2009-04-14

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Recommended Citation

Wasko, Dennis K., "Spatial and Feeding Ecology of the Fer-de-Lance (Bothrops asper) in Costa Rica" (2009). *Open Access Dissertations*. 206.
https://scholarlyrepository.miami.edu/oa_dissertations/206

UNIVERSITY OF MIAMI

SPATIAL AND FEEDING ECOLOGY OF THE FER-DE-LANCE (BOTHROPS ASPER) IN COSTA RICA

By

Dennis K. Wasko

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2009

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
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SPATIAL AND FEEDING ECOLOGY OF THE FER-DE-LANCE (*BOTHROPS ASPER*) IN COSTA RICA

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WASKO, DENNIS K. (Ph.D., Biology)
Spatial and Feeding Ecology of the (May 2009)
Fer-de-lance (*Bothrops asper*) in
Costa Rica

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Donald L. DeAngelis.
No. of pages in text. (116)

Understanding the ways in which animals utilize space and obtain food are central themes in modern ecology. Formulating broad principles and elucidating the factors explaining such patterns are limited, however, by the availability of data from a broad range of species and systems. This problem especially true of snakes, a predator group about which even the most basic natural history data are often entirely lacking, even among abundant, widespread, and ecologically-important species. I studied the natural history and ecosystem role of one such species, the fer-de-lance (*Bothrops asper*) in lowland rainforest in Costa Rica. *B. asper* is a large, cryptic pitviper that is highly abundant in many Central American ecosystems and is strongly relevant to human health due to high incidence of snakebite, yet its biology under natural conditions is almost entirely undocumented. I used radiotelemetry to quantify home range, movement patterns, habitat usage, and foraging behavior. *B. asper* was found to have smaller home ranges and reduced movement patterns than similarly-sized temperate pitvipers, likely due to a greater reliance upon ambush foraging in patches of high prey density. Snakes also demonstrated strong selection for swamp habitat, which may reflect efforts to exploit frogs as a primary food source due to low availability of small mammals at the study site.

I subsequently addressed the trophic status of this *B. asper* population using a supplemental-feeding experiment. In comparison to control snakes, individuals receiving supplemental food had smaller home ranges, shorter and less frequent movements, increased mass acquisition, and shifted to primarily forest rather than swamp habitat. These results support the suggestion that *B. asper* at the study site are strongly food-limited. Finally, I tested the hypothesis that fer-de-lance mediate local seed-predation rates by influencing habitat usage and foraging behavior of rodents. A series of behavioral experiments conflicted with many existing studies in failing to support this idea, as three rodent species demonstrated little snake avoidance, and none of likely ecological relevance. Collectively, this dissertation represents the first comprehensive field study of *Bothrops asper* and is among the first for any tropical snake, and suggests several avenues for future research.

Acknowledgements

I am very grateful to the members of my dissertation committee for their support during the completion of this work. My advisor, Donald DeAngelis, offered constant support and encouragement throughout my years at University of Miami. Julian Lee was instrumental in bringing me to Miami to pursue a career in tropical herpetology. Steven Green offered useful insights into the field of animal behavior, as well as extensive advice on writing and statistical analysis. My outside committee member, Mahmood Sasa, was involved conceptually and logistically in virtually every stage of this research. I thank him for introducing me, in his own particular way, to tropical fieldwork, and for helping to perpetuate stereotypes about crazy herpetologists. I am glad to consider all of them friends as well as mentors and colleagues.

Due to his significant theoretical and logistical contributions to this work, Mahmood will also be credited as a co-author on all publications resulting from the submission of Chapters 2 through 5 to peer-reviewed journals. Fabian Bonilla will be credited as a co-author on publications based on the work described in Chapter 5, due to his extensive participation in conducting experimental trials and preliminary data analysis.

Many other people offered logistical support and advice during the course of my doctoral study. Patricia Buendia, Matt Potts, and Aaron Ellison provided assistance with statistical analysis. Fabian Bonilla assisted greatly with data collection for behavioral experiments, Franklin Aguilar often helped with radio-tracking and other field projects, and Willie Pineda helped with my mammal-trapping efforts. Detlev Kelm and Christian Voigt collaborated with me on several projects exploring snake physiology, despite their

own misgivings about working with venomous subjects. They also generously donated their own radiotelemetry equipment when mine failed. Marcia Snyder taught me most of what I know about using ArcView to work with spatial data, and Chris Hanson offered further advice. Beth Goad frequently helped me to navigate the dense jungles of paperwork that are so common to academia.

I was fortunate to obtain financial support from many sources. At the University of Miami, my extended field work and subsequent preparation of this dissertation were made possible by the Department of Biology Tropical Research Fellowship and Arts and Sciences Doctoral Dissertation Fellowship. Numerous awards from UM's Kriloff Fund, Provost Fund, and the Graduate Activity and Funding Allocation Committee allowed me to share the results of my work at several international conferences. I was also supported by generous grants from the American Society of Ichthyologists and Herpetologists' Gaige Award, the American Society of Naturalists, and Universidad de Costa Rica's Vicerrectoría de Investigación.

