NATURAL HISTORY AND CONSERVATION OF THE EYELASH PALM-PITVIPER (*BOTHRIECHIS SCHLEGELII*) IN WESTERN PANAMÁ

Except where reference is made to others, the work described in this thesis is my own or was done in collaboration with my advisory committee. This thesis does not include proprietary or classified information.

Geoffrey Gordon Sorrell

Certificate of Approval:

Sharon M. Hermann
Visiting Assistant Professor
Biological Sciences

Craig Guyer, Chair
Professor
Biological Sciences

George W. Folkerts
Professor
Biological Sciences

Mary T. Mendonça
Associate Professor
Biological Sciences

George T. Flowers
Interim Dean
Graduate School

NATURAL HISTORY AND CONSERVATION OF THE EYELASH PALM-PITVIPER (*BOTHRIECHIS SCHLEGELII*) IN WESTERN PANAMÁ

Geoffrey Gordon Sorrell

A Thesis

Submitted to

the Graduate Faculty of

Auburn University

in Partial Fulfillment of the

Requirements for the

Degree of

Master of Science

Auburn, Alabama
December 17, 2007

NATURAL HISTORY AND CONSERVATION OF THE EYELASH PALM-PITVIPER (*BOTHRIECHIS SCHLEGELII*) IN WESTERN PANAMÁ

Geoffrey Gordon Sorrell

Signature of Author

Date of Graduation

VITA

Geoffrey Gordon Sorrell, son of Fredrick Gordon Sorrell III and Fay McClendon Newton, was born 28, April 1976 in Durham, North Carolina. He graduated from Riverside High School, Durham, North Carolina in 1994. He entered Auburn University in fall of the same year and graduated with a Bachelor's Degree of Science in Wildlife Science in March 2000. During the next several years he worked on various field projects in Central America, the southeastern U.S. and in California. Several of the projects that he worked on during this period were directed by Craig Guyer of Auburn University. It was this association Dr. Guyer that lead, in large part, to an opportunity for graduate study. In January of 2004 he entered graduate school at Auburn University in the Department of Biological Sciences.

THESIS ABSTRACT

NATURAL HISTORY AND CONSERVATION OF THE EYELASH PALM-PITVIPER (*BOTHRIECHIS SCHLEGELII*) IN WESTERN PANAMÁ

Geoffrey Gordon Sorrell

Master of Science, 17 December 2007
(B.S., Auburn University, 2000)

66 Typed Pages

Directed by Craig Guyer

The focus of this thesis was to examine various components of the natural history, ecology, and conservation biology of the *Bothriechis schlegelii*. The sections that follow include studies of foraging ecology, demography, and effects of fragmentation on *Bothriechis schlegelii*.

In the first section I examined the effects of color, body size, and sex on growth and survival in an arboreal Neotropical snake, the eyelash palm-pitviper, *Bothriechis schlegelii*. This species exhibits polychromatism in populations throughout its range. Growth and survival were estimated during a seven-year, mark-recapture study of a population in western Panamá. My results indicate that body size has the strongest influence on growth and that sex and color morph have little impact on this variable. Sex had the greatest ability to explain variation in survival whereas body size and color were less informative. However, sex and body size were correlated in this species because females grew to a larger size than males.

The second section focuses on movement and foraging ecology of *Bothriechis schlegelii*. This species is reported to be a nocturnal ambush predator that preys upon a wide variety of vertebrates. However, this study demonstrates that *B. schlegelii* has a greater temporal activity range than previously documented. Specifically, I document that this snake moves most frequently at night, is capable of capturing mobile prey from daytime perches, and consumes diurnally- and nocturnally-active prey. An ability to consume prey during both night and day increases the importance of the role of *B. schlegelii* as a predator of small vertebrates.

The final section of my thesis examines the response of *Bothriechis schlegelii* to anthropogenic fragmentation. Cattle production has had a widespread impact on the Neotropical landscape, which has increased in closing decades of the twentieth century. Although the deleterious effects of conversion of native vegetation to pasture have been acknowledged, research on mitigation of such practices is lacking. In this study I focus on the use of tree islands in pasture by an arboreal predator, the eyelash palm-pitviper (*Bothriechis schlegelii*). The effects of tree island isolation, size, and structural heterogeneity, on snake occupancy were measured. My results indicate that isolation form intact forest, and the structural heterogeneity found within islands were the most important predictors of snake occupancy. Management implications are discussed in light of these findings.

ACKNOWLEDGMENTS

I am very thankful for the opportunity to pursue graduate studies at Auburn. I thank my advisor, Craig Guyer, for the patience, insight, and understanding with which he leads and mentors our lab. Without Craig’s interest in my work and in my professional development I would have not have had the success that I have enjoyed at Auburn.

I also thank my committee, George Folkerts, Mary Mendonça, and Sharon Hermann for their valuable suggestions throughout my academic career. Barry Grand was very helpful with certain aspects of this thesis. My experience at Auburn has been positively shaped by my lab-mates: S. Boback, M. Williams, C. Romagosa, R. Birkhead, K. Barrett, J. Steffen, T. Kesler, S. Hoss, A. Rall, and A. Sorenson. My parents Fred and Fay, and other family members provided endless support and encouragement. Lesley de Souza has provided love and encouragement as well as editorial and fieldwork assistance and I hope to reciprocate in all of those categories as we move through life together. Thanks to T. Jones, S. Lindey, J. Roper, K. Keefe, R. Babb, J. Burkhart, R. Serrano, and G. Serrano for assistance with fieldwork. I also thank P. Lahanas and the students and staff of the Institute for Tropical Ecology and Conservation for logistical and field support. I thank A. de la Lastra M. for allowing access to the field site. For funding I thank the Chicago Herpetological Society, the American Society of Ichthyologists and Herpetologists, and the Auburn Univ. College of Agriculture International Scholars Program.

Style manual or journal used:

Copeia (Chapter 1)

Copeia (Chapter 2)

Copeia (Chapter 3)

Computer software used:

SAS Statistical Package, R Statistical Package, Microsoft Word, Microsoft Excel, ARCGIS®

TABLE OF CONTENTS

CHAPTER II. THE INFLUENCE OF COLOR POLYMORPHISM, BODY SIZE, AND SEX, ON GROWTH AND SURVIVAL OF *BOTHREICHIS SCHLEGELII*

CHAPTER III. DIEL MOVEMENT AND PREDATION ACTIVITY PATTERNS OF THE EYELASH PALM-PITVIPER (*BOTHREICHIS SCHLEGELII*)

CHAPTER IV. PATTERNS OF USE OF ANTHROPOGENICALLY-FRAGMENTED HABITAT BY AN ARBOREAL PITVIPER

LIST OF TABLES

CHAPTER II.

CHAPTER III.

CHAPTER IV.

LIST OF FIGURES

CHAPTER II.

CHAPTER III.

CHAPTER IV.

CHAPTER I

INTRODUCTION

The importance of studying the ecology of predators is often acknowledged, yet little work on this trophic level has occurred in the tropics (Greene, 1988). The impact of predators on terrestrial communities may range from direct effects on prey populations to indirect influences on processes such as pollination and seed dispersal (Greene and Santana, 1983; Greene, 1997). The potential for multiple direct and indirect effects exists, especially where generalist predators are present in high densities (Hairston et al., 1960). Although many theories concerning the role of predators have been developed the basic natural history of many of these organisms remains poorly studied, especially in tropical forests (Sih et al., 1985).

It is well documented that the fauna of tropical forests are generally the most diverse of any terrestrial habitat type. This trend is reflected in the predator assemblages present in the tropics. Tropical squamates, snakes in particular, represent an extremely diverse group of vertebrate predators. At some sites, the richness of snake species that prey upon vertebrates is approximately equal to that of all other vertebrate predators (Greene, 1988). This fact highlights the importance of research with snakes in general (Seigel, 1993), especially tropical species.

Among the groups of Neotropical snakes that are least studied are the arboreal viperids. Of this suite of snakes, the eyelash palm-pitviper (*Bothriechis schlegelii*) is the most widely distributed. Although this snake ranges throughout much of the lowland and montane wet forests of Central America and northern South America, there have been no population level studies of this species (Campbell and Lamar, 2004). This species is the basal member of the *Bothriechis* clade (Crother et al., 1992), and has the broadest distribution of any of the species in this genus. This medium-sized pit viper (maximum total length of 80 cm) ranges from Chiapas, Mexico to northwestern Ecuador and western Venezuela, where it is widely distributed in lowland and premontane wet forests (Campbell and Lamar, 1989; Campbell and Lamar, 2004). Coloration is extremely variable with olive green being the most common ground color. Other color morphs include grey, brown, or yellow specimens. Extreme color variation may be exhibited within populations, and within litters. These colors provide crypsis for *B. schlegelii* in its arboreal habitat where it is a sit-and-wait predator that is often described as being nocturnal (Savage, 2002; Lee, 2000). *Bothriechis schlegelii* is known to consume frogs, lizards, birds, bats, and other small mammals (Greene, 1988).

Despite the wide distribution of *B. schlegelii* all published accounts are based on a relatively few isolated observations of individuals in the wild or captive animals. The logistic difficulties associated with observing and working with arboreal organisms are likely the principal reason why there is a paucity of literature on organisms like *B. schlegelii* (Kays and Allison, 1998; Henderson, 2002; Henderson, 1974). To fill this void, I have investigated the demographics, natural history, and conservation of *B. schlegelii* on the Soropta Peninsula, Bocas del Toro, Panamá. The high density of snakes at the study site, along with its unique arrangement of habitat types provides an extraordinary opportunity to study the spatial ecology of this tropical predator.

The general objective of this work is to provide information about a tropical arboreal snake that is potentially an important generalist predator throughout its range. Specifically I have addressed the following questions: 1) How does color, size, and sex influence growth and survival? 2) What predictions can be made about foraging activity based on diet? 3) Which habitat characteristics influence snake occupancy of tree islands in forest fragmented by cattle pasture?

