulatus*, but perhaps it simply was not exhibited by any individuals tested during this study. This criticism is supported by the quantitative data collected for *Contia tenuis*. Although defensive behaviors did not different in frequency between Trial 1 and Trial 2 (Table 5.4), even the most common behaviors were not always exhibited during those tests (Table 5.5). In an effort to comprehensively document the defensive behaviors, continued research should increase sample sizes and allow a greater chance that rare behaviors will be observed.

Several species of mollusk-eating snakes have been suggested to mimic sympatric venomous species (Solórzano, 2004; Table 4.1). For example, Greene (1997) suggests that *Sibon argus* and *S. longifrenis* mimic *Bothriechis schlegelii* (see also Solórzano, 2002, 2004). However, *B. schlegelii* is highly variable in color pattern, ranging from mottled red and green (with either of the two colors being dominant in an individual) to solid golden yellow (Solórzano, 2004). *B. schlegelii* is relatively slow-moving, but will strike when disturbed (pers. obs.), whereas *S. argus* and *S. longifrenis* do not attempt to strike or bite. *S. argus* readily forms a flat or raised coil with the body (Fig. 5.5), a behavior never observed in *B. schlegelii*; *S. longifrenis* was not observed to exhibit body coiling.

Sazima (1989) suggested that *Dipsas indica* may mimic *Bothrops jaracaca*. The two species have similar color patterns and perform some of the same behaviors, including head flaring, S-coiling, and false striking (Sazima, 1989; Chapter IV). However, in general, vipers are not considered to be closely mimicked by these taxa (Pough, 1988). It is unlikely that *Dipsas* sp. in Panama is mimicking any species of sympatric viper. I documented four species of vipers in PNGDOTH during my study: *Atropoides nummifer, Bothriechis schlegelii*, *Bothrops asper*, and *Lachesis stenophrys*; all are terrestrial except *B. schlegelii* (Solórzano, 2004). The mottled pattern of *B. schlegelii* (Solórzano, 2004) does not resemble the banded pattern of *Dipsas* sp. (Fig. 5.3).

Some species of *Dipsas* may mimic *Micrurus* (Kofron, 1982; Pough, 1988; Sazima, 1989). Defensive behaviors of many *Micrurus* species include rapid locomotion and a head-tail confusion display (Greene, 1988). However, *Dipsas* sp. is nocturnal and arboreal (pers. obs.), whereas *Micrurus* spp. are diurnal or crepuscular and terrestrial or semi-fossorial (Solórzano, 2004). Three species of coral snakes have been reported at PNGDOTH, including *Micrurus multifasciatus, M. nigrocinctus,* and *M. mipartitus*. Although *Dipsas* sp. is bicolored, it is unlikely that it mimics the black and red, orange, or white *M. mipartitus*. Alternatively, the brown and black color pattern of *Dipsas* sp. may be cryptic against the leaf litter of the secondary forest where they regularly occur.

Mollusk-eating snakes may use mimicry or crypsis as an initial, passive defense, and employ more active defensive behaviors if a predator continues to attack. Currently, data on the natural predators of mollusk-eating snakes are limited, and accounts of predation on them have rarely been reported. Maitland (2003) reported predation on a

Sibon nebulatus by a large crab. Similar crabs are found at my study sites (M. Whiles, pers. comm.; pers. obs.).

Ophiophagus snakes, including *Micrurus* spp., *Clelia clelia*, and *Erythrolampus mimus* (Table 4.8), probably constitute a major source of predation on molluscivorous snakes, among other taxa. *Ninia* spp., which are found in the leaf litter, may be prey for these terrestrial ophiophagus snakes. Owls and other nocturnal birds (Table 4.6) may consume the nocturnal *Dipsas* or *Sibon* species, whereas diurnal birds may feed upon the diurnal species of mollusk-eating snakes or on nocturnal species that are found sleeping. Finally, mammals such as opossums and kinkajous (Table 4.7) may prey upon the nocturnal species or sleeping diurnal snakes.

This study provides additional data on the defensive tactics of Neotropical mollusk-eating snakes. Clearly, more data are needed to understand the patterns of defensive behaviors among these snakes and, in possible cases of mimicry, between the mollusk-eating snakes and their potential models. A more complete analysis of the defensive behaviors of mollusk-eating snakes, preferably including the independently evolved taxa in the Old World, is needed to examine further whether similarities in diet are reflected in independently evolved defensive behaviors. Furthermore, complete behavioral repertoires of such species in both arboreal and terrestrial situations are needed in order to understand how defensive behaviors differ when performed in various locations. Finally, a better understanding of the natural predators of mollusk-eating snakes is needed to understand the conditions under which certain behaviors may be utilized.

CHAPTER VI

DIET OF THE NEOTROPICAL SNAKE GENERA *DIPSAS* AND *SIBON*

The natural history of many tropical snakes remains understudied (Martins 1996), despite recent publications on Neotropical herpetofaunas (e.g., Lee, 2000; Savage, 2002; Campbell and Lamar, 2004; Duellman, 2005). Diet of tropical snakes is often generalized across genera or larger lineages based on stomach contents or fecal samples from modest numbers of museum specimens or live, wild-caught individuals (e.g., Sazima, 1989; Solórzano, 2004). The extensively kinetic skulls of snakes have been modified in response to prey specialization and prey is diverse among the group (Greene, 1997; Cundall and Greene, 2000). For species that consume soft-bodied prey (worms, slugs, snails, etc.), rapid and complete digestion makes diet evaluation difficult (Kofron, 1982; MacCulloch and Lathrop, 2004). Morphological adaptations, such as skull modification, for the consumption of terrestrial snails and slugs have evolved at least five times, with varying degrees of specialization (Gruz, 2002). Snakes exhibiting these modifications reside in Africa, Asia, North America, and Central and South America (Gruz, 2002). The radiation of molluscan specialists is greatest in South and Central America and includes the Dipsadini. This tribe of Dipsadinae includes four genera of putatively mollusk-eating snakes, *Dipsas, Sibon, Sibynomorphus*, and *Tropidodipsas* (Peters, 1960; Cadle, 2007). The Dipsadini are united by synapomorphies of the skull and cephalic musculature that presumably enable them to consume molluscan prey (Dunn, 1951; Savitzky, 1983), with gastropods regarded as the "nearly sole constituent of [their] diet" (Cadle, 2007; Cadle and Greene, 1993, Wallach, 1995).

Consuming molluscan prey poses many challenges, especially since many dipsadins are arboreal, and most remove soft parts from the snail shell before consumption. The consumption of slugs by limbless snakes is complicated by the prey's dynamic body structure (Sazima, 1989; pers. obs.), production of copious mucous and in some species the possession of defensive toxins (Schroeder et al., 1999). Defensive diterpene toxins have been documented in the eggs of one species of slug (Schroeder et al., 1999), and unspecified toxins reportedly are present in the slime of slugs and snails (Gordon, 1994). Consumption of toxin-possessing mollusks has been confirmed in a temperate snake, *Contia tenuis* (Shaw and Campbell, 1974; G. Pauly, pers. comm.). Finally, slugs are low-energy prey items, containing only 25% of the mass-specific energy content of mice (Arnold, 1993). Given the effort required to extract a mollusk from its shell and ingest the soft parts (Sazima, 1989; Rossman and Myer, 1990), snails (but not necessarily slugs) may be a relatively unprofitable food source (Arnold, 1993).

Ophidian adaptations for the consumption of mollusks.---Snakes of the genus *Dipsas* and, to a lesser degree, *Sibon* are morphologically specialized to feed on terrestrial mollusks (Sousa do Amaral, 1999, 1999, Dunn, 1951; Peters, 1960; Savitzky, 1983; Savage, 2002). Specialized dentition and highly kinetic skulls facilitate the extraction and handling of mollusks (Dunn, 1951; Peters, 1960; Cundall and Greene, 2000; Gruz, 2002; Savage, 2002). Highly specialized mollusk-eating snakes, including members of Dipsadini and Pareatinae (Cundall and Greene, 2000), employ mandibular transport of prey, in which the left and right lower mandible move independently to aid feeding. Mandibular transport is a tactic limited to these molluscivore snakes and the scolecophidian Leptotyphlopidae (Kley, 2001). Furthermore, Hoso et al. (2007) note that in the Asian snail specialists *Pareas* the number of teeth differs between the right and left mandibles. More teeth on the right mandible facilitate consumption of dextral shells but reduce the ability to feed on snails with sinistral shells. Such morphological differences have not yet been explored for Neotropical snail-eaters.

Peters (1960) describes five adaptations of the skull and musculature of the Dipsadini, the largest group of mollusk-eating snakes. Modifications include (1) an inwardly tilted maxilla, (2) a pterygoid that is free posteriorly and lacking an articulation with the quadrate, (3) reduction in pterygoic tooth number, (4) a prominent intra-mandibular hinge, and (5) changes in cephalic musculature (Kofron, 1982). Savitzky (1983) elaborates on the specialization of the cranial morphology for the ingestion of molluscan prey.

Another possible adaptation involves secretions from various glands, as reported for the dipsadin *Sibynomorphus mikani* (Da Graca Salomão and Laporta-Ferreira, 1994). Such secretions may reduce the production of mucus and/or the mobility of the prey. Application of glandular extract to the surface of a slug yielded the same results as injection, indicating that specialized teeth are not necessary to deliver the glandular compounds (Da Graca Salomão and Laporta-Ferreira, 1994). Further research is required to determine how widespread such compounds are between Dipsadini and other molluscivores.

Different species of snakes may employ alternative means of removing molluscan mucous from their labial scales after feeding (Cummingham and Burghardt, 1999). *Dipsas variegata* (Mertens, 1952) and *D. indica* (Sazima, 1989) rub their mouths on the substrate after swallowing a mollusk. *Storeria occipitomaculata* and *Thamnophis* spp. may avoid the accumulation of slime near the mouth by flaring the labials during ingestion (De Queiroz, 1997; Sousa do Amaral, 1999).

Members of the Dipsadini provide an excellent example of the generalization of diet across taxa, with all members referred to as "mollusk-eaters" (Peters, 1960) or "snail-suckers" (Solórzano, 2004) because ingestion of other soft-bodied prey items has been documented for *Sibon* and *Dipsas*. To date non-molluscan prey items have not been reported for *Sibynomorphus* or *Tropidodipsas*.