In Costa Rica, I was lucky to work with some of the best field assistants one could ask for. Vincent Farallo, Steven Mickletz, Logan Olberg, James Tumulty, Kiri Wallace, and Nigel Watson worked with me exhaustively on challenging field projects and often under less-than-comfortable circumstances. I appreciate their dedication and hard work, and I like to think they even enjoyed themselves. I also got to become part of the incredible La Selva community. There are more people than I can possibly name here, but I especially appreciate the friendship of Marcia Snyder, Susan Letcher, Alex Gilman, Katja Rex, Molly Cavaleri, Alice Boyle, Matt Williams, Malia Fincher, Andrea Romero, Dina Roberts, Beth Anderson, Paolo Olivas, Deedra McClearn, David and Deborah

Clark, and Luis Diego Gómez. Thanks for making my time there one of the most enjoyable periods in my life.

I would never have made it through graduate school without the friendship and support of fellow graduate students at University of Miami. I thank the O-Lab – Jim O'Reilly, Lisa Ganser, Ron Rozar, Mark Mandica, and Gabriel Gartner – for taking me in when I first arrived. I owe special thanks to Christy Wolovich, Jen Ciaccio, Ana Ibarra, Vanessa McDonough, Miguel Fernandes, Nate Muchhala, Eric Manzane, David Matlaga, Venetia Briggs, Adrienne DuBois, Thaddeus McRae, and many others… my experience at UM would have been radically different without every one of you.

My (increasingly) old friends Joal Tallant, Scott Harvey, Eric Toscano, Rob Strauss, Chris Fitzpatrick, and their families always provided a welcome distraction from academia. Thanks for making me feel like family too.

Finally, I thank my own family – Donna, Dennis, and Kimberly Wasko, Lilyanne, Damian, and Leslie Mitchell, James Dippolito, and everyone else – for their love and for always supporting (or at least humoring) my often-baffling career choices. I wouldn't be here without you.

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CHAPTER 1

INTRODUCTION

Most organisms are distributed neither randomly nor uniformly across space, but rather occur in patches (Dalthorp et al. 2000). Spatial ecology involves not only the description such patches, but also our attempts to understand the factors explaining them. For example, animals' space usage at the individual or population scale is often quantified in terms of home range (Burt 1943, Jennrich and Turner 1969, Macdonald et al. 1980, Worton 1987, Powell 2000). The size, shape, and location of home ranges may be influenced by numerous extrinsic biotic and abiotic factors including habitat suitability, climate, population density, the presence of predators and competitors, and the availability of mates (Waser and Wiley 1979, Schoener and Schoener 1982, Beck 1995, Hubbs and Boonstra 1998, Brown and Weatherhead 1999, Grubb and Doherty 1999, McLoughlin and Ferguson 2000). In the case of predators, however, prey resources often remain among the most important forces determining distribution and spacing (Gittleman and Harvey 1982, Village 1982, Litvaitis et al. 1986, Zabel et al. 1995, Bernstein et al. 1999).

The ability to obtain food is of paramount importance to individuals, as energetic resources are related to survival, growth, and reproduction (White 1978, Sebens 1987, Richner 1992, Taylor et al. 2005). Resolving feeding dynamics is also relevant beyond the species scale, as the top-down forces exerted by predators may have community-wide effects detectable throughout multiple trophic levels (Letourneau and Dyer 1998, Pace et al. 1999, Schmitz et al. 2000, Schmidt 2006). The ways in which animals obtain food vary widely across taxa with dissimilar foraging strategies, but should be optimized to balance maximum nutritional input with minimal energetic expenditure. Individuals often do so by refining foraging efficiency so that the locomotion and space usage required are minimal (Schoener 1971, Charnov 1976, Ford 1983).

Spatial and feeding biology are thus central themes in modern ecology and conservation, and their inherent relatedness makes them particularly complementary fields of study. Indeed, it can be difficult to address one effectively without accounting for the other. The identity of prey species and the context in which they are taken is largely dictated by the timing and location of predator activity, while the distribution of food resources plays a large role in determining these activities for many predators. Formulating generalizations about the connection between spatial and feeding ecology is limited, however, by the scarcity of empirical data for many species.

This dearth of information is especially pronounced for snakes, which have been historically less represented in ecological literature than any other major vertebrate taxon (Shine and Bonnett 2000, Bonnett et al. 2002). Several factors probably contribute towards this disparity; snakes are often highly cryptic, nocturnal, and have low population densities (Parker and Plummer 1987, Greene 1997), and many species occur in tropical regions which themselves have been little-studied (Vitt 1993). Yet perhaps more relevant is personal bias by human researchers. Fear of snakes seems innate among many non-human primates, and is pervasive across human societies (Öhman and Mineka 2003, LoBue and DeLoache 2008). Scientists are far from immune to such prejudice; Linnaeus (1758) himself proclaimed of snakes and other reptiles, “these foul and loathsome creatures are abhorrent because of their cold body, pale color, cartilaginous skeleton, filthy skin, fierce aspect, calculating eye, offensive smell, harsh voice, squalid habitation, and terrible venom; and so their Creator has not exerted his powers to make more of them." Such disparaging (and somewhat inaccurate) perceptions apparently persisted among many naturalists until the latter part of the 20th century when the number of studies involving snakes began to approach those of other groups (Shine and Bonnett 2000).