CHAPTER II

THE INFLUENCE OF POLYCHROMATISM, BODY SIZE, AND SEX, ON GROWTH AND SURVIVAL OF *BOTHREICHIS SCHLEGELII*

ABSTRACT

In this study I examined the effects of color, body size, and sex on growth and survival in an arboreal Neotropical snake, the eyelash palm-pitviper, *Bothriechis schlegelii*. This species exhibits polychromatism in populations throughout its range. Growth and survival were estimated during a seven-year, mark-recapture study of a population in western Panamá. My results indicate that body size has the strongest influence on growth and that sex and color morph have little impact on this variable. Sex had the greatest ability to explain variation in survival whereas body size and color were less informative. However, sex and body size were correlated in this species because females grew to a larger size than males. So, the influence of these two variables on demographic parameters was difficult to disentangle.

INTRODUCTION

Polychromatism has evolved independently in a number of lineages, and it has been studied in a variety of vertebrate taxa (Shine et al., 1998a). The maintenance of multiple color patterns in a given population suggests that there is an adaptive significance associated with each pattern (Madsen and Shine, 1992). Therefore, certain aspects of a species' biology must be correlated to its color pattern in order for multiple color states to persist. Biological traits that vary with color pattern include body size and shape, diet, energy stores, parasite loads, predation rates, and sex ratios (King, 1992; Andren and Nilson, 1981; Shine et al., 1998a). Many of these traits have the potential to influence growth rates as well as survival.

Squamates exhibit polychromatism in a number of divergent lineages. In snakes there are polychromatic species in at least five families. The family Viperidae contains more such species than the other four families combined, perhaps because vipers are ambush foragers (Shine et al., 1998a). *Bothriechis schlegelii*, an arboreal snake that relies in part on ambush foraging (Sorrell, *In revision*), is unique among Neotropical viperids in that it exhibits pronounced polychromatism. Color patterns from a single population range from yellow individuals that are typically monochromatic to individuals whose dorsal coloration exhibits variations of green, gray or brown. Unlike other arboreal species (eg. *Corallus caninus*, *Bothriechis lateralis*), *B. schlegelii* does not exhibit an ontogenetic shift in coloration. Furthermore there is no obvious pattern of sexual dichromatism in *B. schlegelii* such as that present in other viperids (eg. *Agkistrodon taylori*, *Vipera ammodytes*, and *V. berus*). Therefore, the presence of multiple color patterns that are fixed at birth and do not appear to be sex-linked allows us to examine whether *B. schlegelii* exhibits color- size- or sex-specific growth or survival rates.

MATERIALS AND METHODS

Study species.-Bothriechis schlegelii is a small Neotropical viper that attains a maximum total length of approximately 80 cm. Neonates average 18.5 cm in total length [mean for 10 litters reported in (Campbell and Lamar, 2004)]. Although females are known to be "longer and more robust than males" (Solorzano, 2004), an investigation of sexual size dimorphism has not been conducted for any snake in this genus.

Site description.-This study was conducted on the Soropta Peninsula, Bocas del Toro, Panamá during 15 July - 28 August 1999, 6 July - 23 August 2000, 9 June - 2 July 2001, 5 May - 14 June 2002, 21 June - 12 August 2003, 22 June - 14 August 2004, and 25 March - 12 May 2005. I worked in primary forest where the habitat type is best characterized as Atlantic lowland tropical moist forest (Holdridge, 1967). Common canopy and emergent trees on the forested portion of the site include *Apeiba membrenacea*, *Prioria copaifera*, and *Virola surinamensis*. *Cecropia insignis* is also commonplace in the midstory and subcanopy. Among the more abundant species of midstory trees are *Brosimum* sp., *Heisteria longipes*, *Protium panamense*, and *Unonopsis pittieri*. Large palms include *Euterpe precatoria* and *Welfia regia*. Understory palms include *Geonoma* spp.

Field methods.-Snakes were located during visual encounter surveys, which were conducted during the day. Surveys most often involved two observers. The entire site was surveyed every two days, on average. Snakes were captured using tongs or hooks, and restrained in clear plastic tubes during processing. Data collected included weight, snout-vent length (SVL), tail length, sex, and color pattern. Individuals below 27 cm SVL were recorded as juveniles due to difficulty in distinguishing males from females at this size. All snakes were marked in year one with ventral scale clips, and all adults in years 2-7 were marked with Passive Integrated Transponder (PIT) tags. All neonates and juveniles below 28 cm SVL and 8 g were scale clipped due to the potential danger of injecting PIT tags in animals of this size.

Data analysis.-A G-test for goodness-of-fit was used to determine if the sex and color-pattern ratios observed in the study population differed from the null expectation of 1:1. A G-test for association was used to determine if proportion of color patterns differed within males, females, and juveniles. A t-test was used to examine differences in average SVL between males and females. Analysis of covariance (ANCOVA) was used to compare regressions of growth rate on mean SVL for males and females as well as for yellow and brown/gray snakes (SAS Version 9.1). An alpha of 0.10 was used for all tests. Estimates of survival and detectability were generated using the Huggins Closed Capture model within the Robust Designs set of models in Program MARK (version 4.3). Three covariate categories were entered into the design matrix. Sex could be consistently determined by probing the tail for the presence of hemipenes for snakes > 26 cm SVL; animals below this size were referred to as juveniles, although the size at sexual maturity is unknown. Color was treated as a binary covariate, with yellow and brown/gray colors as the two categories. Brown snakes and gray snakes were combined into a single category because they are cryptic against similar backgrounds such as tree buttresses and trunks. Size (SVL) was entered into the matrix for each year that a snake was captured, which accounted for growth. Akaike's Information Criterion was used to evaluate competing models and delta AIC values less than 2.0 were used distinguish informative from uninformative models (Burnham and Anderson, 2002).

RESULTS

Sex and color morph ratios.- A G-test for goodness-of-fit indicated that there were significantly more males (n = 67) and fewer juveniles (n = 25) in the population than females (n = 45; G = 19.79, p = < 0.0001, df = 2). Similarly, yellow snakes (n = 85) were more abundant than gray/brown snakes (n = 52;G = 12.5, p = 0.0004, df = 1). A G-test of association documented an interaction between color and sex (G = 8.41, p = 0.0149, df = 2). However, this pattern was driven by the high proportion of yellow juveniles compared to adults (Table 1). When juveniles were omitted, no such interaction remained (G = 1.09, p = 0.2974, df = 1).

Growth rates and sexual size dimorphism.-Growth rates correlated with SVL (F = 4.69, p = 0.03), however slopes and elevations did not differ between regressions for males (n = 26) and females (n = 14; F = 0.91 p = 0.3 for slopes; F = 0.65, p = 0.4 for elevations). The parameters associated with the regression of growth rate for yellow individuals (n = 24) and that of brown/gray individuals (n = 16; F = 0.92 p = 0.3 for slopes; F = 0.96, p = 0.5 for elevations) did not differ (Figure 1). Results for a test of an interaction between SVL, sex, and color were not significant (F = 0.49, p = 0.4). For adult snakes, females attained a larger body size (mean SVL = 39.38 cm, range 24 - 62 cm, n = 42) than males (mean SVL = 36.69 cm, range 25 - 48 cm, n = 60, t = 1.179, p = 0.077).

Survival.-Estimates for survival were based on 303 captures of 123 individuals. The most parsimonious model of survival included only sex (males, females, and juveniles) as a covariate. However, models that included sex plus SVL and sex plus color also yielded informative models (Table 2). Survival estimates for the groups were highest for males followed by females and juveniles (Table 3).

DISCUSSION

The population biology of *B. schlegelii* on the Soropta Peninsula is characterized by three interesting patterns. First, the relative number of yellow snakes changes dramatically from juvenile to adult. Second, adult females are, on average, larger than males. Third, the sex ratio of adults is skewed towards males. These three patterns suggest that growth, survival, and/or detectability differ among color and sex groups.

The reduction in the number of yellow individuals as snakes develop from the juvenile to the adult stage could result from decreased growth, decreased survival, or increased immigration/emigration of yellow juveniles relative to snakes of other ages and colors. Of these explanations we have no reason so suspect that color morphs migrate at differing rates and we found no support for a difference in growth rate between the two color groups. Thus, color in *B. schlegelii* does not influence foraging success or feeding frequency in a way that would result in growth rate differences between the color patterns as it does in other species (Shine et al., 1998a). However, this finding differs from that for *Vipera berus*, in which a genetic link between color and growth was documented (Madsen and Shine, 1992).

We found limited support for the hypothesis that the reduced frequency of yellow snakes in adults results from differing survival rates between the two color groups. Our data indicate that juvenile survival was markedly lower than that of adult males and females. This pattern of low juvenile survival relative to adults is similar to that observed in other studies that employed similar analyses (Webb et al., 2003; Diller and Wallace, 2002). Although color was not included in the most parsimonious survival model it was included in a competitive model along with sex. Body size (SVL) was also retained in the competitive models (along with sex) but the three parameter model (size, sex, and color) was uninformative. Thus, our data provide only weak support for the hypothesis that yellow juveniles survive at a lower rate than brown and gray juveniles.

Why are yellow and brown/gray adults equally abundant in the study population? One possible explanation is that predation on *B. schlegelii* is frequency dependent. Under this interpretation, yellow and brown/gray adults would have to be equally cryptic in their environment and thus subject to equal predation pressure. An alternative interpretation, based on the theory of disruptive selection, suggests that species experiencing variable light conditions benefit from polychromatism (Galeotti et al., 2003). Under this scenario, the structural complexity of a lowland tropical forest creates many combinations of perch background colors and light environments (Endler, 1993) that offer concealment for the various color patterns exhibited by *B. schlegelii*. For example, a yellow snake may be obvious to predators in some settings while being cryptic in other perch positions. Because this species utilizes a range of perches and heights and exhibits a range of color patterns the population as a whole might benefit because predators cannot develop a well-defined search image.