Review of Dipsas and Sibon diet.---The Neotropical genus *Dipsas* ranges from Mexico to central South America. *Dipsas* species are highly specialized morphologically for feeding on terrestrial mollusks (Dunn, 1951; Peters, 1960). *D. albifrons* and *D. variegata* have been observed to feed on snails (Lankes, 1930 in Mertens, 1952; Rembold, 1934; Mertens, 1952), and *D. indica* feeds on snails and slugs (Sazima, 1989). Such observations support the proposition that members of the genus *Dipsas* feed exclusively on mollusks, although individual species may specialize on specific molluscan prey (Dunn, 1951; Queiroz-Alves et al., 2003). No comprehensive study has contradicted the widely held assumption that *Dipsas* exhibits a mollusk-dominated diet (but see Kofron, 1982). Brief notes have reported non-molluscan prey in the stomachs of *Dipsas* spp., including wood roaches (Peters, 1960), unspecified insects (Beebe, 1946; Cunha and Nacimento, 1978), a lizard's foot (Martins, 1999), and an earthworm (Cisneros-Heredia, 2005). However, such occurrences were attributed to incidental ingestion while foraging in bromeliads or other forest habitats (Peters, 1960; Cisneros-Heredia, 2005).

Sibon spp. are distributed from southern Central America to northern South America (Solórzano, 2004). Bulbous heads and modified skulls with features similar to those of *Dipsas* suggest that *Sibon* spp. are specialized for feeding on mollusks as well (Dunn, 1951; Savitzky, 1983). Few accounts document the diet of *Sibon* spp., and most general faunistic studies cite slugs or snails as prey (e.g., Savage, 2002; Solórzano, 2004). Kofron (1987) found remains of slugs in the stomach of *S. anthracops*. In addition to slugs and snails, Solórzano (2002; 2004) mentioned that a juvenile *S. argus* consumed unidentified centrolenid frog eggs and a *S. longifrenis* may have consumed an earthworm in captivity. Predation by various species of *Sibon* on centrolenid eggs have also been reported from Central Panama. *S. argus* consumes *Centrolene prosoblepon* (Ryan and Lips, 2004) and *C. ilex* (pers. obs.) and *S. longifrenis* consume *Cochranella albomaculata* eggs (Montgomery et al., 2007). Furthermore, Ryan and Lips (2004) suggest that *S. nebulatus* may feed on eggs of *Agalychnis callidryas*, and Ray et al. (in review) confirmed that eggs of *A. callidryas* are eaten by *S. argus*.

In light of recent observations that some species of putatively molluscivorous snakes feed on amphibian eggs, and given the rapid loss of amphibians from within the range of these snakes, it is important to understand diet of mollusk-eating snakes. Therefore, I studied the diets of all dipsadin snakes at a site in central Panama where amphibian declines have been ongoing for several years.

MATERIALS AND METHODS

At least six species of Dipsadini have been documented in central Panama, including four species of *Sibon* (*S. annulatus, S. argus, S. longifrenis, and S. nebulatus*) and at least two species of *Dipsas*. *D. nicholsi* is rare throughout its range (Myers et al., 2007), whereas the other *Dipsas* residing in Parque Nacional General de División Omar Torrijos Herrera (PNGDOTH) may comprise as many as three morphologically cryptic species (Cadle and Myers, 2003; Myers et al., 2007; R. Ibáñez, pers. comm.). For this study I treat the species of *Dipsas* encountered at my field site, other than *D. nicholsi*, as one taxon, *Dipsas* sp. Furthermore, *S. argus* and *S. longifrenis* were not consistently distinguished from one another. Their independent recognition has been debated (Peters, 1960, Savage and McDiarmid, 1992), although they are currently considered valid species. For some analyses, individuals of these two species were combined (referred to as "*S. argus/longifrenis*" below).

I analyzed fecal samples to facilitate non-lethal sampling of individuals across seasons. Although soft-bodied prey is difficult to identify (Kofron, 1982), chitinous structures (e.g., oligochaete chaetae, molluscan radulae and shells) are not digested. Fecal samples were collected from *Dipsas* and *Sibon* from 20 May – 23 October 2005, 12-13 May 2006, and 06 September 2006 – 20 August 2007 at PNGDOTH (Chapter I).

In addition to the study conducted in PNGDOTH, fecal samples were collected between 06 May and 10 July 2006 from Altos del Maria (ADM; Chapter I). Snakes were collected along riparian and terrestrial distance-constrained transects prior to significant chytridiomycosis-induced amphibian decline (first dead frog found on 22 May 2007; pers. obs.).

Upon capture of each snake, I recorded the time, location, and habitat data (including height and distance to stream; Chapter I). All snakes were transported to the field house (7.5-10 km away), where I recorded snout-vent length (SVL) and tail length to the nearest 0.1 cm using a squeeze box (Quinn and Jones, 1974); mass was recorded to the nearest 0.1 g with an electronic balance. I also recorded sex and reproductive condition (presence of enlarged follicles or eggs in females), and individually marked snakes using scale clips (Brown and Parker, 1976) or PIT tags (Gibbons and Andrews, 2004). Fecal samples were collected by gently squeezing the snake just anterior to the cloaca to extract feces. All snakes were returned to the exact location of capture within 48 hours.

Fecal samples were examined using a dissecting microscope (Wild M3 or M8) for any undigested hard structures (e.g., bones, shells, radulae). Such structures were further examined using a compound or scanning electron microscope and were identified to the lowest taxonomic level by colleagues at the Old Dominion University Benthic Ecology Laboratory or myself. Fecal samples not containing any hard structures are included as samples with "no identifiable prey".

In May 2006 surveys of available prey were performed along one forest transect (Rocky Road; Chapter I) where *Dipsas* spp., *Sibon annulatus*, and *S. nebulatus* were regularly found and one riparian transect (Silenciosa; Chapter I) where *S. argus* and *S. longifrenis* were regularly found. Surveys involved searching bromeliads for mollusks, oligochaetes, and other soft-bodied prey along both transects. Leaves were surveyed along the riparian transect for the presence of amphibian eggs. Potential prey items were noted to lowest possible taxonomic level.

Statistics.---Statistics were performed with SPSS 13.0 and α was maintained at 0.05 for all analyses (Zar, 1999). Logistic regression was used to test for differences in the presence of chaetae seasonally and intraspecifically (between size classes). A χ^2 test was used to determine interspecific differences in dietary components recovered from fecal samples (oligochaetes, mollusks, and amphibian eggs) among *Sibon annulatus*, *S. argus/longifrenis*, and *S. nebulatus*.

An analysis of covariance (ANCOVA) was used to test for differences in body condition between *Sibon argus/longifrenis* captured along stream or forest transects where frogs had declined and those captured at the Pond, where the leaf-breeding hylid *Agalychnis callidryas* persisted and continued to breed. The dependent variable was mass, the covariate was SVL, and the fixed factor was location. For ANCOVA, all captures from 2005-2007 were included. Females and males were analyzed separately because of sexual dimorphism.

RESULTS

Dipsas sp. was found primarily in the mature secondary forest (n = 123 captures; 78.9%) and occasionally in vegetation along stream transects (n = 26 captures; 21.1%). *Sibon annulatus* and *S. nebulatus* were found primarily in mature secondary forest and occasionally along streams. *S. argus* and *S. longifrenis* were found primarily along streams or at a small pond (Chapter I).

A total of 59 fecal samples were collected for *Dipsas* sp., with at least one sample (mean = 3.28, range: 1-7) from each month of the sampling period, except June 2007. Molluscan parts (two small snail shells, Helicoidea) were recovered from one (1.7%) of the samples. Nine samples (15.3%) yielded no identifiable prey. The remaining 49 of 59 samples (83.1%) contained chaetae that were identified as belonging to oligochaetes of the family Lumbriculidae (H. K. Mahon and A. Rodi, pers. comm.; Fig. 6.1). The chitinous bristles, which pass through the digestive tract of a snake without damage, allow worms to grip the substrate, presumably aiding in locomotion (Roembke and Schmidt, 1990). Ten individual chaetae were measured from digital photographs and had a mean length of 860 μm.

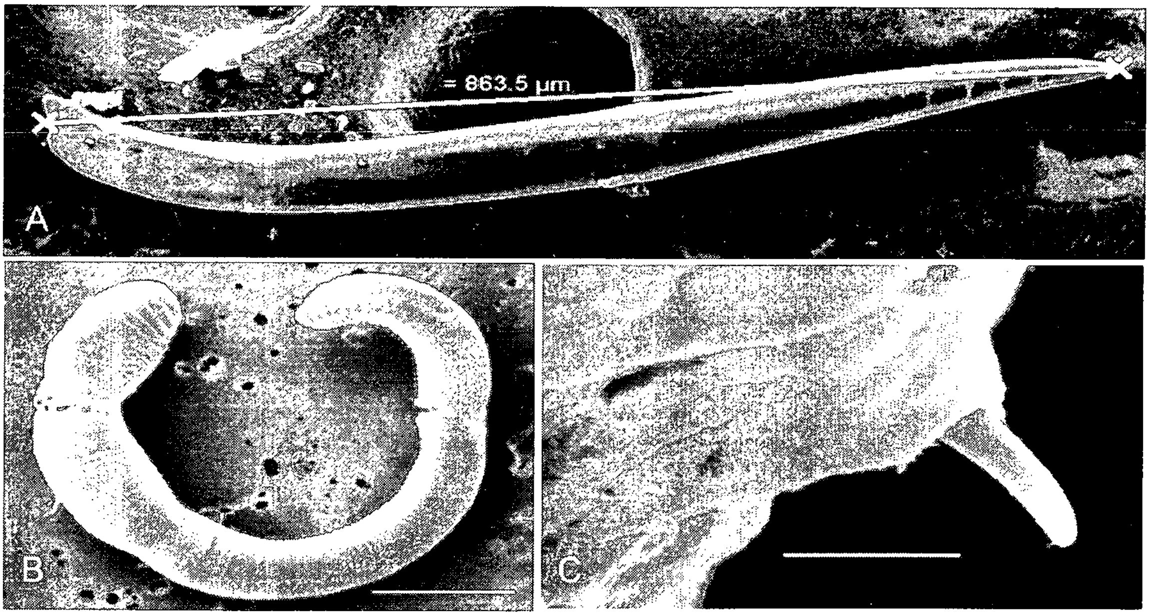

Fig. 6.1. Scanning electron micrograph of Lumbriculid worm. (A) chaeta recovered from fecal sample of *Dipsas* sp., (B) oligochaete recovered from bromeliad, and (C) chaeta *in situ*, similar to that recovered from fecal sample (H. K. Mahon and A. Rodi, pers. comm.).