Regardless of the subjective opinions of researchers, it is now clear that snakes are integral components of ecological systems. Snakes are among the most dominant predators in many ecosystems, exerting heavy mortality on prey species (Daly et al. 1990, Weatherhead and Blouin-Demers 2004, Robinson et al. 2005, Sperry *et al*. 2008), while serving as important prey in others (Janzen 1976, DuVal et al. 2006, Moreno-Rueda and Pizarro 2007. Predation pressure by snakes may also influence prey behaviorally, influencing habitat usage, foraging, and other activities (Weldon et al. 1987, Dickman 1992, Kotler et al. 1993, Bouskila 1995). Predation risk specifically from snakes has been proposed as a driving factor in the evolution of some avian migratory patterns (Boyle 2008), and even in the development of the primate brain (Isbell 2006). Finally, venomous species can be of strong interest from a human health perspective, as mortality rates due to snakebite are high in some regions (Hardy 1994*a*,*b*, Chippaux 1998).

This dissertation focuses on the snake *Bothrops asper* (Fig. 1.1), an ideal study organism in many of these aspects. Commonly known as the "fer-de-lance" or "lancehead" in the English-speaking world, *B. asper* is widespread, ranging from southern Mexico into northern Colombia and Ecuador (Campbell and Lamar 2004). *B. asper* is likely to be an important predator in much of its range due to its large body size (up to 2.5m total length), often high local abundance, and opportunistic feeding habits (Martins et al. 2002). Due to their highly cryptic coloration, willingness to inhabit human-disturbed areas, and propensity for active self-defense, fer-de-lance are also responsible for more human snakebites and snakebite mortalities than any other snake in the New World. While fairly well-represented in medical and toxicological literature, the natural history of *B. asper* remains almost completely undocumented despite the species' potential ecological significance and strong relevance to human health. This work represents the first comprehensive study of *Bothrops asper* conducted under natural conditions

My overarching goals in conducting this research were to improve our understanding of *B. asper*'s life history and to elucidate its role within the ecosystem. In Chapter 1 I use radiotelemetry data to quantify patterns of space usage exhibited by *B. asper*, including home ranges, movement rates, and a general depiction of habitat selection. I also describe daily activity and foraging behavior, which I propose as a driving factor explaining many of the observed spatial patterns. I also compare the relative merits of various home range and habitat-availability estimation techniques, and discuss the importance of selecting methodology appropriate for a given study organism.

In Chapter 2 I analyze patterns of habitat usage in more rigorous detail and at multiple scales. Specifically, landscape-level macrohabitat selection is addressed by comparing the proportions of general habitat types that were used by and available to study snakes. I examine microhabitat selection by identifying structural characteristics of the environment most likely to be of importance to snakes. This chapter also emphasizes the importance of considering an animal's activity patterns in habitat studies, as *B. asper* exhibited differential microhabitat utilization at different times and for different activities.

During data collection for the first two chapters, my observations suggested that small mammals, adult *B. asper*'s usual prey, were rare at the study site, and that as a result fer-de-lance were disproportionately selecting swamps in order to feed on amphibians as a primary food source. In Chapter 3 I use a supplemental-feeding experiment to address the hypothesis that this *B. asper* population was strongly food-limited. One group of control snakes foraged normally, while an experimental group was offered a pre-killed rat in the field once every two weeks, in addition to any food obtained on their own. I proposed that if the study population was limited by food availability, fed snakes would exhibit smaller home ranges, reduced movement, and selection of forest rather than swamp habitat, expectations that were upheld by the results. This study was among the first to apply food-supplementation techniques to any snake, and the only study to date experimentally demonstrating ecological and behavioral resource dependence among snakes.

Finally, in Chapter 4 I investigate the influence of *B. asper* on the behavior of three sympatric rodent species. Specifically, I address whether rodents avoid areas featuring snakes or snake cues, whether they alter foraging efforts in the presence of snakes or snake cues, and whether these responses differ under laboratory, semi-natural, and field conditions. Such experiments conducted in a tropical system present an interesting comparison with existing studies of small mammals, the majority of which have taken place in temperate regions, and typically report strong anti-snake responses. I conclude this chapter by offering several possible explanations for why the importance of snake predation as a selective force may differ for rodents in temperate and tropical ecosystems.

Figure 1.1. Adult female *Bothrops asper*, approximately 1.5m SVL.

CHAPTER 2

ACTIVITY PATTERNS OF A NEOTROPICAL AMBUSH PREDATOR: SPATIAL ECOLOGY OF THE FER-DE-LANCE (*BOTHROPS ASPER*, SERPENTES: VIPERIDAE) IN COSTA RICA

SUMMARY:

Patterns of movement and space usage are important components of the ecology of any organism. Among snakes, this information is often lacking even for species that are abundant, ecologically important, and/or relevant to human health. We used radiotelemetry to examine the spatial ecology and behavior of the fer-de-lance (*Bothrops asper*), a highly venomous pitviper that is ubiquitous throughout much of Central America. Sixteen adult snakes were tracked over two years in lowland rainforest of Costa Rica in order to determine home range, movement patterns, and foraging behavior. Consistent with previous descriptions, *B. asper* was found to be a highly nocturnal ambush predator, exhibiting virtually no activity during the day. Overall home range was determined using both minimum convex polygon (mean size=5.95ha) and 95% and 50% kernel density (mean size=3.71 and 0.370ha respectively); home range size did not differ between males and females by any estimation method. Movement pattern was largely aseasonal and not related to any observed environmental conditions other than the daily low temperature. Most movements consisted of short (<10m) movements between daytime shelter and nocturnal ambush sites within a given area, interspersed with longer distance (>50m) movements to new foraging areas. Compositional analysis of habitat usage indicated an avoidance of developed areas and selection of swamp habitat. Most snakes had several activity cores (50% kernel density), the majority which were in or

near swamps. These patterns suggest that space and habitat usage of fer-de-lance may be related to foraging strategy.