Although the two color forms were equally abundant in the adult population the two sexes were not. Males were more abundant than females but growth and survival rates did not differ between sexes. This is interesting because females reach a greater maximum size in this species, as they do in many other snake species (Shine, 1978). These features might be used to describe a female-biased sexual size dimorphism in *B. schlegelii*. However additional data do not support this conclusion because males and females grow at similar rates. Thus, our data are consistent with taxa in which males and females grow at similar rates, but females mature later than males, resulting in a male-biased sex ratio and females reaching larger sizes than males (Madsen and Shine, 1994; Gibbons, 1990). The only trend that emerged from the analysis of growth was that the smallest (and presumably youngest) animals exhibited the highest growth rates, which is consistent with growth patterns observed in many other reptiles (Dunham and Gibbons, 1990).

Although *B. schlegelii* is well known for its pronounced color variation, our data indicate that the different color patterns experience similar natural histories. The fact that polychromatism persists in *B. schlegelii* indicates that color variation in this species has adaptive significance. In a review of polychromatism in snakes by Shine et al. (1998) 50% of the 18 species (including *B. schlegelii*) listed are semiarboreal or fully arboreal. Because the proportion of arboreal species in most snakes faunas is much less than 50% (e.g. Guyer and Donnelly, 1990), polychromatism appears to be an a more frequent phenomena in snakes that occupy arboreal habits (Lillywhite and Henderson, 1993). *Bothriechis schlegelii* is known to hunt day and night across a range of heights and microhabitat types (Sorrell, unpubl. ms.). Such plasticity in foraging behavior may benefit from the maintenance of the pronounced polychromatism observed in this species.

Table 1. Relative abundance of color patterns among adult male, adult female, and juvenile *B. schlegelii* at the Soropta Peninsula, Panamá.

Color	Sex		
	Juvenile	Male	Female
Yellow	22	35	28
Brown/Gray	3	32	17

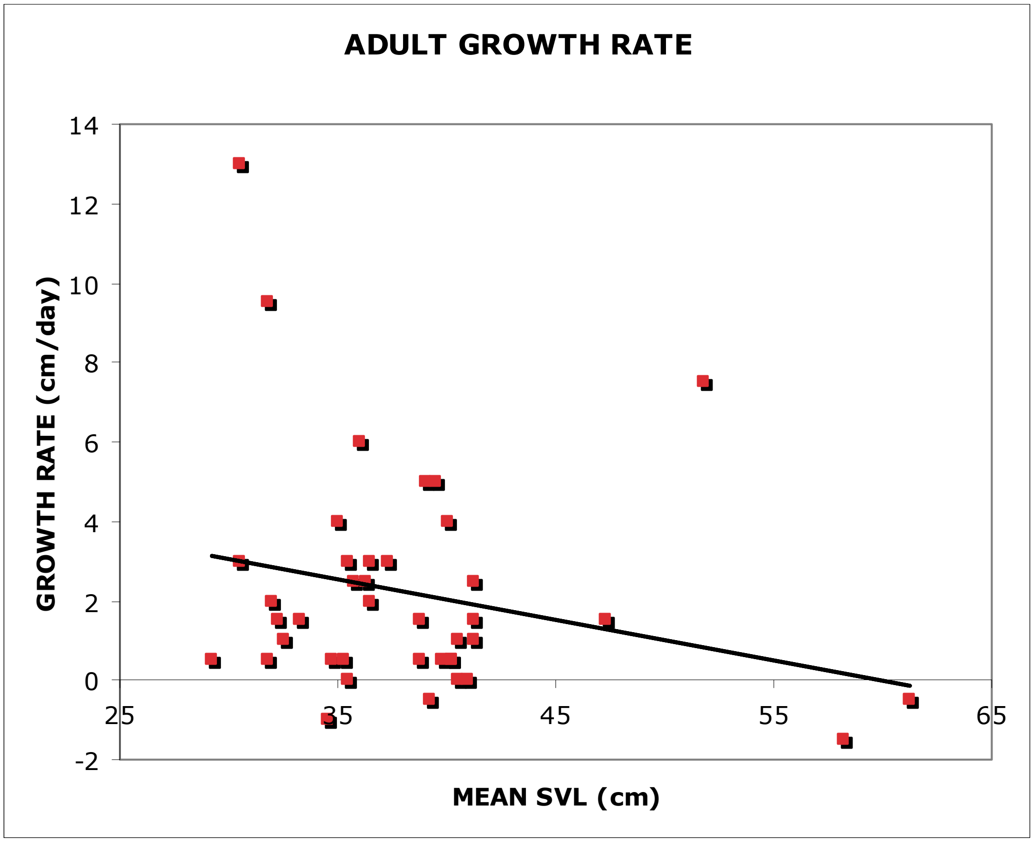

Figure 1 Growth data for *B. schlegelii* at the Soropta Peninsula, Panama. Regression parameters: $y = -0.1024x + 6.1333$, $R^2 = 0.0574$).

Table 2. Summary of Huggins closed-capture, mark-recapture models run in Program MARK.

Model	AIC	ΔAIC	Akaike weight
Sex	1399.08	0	0.421
Sex and body size	1399.8	0.72	0.294
Sex and color	1401	1.92	0.161
Sex, body size, and color	1401.52	2.45	0.124

Table 3. Beta values for *Bothriechis schlegelii* by sex. These values are a statistical surrogate for survival rates and they are based on the link logit function of the most parsimonious model generated by Program MARK.

Sex	Beta values	SE
Male	4.058	219.03
Female	3.472	207.79
Juv.	-3.015	197.69

CHAPTER III

DIEL MOVEMENT AND PREDATION ACTIVITY PATTERNS OF THE EYELASH PALM-PITVIPER (*BOTHRIECHIS SCHLEGELII*)

ABSTRACT

The eyelash palm-pitviper, *Bothriechis schlegelii*, is reported to be a nocturnal ambush predator that preys upon a wide variety of vertebrates. However, this study demonstrates that *B. schlegelii* has a greater temporal activity range than previously documented. Specifically, I document that this snake moves most frequently at night, is capable of capturing mobile prey from daytime perches, and consumes diurnally- and nocturnally-active prey. An ability to consume prey during both night and day increases the importance of the role of *B. schlegelii* as a predator of small vertebrates.

INTRODUCTION

Understanding movement and foraging activity are fundamental to gaining insights into the ecology of any predator. Although such information is basic, it is lacking for many species, especially in tropical systems (Kays and Allison, 1998). Development of a better understanding of the activities of predators is essential because of the potential importance of trophic level in ecosystem regulation (Terborgh et al., 2006).

Among tropical predators, reptiles in general, and snakes in particular, are rarely studied despite the fact that they are an extremely diverse and abundant group (Greene, 1988). An essential first step towards predicting how a snake fits into its environment is development of a working knowledge of its natural history. A rudiment of such information is determination of whether an animal is active by day or by night. Such a determination is frequently based on the portion of the diel cycle during which the species in question is most frequently observed to move. This use of a diurnal/nocturnal dichotomy suggests that if an animal is not moving then it must be sleeping or resting. This assumption is reasonable for animals that must move about to acquire prey. For animals that employ an ambush or sit-and-wait strategy it becomes more difficult to determine whether an immobile animal is resting or hunting. Snakes, especially of the family Viperidae, exemplify extreme cases of sit-and-wait predatory tactics. Due to low metabolic rates, vipers can remain motionless for long periods waiting for prey to approach (Greene, 1997). Although such predators are assumed to be hunting, it is difficult to determine this by observation alone. Thus, diel activity patterns are complex, and natural history studies that document biologically relevant activities during both phases of the diel cycle are needed to interpret diel patterns.

In this work I examined movement and predatory activity in the eyelash palm-pitviper (*Bothriechis schlegelii*) during day and night observations. Additionally, diet analysis and experimental prey introduction techniques were employed to infer patterns of movement and to test the ability of individuals to respond to potential prey. Specific questions of interest were: 1) is *B. schlegelii* active, in terms of both locomotor and predatory activity, throughout the diel cycle and 2) what does diet suggest about diel activity pattern.

MATERIAL AND METHODS

Study organism.-The eyelash palm-pitviper, *Bothriechis schlegelii*, has been described to be a nocturnal, arboreal snake that feeds on small vertebrates including frogs, lizards, birds, bats, rodents, and marsupials (Savage, 2002; Lee, 2000; Greene, 1988; Campbell and Lamar, 2004). This medium-sized pitviper (maximum total length of ~80 cm) ranges from Chiapas, Mexico to northwestern Ecuador and western Venezuela, where it inhabits lowland and premontane wet forests (Campbell and Lamar, 2004).

Site description.- This study was conducted on the Soropta Peninsula, Bocas del Toro, Panamá during 15 July - 28 August 1999, 6 July - 23 August 2000, 9 June - 2 July 2001, 5 May - 14 June 2002, 21 June - 12 August 2003, 22 June - 14 August 2004, and 25 March - 12 May 2005. The site is part of a farm that is mostly undisturbed forest, but also contains pastureland. The general habitat type is best characterized as Atlantic lowland tropical moist forest (Holdridge, 1967). Common canopy and emergent trees at this site include *Genipa americana* (Rubiaceae), *Luehea seemannii* (Tiliaceae), *Pachira aquatica* (Bombacaceae), *Prioria copaifera* (Fabaceae), and *Virola surinamensis* (Myristicaceae). The elevation ranges from 0-10 m above sea level.

Movement patterns.- Data were generated using two methods. The first method was based on repeated observations of the same individual within a set period of time. One pair of repeated observations was made during daylight hours (1000-1700 hr; n = 9; same day) and the other pair consisted of one sighting during the afternoon (1400-1700 hr) and the other that night (2000-2200; n = 18; same night). During the second observation of each set I noted whether a snake was in the same location or had moved. A G-test of independence was used to test the null hypothesis of no difference in the proportion of individuals moving for same-day and same-night samples.