I collected 37 fecal samples from *Sibon annulatus* at PNGDOTH between May 2006 and August 2007 (mean per month = 2.06, range = 0 - 6; Table 6.1, Fig. 6.2), of which nine (24.3%) contained a mean of 3.3 (range: 1 – 6) molluscan opercula, seven (18.9%) contained chaetae from lumbriculid oligochaetes, and 22 samples (59.5%) contained no identifiable prey (Table 6.1, Fig. 6.2). I collected 40 fecal samples from *S. argus* at PNGDOTH between May 2006 and August 2007 (mean per month = 2.22, range = 0 – 8), including two samples (5%) that contained one and two opercula, respectively, five (12.5%) samples presumably contained gelatinous amphibian eggs, and 26 samples (65%) contained chaetae from oligochaetes (Table 6.1, Fig. 6.2). I collected only three fecal samples of *S. longifrenis* at PNGDOTH (mean per month = 0.11, range = 0 – 1); two (66.6%) contained chaetae and the other contained no identifiable prey (33.3%; Table 6.1, Fig. 6.2). Finally, I collected five fecal samples from *S. nebulatus* at PNGDOTH (mean per month = 0.28, range = 0 – 2), but no identifiable prey were found (Table 6.1, Fig. 6.2). However, a large slug was palpated from the stomach of one *S. nebulatus* from PNGDOTH; the slug was still alive, indicating that it had recently been consumed.

Samples collected from Altos del Maria were more limited in number (Table 6.1, Fig. 6.2). Only one sample was collected from *S. annulatus*; it contained 16 molluscan opercula. Fourteen samples were collected from *S. argus*, of which six (42.9%) were gelatinous and assumed to consist of amphibian eggs, five samples (35.7%) contained oligochaete chaetae, and three samples (21.4%) did not contain any identifiable structures. Seven samples of *S. longifrenis* were collected, including one (14.3%) that was gelatinous, two (28.6%) contained chaetae, and the other four (57.1%) contained no identifiable prey (Fig. 6.2).

Table 6.1. Dietary remains in fecal samples of *Sibon* spp. Includes number and percentage of total samples for mollusks, amphibian eggs, and chaetae in four species of *Sibon* from PNGDOTH and three species of *Sibon* from ADM. Fecal samples without hard structures are included in the no prey column.

Species	n	Mollusks	Eggs	Oligochaetes	No Identifiable Prey
			PNGDOTH		
S. annulatus	37	9 (24.3%)	-	7 (18.9%)	22 (59.5%)
S. argus	40	2 (5.0%)	5 (12.5%)	26 (65.0%)	7 (17.5%)
S. longifrenis	3	-	-	2 (66.7%)	1 (33.3%)
S. nebulatus	5	-	-	-	5 (100%)
			ADM		
S. annulatus	1	1 (100%)	-	-	-
S. argus	14	-	6 (42.9%)	5 (35.7%)	3 (21.4)
S. longifrenis	6	-	1 (16.7%)	2 (33.3%)	3 (50.0%)

Logistic regression was used to test for significant differences in presence of chaetae between seasons and across sizes of *Dipsas* sp. Chaetae were equally frequent in fecal samples during both rainy and dry seasons (P = 0.194; Fig. 6.3). However, there was a significant difference in the presence of chaetae as a function of body size (SVL) of snakes (P = 0.003; Fig. 6.4). The mean SVL (±SD) of snakes lacking chaetae in their fecal samples was 23.6±7.3 cm, whereas the mean SVL of those with chaetae in their fecal samples was 36.2±9.3 cm.

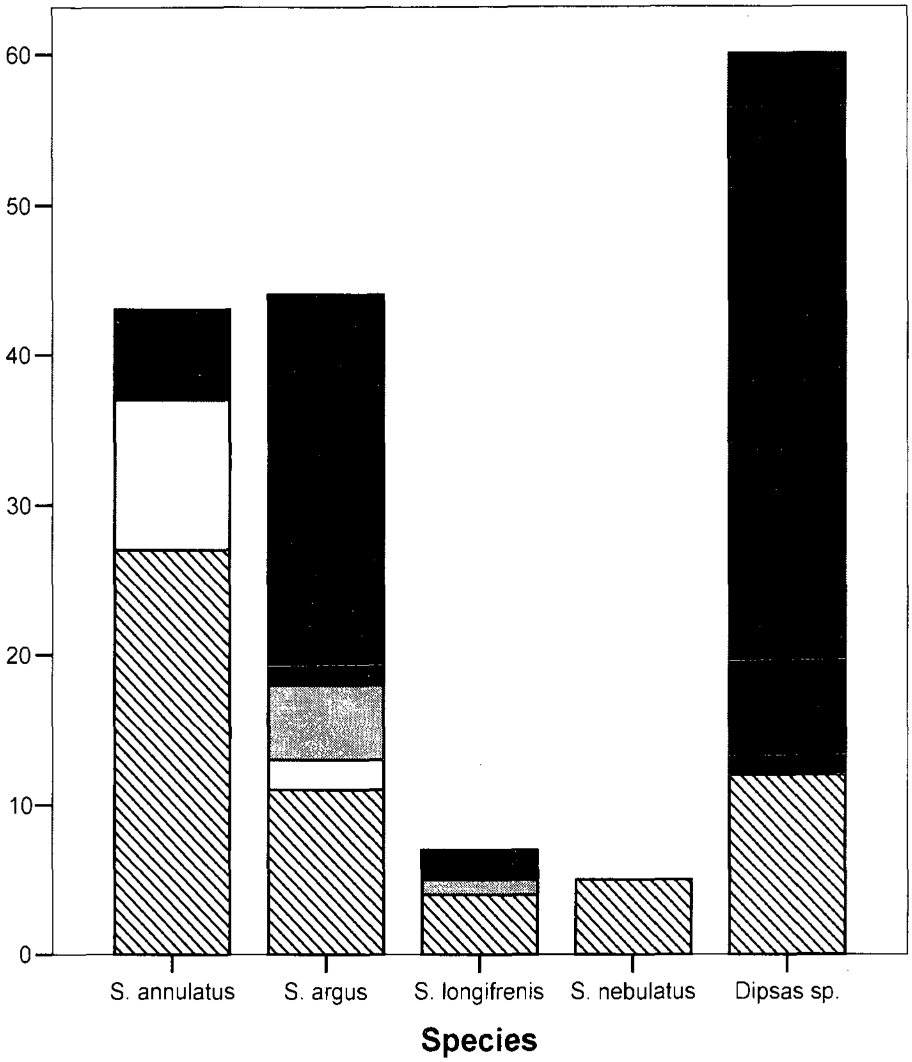

Fig. 6.2. Dietary remains from fecal samples of Dipsadini in PNGDOTH. Diagonal stripes represent samples that contained no identifiable prey, light gray represents molluscan prey (opercula or shells), dark gray represents presumptive amphibian eggs, and black represents oligochaete remains (chaetae).

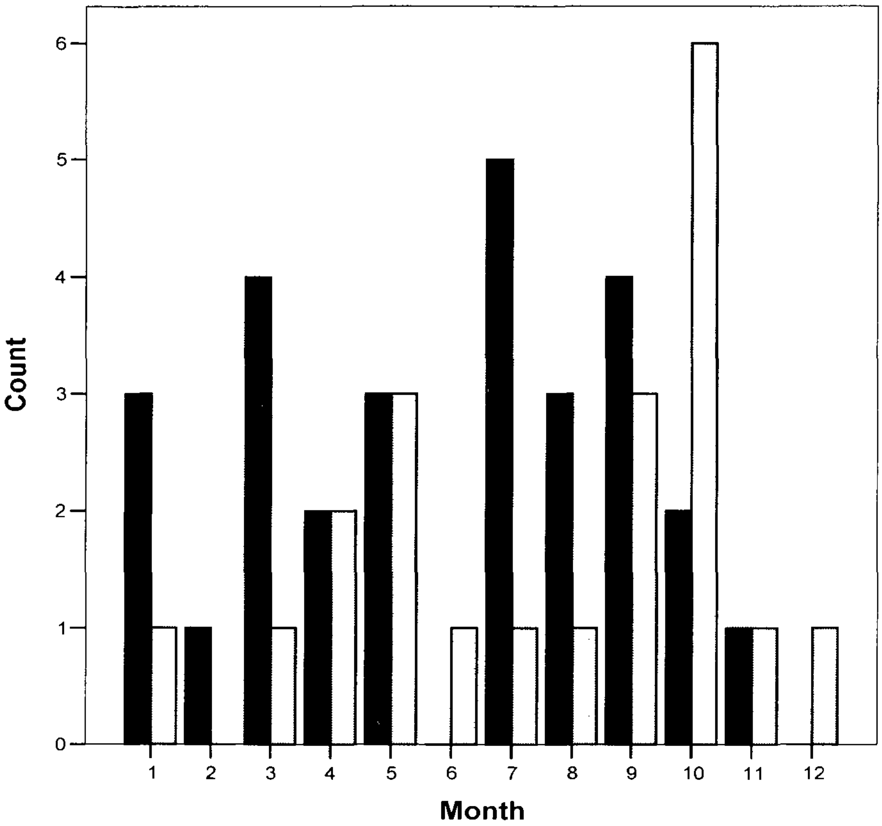

Fig. 6.3. Presence of chaetae in fecal samples of *Dipsas* sp., across time by sex (males, black; females, gray). Months 1 - 3 represent the dry season and 4 - 12 represent the rainy season.

There was a significant difference in the components of diet recovered from fecal samples for *Sibon annulatus*, *S. argus/longifrenis*, and *Sibon nebulatus* ($\chi^2 = 36.606$, $P < 0.001$). *Sibon argus/longifrenis* found at the pond had a significantly higher frequency of eggs in their fecal samples ($\chi^2 = 29.824$, df = 1, $P \leq 0.001$), but there was no significant difference in the presence of oligochaete chaetae between snakes at the pond and the stream transects ($\chi^2 = 0.490$, df = 1, P = 0.484). In addition, both male and female *S. argus* from the pond had higher body condition (greater mass per unit SVL) than snakes along the stream (males: n = 19 pond and n = 39 stream, F = 21.803, df = 1, $P < 0.001$, Fig. 6.5; females: n = 62 stream and n = 27 pond, F = 45.651, df = 1, $P < 0.001$, Fig. 6.6).