BACKGROUND:

Understanding the ways in which mobile animals utilize space is important for addressing broader questions of ecology, behavior, and conservation. This is especially true for snakes, where patterns of movement and space usage may be tied directly to life-history parameters such as reproduction (Gregory et al. 1987, Reinert and Zappalorti 1988, Shine 2003), growth (Wharton 1966, Diller and Johnson 1988, Bronikowski 2000), and food acquisition (Secor and Nagy 1994, Luiselli 2006*a*). However, due to their often secretive nature and difficulty of study under field conditions, the body of literature regarding snake spatiotemporal distributions has historically been limited. The development of radio-transmitters modified for internal implantation (Reinert and Cundall 1982, Weatherhead and Anderka 1984) permitted long-term monitoring of snakes in the field, yet basic natural history data are often lacking even for abundant and widespread species. This is especially true of snakes occurring in the tropics, despite the fact that snake species richness and diversity are far higher in tropical than in temperate regions (Pough et al. 2001). This absence may represent a substantial gap in our understanding of tropical ecosystem dynamics, as snakes play important ecological roles in many systems (Bouskila 1995, Luiselli 2006*b*).

In temperate vipers, movements and spatial patterns are often dependent upon daily thermal refugia (Brown and Lillywhite 1992, Beaupre 1995) or overwintering hibernacula (Macartney et al. 1988). Such behaviors may also be driven by the need to exploit seasonally-abundant prey and acquire sufficient energy reserves for survival during extended periods without feeding (Reinert and Zappalorti 1988, Beck 1995, Ashton 2001). In contrast, tropical snake species might be less affected by daily or seasonal thermal constraints (Shine and Madsen 1996, Luiselli and Akani 2002) although foraging habits may still vary throughout the year in response to shifting prey availabilities (Madsen and Shine 1996, Sant'Anna and Abe 2007). Further generalizations regarding spatial habits of tropical snakes remain elusive without additional study.

Bothrops asper (Serpentes: Viperidae), most often called the terciopelo in Costa Rica and (collectively with *B. atrox*) the fer-de-lance or lancehead in the English-speaking world, is a large-bodied pitviper (maximum total length 2.5m, Savage 2002) ranging from southern Mexico into northern Ecuador and Colombia and found in a variety of ecosystems at elevations below 1500m asl (Campbell and Lamar 2004). This species is relatively abundant throughout much of its distribution, and in some localities is perhaps one of the most conspicuous snakes. Like many other members of the genus *Bothrops*, fer-de-lance are sit-and-wait ambush predators that feed opportunistically on a wide variety of prey, although there seems to be a general shift from ectothermic to mammalian prey specialization with ontogeny (Martins et al. 2002, Campbell and Lamar 2004). Due to its cryptic nature, prevalence in agricultural regions, high venom yield and potency (Bolaños 1972), and propensity for aggressive self-defense, *B. asper* is also responsible for the majority of human envenomations and snakebite mortalities in Central America (Hardy 1994*a*,*b*, Rojas et al. 1996, Saborío et al. 1998).

Despite its relatively high abundance, widespread distribution, and relevance to human health, the species has received little scientific attention outside of systematics and toxicology, and its ecology and behavior in the field remain almost completely undocumented. Here we present data on the spatial ecology of 16 fer-de-lance obtained through radiotelemetric monitoring in Costa Rica over two years. The specific objectives of this study were to 1) describe home range size and movement rates of free-ranging fer-de-lance, 2) determine whether observed movement rates correlate with individual snake characteristics or environmental conditions such as temperature and precipitation, and 3) identify patterns of macrohabitat selection.

METHODS AND MATERIALS:

STUDY SITE. – Field research was conducted from November 30, 2004 through December 10, 2006 at La Selva Biological Station (LSBS) in Puerto Viejo de Sarapiquí, Heredia Province, northeastern Costa Rica (84˚00'12.959 W, 10˚25'52.513 N). LSBS is a 1700ha reserve consisting of primary and secondary lowland tropical wet forest, with numerous small forested swamps, and some developed areas and disturbed sites (see McDade and Hartshorn 1994 for detailed description and history of the site). The region is fairly aseasonal in temperature, but does typically experience periods of reduced rainfall from January through April and in September; rainfall is abundant throughout the remainder of the year. Comprehensive descriptions of climate at LSBS are provided elsewhere (Fetcher et al. 1985, Guyer 1988, Sanford *et al.* 1994) and vegetation cover (Frankie et al. 1974, Holdridge et al. 1971). LSBS features a 50m by 100m grid of numbered posts with known GPS coordinates; this infrastructure greatly facilitated our ability to orient and map snake relocations at the study site, as handheld GPS units typically functioned poorly under the heavy forest canopy.