The second method involved observations of individual *B. schlegelii* during visual-encounter surveys for which time of day (n = 111 individuals, 501 total observations of) or night (n = 19 individuals, 25 total observations), and activity status (sedentary or mobile) were noted. A G-test of independence was used to test the null hypothesis of no difference in the proportion of individuals observed moving during the day versus at night. Alpha was set at 0.05 for both tests.

Perch residency.- This data was collected as an ancillary portion of a mark-recapture study where all individuals were painted with a unique number using a non-toxic paint marker during processing. The number of consecutive sampling occasions during which a snake was observed at the same perch site was used to determine perch residency time. This series included the first post-release observation of an individual and all subsequent daytime observations. Snakes that were observed only once at a perch were scored as 0, individuals that were observed on two consecutive occasions at the same perch location were scored as 1, and so on.

Diet records.-Information on the diet of *B. schlegelii* was gathered from the literature and by palpation of live individuals captured during this study. Prey items recovered were identified to species when possible.

Prey introductions.-This experiment consisted of 16 trials, each with a different snake. *Norops limifrons* was used as prey because it is a diurnal anole that is commonly eaten by

B. schlegelii (pers. obs.). Each snake was given one opportunity to respond to the prey item and anoles were not used in more than one trial. Anoles were captured by hand and immediately placed in a plastic bag with leaf litter (held captive less than eight hours) prior to being introduced as a potential prey item. Of snakes encountered during this work, only those that were in a hunting posture were used. Two criteria were used collectively to define a hunting posture: 1) the anterior half of the snake's body was in a tight figure-eight or S-shaped coil (Campbell and Lamar, 2004) and 2) the snake was facing an object that could serve as a prey runway (e.g., liana, tree bole, or tree buttress). My observations indicate that, by day, *B. schlegelii* is most frequently located in a hunting posture (85.8%, n = 497 total observations of 108 individuals). Thus, the individuals selected for prey introductions represent the vast majority of diurnal observations.

Introductions were made via a clear plastic tube connected to a polyvinyl chloride (PVC) pipe. The clear tube facilitated exact placement of the anole by allowing observation just prior to introduction. The combined length of this assembly was approximately 2 m, with an approximate diameter of 3 cm. This length was chosen so that disturbance to the snake would be minimized, yet allow for controlled placement of each prey item. During each introduction a single anole was placed into the PVC end of the tube and prodded with a dowel to exit the opposite (clear) end near a perched snake. All trials took place between 1000-1700 hr.

Each introduction was categorized in terms of the snake response; either the snake struck at the anole or it did not. The response of the snake was recorded after the prey item moved to within 10 cm of the snake. Additionally, each snake was palpated in order to detect any prey item that had recently been ingested prior to the trial. Snakes containing prey were excluded from the experiment. This was done in an attempt to remove the confounding effects of satiation. The results of this experiment were analyzed using a G-test of goodness of fit and examined the null hypothesis that strike and no-strike responses occurred with equal frequency. Alpha was set at 0.05.

RESULTS

Movement patterns.-Series of repeated observations during same-day and same-night periods indicate that snakes were significantly more likely to move at night ($G = 6.3$, $\alpha = 0.012$; Table 1A). The numbers of individuals moving during the day or night reinforce the above results. These data showed that a greater percentage of *B. schlegelii* were moving when first observed during the night than during the day (G-test for independence, $G = 4.46$, $\alpha = 0.035$; Table 1B). Snakes frequently changed perch sites between observations, presumably at night. Of the 50 snakes observed over multiple consecutive sampling days, 68% were not relocated at the same perch site the next day, suggesting that the majority of snakes move each night (Fig. 2).

Diet records.-A total of 10 prey items representing 7 taxa were recovered from snakes in this study; 5 prey species were not previously reported for *B. schlegelii*. Including literature records, a total 15 prey categories (mostly identified to species) are reported (Table 2). Of these, 7 are considered primarily diurnal, and 8 are primarily nocturnal in activity.

Prey introductions.-The prey introductions resulted in a strike rate of 81.25% ($n = 16$) for snakes in a stationary, ambush posture (Fig. 3). These trials demonstrate that motionless

B. schlegelii observed during the daylight hours are significantly more likely to strike lizard prey during the day than to not strike this prey item ($G = 6.74$, $\alpha = 0.009$). Of 13 strikes, 9 (69.2%) resulted in prey capture.

DISCUSSION

The observations presented above indicate that *B. schlegelii* is active throughout the diel cycle but that the type of activity differs between day and night. If activity is defined by the proportion of individuals moving during a specific phase of the diel cycle, then *B. schlegelii* is best categorized as nocturnal based on my observations of movement activity. Of 111 individual daytime observations, only three snakes were observed moving. This is consistent with most published accounts, which also describe this snake to be nocturnal.

Additionally, the list of prey items known for *B. schlegelii* includes frogs, which indicates that this species actively forages at night because sedentary, nocturnal prey items (eg. *Eleutherodactylus*) are unlikely to be encountered by a snake that uses only ambush methods. Although most viperids rely on ambush tactics, there is an increasing body of literature indicating that active foraging may be more common in this group than previously thought (Martins et al., 2002; Shine et al., 1998b; Campbell and Solorzano, 1992). In light of such information on related taxa, and on the basis of my observations, I interpret the nocturnal mobility of *B. schlegelii* to include active searching for prey such as frogs. Unlike diurnal lizards, which move along routes such as vines and buttresses that make ambush possible, frogs seldom use such predictable routes.

One individual *B. schlegelii* was observed over a span of four days at the same perch site and was found in the same position each day, whereas each night it moved approximately 1m, was alert, and moved slowly about on the surface of a large leaf. This snake paused intermittently and raised its head and tongue-flicked actively. It appeared to be actively foraging, and on the fourth night when a *Hyla phlebodes* was placed on the leaf, the snake struck and consumed the frog. Another *B. schlegelii* was observed at night moving in a similar fashion and when this individual was offered an *Eleutherodactylus diastema* it captured and ingested it. Such observations suggest that *B. schlegelii* is capable of employing an active-foraging strategy at night.

Although *B. schlegelii* has the ability to actively forage by night, most snakes observed during the daytime are in an ambush posture. Therefore, the selection of ambush sites should significantly influence a snake's diurnal foraging success. Thus, unsuccessful sites may be quickly abandoned for more productive ones which maximize encounter rates for prey such as *Norops limifrons*, and such sites may be used for longer periods (Greene, 1986; Greene, 1992; Clark, 2006). Observations of perch residency illustrate that most snakes (68%) relocate each night, and only 10% of individuals (n = 50) remain at the same daytime perch site for more than two days. However, there is great deal of variation in the duration of use for a single perch site. One *B. schlegelii* was observed in the same daytime ambush site 14 times over a span of 23 days. Based on these diurnal observations one might conclude that certain individuals sit motionless for long spans of time, yet such assumptions may be misleading.

In some species, such as *Bothrops atrox* and *Lachesis* spp., individuals move at night to an ambush site and then return by day to a nearby resting site (Henderson et al., 1976; Campbell and Lamar, 2004). *Lachesis stenophrys* has been observed shuttling between the same day and night sites for 24 days (Greene and Santana, 1983). A similar site fidelity pattern may be exhibited by *B. schlegelii*. However, the primary difference is that the terrestrial species are thought to rest during the day and hunt primarily at night based on the fact that their diet is composed of nocturnally-active endotherms. *B. schlegelii* differs from this pattern by frequently using daytime perches as ambush sites in addition to utilizing ambush and active-foraging tactics at night. Although it has been suggested that *B. schlegelii* preys on diurnal, nectarivorous birds, and consumption of diurnally-active prey during the day has been documented, it has not previously been demonstrated that this species frequently employs daytime ambush tactics (Hardy, 1994; Sherbrooke, 1996; Greene, 1992). The experimental approach taken in this portion of the study indicates that *B. schlegelii* is alert to the presence of prey during the day and that they will frequently strike and successfully capture *Norops limifrons* that approach a snake's ambush site. This allows them to utilize an abundant food resource.

The plasticity of the hunting behavior observed in *B. schlegelii* during this study illustrates ways in which a snake may cope with the constraints of predation pressure and food availability. Although this snake rarely moves by day, it will frequently ambush anoles during the daytime. By limiting diurnal movements *B. schlegelii* minimizes exposure to raptors, which are the only known predators of this snake (Laurencio, 2005; Gerhardt et al., 1993). Observations of *B. schlegelii* actively foraging at night may indicate that predation risks are low during the time which anuran prey is most abundant, allowing for additional opportunities to consume prey.

This knowledge of the natural history of *B. schlegelii* allows for a reassessment of this snake's role as a predator thanks to a greater understanding of the breadth of its feeding niche. In light of the information presented it is obvious that this snake's activity is best described along a continuum including both diurnal and nocturnal activity, as well as active-foraging and ambush hunting. In a broader context, this study adds to the growing body of evidence that illustrates the fact that the use of dichotomies to describe nature can be misleading (Perry, 1999).