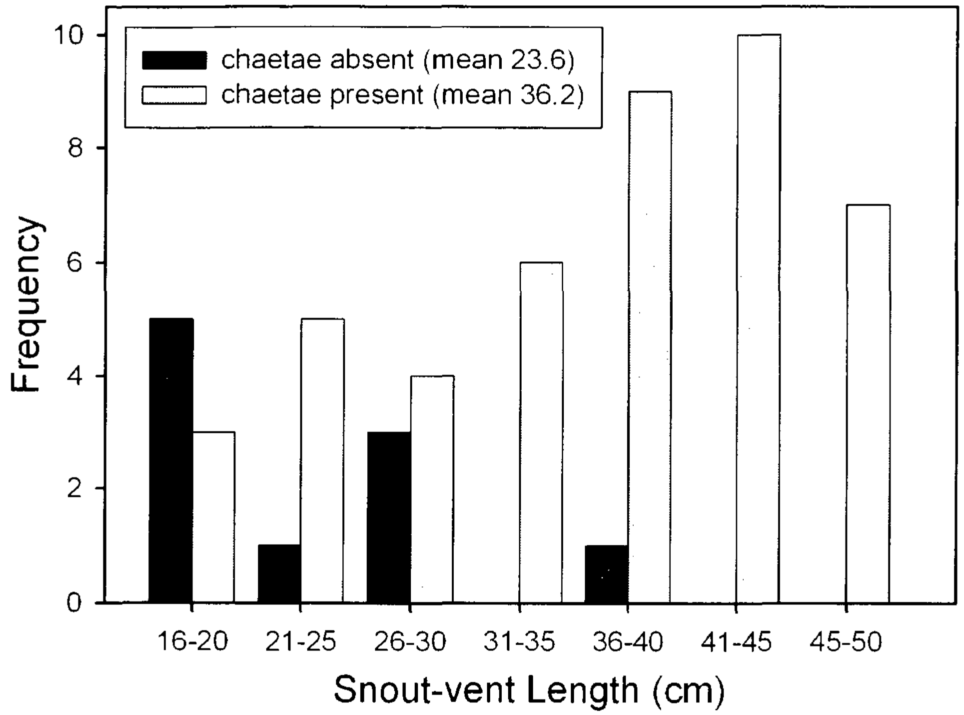

Fig. 6.4. Histogram of presence of chaetae by snout-vent length for *Dipsas* sp.. Chaetae present (gray) and absent (black) in fecal samples.

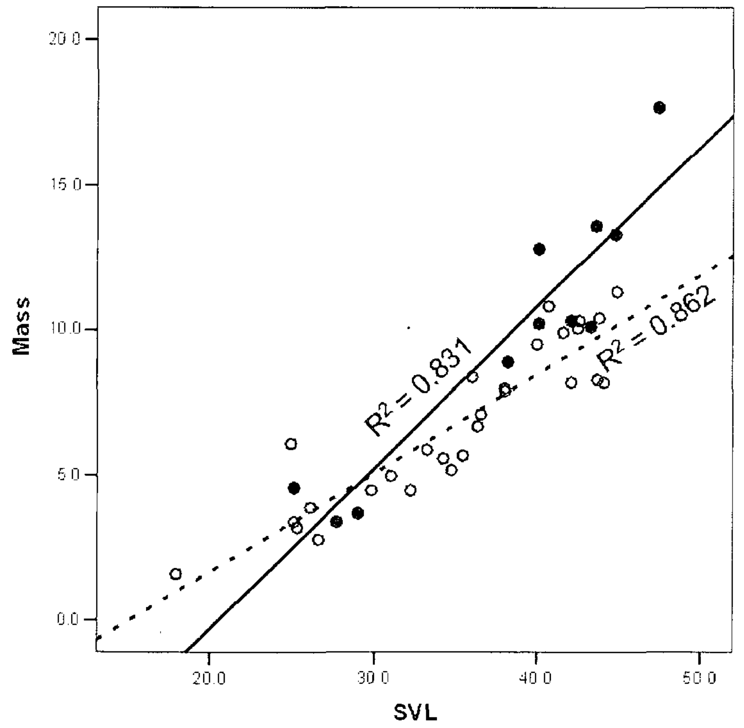

Fig. 6.5. Relationship of SVL to mass for male *Sibon argus/longifrenis*. Solid circles and line represent snakes captured at the Pond; open circles and dashed line represents snakes captured along the stream.

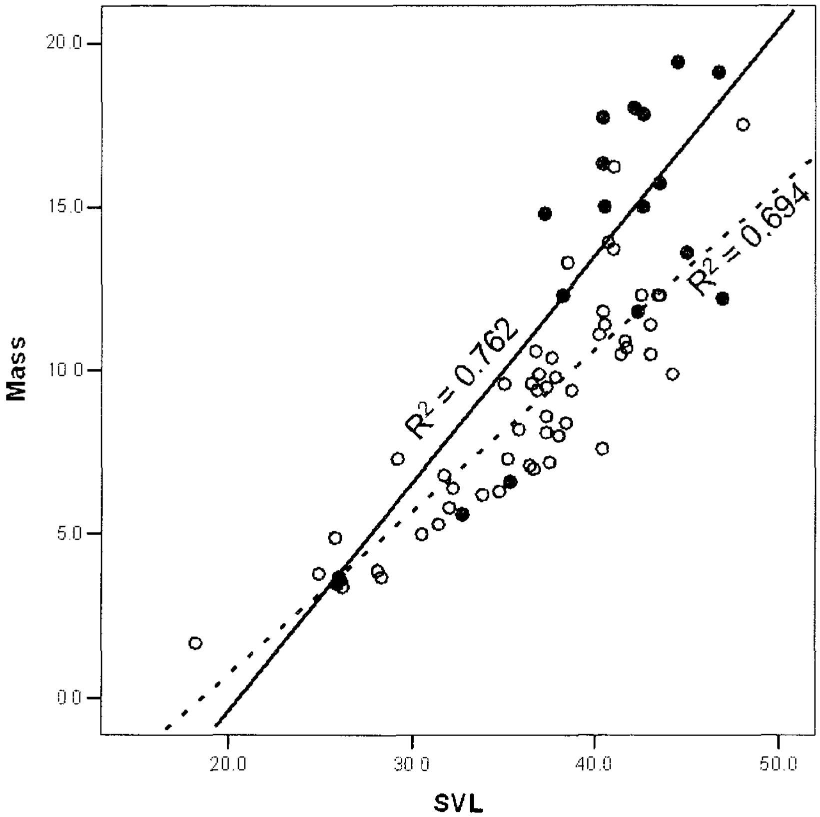

Fig. 6.6. Relationship of SVL to mass for female *Sibon argus/longifrenis*. Solid circles and line represent snakes captured at the Pond; open circles and dashed line represents snakes captured along the stream.

The survey of riparian and terrestrial transects found small snails (Helicoidea) and oligochaetes of the family Lumbriculidae, along with small spiders and insects in the bromeliads (n = 4 tank bromeliads). Random samples of leaf litter revealed small spiders and insects, but no oligochaetes or mollusks. Along the riparian transect, one egg clutch of *Hyalinobatrachium colymbiphyllum* was found. Small snails (Helicoidea) were found in the moss on branches overhanging streams.

DISCUSSION

Although diverse prey items have been reported from the stomachs or intestines of several species of *Dipsas* and *Sibon,* members of the group are generally referred to as mollusk-eaters (Peters, 1960; Cisneros-Heredia, 2005). However, my results indicate that for most *Dipsas* and *Sibon* at PNGDOTH, at least during my study period, non-molluscan prey comprises most of the diet (Fig. 6.2).

Among *Dipsas*, fecal samples of larger individuals were more likely to contain chaetae than were those of smaller snakes (Fig. 6.4). Further study is needed to determine whether this reflects an ontogenetic shift in prey preference. Chaetae were found in 83.1% of fecal samples from *Dipsas* spp. across both rainy and dry seasons, over three years, and in snakes captured along both riparian and terrestrial secondary forest transects. These results suggest that *Dipsas* sp. at PNGDOTH feeds regularly on worms. Surveys of the leaf litter and bromeliads along transects where *Dipsas* sp. was commonly collected found oligochaetes in the organic matter trapped in the axils of tank bromeliads, but not in the terrestrial leaf litter. Oligochaetes are found in bromeliads in mid-elevation tropical forests throughout Central America and can reach high densities (Gates, 1942; Fragoso and Rojas-Fernandez, 1996). Although generally abundant, oligochaetes exhibit patchy distribution (Fragoso and Rojas-Fernandez, 1996).

In addition to mollusks, *Sibon argus* in central Panama consumes oligochaetes, and *S. argus* and *S. longifrenis* take advantage of, at least seasonally, amphibian eggs. Information is not available on the foraging behavior of *Sibon* spp. in Central Panama, aside from observations of the consumption of frog eggs (Ryan and Lips, 2004;

Montgomery et al., 2007; pers. obs.) and the consumption of a small snail by *Sibon annulatus* (C. E. Montgomery, pers. comm.). Further investigations are needed to fully understand the extent of dependency on amphibian eggs and impacts of local amphibian declines on snakes.

My findings may provide insight into the occurrence of *Dipsas* and *Sibon* in and near bromeliads. The few observations of diurnal retreats of *Dipsas* include bromeliads (Porto and Fernandes, 1996; MacCulloch and Lathrop, 2004; Duellman, 2005; pers. obs.). Bromeliads serve as microcosms within tropical forests (Fragoso and Rojas-Fernandez, 1996), and it is likely that *Dipsas* sp. and *Sibon* spp. forage nocturnally in bromeliads and then use the epiphytes as a diurnal retreat sites.

Based on my findings, *Dipsas* sp., *Sibon argus*, and *S. longifrenis* are not stenophagic molluscivores, at least not in all populations and/or at all ages. In Central Panama *Dipsas* sp. feeds primarily on oligochaete prey when available, and *S. argus* and *S. longifrenis* consume both amphibian eggs and oligochaetes when available. However, *Sibon* and *Dipsas* may be able to utilize molluscivorous morphological specializations during times when oligochaetes or other prey are unavailable. Some cichlid fishes residing in Lake Malawi of Africa have been documented to feed generally, but in times of strong interspecific competition those fishes switch to specialized diets (McKaye and Marsh, 1982; Meyer, 1989, Robinson and Wilson, 1998). A similar situation may occur within the context of the arboreal snake assemblage at PNGDOTH, where *Dipsas* sp. and some *Sibon* spp. occur in close proximity to each other and may experience a high level of interspecific competition. This may require them to broaden their diets to more handling-intensive prey, such as shelled mollusks, during times of intense competition.