FIELD AND TELEMETRY METHODS. – Adult *B. asper* were located by active search at night; although search efforts were not strictly controlled, we attempted to spend roughly equal time searching for animals in primary forest, secondary forest, and swamps. Captured animals were brought to the laboratory, measured to the nearest 0.1cm, weighed to the nearest 1g, anesthetized with Sevoflurane administered via inhalation, and implanted with a radiotransmitter (Holohil® 5g model SI-2 or 9g model SB-2, depending on size of the animal) in the body cavity following the methods of Hardy and Greene (1999). All transmitters weighed less than 5% of the snake's body mass. Animals were held in the laboratory for 48hrs post-surgery to monitor for adverse reactions, then released at the point of capture. We located snakes using receivers from Communications Specialists Inc.® (R-1000) and Habit Research® (HR2600 Osprey), and 3-element directional antennae from Wildlife Materials®.

In order to maximize the accuracy and precision of our home range and movement rate estimates, we attempted to relocate snakes once every day, alternating daytime and nighttime observations (as determined by sunrise and sunset) to account for temporal variation in activity. At each snake relocation, we used a compass and tape measure to relate its position to the nearest reference point (LSBS grid system or previously-marked location), and marked the site for subsequent use as a reference point. We also recorded whether we were able to visually detect the snake (otherwise locating it by triangulation), and if so noted its level of shelter and activity. We also conducted three 24-hour continuous-monitoring periods on each of six individuals (three male, three female) to assess daily activity cycles, recording all movements and behaviors in real time; observers remained approximately 10m from the snake and used minimal lighting, movement, and noise to avoid influencing its behavior.

Activity was scored as Inactive if the snake was lying coiled with its head resting when first located, Active if it was moving, and Ambushing if it was lying coiled and alert with the head raised. To characterize shelter usage, a snake was considered Sheltered if it was completely within structural cover (e.g. hollow log or root system of a tree), Semisheltered if it was partially covered (e.g. in dense herbaceous vegetation, adjacent to the base of a tree, or below but not concealed by a raised log), and Unsheltered if it was in the open.

ANALYSES. – Home range, movement, and macrohabitat cover at each relocation were determined using ArcView 3.2 with Animal Movement Extension (Hooge and Eichenlaub 2000), compositional analysis using Resource Selection (Leban 1999), and all other analyses using Systat 12.0. For each snake we calculated Minimum Convex Polygon (MCP), 95% and 50% Kernel Density (KD) (Worton 1989) home range estimates; for kernel estimates, the least-squares crossed validation method recommended by Seaman and Powell (1996) was used to determine smoothing parameter h.

Because home range estimate is strongly affected by number of relocations (Kernohan et al. 2001, Girard et al. 2002), we first used the MCP Bootstrap procedure in Animal Movement with 1000 replications to determine the relationship between MCP size and number of relocations for each snake. Since home range estimate appeared to plateau by approximately 100 relocations (Fig. 2.2), snakes with fewer relocations were excluded from home range analyses due to insufficient data.

We also used bootstrap data to project a "final" MCP size for each individual using the simplest standard equation describing an asymptotic curve MCP=(α*sample size)/(ß+sample size), where α is the asymptote and ß the half-saturation point. Resulting final MCPs were compared to our existing estimates using a Mann-Whitney U-test to determine whether our estimation methods produced a reasonable estimate of home range size. ANCOVA was used with snout-vent length (SVL) as the covariate to determine whether home range size differed between males and females by each estimation method while controlling for effects of body size.

Daily movement was determined as straight-line displacement between subsequent relocations, divided by the number of days between those relocations. For snakes used in 24-hour focal observations, we compared linear displacement and actual cumulative distance moved by each individual in the 24-hour period using a Mann-Whitney U-test, again to assess reliability of our estimation methods. Mean daily movement was calculated for each individual in each month, and months compared using ANOVA. Hierarchical mixed regression permits analysis of repeated measures of multiple individuals (Bryk and Raudenbush 2001), so was used to determine whether daily movement was affected by sex, SVL, month, rainfall, or daily high, low, or mean temperature. These variables were selected because they are known to influence movement rates of snakes (Gregory et al. 1987) and environmental data were readily available from an automated weather station at LSBS. We then regressed the movements of each snake individually against any significant variables, and took the mean of the resulting regression coefficients as a measure of overall effect (Lorch and Myers 1990).

Compositional analysis (Aebischer et al. 1993) was used to determine whether usage of each macrohabitat type varied from its availability. In compositional analysis, habitat usage and availability are expressed as a vector of proportions for each individual, and the log ratios of these proportions are analyzed using MANOVA (Aitchinson 1986). Thus it is an effective procedure for coping with problems of sampling level, non-independence of data, and differential selection across individuals. Macrohabitat types used were determined from available GIS maps by aggregating similar subtypes: Primary Forest (old-growth forest), Secondary Forest (abandoned agroforestry, abandoned plantation, current tree plantation, secondary-growth forests, selectively-logged forest), Swamp (open swamp, swamp edge) and Developed Areas (lab clearing, open pasture, shaded pasture). For all snakes, each relocation point was buffered with a radius equal to that individual's maximum observed single-day movement. The resulting polygons cumulatively defined the total area considered potentially "available" to that snake.