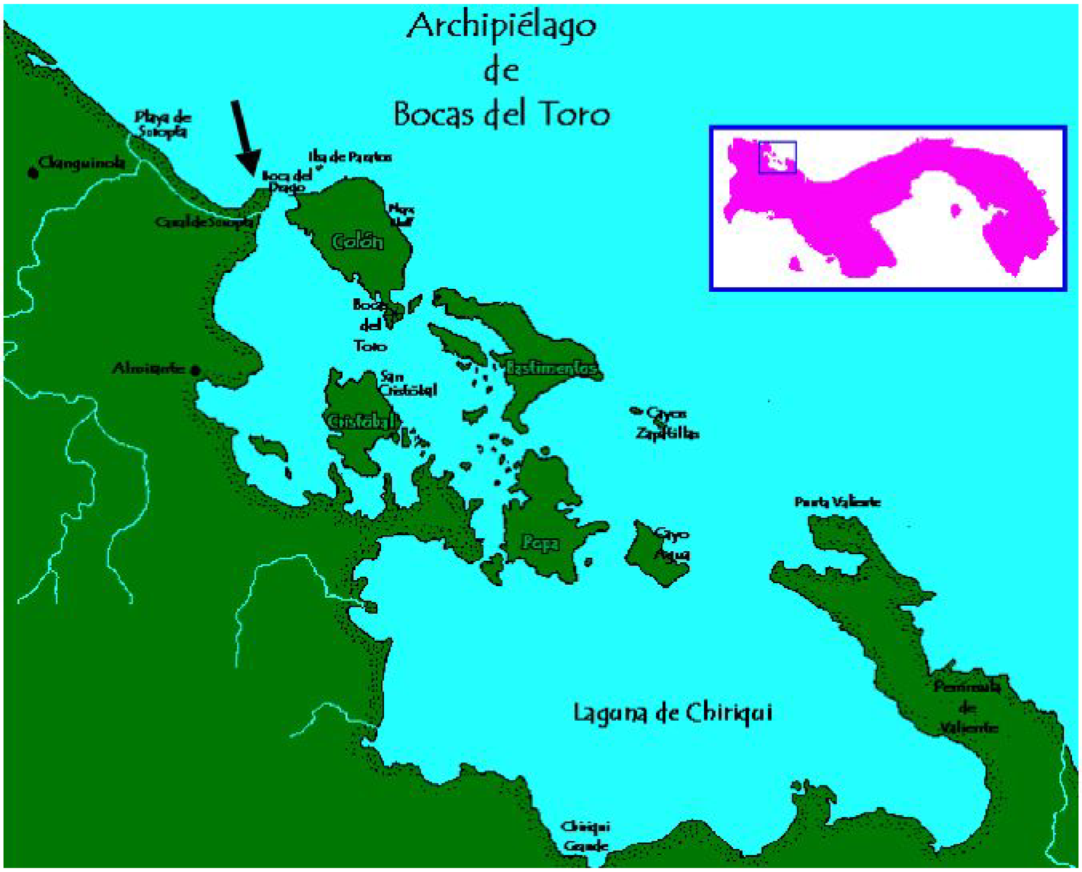

Figure 1. Inset map is of the Republic of Panama, enlarged map is of the Bocas del Toro Archipelago. The arrow indicates the Soropta Peninsula where this study was conducted.

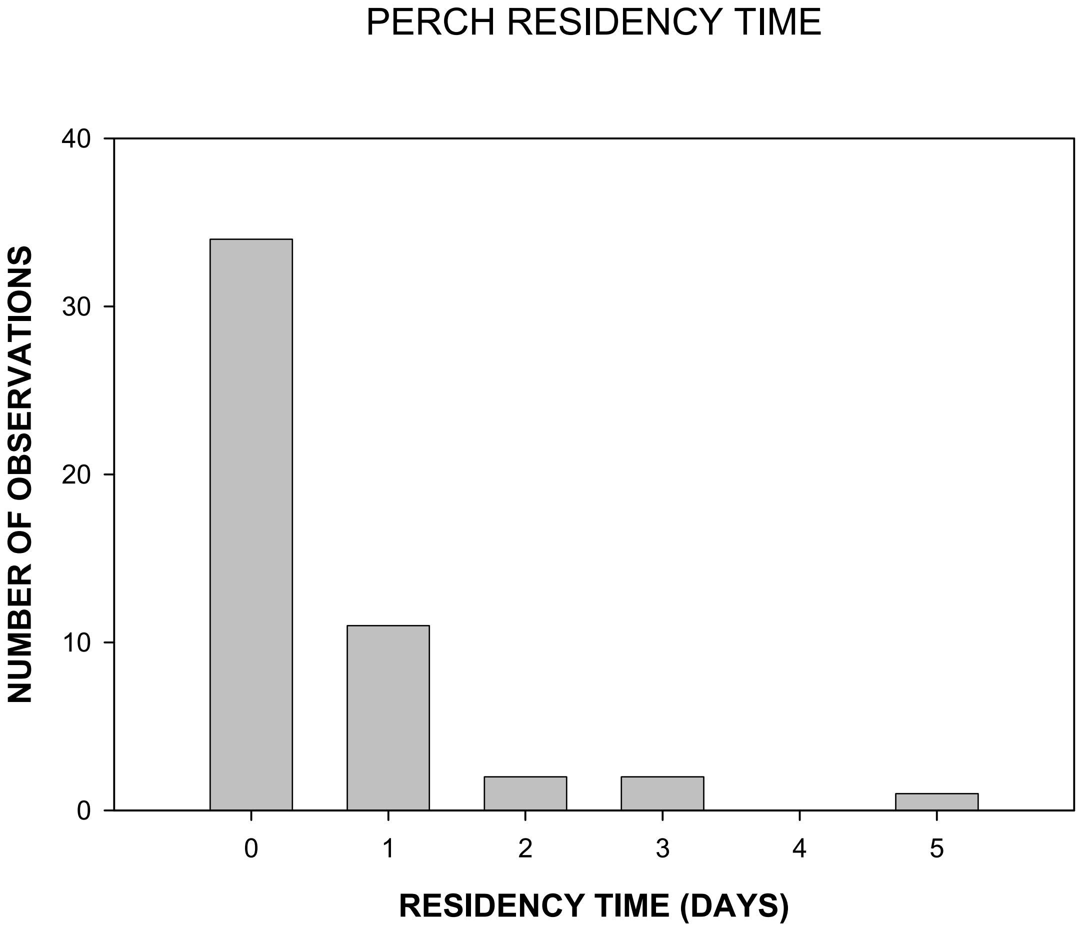

Figure 2. Number of consecutive days during which individual snakes (n = 50) were observed using the same perch site.

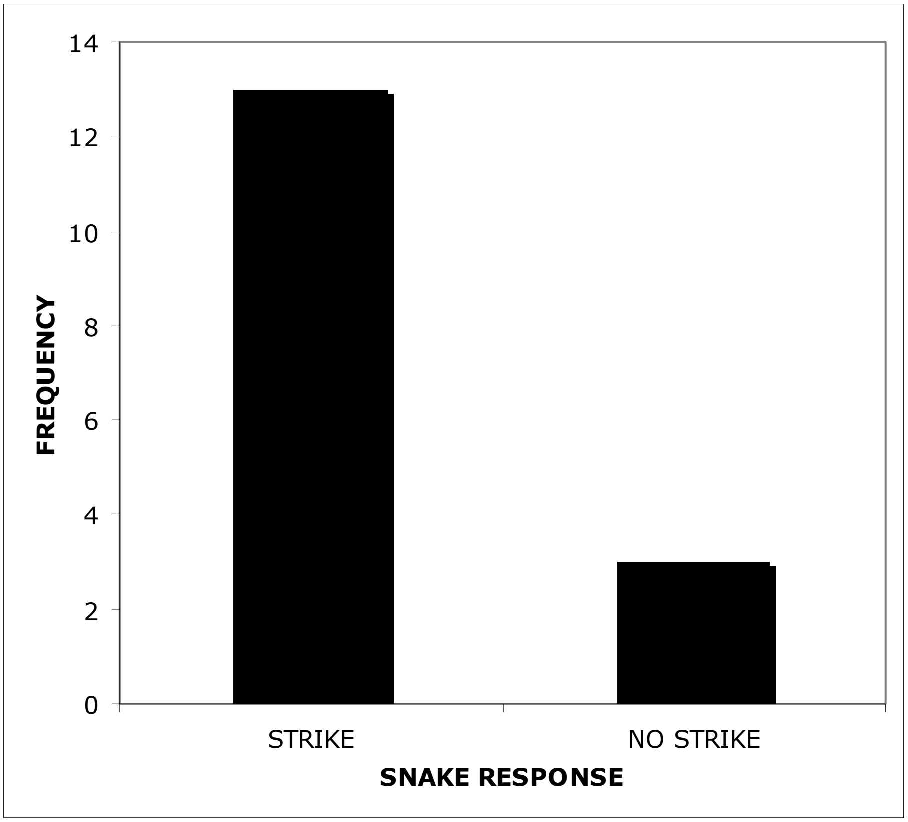

Figure 3. Snake response to prey introductions (n = 16).

Table 1. Number of snake observations during A) paired observations and B) single observations.

A.

Time period	Moved	Did not move	n
Same day	2	7	9
Same night	13	5	18

B.

Time period	Moving	Not moving	n
Day	3 (3)	108 (498)	111 (501)
Night	3 (3)	16 (22)	19 (25)

Table 2. Activity patterns of prey known from stomach contents of *B. schlegelii*. Numbers in parentheses indicate number of snakes observed with a particular prey item during this study.

Diurnal species	Source	Nocturnal species	Source
Norops lemurinus	This study (1)	*Hyla* spp.	(Campbell and Lamar, 2004)
Norops limifrons	(Hardy, 1994); This study (2)	*Ptychohyla panchoi*	(Smith, 1994)
Norops humilis	(Smith, 1994)	*Eleutherodactylus talamancae*	This study (3)
Dactyloa sp.	(Solorzano, 2004)	*Scinax elaeochroa*	This study (1)
Ameiva festiva	This study (1)	*Thecadactylus rapicauda*	(Lindey and Sorrell, 2004)
Gonatodes albugularis	This study (1)	*Marmosa* sp.	(Campbell and Lamar, 2004)
Passerines	(Campbell and Lamar, 2004); This study (1)	Rodentia	(Campbell and Lamar, 2004)
		Chiroptera	(Campbell and Lamar, 2004)

CHAPTER IV

PATTERNS OF USE OF ANTHROPOGENICALLY-FRAGMENTED HABITAT BY AN ARBOREAL PITVIPER

ABSTRACT

Cattle production has had a widespread impact on the Neotropical landscape, which has increased in closing decades of the twentieth century. Although the deleterious effects of conversion of native vegetation to pasture have been acknowledged, research on mitigation of such practices is lacking. In this study I focus on the use of tree islands in pasture by an arboreal predator, the eyelash palm-pitviper (*Bothriechis schlegelii*). The effects of tree island isolation, size, and structural heterogeneity, on snake occupancy was measured. My results indicate that isolation form intact forest, and the structural heterogeneity found within islands were the most important predictors of snake occupancy. Management implications are discussed in light of these findings.