Oligochaetes appear to be common at PNGDOTH (pers. obs), However, the reportedly patchy distribution of oligochaetes (Fragoso and Rojas-Fernandez, 1996) may render them difficult to locate or unavailable in some areas. A broader diet may decrease interspecific competition between *Dipsas* sp. and *Sibon* spp. (but see Solórzano, 2002; Ryan and Lips, 2004; Montgomery et al., 2007) and perhaps among age classes of conspecifics (Swanson et al., 2003). However, the consumption of amphibian eggs recently reported for *Sibon* spp. may place them in competition with *Dipsas* spp. in areas were amphibians have declined, albeit for oligochaetes as well as mollusks. *S. argus/longifrenis* are more frequently observed along streams; it is not known whether their distribution is related to diet (consumption of frog eggs on overhanging vegetation). *Dipsas* sp. outnumbers *Sibon argus/longifrenis* at PNGDOTH, perhaps reflecting their more widespread non-riparian habitat and their greater reliance on oligochaetes, whose abundance presumably has not been greatly affected by the amphibian declines. Furthermore, individuals of *S. argus/longifrenis* found to have fed on oligochaetes and not amphibian eggs were in poorer body condition than conspecifics that had consumed frog eggs, suggesting that the latter may either be less nutritious or simply less available. *S. argus/longifrenis* appears to be at a disadvantage due to the decline of riparian-breeding frogs and may persist primarily at areas where arboreally-breeding frogs continue to persist.

Notably, the first observations of *Sibon argus* and *S. longifrenis* feeding on amphibian eggs (Ryan and Lips, 2004; Montgomery et al., 2007; Ray et al., in review) were made concurrently with local amphibian declines attributed to chytridiomycosis (Lips et al., 2006). Studies directly following the decline (March-October 2005) indicated that the cryptic species *S. argus* and *S. longifrenis*, the two confirmed egg-eating Dipsadini at PNGDOTH, were experiencing a decline in body condition and were likely being lost from the community (C. E. Montgomery and K. R. Lips, unpublished data; pers. obs.). However, since September 2006 only two small individuals of *S. longifrenis* have been captured in PNGDOTH. My limited sampling at Altos del Maria resulted in double the captures of *S. argus* (n = 31) compared to *S. longifrenis* (n = 13). However, if the proportion of the two species had been similar at PNGDOTH prior to the amphibian declines, then *S. longifrenis* has declined significantly. *Sibon argus* remains relatively common, at least during the rainy season and at the Pond.

The limited number of fecal samples (n = 7) collected for *S. longifrenis* and *S. argus* during the first 12 months post-decline contained oligochaete chaetae (n = 1), gelatinous material (n = 2), or no identifiable prey (n = 4). No identifiable prey suggests that nothing substantial had been consumed recently or an unidentifiable prey was consumed and completely digested. Following amphibian decline, anuran egg masses became rare and were limited to the most optimal breeding times for frogs (pers. obs.). Whether the scarcity of *S. longifrenis* relative to *S. argus* reflects a differential response to the reduced availability of anuran eggs as a dietary item cannot be determined from the available data. However, the effects of the amphibian decline on *Sibon* spp. must be considered when working with this group of snakes.

Conservation implications in relation to diet.---Tropical forests and their associated biotas are rapidly being lost (Kricher, 1999). Now that amphibian eggs and oligochaetes, as well as terrestrial mollusks, have been identified as dietary components of Dipsadini, any loss of diversity among these disparate taxa can be expected to impact populations of *Dipsas* and *Sibon*. As chytridiomycosis continues to spread throughout the range of Dipsadini (e.g., Peters, 1960; Lips et al., 2006), it is unknown whether additional species within this lineage will also be affected by the absence of amphibian eggs as prey.

Furthermore, non-marine mollusks are in global decline, for reasons that are unclear (Lydeard et al., 2004). Little research has been conducted on terrestrial mollusks in the montane region of Central Panama, so it is difficult to assess the current status of mollusks at my study sites. Molluscan opercula are regularly found in the feces of *S. annulatus*. Very few terrestrial mollusks (slugs or snails) are observed in the open, but targeted searching reveals small snails among epiphytic mosses in the forest and near streams (pers. obs.).

Finally, illegal collection of epiphytes, including bromeliads that harbor the oligochaetes consumed by *Dipsas* and *Sibon*, has been intense in some sites in Central Panama (pers. obs.). Park rangers and a rugged access road provide some level of protection to my study area, so illegal collection of such plants is limited. However, the effect of such collection should be considered a conservation threat in some other areas where *Dipsas* and *Sibon* reside.

Relationships within Dipsadinae.---The taxonomic relationship of the Dipsadini to other genera within the Dipsadinae, such as *Geophis*, *Atractus*, and *Ninia* (Fernandes, 1995; Wallach, 1995; Cadle, 2007; Mulcahy, 2007), is unclear (e.g., Peters, 1960; Wallach, 1995; Cadle, 2007). The demonstration that *Dipsas* and *Sibon* consume oligochaetes may indicate that this is a dietary synapomorphy shared with closely related taxa. However, it is not known whether *Tropidodipsas* or *Sibynomorphus* consume oligochaetes. Published records indicate that members of *Sibynomorphus* (e.g., Laporta-Ferreira et al., 1986; Laporta-Ferreira and Da Graca Salomão, 1991; Da Graca Salomão and Laporta-Ferreira, 2004; Cadle, 2007) and *Tropidodipsas* (e.g., Smith, 1943; Stuart, 1948; Martin, 1958; Kofron, 1985; Wallach, 1995) feed primarily, if not solely, on gastropods, but further investigation into the diets of those genera are needed. Furthermore, the demonstration the presumably molluscivorous specialists *Dipsas* and *Sibon* frequently consume alternative prey suggests that detailed studies are needed on congeneric species from across the broad range of these genera.

Future directions.---Although many mollusk-eating snakes are presumed to be highly specialized to consume shelled or unshelled molluscan prey, results from my work suggest that *Dipsas* spp. and *Sibon* spp., at least in Central Panama, will consume mollusks, but in general utilize oligochaete or anuran egg prey far more frequently. Further analyses must be conducted throughout the range of *Dipsas* and *Sibon* to better understand the dependency of different populations of these species on oligochaete or anuran egg prey. Systematic surveys to determine the population status of terrestrial mollusks and oligochaetes should be performed so the availability of prey for *Dipsas* and *Sibon* is realized. Understanding the relative importance of prey other than mollusks as part of the diet throughout the range of Dipsadini may have important conservation implications as *Sibon* spp. is affected by the loss of amphibian eggs as a prey source and potentially put into competition with other *Sibon* spp., as well as *Dipsas* spp., for alternative prey sources such as oligochaetes.

CHAPTER VII

GENERAL CONCLUSIONS

I evaluated several aspects of the ecology and behavior of snakes comprising a Neotropical community. Among these were defensive behaviors of the ophidian community; interspecific differences in morphology of the arboreal snake community; environmental characteristics of the locations where those arboreal snakes were captured; and the diets of the mollusk-eating snakes.

My evaluation of the arboreal snake assemblage demonstrated variation in morphology, with a range of adaptations to arboreality. Differences also were found in maximum cantilever distance among five abundant members of the arboreal snake assemblage. The ability to bridge gaps in the aboveground vegetation likely facilitates arboreal movement. Arboreal species partition the habitat, with distance from the ground, distance from water, and the diameter of the perch being the most important factors. Correlations were found between the size of the snake and the areas where it was found; larger snakes were restricted to larger branches and lower perch heights. This study addressed interspecific differences in morphology and habitat. Future studies of such differences would be strengthened by the inclusion of the larger members of the arboreal assemblage (e.g., *Boa, Spilotes, Pseustes*). Future studies also should include the full range of the vertical dimension of habitat structure.

I also studied the defensive behaviors of the central Panamanian snake community. The repertoire of defensive behaviors for several species was documented for the first time. Body thrashing, cloacal discharge, and head flaring were among the most commonly observed behaviors, whereas the formation of a conical pyramid was observed only in some species of *Dipsas* and *Sibon*. Birds, mammals, and other snakes are presumed to be the major predators on members of the snake community in central Panama. Future studies should include further documentation of potential predators and should document snakes' responses to specific predators.

Recent documentation that mollusk-eating snakes feed on amphibian eggs lead me to evaluate the diets of *Dipsas* and *Sibon* in central Panama. As expected, *Dipsas* sp., *S. annulatus, S. nebulatus* fed on terrestrial snails, but *S. argus* and *S. longifrenis* fed primarily on amphibian eggs and *Dipsas* sp., *S. argus, S. longifrenis,* and *S. annulatus* also consumed oligochaetes. Future studies should include dietary investigations of *Dipsas* and *Sibon* at other sites in Central and South America. A thorough survey of mollusks at the study site would be required to determine whether the diet of *Dipsas* and *Sibon* is influenced by the availability of molluscan prey.

The Neotropics remain a relatively understudied region, and broad generalizations about natural history are common. Efforts should be made to expand our knowledge of this biologically diverse region to aid in the development of management plans and conservation efforts.

REFERENCES

Allee, W. C. 1926. Measurement of environmental factors in the tropical rain-forest of Panama. Ecology 7:273:302.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Sanders, Philadelphia, Pennsylvania.

Alvarado, R. 2000. Evaluación Ecológica Rápida. Parque Nacional G. D. Omar Torrijos Herrera. Consultores Ecológicos Panameños, S.A., Panama City, Panama.

Arnold, S. J. 1993. Foraging theory and prey-size-predator-size relationships in snakes. *In* Snakes Ecology and Behavior. Seigel, R. A. and J. T. Collins (eds.). McGraw-Hill, Inc., New York, New York.

Barker, M. G. and M. A. Pinard. 2001. Forest canopy research: sampling problems, and some solutions. Plant Ecology 153:23-38.

Bartram, S. and W. Boland. 2001. Chemistry and ecology of toxic birds. ChemBioChem 2:809-811.

Beebe, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Zoologica 31:11-51.

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.

Blanchard, F. N. 1937. Data on the natural history of the red-bellied snake, *Storeria occipitomaculata* (Storer), in northern Michigan. Copeia 1937:151-162.

Brem, F. 2006. Comparing *Batrachochytrium dendrobatidis* infection prevalence among habitats before, during, and after an epizootic in central Panama. Unpublished Masters Thesis. Southern Illinois University, Carbondale, Illinois.

Brem, F., J. R. Mendelson III, and K. R. Lips. 2007. Field-sampling protocol for *Batrachochytrium dendrobatidis* from living amphibians, using alcohol preserved swabs. Verison 1.0 (18 July 2007). Electronic document accessible at http://www.amphibians.org Conservation International.

Brodie, E. D. III. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution 47:227-235.

Brodie, E. D. III and E. D. Brodie, Jr. 1999. Tetrodotoxin resistance in garter snakes: An evolutionary response of predators to dangerous prey. Evolution 44:651-659.

Brodie, E. D. III and F. J. Janzen. 1995. Experimental studies of coral snake mimicry: Generalized avoidance of ringed snake patterns by free-ranging avian predators. Functional Ecology 9:186-190.

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.

Buckley, L. B. and J. Roughgarden. 2005. Lizard habitat partitioning on islands: the interaction of local and landscape scales. Journal of Biogeography 32:2113-2121.