RESULTS

Data are reported here from eleven female and five male *B. asper*. For three individuals we recorded fewer than 33 observations before loss due to equipment malfunction, failure to relocate the animal, or death; all other individuals had between 121 and 371 relocations (Table 2.1). We were able to visually detect the snakes during 1198 of 1498 (80.0%) daytime and 1163 of 1430 (81.3%) nighttime observation attempts. Fer-de-lance were typically inactive throughout the day, remaining either coiled in the leaf litter or in shelter, emerging from such cover and assuming ambush posture (coiled and alert with the head raised) within about an hour of sunset. Snakes were more often inactive during the day than at night (Fig. 1; mean value= 98.1% of days, 34.1% of nights; Wilcoxon matched-pair rank sum test z=-3.41, n=16, p<0.001) and were observed ambushing more often at night than during the day (1.6% day, 62.8% night; z=3.41, p<0.001), with most daytime-ambush events recorded just prior to sunset. Foraging behavior consisted almost entirely of sit-and-wait tactics, with behavior characteristic of active searching or scent-trailing of previously-envenomated prey (moving slowly with frequent probing and tongue flicking) observed on less than 2% of all occasions, more often at night (0.3% day, 3.2% night; z=2.93, p=0.003). Snakes tended to utilize more exposed Unsheltered areas at night when they usually ambushed than during the day (35.5% day, 65.6% night; z=3.51, p<0.001), and were more often in Sheltered (31.2% day, 12.0% night; z=-3.30, p<0.001) or Semisheltered (33.4% day, 22.3% night; z=-3.52, p<0.001) conditions while resting during the day than at night.

During 24-hour observations (n=18), no daytime movement or other activity was recorded. At night, two individuals had one evening each during which they did not emerge at all from shelter; five individuals had one evening each during which they ambushed in place, but did not move. During the remaining observations (n=11), ambushing snakes utilized from 1-4 (mean=1.83±0.29) separate ambush sites over the course of a single evening, with little activity observed other than movement between these sites. Mean linear distance between ambush sites was 8.11±1.30m, and the mean cumulative duration of an individual's movements in a single evening was 37.3±7.9min. Although it is possible that snakes' movements were influenced by the proximity of an observer, the proportion of evenings in which snakes did not move at all (displacement=0.0m) during 24-hour sampling (38.89%) was similar to the proportion across all other evenings, when no observers were present (30.54%).

HOME RANGE. – MCP bootstrapping showed that home range estimate increased with number of relocations, and began to plateau after approximately 100 relocations (Fig. 2.2), but individuals with a high number of relocations did not necessarily have larger home ranges than those with fewer relocations. Home range estimates ranged from 0.59 to 13.81ha, mean 5.95±3.86 (MCP) and from 0.40 to 8.17ha, mean 3.71±2.56 (95% KD), while core areas (50% KD) ranged from 0.04 to 0.88ha, mean 0.37±0.28. Projected MCP size did not differ from our own estimates (U=95.0, df=1, p=0.30), so we considered those estimates a reasonable measure of home range size for comparative purposes, despite unequal number of relocations between individuals. After controlling for SVL, sex had no influence on home range size by MCP (F=0.11, df=1, p=0.74), 95% KD (F=0.13, p=0.72), or 50% KD estimates (F=0.56, p=0.47).

MOVEMENT. – Cumulative distances recorded for each individual during 24-hour observations did not differ significantly from straight-line displacement measures obtained from ArcView for those same dates (U=149.0, df=1, p=0.672); we therefore use displacement as a reasonable, if minimum, estimate of actual movement. Most daily displacements were less than 10m (Fig. 2.3) and consisted of short evening movements within a given area, interspersed with occasional longer-distance movements up to a maximum observed single-day displacement of 373.0m. Little seasonality in movement rate was detected, with mean daily movement rate of all individuals not differing among months (F=1.34, df=11, p=0.21).

Of all recorded variables (sex, SVL, month, rainfall, daily high, low, and mean temperature), only daily low temperature had a significant effect on movement rate (z=2.26, p=0.02), with lower temperatures seeming to constrain movement. However, an increase in temperature of 1°C predicted an increase in single-night displacement of just 0.73m, and regression coefficients for low temperature were small and highly variable across all snakes (mean= 0.013±0.025), suggesting that regression models explained very little of the overall variation in observed movement rates.

MACROHABITAT SELECTION. – Compositional analysis indicated overall nonrandom habitat usage relative to availability ($\lambda = 0.2323$, $\chi^2 = 18.977$, df=3, $p < 0.001$). Proportional use and availability of each habitat type are summarized in Fig. 2.4. *Bothrops asper* showed significantly greater usage of Swamp habitat relative to other types, and avoidance of Developed areas (Table 2.2). Usage of Primary and Secondary forests did not differ. The study area contained several rivers of up to >60m in width, which were excluded from habitat analysis. However, at least three individuals did swim across the rivers on several occasions during the course of this study.

DISCUSSION

These results represent the first detailed information regarding spatial ecology of fer-de-lance, and are among the first regarding long-term telemetric study of any Neotropical snake. Our results support characterization of *B. asper* as a highly nocturnal, sit-and-wait predator, with snakes observed ambushing on the majority of evenings (Fig. 2.1). Foraging sites were usually more exposed than daytime retreat sites; fer-de-lance did not seem to incorporate fallen logs or other structural features in their predatory tactics as reported for other ambush-hunting vipers (Reinert et al. 1984, Theodoratus and Chiszar 2000, Brito 2003). Diurnal ambushing behavior was rarely observed, nearly always by individuals that appeared extremely thin, with distinctly protruding vertebrae. During the course of the study, three individuals (animals #6, 8, and 37) began to show such emaciation, stopped moving between sites, and died within 1-2 weeks of the cessation of locomotion. It is therefore possible that diurnal ambushing represents atypical hunting behavior by starving individuals. We do not believe this to be related to transmitter implantation as each was able to forage normally for several months prior to death.