INTRODUCTION

Throughout history, the clearing of land for agricultural use has been a major cause of habitat fragmentation (Saunders et al., 1991). Pressure exerted on natural resources due to livestock grazing represents a significant contribution to this pattern.

This process of resource degradation is driven largely by cattle production, especially in the Neotropics, where conversion to pasture represents the most prevalent motive for deforestation (Carroll and Kane, 1999; Buschbacher, 1986). The impact of pasture clearing on the tropical biota is generally negative, and this practice has been documented to have adverse effects on the diversity and abundance of many species, especially birds (Saab and Petit, 1992; Lynch, 1989). Some species are able to persist in such ruderal habitats. However, their persistence may be dependent on the nature of the remnant patches of forest. In Central America, scattered trees are often left standing during the pasture clearing process (Harvey and Haber, 1999). These remnants are essentially tree islands within a matrix of pasture grasses, and the smallest fragments often consist of a single tree.

Investigations of the value of small fragments (where trees number in the single digits) have indicated that they are biologically important for several reasons including perch sites for birds, and foraging sites for bats and birds (Holl et al., 2000; Galindo-Gonzalez et al., 2000). Many of these species are frugivorous and are important seed dispersers in tropical forests. Therefore, the use of pasture tree islands by these taxa illustrates the importance of these small habitat patches for seedling establishment, and thus the potential of isolated trees in aiding regeneration of abandoned pastures (Holl et al., 2000; Galindo-Gonzalez et al., 2000). Various predatory species (e.g. raptors, snakes; pers. obs.) are also attracted to isolated pasture trees, but no work has focused on the use of tree islands by these taxa. Other work has indicated the importance of predators on maintaining ecosystem function of habitat fragments (“true islands”) in the tropics where processes including herbivory, pollination, and seed dispersal are regulated by the presence of predators (Terborgh et al., 2006; Terborgh et al., 2001). Therefore understanding the attributes of tree islands that facilitate use by predators is an important step toward a holistic approach to managing for predators and incorporating them into the pasture restoration process.

Among Neotropical predators, snakes occupy a wide range of trophic niches (Greene, 1988), and they have the potential to play an important role in regulating ecological processes on habitat fragments in an agricultural landscape. Specifically, snakes of the genus *Bothriechis* are known to use agricultural sites ranging from cacao and coffee plantations to cattle pasture (Solorzano, 2004). This information is based on a number of isolated observations, yet no studies have evaluated habitat use by the snakes of this genus. The focal species of the present study is *Bothriechis schlegelii*, the most widely distributed member of the genus. Although it is found throughout the lowland and montane tropical forests of Central America and northern South America, *B. schlegelii* has declined due to deforestation through out much of its range (Campbell and Lamar, 2004). *Bothriechis schlegelii* is an arboreal snake that is rarely observed on the ground (Savage, 2002). Arboreal snakes possess many traits that are specialized for life in vegetation above the ground. Thus, it is somewhat surprising that this species uses habitat patches that are separated from forest by a matrix of pasture grasses (Lillywhite and Henderson, 1993).

To better understand how this species utilizes habitat fragmented by pastureland I have sought to determine the features of tree islands that are most significantly associated with occupancy by *B. schlegelii*. The size of habitat fragments and their isolation from unfragmented habitat are often cited as important factors influencing the probability that animals will utilize fragments (Watling and Donnelly, 2006). In addition, the distribution of fragments within a matrix of dissimilar habitat has been examined as a predictor of occurrence on habitat fragments (Baum et al., 2004). Other workers have investigated how factors within the habitat fragments differ between fragments. One means of assessing such variability among islands is by evaluating the heterogeneity of habitat structures predicted to be important for a particular taxon (McCoy and Mushinsky, 1999). I hypothesize that snake use of tree islands is influenced by the size, isolation, and structural heterogeneity of each island. The predictions associated with these hypotheses are as follows: 1) snake occupancy will increase with island size, 2) occupancy will be inversely proportional to island distance from intact forest, 3) distance to neighboring islands will have an inverse relationship with snake occupancy, and 4) occupancy will increase with increasing structural heterogeneity of islands.

METHODS

Study site.-This study was conducted on the Soropta Peninsula, Bocas del Toro, Panamá during 22 June - 14 August 2004, and 25 March - 12 May 2005. The site is a plot of pasture that was cleared in 1985 (A. de la Lastra M., pers. comm.). The plot is immediately bordered by additional pasture, with ocean to the south and east, and abuts forest to the north and west (Figure yet to be included). The forested habitat type is best characterized as Atlantic lowland tropical moist forest (Holdridge, 1967). It is common practice for farmers to leave trees scattered throughout pastures to provide shade for cattle. Farmers also value these trees as a source of timber, fence posts, and even as wildlife habitat (Harvey and Haber, 1999). Common canopy and emergent trees that remain after the conversion to pasture at this site include *Genipa americana* (Rubiaceae), *Luehea seemannii* (Tiliaceae), *Pachira aquatica* (Bombacaceae), and *Virola surinamensis* (Myristicaceae). The elevation ranges from 0-10 m above sea level.

Field Methods-

There were 47 tree islands included in the 4.7 ha study plot. A tree island was defined as a single tree, or group of trees, with no canopy connection to other islands or the neighboring intact forest. Islands and the forest edge were mapped using a handheld GPS unit (Garmin 12). One waypoint was taken as close to the center of each island as possible, and all points were accurate to within 6 m. Canopy volume was estimated by calculating the volume of a spherical ellipse where the major (length) axis of the ellipse was the horizontal, long axis of the island and island width was the minor horizontal axis. Canopy length and width were measured from the ground using a meter tape. Canopy height (crown ratio, proportion of bole to live crown) was measured using a clinometer and was calculated by subtracting the portion of the tree where branches were present from the total height of the tree. The product of length, width, and height multiplied by $\pi/6$ equaled canopy volume. This was used as a measure of tree island size because the canopy provides the greatest amount of structural habitat for *B. schlegelii*. Vine coverage and the proportion of buttressed trees within an island were the two variables used to quantify structural heterogeneity. The amount of vine coverage was assessed by visual estimation and five categories based on percentages were used: 0-20%, 21-40%, 41-60%, 61-80%, and 81-100%. The proportion of the buttressing present in each island was quantified by dividing the total diameter-at-breast-height (DBH) of buttressed trees found in a particular island into the total DBH for all trees in a particular tree island. Islands were then grouped in the following three categories: 1) 0%, 2) 1-99%, and 3) 100% because most islands were either devoid of buttressed trees or composed entirely of buttressed trees.

Snakes were located using visual encounter surveys conducted during the daylight hours. Surveys were conducted by two observers who inspected each tree in each island for the presence of snakes. Only data from the 2005 field season was used to develop the island occupancy model. When a snake was located the identification number of the tree island was recorded. Snakes were captured using snake hooks or tongs and then restrained using transparent plastic tubes. Individual snakes were marked for long-term identification by injecting a PIT tag (passive integrated transponder) subcutaneously. In addition, a unique number was applied to the dorsum of each snake using a non-toxic paint pen. This allowed for quick recognition of individuals and minimized the disturbance of snakes during subsequent observations.

Statistical analysis.-Waypoint data from the GPS unit was uploaded into ArcGIS 9.1 (ESRI, Redlands, California). These data were used to plot a map of the study area that included the forest edge and all tree islands. I then used this map to generate distance data between each island and its nearest neighbor and each island and the forest edge. All distance measurements (in meters) were made using ArcGIS (Near and Hawth's Tools extensions).

The presence or absence of snakes on each island was coded as a binary response. There were five predictor variables included in the modeling procedure: isolation (distance to forest), distance to nearest neighboring island, canopy volume, vine coverage percentage, and buttress percentage. The three continuous predictor variables (isolation, distance to nearest neighboring island, and canopy volume) were log-transformed to normalize their distribution. Vine coverage percentage and buttress percentage were entered as categorical parameters. Stepwise logistic regression was used to determine which habitat variables influence snake occupancy on a particular island. Akaike's Information Criterion (AIC) was used to select the best logistic regression model. All analyses were run using R version 2.4.1.

RESULTS

A total of 17 individual snakes were located on nine of the 47 islands (19.15%) within the study plot. The distance from the forest, buttress percentage, and vine coverage percentage were included in the most parsimonious model based on AIC values (Table 1). An evaluation of delta AIC values indicates that a four-parameter model including distance from the forest, proportion of buttressed trees, vine coverage, and distance to nearest neighbor was also competitive. The global model including all five variables has less support but should also be considered because of the relatively low delta AIC value (2.43) (Burnham and Anderson, 2002). A plot of the isolation from the forest of each island along with the proportion of buttressed trees present indicates that the distance from the forest has and a strong influence on snake use of an island that is enhanced by the presence of buttressed trees. This trend is most obvious where there is a high proportion of buttressed trees on islands that are near the forest (Figure 1).

DISCUSSION

The influence of isolation on the use of habitat fragments has been recognized as an important variable by several previous authors (Watling and Donnelly, 2006; Vos and Stumpel, 1995). In the present study the degree of isolation from intact forest emerged as one of two best predictors of which tree islands *B. schlegelii* used. This finding suggests that distance limits the ability of *B. schlegelii* to colonize habitat fragments. Because this snake is an arboreal species it may be constrained by predation pressures or simply by an inability to traverse expanses of pasture that lack suitable habitat structure (Baum et al., 2004).