Cadle, J. E. 2007. The snake genus *Sibynomorphus* (Colubridae: Dipsadinae: Dipsadini) in Peru and Ecuador, with comments on the systematics of Dipsadini. Bulletin of the Museum of Comparative Zoology 158:183-283.

Cadle, J. E., and H. W. Greene. 1993. Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. Pp. 281-293 in Species Diversity in Ecological Communities: Historical and Geographical Perspectives Ricklefs, R. E. and D. Schluter (eds.). University of Chicago Press, Chicago, Illinois.

Cadle, J. E. and C. W. Myers. 2003. Systematics of snakes referred to *Dipsas variegata* in Panama and Western South America, with revalidation of two species and notes on defensive behaviors in the Dipsadini (Colubridae). American Museum Novitates 3409:1-47.

Campbell, J. A. and W. W. Lamar. 1989. Venomous Reptiles of Latin America. Cornell University Press, Ithaca, New York.

Campbell, J. A. and W. W. Lamar. 2004. The Venomous Reptiles of the Western Hemisphere, 2 Volumes. Comstock Books in Herpetology. Cornell University Press, Ithaca, New York.

Carl, C. 1949. The sharp-tailed snake in British Columbia. Herpetologica 6:116.

Carl, C. 1968. The Reptiles of British Columbia. Handbook 3. Proceedings of the Museum, Victoria, British Columbia.

Castoe, T. A., M. M. Sasa, C. L. Parkinson. 2005. Modeling nucleotide evolution at the mesoscale: the phylogeny of the neotropical pitvipers of the *Porthidium* group (Viperidae: Crotalinae). Molecular Phylogenetics and Evolution 37:881-898.

Cei, J. M. 1993. Reptiles del noroeste, nordeste, y este de la Argentina. Herpetofauna de las selva subtropicales, puna y pampas. Museo Regionale di Scienze Naturali Torino, Monografia, Italy 14:1-949.

Cisneros-Heredia, D. F. 2005. Report of molluscivory in *Atractus carrioni* Parker, 1930. Herpetozoa 18:185-186.

Coates, M. and M. Ruta. 2000. Nice snake, shame about the legs. Trends in Ecology and Evolution 15:503-507.

Cody, M. L. 1966. The consistency of intra- and inter-continental grassland bird species counts. The American Naturalist 100:371 – 376.

Coley, P. D. and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:30-35.

Collins, S. L. 2003. Defense posture of *Contia tenuis*. Journal of Kansas Herpetology 5:9.

Cook, S. Jr. 1960. On the occurrence and life history of *Contia tenuis*. Herpetologica 16:163-173.

Crother, B. I. 1999. Phylogenetic relationships among west Indian Xenodontinae snakes (Serpentes; Colubridae) with comments on the phylogeny of some mainland xenodontines. Contemporary Herpetology. http://www.contemporaryherpetology.org/ch/1999/2/index.htm. Downloaded 28 December 2008.

Cummingham, D. S. and G. M. Burghardt. 1999. A comparative study of facial grooming after prey ingestion in Colubrid snakes. Ethology 105:913-936.

Cundall, D. and H. W. Greene. 2000. Feeding in Snakes. In Feeding: Form, Function, and Evolution in Tetrapod Vertebrates. Schwenk, K. (ed.). Academic Press, San Diego, California.

Cunha, O. R. and F. P. do Nascimento. 1978. Ofídios da Amazônia. X-as cobras de região leste do Pará. Publ. Avul. Mus. Par. Emilio Goeldi. 31:1-218.

Da Graca Salomão, M. and I. L. Laporta-Ferreira. 2004. The role of secretions from the supralabial, infralabial, and Duvernoy's glands of the slug-eating snake *Sibynomorphus mikani* (Colubridae: Dipsadinae) in the immobilization of molluscan prey. Journal of Herpetology 28:369-371.

Darda, D.M. 1995. *Contia tenuis*. Pp. 102-105. In Reptiles of Washington and Oregon. Storm, R. M. and W. P. Leonard (eds.). Seattle Audubon Society, Seattle, Wahsingon.

De Queiroz, A. 1997. Lip-flaring in Thamnophine snakes and its possible association with feeding on soft-bodied, sticky prey. Herpetological Review 28:28-29.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc. Publications of the Museum of Natural History. University of Kansas 65:1-352.

Duellman, W. E. 2005. Cusco Amazonico: The Lives of Amphibians and Reptiles in an Amazonian Rainforest. Comstock Publishing Associates, Ithaca, New York.

Duellman, W. E. and A. W. Salas 1991. Annotated Checklist of the amphibians and reptiles of Cusco Amazonico, Peru. Occasional Papers of the Museum of Natural History. University of Kansas Press. Lawrence (KS). 143:1-13.

Dumbacher, J. P., A. Wako, S. R. Derrickson, A. Samuelson, T. P. Spande, and J. W. Daly. 2004. Melyrid beetles (Choresine): A putative source for the batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. Proceedings of the National Academy of the Sciences 101:15857-15860.

Dunn, E. R. 1935. The snakes of the genus "*Ninia*". Proceedings of the National Academy of Science 21:9-12.

Dunn, E. R. 1951. The status of the snake genera *Dipsas* and *Sibon*, a problem for "quantum evolution". Evolution 5:355-358.

DuVal, E. H., H. W. Greene, and K. L. Manno. 2006. Laughing falcon (*Herpetotheres cachinnans*) predation on coral snakes (*Micrurus nigrocinctus*). Biotropica 38:566-568.

Eisenberg, J. F. 1989. Mammals of the Neotropics: The Northern Neotropics. Volume 1: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. The University of Chicago Press, Chicago, Illinois.

Emmons, L. H. 1987. Comparative feeding ecology of felids in a Neotropical rainforest. Behavioral Ecology and Sociobiology 20:271-283.

Endler, J. A. 1981. An overview of the relationships between mimicry and crypsis. Biological Journal of the Linnaean Society 16:25-31.

Endler, J. A. 1986. Defense against predators. In Predator-prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. Feder, M. E. and G. V. Lauder (eds). University of Chicago Press, Chicago, Illinois.

Engelstoft, C. and K. Ovaska. 2000. Natural history of the sharp-tailed snakes, *Contia tenuis*, on the Gulf Islands, British Columbia. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk. Kamloops, BC. 15-19 February 1999. Volume One. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, British Columbia.

Evans, D. L. and J. O. Schmidt. 1990. Insect defenses: adaptive mechanisms and strategies of prey and predators. State University of New York Press, Albany, New York.

Fernandes, R. 1995. Phylogeny of the Dipsadinae Snakes. Ph.D. Dissertation, University of Texas of Arlington, Arlington, Texas.

Fitzgerald, M., R. Shine, and F. Lemckert. 2002. Radiotelemetric study of habitat use by the arboreal snake *Hoplocephalus stephensii* (Elapidae) in eastern Australia. Copeia 2002:321-332.

Fragoso, C. and P. Rojas-Fernandez. 1996. Earthworms inhabiting bromeliads in Mexican tropical rainforests: Ecological and historical determinants. Journal of Tropical Ecology 12:729-734.

Franca, F. G. R., D. O. Mesquita, C. C. Nogueira, and A. F. B. Araújo. 2008. Phylogeny and ecology determine morphological structure in a snake assemblage in the Central Brazilian Cerrado. Copeia 2008:23-38.

Gallardo, J. M. 1972. Observaciones biológicas sobre una falsa yarará *Tomodon ocellatus* Duméril, Bibron et Duméril. Neotropica 18:57-63.

Gates, G. E. 1942. Check list and bibliography of North American earthworms. American Midland Naturalist 27:86-108.

Gentry, A. H. 1992. Tropical forest biodiversity: Distributional patterns and their conservational significance. Oikos 63:19-28.

Gibbons, J. W. and K. M. Andrews. 2004. PIT tagging: Simple technology at its best. BioScience 54:447-454.

Goldman, E. A. 1920. Mammals of Panama. Smithsonian Institution. Washington, D.C.

Gordon, D. G. 1994. Field Guide to the Slug. The Western Society of Malacologists. Sasquatch Books, Seattle, Washington.

Gosner, K. L. 1942. Lip curling of the red-bellied snake. Copeia 1942:181-182.

Greene, H. W. 1975. Ecological observations on the red coffee snake, *Ninia sebae*, in southern Veracruz, Mexico. The American Midland Naturalist 93:479-484.

Greene, H. W. 1988. Antipredator mechanisms in reptiles. In Biology of the Reptilia. Vol. 16, Ecology B, Defense and Life History. Gans, C. & R. B. Huey (eds.). Alan R. Liss, New York, New York.

Greene, H. W. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley, California.

Gruz, M. 2002. The feeding behavior of the snail-eating snake *Pareas carinatus* Wagler 1830 (Squamata: Colubridae). Amphibia-Reptilia 23:487-493.

Guyer, C. and M. A. Donnelly. 1999. Length-mass relationships among an assemblage of tropical snakes in Costa Rica. Journal of Tropical Ecology 6:65-76.

Handley, C. O. Jr. 1966. Checklist of the mammals of Panama. In Ectoparasites of Panama. Wenzel, R. L. and V. J. Tipton (eds.). Field Museum of Natural History, Chicago, Illinois.

Hartmann, M. T., M. L. del Grande, M. J. Gondim, M. C. Mendes, and O. A. V. Marques. 2002. Reproduction and activity of the snail-eating snake, Dipsas albifrons (Colubridate), in the southern Atlantic forest in Brazil. Studies on Neotropical Fauna and Environment 37:111-114.

Harvey, M. B. and A. Muñoz. 2004. A new species of *Tomodon* (Serpentes: Colubridae) from high elevations in the Bolivian Andes. Herpetologica 60:364-372.

Harwood, P. D. 1945. The behavior and growth of young DeKay's snakes (*Storeria dekayi dekayi*) in captivity. The American Midland Naturalist 34:523-525.

Henderson, R. W. and M. H. Binder. 1980. The ecology and behavior of vine snakes (*Ahaetulla, Oxybelis, Thelotornis, Uromacer*): a review. Milwaukee Public Museum Contributions in Biology and Geology 37:1-38.

Henderson, R. W. and M. A. Nickerson. 1976. Observations on the behavioral ecology of three species of *Imantodes* (Reptilia, Serpentes, Colubridae. Journal of Herpetology 10:205-210.

Highton, R., S. B. Hedges, C. A. Hass, and H. G. Dowling. 2002. Snake relationships revealed by slowly-evolving proteins: further analysis and a reply. Herpetologica 58:270-275.