We analyzed home ranging behavior using both MCP and KD methods. Kernel-based methods in many cases produce larger estimates than polygons (Reinert and Zappalorti 1988, Fitzgerald et al. 2002, Diffendorfer et al. 2005), as they generate nested probabilistic contours that may extend beyond the outermost boundaries of polygons. However, for our data 95% KDs were a more conservative estimate of home range size (Fig. 2.5; Table 2.1). This finding may be due to the fact that unlike many large terrestrial vertebrates, *B. asper* wander very little on a daily basis, creating large pockets of unused space within the overall home range. For example, one individual (#29) repeatedly circled the LSBS laboratory clearing over several weeks, but observations and the direction of its day-to-day movements suggest it never actually entered the area. This area would be included in an MCP, but omitted from KD estimates. We include MCP estimates here to represent the overall area experienced by an individual and to facilitate comparison with existing studies of other snake species, but believe 95% KDs to be a more biologically meaningful reflection of actual space usage.

Mean home ranges as estimated by either method (MCP 5.95ha, 95% KD 3.71ha) are relatively small compared to those reported for similar-size terrestrial viper species in temperate regions that make annual migrations to overwintering hibernacula; for example, a mean home range size of 8.0ha (MCP) has been reported for *Crotalus oreganus* (formerly *viridis*) in British Columbia (Macartney 1985), 27.4 ha MCP and 45.2ha 95% KD for *C. horridus* in New Jersey (Reinert and Zappalorti 1988), and 23.2ha MCP and 20.9ha 95% KD for *C. cerastes* in California (Secor 1994). Our results are more similar to those reported by Beck (1995) for *C. atrox*, *C. molossus*, and *C. tigris* in southeastern Arizona (MCP 5.42, 3.49, and 3.48ha respectively) and by Angelici et al. (2000) for the larger *Bitis gabonica* in tropical Nigeria (MCP 1.6ha for males and 0.8ha for females, albeit over a shorter time period), populations that are independent of seasonal refugia.

Kernel methods also allow the identification of higher-usage areas within the home range; 50% KDs are considered the "core" of the home range (Hooge et al. 2001). Most snakes had two or more small core areas, with a mean cumulative size of less than 0.5ha (Table 2.1); Fig. 2.5 illustrates the home ranges of two representative individuals. These cores did not seem to be simply clusters of temporally-constrained points, but small areas between which the snakes traveled repeatedly and aseasonally. This pattern may be attributable to the observed foraging strategy, with snakes hunting within a given area for days to weeks at a time, before moving on to the next foraging area. Each 50% KD may therefore consist of an aggregation of nearby foraging areas.

Observed movement patterns support the idea of *B. asper* using several clusters of hunting areas, with most single-night displacements being short (<10m) movements between clusters of daytime shelter sites and nocturnal ambush sites. This was interspersed with occasional longer-distance movements (<50m) to new areas where the pattern was repeated. Snakes rarely traveled more than 100m on two consecutive evenings, suggesting that such movements represent dispersal across relatively unused areas to a given target site, although the factors reflecting the suitability of used and unused areas were not obvious to human observers. No evidence for territorial defense or synchronicity in use of foraging areas was observed.

Travel between disjunct foraging areas may be dictated by relative differences in resource availability at each area. Such a pattern may also reflect an inherent behavior of the species, roughly analogous to the "traplining" strategy of nectar-feeding insects (Janzen 1971, Thompson et al. 1987), birds (Stiles 1975, Gill 1988), and mammals (Janson *et al*. 1981, Garber 1988). However, it is not clear whether all foraging areas are predetermined destinations or selected upon random encounter, and the cues used by fer-de-lance in selecting foraging areas are unknown. Resolving these possibilities requires further investigation of the relationship between resource availability, foraging, and space usage by *B. asper*.

Movement pattern was largely aseasonal, with mean daily movement not differing across months. Movement also was not affected by most recorded environmental conditions (rainfall, daily high, low, and mean temperature); of all variables, only daily low temperature was significant. Snakes were observed moving and foraging normally during all but extremely heavy rains. Although daytime temperatures reached a maximum of 36.7°C, snakes were usually inactive at this time and under dense canopy cover or direct shelter. Fer-de-lance were seen basking in direct sunlight during only nine observations, six of them involving the same individual (#8, a female). Low temperatures always occurred at night, the time during which locomotion is most likely to occur. However, linear regression indicated that an increase of 1°C predicts an increase in daily displacement of only 0.73m, explaining very little of the overall variation in movement rate. LSBS may not experience temperatures low enough to greatly constrain movement (temperatures <19.0°C were recorded on only 16 nights during the study, all from November-February), or movement may be dictated more by factors such as foraging strategy than by environmental conditions.

We also found that movement pattern and home range were unaffected by sex. This was somewhat surprising, as males of many viper species tend to have greater movement rate or home range size than females, often presumably due to mate-searching behavior (Reinert and Zappalorti 1988, Secor 1994, Duvall and Schuett 1997, Marshall et al. 2006). Due to their extremely effective crypsis, it was not possible to tell whether additional fer-de-lance were present but undetected during observations, or to assess the overall distribution of conspecifics. In April 2006, we tracked one male that for three weeks closely followed and remained in close proximity to a female (neither animal is included in this study), including two movements across a 60m-wide river. Although breeding of *B. asper* may not be as markedly seasonal as that of temperate species, there seems to be a peak of mating activity in March (Campbell and Lamar 2004). On several occasions in March and April, we recorded unmarked male fer-de-lance coiled within 1m of telemetered females, though no mating was actually observed and no females were found to be gravid during the study.