Structural heterogeneity was the other variable with the most predictive power. Heterogeneity within islands has been recognized as an important variable when examining patterns of species presence/absence on habitat fragments (McCoy and Mushinsky, 1999; Fox and Fox, 2000). The assessment of the influence of heterogeneity in the present study provides further support for this concept. Upon reaching an island, snakes require suitable perches for ambushing prey which are frequently provided by buttresses and vines or lianas (Shine and Li-Xin, 2002)Sorrell et al., unpub. manuscript). Due to the importance of these structures to the foraging ecology of *B. schlegelii* it becomes clear that habitat structure has the potential to influence the use of islands by snakes.

The biological significance of the alternative models (Table 1) generated by my analysis should be considered as well. The distance from a tree island to its nearest neighbor is included as a parameter in the next most likely model. Nearby islands can serve as aids to dispersal by providing stepping stones to and from source populations and between habitat fragments (Baum et al., 2004). The presence of neighboring islands should facilitate snake movement by decreasing the amount of time spent traveling through the grassy pasture matrix. These should also limit exposure to predators even if many islands are only used as temporary refugia. The global model also incorporates island size (quantified using canopy volume). Although it has the least predictive power in this study, it has been found to be an important explanatory variable for patterns of species richness in other studies (Watling and Donnelly, 2006). A similar trend has been observed other work investigating abundance patterns of single species (Conner et al., 2000).This may be due to several factors, one of which is a positive correlation with island area and single species abundance, a pattern that has been attributed to the increasing heterogeneity of available habitat in larger islands (Fox and Fox, 2000). It may also be because larger islands have a greater probability of intercepting dispersers, assuming that the direction of dispersal is random (Bowman et al., 2002).

Although *B. schlegelii* inhabits these small habitat fragments my findings are not sufficient to say that such habitat will sustain this species without the presence of a dense population nearby that may act as a source of individuals that can immigrate to the fragmented habitat (Daily et al., 2001). Data from a pilot study conducted on the site in 2004 however, suggests that these tree islands provide more than a temporary refuge. During a period of approximately six weeks, 14 *B. schlegelii* were captured and marked using PIT-tags. Of those marked individuals, four (recapture rate of 28.6%) were recaptured during this study. Of the four individuals recaptured, one was located on the same tree island as it had been the previous year. These observations indicate that snakes are at least revisiting tree islands if they are not short-term (> 1 yr) residents. Additional evidence that *B. schlegelii* may persist in this habitat is drawn from observations of inter-island movement. Of the four recaptured snakes three had moved to different tree islands within the site between observations. Furthermore, one individual was recorded to have moved as far 100m between tree islands when it would have been closer for it to return to the forest.

Observations that *B. schlegelii* can persist (at least in the short term) on these habitat fragments further illustrates the importance of tree islands in terms of conservation. It is also noteworthy that the tree islands on the study site are used by a number of reptile and amphibian species including five species of snakes (excluding *B. schlegelii*), which represents 25% of the snake fauna documented for this peninsular site (Sorrell et al., unpbl. data). If pastures are maintained in an active state for cattle production then the practice of retaining numerous trees not only benefits *B. schlegelii* but also a host of other organisms (Slocum, 2000). In the event that a pasture is taken out of production these tree islands will accelerate reforestation. This study illustrates that the practice of providing the appropriate habitat features will also attract predators who may play an important role in regulating ecological processes on small forest fragments (Terborgh et al., 2006; Terborgh et al., 2001).

The ability of *B. schlegelii* to use fragmented habitat indicates that this species (at least at this site) is resilient to changes of habitat structure. However, this species, like other arboreal snakes (e.g. *Corallus enhydris*; (Henderson and Winstel, 1995), is limited in its ability to inhabit isolated fragments of habitat. In general *B. schlegelii* would benefit from pastures that are smaller in size where distances required for dispersal to islands are minimal. The importance of buttressed trees for these snakes underscores the need to leave large mature trees (which are often buttressed) standing. In addition, the common practice of cleaning vines off of trees is one that should be discontinued. In most cases current management efforts do not focus on the conservation of snakes. However, if we understand that snakes are important predators that share habitat requirements with other ectotherms then we can apply these results as guidelines at sites where pastures are managed for wildlife value, especially if the herpetofauna are considered.

Table 1. Model selection for habitat choice by *Bothriechis schlegelii* on the Soropta Peninsula, Panamá. Akaike's Information Criterion (AIC), a method of measuring model strength, was used to evaluate competing models.

MODEL	**# PARAMETERS**	**AIC**	**DELTA AIC**
DIST., BUTTRESS, VINE	**3**	**41.57**	**0**
DIST., BUTTRESS, VINE NEIGHBOR	**4**	**42.71**	**1.14**
DIST., BUTTRESS, VINE, NEIGHBOR, VOLUME	**5**	**44**	**2.43**

FIG. 1 Influence of islolation and buttresses on snake occurrence

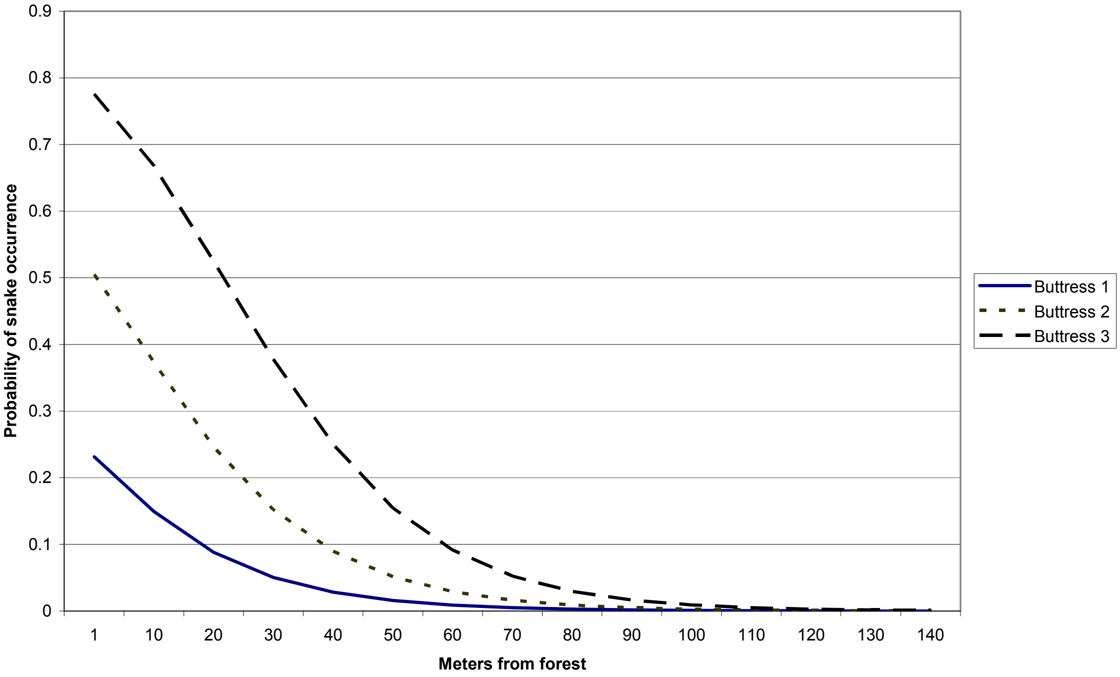

Figure 1. The probability of snake occurrence on islands as influenced by distance from forest and buttress category (1=0%, 2=1-99%, 3=100%).

CHAPTER V

CONCLUSIONS

1) *Bothriechis schlegelii* exhibits pronounced polychromatism and this feature is correlated with survival in this species. The yellow color morph is most abundant in the study population and the difference in the ratio of yellow to brown/gray juveniles seems to be responsible for the yellow-biased color ratio. There is a male biased sex ratio, but females are the largest sex. However, males and females grow at a similar rate, which indicates that females mature later in life than males.

2) *Bothriechis schlegelii* is a species known to take both diurnally-active and nocturnally-active prey. This snakes moves most frequently at night to search for new ambush sites as well as for active foraging. This species also hunts during the day by employing ambush tactics, and is successful at taking prey using this method. The plasticity of foraging behavior exhibited by *B. schlegelii* allows this species to minimize exposure to visually oriented predators while maximizing the likelihood of capture for a wide variety of vertebrate prey types.

3) Snake occupancy of tree islands in pasture is most likely on islands that are closest to intact forest in addition to ones that retain the most vine coverage. Trees characterized by buttresses are important for *B. schlegelii* as well. These data indicate that smaller pastures or at least pastures where dispersal distances are small will benefit this species of arboreal

snake. Furthermore, my data illustrate that the cleaning of vines from pasture trees should be minimized. Because older trees are frequently buttressed they should be protected in order to provide sufficient perch sites. In the long-term, recruitment of younger trees will be necessary to perpetuate tree islands availability. The findings of this work can translate to management protocols for areas where cattle are retained but where conservation is also considered. These findings are also important for restoration efforts.

CUMULATIVE BIBLIOGRAPHY

ANDREN, C., and G. NILSON. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. Biological Journal of the Linnean Society. 15:235-246.

BAUM, K. A., K. J. HAYNES, F. P. DILLEMUTH, and J. T. CRONIN. 2004. The matrix enhances the effectivenss of corridors and stepping stones. Ecology. 85:2671-2676.

BOWMAN, J., N. CAPPUCCINO, and L. FAHRIG. 2002. Patch size and population density: the effect of immigration behavior. Conservation Ecology. 6:9.

BURNHAM, K. P., and D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

BUSCHBACHER, R. J. 1986. Tropical deforestation and pasture development. BioScience. 36:22-28.

CAMPBELL, J. C., and W. W. LAMAR. 1989. The venomous reptiles of Latin America. Cornell University Press: Ithaca.

—. 2004. The venomous reptiles of the Western Hemisphere. Comstock Publishing Associates, Ithaca, NY.