Hollis, J. L. 2006. Phylogenetics of the genus Chironius Fitzinger, 1826 (Serpentes, Colubridae) based on morphology. Herpetologica 62:435-453.

Hoso, M., T. Asami, and M. Hori. 2007. Right-handed snakes: Convergent evolution of asymmetry for functional specialization. Biology Letters 3:169-172.

Hutchinson, D. A., A. Mori, A. H. Savitzky, G. M. Burghardt, X. Wu, J. Meinwald, and F. C. Schroeder. 2007. Dietary sequestration of defensive steroids in nuchal glands of the Asian snake *Rhabdophis tigrinius*. Proceeding of the National Academy of Sciences. 104:2265-2270.

Ibáñez D., R., F. A. Arosemena, F. A. Solís, and C. A. Jaramillo. 1995. Anfibios y reptiles de La Serrania Piedras-Pacora, Parque Nacional Chagres. Scientia 9:17-31.

Jackson, J. F., W. Ingram III, and H. W. Campbell. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: A multivariate approach. The American Naturalist 110:1029-1053.

Jayne, B. C. and M. A. Riley. 2007. Scaling of the axial morphology and gap-bridging ability of the brown tree snake, *Boiga irregularis*. Journal of Experimental Biology 210:1148-1160.

Jordon, R., Jr. 1970. Death-feigning in a captive red-bellied snake, *Storeria occipitomaculata* (Storer). Herpetologica 26:466-468.

King, R. B., T. D. Bitner, A. Queral-Regil, and J. H. Cline. 1999. Sexual dimorphism in neonate and adult snakes. Journal of Zoology 247:19-28.

Kley, N. J. 2001. Prey transport mechanisms in blindsnakes and the evolution of unilateral feeding systems in snakes. American Zoologist 41:1321-1337.

Kofron, C. P. 1982. A review of the Mexican snail-eating snakes, *Dipsas brevifacies* and *Dipsas gaigeae*. Journal of Herpetology 16:270-286.

Kofron, C. P. 1985. Systematics of the Neotropical gastropod-eating snake Genera, *Tropidodipsas* and *Sibon*. Journal of Herpetology 19:84-97.

Kofron, C. P. 1987. Systematics of Neotropical gastropod-eating snakes: the *fasciata* group of the genus *Sibon*. Journal of Herpetology 21:210-225.

Kricher, J. 1999. A Neotropical Companion. 2nd revised edition. Princeton University Press, Trenton, New Jersey.

Laporta-Ferreira, I. L., M. G. Salomao, and P. Sawaya. 1986. Biology of *Sibynomorphus* (Colubridae-Dipsadinae) – reproduction and feeding habits. Revista Brasileira de Biologia 46:793-799.

Laporta-Ferreira, I. L. and M. da Graca Salomão. 1991. Morphology, physiology, and toxicology of the oral glands of a tropical cochleophagous snake, *Sibynomorphus neuwiedi* (Colubridae-Dipsadinae). Zoologischer Anzeiger 227:198-208.

Laurence, W. F. and C. A. Peres. 2006. Emerging Threats to Tropical Forests. The University of Chicago Press. Chicago (IL). 520 pp.

Lawson, R., J. B. Slowinski, B. I. Crother, and F. T. Burbrink. 2002. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 37:581-601.

Lee, J. C. 1996. The Amphibians and Reptiles of the Yucatan Peninsula. Comstock Publishing Associates, Cornell University Press, Ithaca, New York.

Lee, J. C. 2000. A Field Guide to the Amphibians and Reptiles of the Maya World: The Lowlands of Mexico, Northern Guatemala, and Belize. Cornell University Press, Ithaca, New York.

Leonard, W. P. and K. Ovaska. 1998. *Contia tenuis*. Catalogue of American Amphibians and Reptiles. 677.1–677.7

Leonard, W. P. and R. C. Stebbins. 1999. Observations of antipredator tactics of the sharp-tailed snake (*Contia tenuis*). Northwestern Naturalist 80:74-77.

Lillywhite, H. B. and R. W. Henderson. 1993. Behavioral and Functional Ecology of arboreal snakes. *In* Snakes Ecology and Behavior. Seigel, R. A. and J. T. Collins (*eds*.). McGraw Hill Inc., New York, New York.

Lillywhite, H. B., J. R. LaFrentz, Y. C. Lin, and M. C. Tu. 2000. The cantilever abilities of snakes. Journal of Herpetology 34:523-528.

Lin, Y., J. Hwang, and M. Tu. 2003. Does the saccular lung affect the cantilever ability of snakes? Herpetologica 59:52-57.

Lips, K. R., F. Brem, R. Brenes, J. D. Reeve, R. A. Alford, J. Voyles, C. Carey, L. Livo, A. P. Pessier, and J. P. Collins. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proceedings of the National Academy of Sciences 103:3165-3170.

Longcore, J E., A. P. Pessier, D. K. Nichols. 1999. Batrachochytrium Dendrobatidis gen. et sp. nov., a chytrid pathogenic to amphibians. Mycologia 91:219-227.

Lowman, M. D. and M. Moffett 1993. The ecology of tropical rain forest canopies. Trends in Ecology and Evolution 8:104-107.

Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Heshler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong, and F. G. Thompson. 2004. The global decline of nonmarine mollusks. BioScience 54:321-330.

MacCulloch, R. D. and A. Lathrop. 2004. A new species of *Dipsas* (Squamata: Colubridae) from Guyana. Revista de Biologia Tropical 52:239-247.

Madsen, T. 1987. Are juvenile grass snakes, *Natrix natrix*, aposematically coloured? Oikos 48:265-267.

Maitland, D. P. 2003. Predation on snakes by the freshwater land crab *Eudaniela garmani*. Journal of Crustacean Biology 23:241-246.

Martin, P. S. 1958. A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Miscellaneous Publications of the Museum of Zoology number 114, University of Michigan, Ann Arbor, Michigan.

Martins, M. 1996. Defensive tactics in lizards and snakes" the potential contribution of the Neotropical fauna. Pp. 185-199. In Anais do XIV Encontro Annual de Etologia. Sociedade Brasileira de Etologia. del Claro, K. (ed.). Universidade Federal de Uberlandia, Brasil.

Martins, M., M. S. Araujo, R. J. Sawaya, and R. Nunes. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a momphyletic group of Neotropical pitvipers (*Bothrops*). Journal of Zoology 254:529-638.

Martins, M. and M. E. Oliveira. 1998. Natural History of snakes in forests of the Manaus region, central Amazonia, Brazil. Herpetological Natural History 2:78-150.

Martins, M. O. A. V. Marques, and I. Sazima. 2008. How to be arboreal and diurnal and still stay alive: Microhabitat use, time of activity, and defense in Neotropical forest snakes. South American Journal of Herpetology 3:58-67.

McCormick, S. and G. A. Polis. 1982. Arthropods that prey on vertebrates. Biological Review 57:29-58.

McCranie, J. R., J. H. Townsend, and L. W. Wilson. 2003. Three snakes new to the herpetofauna of Honduras. Herpetological Review 34:391-392.

McKaye K. R. and A. Marsh. 1982. Food switching by two specialized algae-scraping cichlid fishes in Lake Malawi, Africa. Oecologica 56:245-248.

Merilanita, S., J. Tuomi, V. Jormalainen. 1999. Optimization of cryptic coloration in heterogeneous habitats. Biological Journal of the Linnean Society 67:151-161.

Mertens, R. 1952. On snail-eating snakes. Copeia 1952:279.

Meyer, A. 1989. Cost of morphological specialization: feeding performance of the two morphs in the tropically polymorphic cichlid fish, *Cichlasoma citrinellum*. Oecologia 80:431-436.

Mitchell, C. A. 2008. The ultimate field guide for South African snakes. The African Safari Serices. http://www.ultimatefieldguide.com. Downloaded 06 December 2008.

Montgomery, C. E., J. M. Ray, A. H. Savitzky, E. J. Griffith-Rodriguez, H. L. Ross, and K. R. Lips. 2007. *Sibon longifrenis* (Drab Snaileater) diet. Herpetological Review 38:343.

Motychak, J. E., E. D. Brodie, Jr., and E. D. Brodie III. 1999. Evolutionary response of predators to dangerous prey: Preadaptation and the evolution of tetrodotoxin resistance in garter snakes. Evolution 53:1528-1535.

Mulcahy, D. G. 2007. Molecular systematics of Neotropical cat-eyed snakes: a test of the monophyly of Leptodeirini (Colubridae: Dipsadinae) with implications for character evolution and biogeography. Biological Journal of the Linnaean Society 92:483-500.

Myers, C. W. 1969. The Ecological Geography of Cloud Forest in Panama. American Museum Novitates 2396:1-52.

Myers, C. W. 1982. Blunt-headed vine snakes (*Imantodes*) in Panama, including a new species and other revisionary notes. American Museum Novitates 2738:1-50.

Myers, C. W., R. D. Ibañez, and J. E. Cadle. 2007. On the uniquely fragmented distribution of a rare Panamanian snake, *Dipsas nicholsi* (Colubridae: Dipsadinae). American Museum Novitates 3554:1-18.

Nussbaum, R. A., E. D. Brodie Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.

Ovaska, K. E. and C. Engelstoft. 1999. *Contia tenuis*. Defensive behavior. Herpetological Review 30.

Peters, J. A. 1960. The snakes of the subfamily Dipsadinae. Miscellaneous Publications, Museum of Zoology number 114. University of Michigan, Ann Arbor, Michigan.

Peters, J. A. and B. Orejas-Miranda. 1970. Catalogue of the Neotropical Squamata. Part I. Snakes. U.S. National Museum Bulletin 297:1-347.

Pinou, T., S. Vicario, M. Marschner, and A. Caccone. 2004. Relict snakes of North America and their relationships with Caenophidia, using likelihood-based Bayesian methods on mitochondrial sequences. Molecular Phylogenetics and Evolution 32:563-574.

Pizzatto, L., M. Cantor, J. Lima de Oliveira, O. A. V. Marques, V. Capovilla, and M. Martins. 2008. Reproductive ecology of Dipsadine snakes, with emphasis on South American species. Herpetologica 64:168-179.

Porto, M. and R. Fernandes. 1996. Variation and natural history of the snail-eating snake *Dipsas neivai* (Colubridae: Xenodontinae). Journal of Herpetology 30:269-271.

Pough, F. H., Jr. 1964. A coral snake "mimic" eaten by a bird. Copeia 1964:223.

Pough, F. H., Jr. 1988. Mimicry and related phenomena. In Biology of the Reptilia. Vol. 16, Ecology B, Defense and Life History. Gans, C. & R. B. Huey (eds.). Alan R. Liss, New York, New York.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2003. Herpetology 3rd Edition. Benjamin Cummings. 736 pp.

Queiroz Alves, F., A. J. Suzart Argôlo, and J. Jim. 2003. *Dipsas catesbyi* (Catesby's Snail-eater) Prey. Herpetological Review 34:373-374.

Quinn, H. and J. P. Jones. 1974. Squeeze box technique for measuring snakes. Herpetological Review 5:32.

Ray, J. M. and R. B. King. 2006. The temporal and spatial scale of microevolution: fine-scale colour pattern variation in the Lake Erie watersnake, *Nerodia sipedon insularum*. Evolutionary Ecology Research 8:915-928.

Ray, J. M., B. Wilson, E. J. Griffith-Rodriquez, & H. L. Ross. *Sibon argus* (Blotched Snail Sucker) Diet. Herpetological Review. In Review.

Reagan, D. P. 1992. Congeneric species distribution and abundance in a three-dimensional habitat: The rain forest anoles of Puerto Rico. Copeia 2:392-403.

Rembold. R. 1934. *Dipsas albifrons*, Dickkopfschlange. Blatt. Aquar. Terr. 45:38-385.

Rhoades, D. F. 1979. Evolution of plant chemical defenses against herbivores. In Herbivores: Their Interaction with Secondary Plant Metabolites. Rosenthal, G. A. and D. H. Janzen (eds.). Academic Press, New York, New York.

Ridgely, R. S. and J. A. Gwynne. 1992. A Guide to the Birds of Panama. 2nd Ed. Princeton University Press, Princeton, New Jersey.

Robinson, B. W. and D. S. Wilson. 1998. Optimal foraging, specialization, and a solutions to Liem's Paradox. The American Naturalist 151:223-235.

Robinson, S. K. 1994. Habitat selections and foraging ecology of raptors in Amazonian Peru. Biotropica 26:443-458.

Roembke, J. and M. Schmidt. 1990. Setal morphology of some species of terrestrial Enchytraeidae (Oligochaeta). Transactions of the American Microscopical Society 109:44:51.

Rossman, D. A. and P. A. Myer. 1990. Behavioral and morphological adaptations for snail extraction in the North American Brown Snake (Genus *Storeria*). Journal of Herpetology 24:434-438.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2004. Avoiding Attack: The Evolutionary Ecology of Crypsis, Warming Signals. Oxford University Press, United Kingdom.

Ryan, M. J. and K. R. Lips. 2004. *Sibon argus* (NCN) diet. Herpetological Review 35:278.

Saporito, R. A., H. M. Garraffo, M. A. Donnelly, A. L. Edwards, J. T. Longino, and J. W. Daly. 2004. Formicine ants: an arthropod source for the pumiliotoxin alkaloids of dendrobatid poison frogs. Proceedings of the National Academy of Sciences 101:21:8045-8050.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinios.

Savage, J. M. and R. W. McDiarmid. 1992. Rediscovery of the Central American colubrid snake, *Sibon argus*, with comments on related species from the region. Copeia 1992:421-432.

Savitzky, A. H. 1983. Coadapted character complexes among snakes: Fossoriality, piscivory, and durophagy. American Zoologist 23:397-409.

Sazima, I. 1988. Um estudo de biologia comportamental da jararaca, *Bothrops jararaca*, com uso de marcas naturais. Mem. Inst. Butantan 50:88-99.

Sazima, I. 1989. Feeding behavior of the snail-eating snake, *Dipsas indica*. Journal of Herpetology 23:464-468.

Sazima, I. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in southeastern Brazil. In Biology of Pitvipers. Campbell, J. A. and E. D. Brodie (eds). Selva, Tyler. 199-216.

Schroeder, F. C., A. González, T. Eisner, and J. Meinwald. 1999. Miriamin, a defensive diterpene from the eggs of a land slug (*Arion* sp.). Proceedings of the National Academy of Sciences 96:13620-13525.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Shaw, C. E. and S. Campbell. 1974. Snakes of the American West. Alfred A. Knopf Publisher, New York, New York.

Shine, R., P. S. Harlow, W. R. Branch, and J. K. Webb. 1996. Life on the lowest branch: sexual dimorphism, diet, and reproductive biology of an African twig snake *Thelotornis capensis* (Serpentes, Colubridae). Copeia 1996:290-299.

Smith, A. P. 1973. Stratification of temperate and tropical forests. The American Naturalist 107:671-683.

Smith, H. M. 1943. Summary of the collections of snakes and crocodilians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. Proceedings of the U.S. National Museum 93:393-504.

Smith, H. M. and F. N. White. 1955. Adrenal enlargement and its significance in the hognose snakes (Heterodon). Herpetologica 11:137-144.

Smith, N. G. 1969. Avian predation of coral snakes. Copeia 1969:402-404.

Solórzano, A. 2002. Una nueva especie de serpiente del género *Sibon* (Serpentes:Colubridae) de la vertiente del Caribe de Costa Rica. Revista de Biología Tropical 49:1111-1120.

Solórzano, A. 2004. Serpientes de Costa Rica: Distribución, Taxonomía, e Historia Natural/Snakes of Costa Rica: Distribution, Taxonomy, and Natural History. Instituto Nacional de Biodiversidad. 792 pp.

Sousa do Amaral, J. P. 1999. Lip-curling in redbelly snakes (*Storeria occipitomaculata*): functional morphology and ecological significance. Journal of Zoology of London 248:289-293.

Stebbins, R. C. 1972. Amphibians and Reptiles of California. University of California Press, Berkeley, California.

Stiles, F. G. and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Comstock Publishing Associates. Cornell University Press, Ithaca, New York.

Stuart, L. C. 1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Miscellaneous Publications of the Museum of Zoology Number 69. University of Michigan, Ann Arbor, Michiga.

Swanson, B. O., A. C. Gibb, J. C. Marks, and D. A. Hendrickson. 2003. Trophic polymorphism and behavioral differences decrease intraspecific competition in a cichlid, *Herichthys minckleyi*. Ecology 84: 1441-1446.

Taggart, T. W., B. I. Crother, and M. E. White. 2001. Palm-pitviper (*Bothriechis*) phylogeny, mtDNA, and consilience. Cladistics 17:355-370.

Taylor, W. E. 1892. Catalogue of the snakes of Nebraska with notes on their habits and distribution. The American Naturalist 26:742-752.

Trapido, H. 1944. The snakes of the genus *Storeria*. The American Midland Naturalist 31:1-84.

Tu, M., S. Wang, and Y. Lin. 2000. No divergence of habitat selection between male and female arboreal snakes, *Trimeresurus s. stejnegeri*. Zoological Studies 39:91-98.

Vidal, N., S. G. Kindl, A. Wong, and S. B. Hedges. 2000. Phylogenetic relationships of Xenodontinae snakes inferred from 12S and 16S ribosomal RNA sequences. Molecular Phylogenetics and Evolution 14:389-402.

Vitt, L. J. and L. D. Vangilder. 1983. Ecology of a snake community in northeastern Brazil. Amphibia-Reptilia 4:273-296.

Wallach, V. 1995. Revalidation of the genus *Tropidodipsas* Günther, with notes on the Dipsadini and Nothopsini (Serpentes: Colubridae). Journal of Herpetology 29:476-481.

Werman, S. D, B. I. Crother, and M. E. White. 1999. Phylogeny of some Middle American pitvipers based on a cladistic analysis of mitochondrial 12S and 16S DNVA sequence information. Contemporary Herpetology 1999. http://www.cnah.org/CH/1999/3/index.htm. Downloaded 22 December 2008.

Wilson, L. D. and J. H. Townsend. 2006. The herpetofauna of the rainforests of Honduras. Caribbean Journal of Science 42:88-113.

Willson, J. D. and M. E. Dorcas. 2004. Aspects of the ecology of small fossorial snakes in the western Piedmont of North Carolina. Southeastern Naturalist 3:1-12.

Zaher, H. 2000. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monopyletic Xenodontinae and a reappraisal of colubroid hemipenes. Bulletin of the American Museum of Natural History 240:1-168.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.

Zweifel, R. G. 1954. Adaptation to feeding in the snakes *Contia tenuis*. Copeia 1954:299-300.

VITA

Julie M. Ray;
Department of Biological Sciences; 110 Mills Godwin Building; Old Dominion University; Norfolk, Virginia 23529 USA

Education

Doctorate of Philosophy in Ecological Sciences – Old Dominion University (Aug. 2009)
Dissertation: Ecology of a Neotropical arboreal snake assemblage and diet and defensive tactics of New World mollusk-eating snakes.

Masters of Science in Biological Sciences - Northern Illinois University (May 2004)
Thesis: Temporal Variation in Color Pattern and Ecological Effects of the Exotic Round Goby on Lake Erie watersnakes, *Nerodia sipedon insularum*

Bachelors of Science – University of Wisconsin – Stevens Point (May 2000)
Biology Major and Broad Field Science Minor

Academic Achievements

2007 Career Achievement Award; Wisconsin Division of Vocational Rehabilitation
2006 Seibert Award of Evolution; Joint Meeting of Ichthyologists and Herpetologist
2006 Best Poster Presentation; Southeastern Ecology and Evolution Conference
2008 First place presentation, Spring Symposium; Old Dominion University
2006 Best Biological Sciences Presentation, Spring Symposium; Old Dominion University
2005-2006 University Fellowship; Old Dominion University

Publications

Walley, H.D., R.B. King, **J.M. Ray**, & T.L. Wusterbarth. 2009. *Nerodia sipedon.* Catalogue of American Amphibians and Reptiles. *In. Press.*

King, R.B., K.M. Stanford, & **J.M. Ray**. 2008. Reproductive consequences of a changing prey base in island watersnakes. South American Journal of Herpetology. *In press.*

Montgomery, C.E., **J.M. Ray**, A.H. Savitzky, E.R. Griffith-Rodriquez, H.L. Ross, & K.R. Lips. 2007. *Sibon longifrenis* (Drab Mollusk-eater) Diet. Herpetological Review 38(3):343.

Ray, J.M. & R.B. King. 2006. The temporal and spatial scale of microevolution: Fine-scale color pattern variation in the Lake Erie watersnake, *Nerodia sipedon insularum*. Evolutionary Ecology Research 8:915-928.

King R.B., **J.M. Ray** & K.M. Stanford. 2006. Gorging on Gobies: Beneficial Effects of Alien Prey on a Threatened Vertebrate. Canadian Journal of Zoology 84:108-115.

Ray, J.M. 2004. Temporal Variation in Color Pattern and Ecological Effects of the Exotic Round Goby on the Lake Erie Watersnake, *Nerodia sipedon insularum.* Northern Illinois University. Unpublished Master of Science Thesis.