CAMPBELL, J. C., and A. SOLORZANO. 1992. The distribution, variation, and natural history of the Middle American montane pitviper, *Porthidium godmani*, p. 223-250. *In:* Biology of the pitvipers. J. C. Campbell and E. D. J. Brodie (eds.). Selva Press, Tyler, Texas.

CARROLL, C. R., and D. KANE. 1999. Landscape ecology of transformed neotropical environments, p. 70-77. *In:* Managed ecosystems: the Mesoamerican experience. L. U. Hatch and M. E. Swisher (eds.). Oxford Univ. Press, Oxford.

CLARK, R. W. 2006. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. Copeia. 2:181-187.

CONNER, E. F., A. C. COURTNEY, and J. M. YODER. 2000. Individuals-area relationships: the relationship between animal population density and area. Ecology. 81:734-748.

CROTHER, B. I., J. C. CAMPBELL, and D. M. HILLIS. 1992. Phylogeny and historical biogeography of the pitvipers. *In:* Biology of the Pitvipers. J. A. Campbell and E. D. J. Brodie (eds.). Selva Press, Tyler, Texas.

DAILY, G. C., P. R. EHRLICH, and A. SANCHEZ-AZOFEIFA. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications. 11:1-13.

DILLER, L. V., and R. L. WALLACE. 2002. Growth, reproduction, and survival in a population of *Crotalus viridis* in north central Idaho. Herpetological Monographs. 16:26-45.

DUNHAM, A. E., and J. W. GIBBONS. 1990. Growth of the slider turtle. *In:* Life history and ecology of the slider turtle. J. W. Gibbons (ed.). Smithsonian Institution.

ENDLER, J. A. 1993. The color of light in forests and its implications. Ecological Monographs. 63:1-27.

FOX, B. J., and M. D. FOX. 2000. Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions, and guild assembly rules. Global Ecology and Biogeography. 9:19-37.

GALEOTTI, P., D. RUBOLINI, P. O. DUNN, and M. FASOLA. 2003. Colour polymorphism in birds: causes and functions. Journal of Evolutionary Biology. 16:635-646.

GALINDO-GONZALEZ, J., S. GUEVARA, and V. J. SOSA. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology. 14:1693-1703.

GERHARDT, R. P., P. M. HARRIS, and M. A. VASQUEZ MARROQUIN. 1993. Food habits of nesting great black hawks in Tikal National Park, Guatemala. Biotropica. 25:349-352.

GIBBONS, J. W. 1990. Sex ratios and their significance among turtle populations. *In:* Life history and ecology of the slider turtle. J. W. Gibbons (ed.). Smithsonian Institution.

GREENE, H. W. 1986. Natural history and evolutionary biology. *In:* Predator-Prey Relationships. M. E. Feder and G. V. Lauder (eds.). University of Chicago Press.

—. 1988. Species richness in tropical predators, p. 259-274. *In:* Tropical Rainforests: diversity and conservation. F. A. a. C. M. Pringle (ed.). California Academy of Sciences, San Francisco.

—. 1992. The ecological and behavioral context for pitviper evolution, p. 107-117. *In:* Biology of the Pitvipers. H. W. Campbell and E. D. J. Brodie (eds.). Selva, Tyler, Texas.

—. 1997. Snakes: the evolution of mystery in nature. Univ. of California, Berkeley.

GREENE, H. W., and M. A. SANTANA. 1983. Field studies of hunting behavior by bushmasters. American Zoologist. 23:897.

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

HAIRSTON, N. G., F. E. SMITH, and L. B. SLOBODKIN. 1960. Community structure, population control, and competition. The American Naturalist. XCIV:421-425.

HARDY, D. L. S. 1994. Venomous snakes of Costa Rica: comments on feeding behavior, venom, and human envenoming - Part I. Sonoran Herpetologist. 7:108-113.

HARVEY, C. A., and W. A. HABER. 1999. Remnant trees and the conservation value of biodiversity in Costa Rican pastures. Agroforestry Systems. 44:37-68.

HENDERSON, R. W. 1974. Aspects of the ecology of a Neotropical vine snake. Herpetologica. 30:19-24.

—. 2002. Neotropical Treeboas: natural history of the *Corallus hortulanus* complex. Krieger, Malabar, FL.

HENDERSON, R. W., M. A. NICKERSON, and S. KETCHAM. 1976. Short term movements of the snakes *Chironius carinatus*, *Helicops angulatus* and *Bothrops atrox* in Amazonian Peru. Herpetologica. 32:304-310.

HENDERSON, R. W., and R. A. WINSTEL. 1995. Aspects of habitat selection by an arboreal boa (*Corallus enydris*) in an area of mixed agriculture on Grenada. Journal of Herpetology. 29:272-275.

HOLDRIDGE, L. R. 1967. Life Zone Ecology, Tropical Science Center, San Jose, Costa Rica.

HOLL, K. D., M. E. LOIK, E. H. V. LIN, and I. A. SAMUELS. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology. 8:339-349.

KAYS, R., and A. ALLISON. 1998. Arboreal tropical forest vertebrates: current knowledge and research trends, p. 121-132. *In:* Proceedings of the ESF Conference. K. E. Linsenmair, A. J. Davis, B. Fiala, and M. R. Spleight (eds.). Oxford University, London.

KING, R. B. 1992. Lake Erie water snakes revisited: morph- and age-specific variation in relative crypsis. Evolutionary Ecology. 6:115-124.

LAURENCIO, D. 2005. *Bothriechis schlegelii*: attempted predation. Herpetological Review. 36:188.

LEE, J. C. 2000. A Field Guide to the Amphibians and Reptiles of the Maya World. Cornell University Press.

LILLYWHITE, H. B., and R. W. HENDERSON. 1993. Behavioral and functional ecology of arboreal snakes, p. 1-48. *In:* Snakes: Ecology and Behavior. R. A. Seigel and J. T. Collins (eds.). McGraw Hill, New York.

LINDEY, S. D., and G. G. SORRELL. 2004. *Bothriechis schlegelii:* predator/prey mass ratio, and diet. Herpetological Review. 35:272-273.

Lynch, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. The Condor. 91:515-544.

Madsen, T., and R. Shine. 1992. A rapid, sexually selected shift in mean body size in a population of snakes. Evolution. 46:1220-1224.

—. 1994. Costs of reproduction influence the evolution of sexual size dimorphism in snakes. Evolution. 48:1389-1397.

Martins, M., O. A. V. Marques, and I. Sazima. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*, p. 307-328. *In:* Biology of the vipers. G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.). Eagle Mountain Press, Eagle Mountain, Utah.

McCoy, E. D., and H. R. Mushinsky. 1999. Habitat fragmentation and the abundances of vertebrates in the Florida Scrub. Ecology. 80:2526-2538.

Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. American Naturalist. 153:98-109.

Saab, V. A., and D. R. Petit. 1992. Impact of pasture development on winter bird communities on Belize, Central America. The Condor. 94:66-71.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology. 5:18-32.

Savage, J. M. 2002. Reptiles and amphibians of Costa Rica. University of Chicago Press.

Seigel, R. A. 1993. Summary: Future research on snakes, or how to combat lizard envy., p. 395-402. *In:* Snakes: Ecology and Behavior. R. A. Seigel and J. T. Collins (eds.). Mcgraw-Hill Inc., N.Y.

SHERBROOKE, W. C. 1996. Reactions of Costa Rican hummingbirds to models of two color-morphs of the eyelash palm-pitviper (Bothriechis schlegelii). Sonoran Herpetologist. 9:2-3.

SHINE, R. 1978. Sexual size dimorphism and male combat in snakes. Oecologica. 33:269-277.

SHINE, R., AMBARIYANTO, P. S. HARLOW, and MUMPUNI. 1998a. Ecological divergence among sympatric colour morphs in blood pythons, *Python brongersmai*. Oecologica. 116:113-119.

SHINE, R., W. R. BRANCH, P. S. HARLOW, and J. K. WEBB. 1998b. Reproductive biology and food habits of horned adders, *Bitis caudalis* (Viperidae), from Southern Africa. Copeia. 2:391-401.

SHINE, R., and S. LI-XIN. 2002. Arboreal ambush site selection by pit-vipers Gloydius shedaoensis. Animal Behaviour. 63:565-576.

SIH, A., P. CROWLEY, M. MCPEEK, J. PETRANKA, and K. STROHMEIER. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review Ecology and Systematics. 16:269-311.

SLOCUM, M. G. 2000. Logs and fern patches as recruitment sites in a tropical pasture. Restoration Ecology. 8:408-413.

SMITH, E. N. 1994. Biology of the snake fauna of the Caribbean rainforest of Guatemala, p. 138. *In:* Biology. Vol. Master of Science. University of Texas at Arlington, Arlington, Texas.

SOLORZANO, A. 2004. Snakes of Costa Rica. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

SORRELL, G. G. *In revision*. Diel movement and predation patterns of the eyelash palm-pitviper (*Bothriechis schlegelii*). Copeia.

TERBORGH, J., K. FEELEY, M. SILMAN, P. NUNEZ, and B. BALUKIJAN. 2006. Vegetation dynamics of predator-free land bridge islands. Journal of Ecology. 94:253-263.

TERBORGH, J., L. LOPEZ, P. NUNEZ V., M. RAO, G. SHAHABUDDIN, G. ORIHUELA, M. RIVEROS, R. ASCANIO, G. H. ADLER, T. D. LAMBERT, and L. BALBAS. 2001. Ecological meltdown in predator-free forest fragments. Science. 294:1923-1926.

VOS, C. C., and A. H. P. STUMPEL. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog *Hyla arborea*. Landscape Ecology. 11:203-214.

WATLING, J. I., and M. A. DONNELLY. 2006. Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conservation Biology. 20:1016-1025.

WEBB, J. K., B. W. BROOK, and R. SHINE. 2003. Does foraging mode influence life history traits? A comparative study of growth, maturation, and survival of two species of sympatric snakes from south-eastern Australia. Austral Ecology. 28:601-610.