Fer-de-lance at the study site utilized primary and secondary forests roughly in proportion to their availability, but showed a significant selection of swamps, which covered relatively little of the overall area (Fig. 2.4, Table 2.2). Similar habitat patterns (nonrandom selection, avoidance of human habitation, preference for swamps) have been reported for the tropical viper *Bitis gabonica* (Angelici et al. 2000). In our study, most (77.8%) 50% KDs were located in or adjacent to swamps (Fig. 2.5), and snakes were often observed sheltering during the day along the wooded banks but ambushing at night within a few meters of the water's edge. As prey availability is known to influence space usage by snakes (Gregory et al. 1987, Weatherhead and Robertson 1990, Madsen and Shine 1996), this habitat selection may be related to foraging on amphibian prey; we observed predation attempts by study animals on both *Leptodactylus pentadactylus* (Leptodactylidae) and *Rana vaillanti* (Ranidae), large-bodied (to >10cm SVL, Savage 2002) frog species that are swamp-associated at LSBS. Several water-associated rodents such as *Hoplomys gymnurus* and *Oryzomys alfari* are native to the area (Reid 1997), but none of these are currently known to be abundant at LSBS; rodents of any kind were very rarely encountered during the study period. More detailed information on prey availability is necessary, however, to draw specific conclusions regarding the link between food resources and spatial ecology of *B. asper*.

Snakes demonstrated significant avoidance of developed areas that typically had reduced canopy cover and ground structure. Although telemetered animals would often circumvent rather than directly cross disturbed clearings, additional non-telemetered *B. asper*, especially juveniles, were often encountered in such areas, including on manmade paths or inside human habitations. Although not likely a preferred habitat, the frequency of such occurrences suggests that *B. asper* is not entirely averse to human activity, or that a change in habitat usage may occur with ontogeny.

Bothrops asper is a ubiquitous and somewhat notorious resident of many Neotropical systems and, as with many venomous snakes, is subject to much mythology and hyperbole. Fer-de-lance are frequently described as being highly aggressive, prone to striking with little provocation. While the high incidence of *B. asper* snakebite indicates this characterization is not entirely without merit, after more than 4000 observations of free-ranging snakes, we recorded no defensive strike attempts by resting animals except when they were directly manipulated for capture. During the day, snakes could often be approached to within less than a meter with no visible reaction; during the evening when they were more alert, snakes were more likely to flee if approached.

Snake ID	Sex	SVL (cm)	No. of relocations	Start date	End date	95% KD (ha)	50% KD (ha)	MCP (ha)	Projected Final MCP (ha)
3	F	125.6	137	1 Dec 2004	7 Jun 2005	4.82	0.53	5.33	5.90
6	M	119.1	155	1 Dec 2004	28 Jun 2005	3.78	0.57	5.18	5.80
8	F	125.5	134	1 Dec 2004	6 Jun 2005	5.13	0.68	9.06	9.90
11	M	116.1	32	1 Dec 2004	11 Jan 2005				
14	F	128.2	27	1 Dec 2004	29 Dec 2004				
15	F	126.1	121	1 Dec 2004	23 May 2005	0.40	0.04	0.59	0.68
16	M	124.7	326	1 Dec 2004	5 Oct 2006	1.96	0.17	3.38	3.84
21	F	139.3	371	25 Feb 2005	7 Oct 2006	8.17	0.53	13.81	14.44
26	F	118.6	31	15 Mar 2005	26 May 2005				
29	M	89.9	200	15 Mar 2005	10 Oct 05	6.05	0.88	9.91	10.64
36	F	113.2	346	3 July 2005	23 Sep 2006	1.29	0.06	2.72	2.90
37	F	121.1	327	20 Jun 2005	9 Jun 2006	1.06	0.15	3.17	3.68
39	F	118.3	129	3 July 2005	15 Nov 2005	0.65	0.05	0.92	1.08
49	F	116.2	289	12 Dec 2005	9 Oct 2006	5.17	0.33	8.18	8.75
63	M	94.6	221	6 Apr 2006	26 Nov 2006	2.77	0.22	6.70	7.70
66	F	145.0	224	16 Apr 2006	10 Dec 2006	6.95	0.60	8.46	9.25
Mean						3.71	0.37	5.95	6.50
SE						0.71	0.08	1.07	1.13

Table 2.1. Identification number, sex, snout-vent length, number of relocations, tracking period, and home-range estimates by minimum-convex polygon (MCP) and kernel density (KD) methods for each snake used in the study. Home ranges were not calculated for individuals with <100 relocations (n=3).

	Swamp	**Primary Forest**	**Secondary Forest**	**Developed Areas**	**Rank**
Swamp		+++	+	+++	3
Primary Forest	−−−		+	+++	2
Secondary Forest	−	−		+++	1
Developed Areas	−−−	−−−	−−−		0

Table 2.2. Comparative usage of habitats by *Bothrops asper*, determined by Compositional Analysis. Signs (+ or −) represent greater or lesser usage of that row habitat relative to column habitat; triple signs indicate a significant difference at $p<0.05$. Rankings are ordered from 3 to 0 (most to least used).

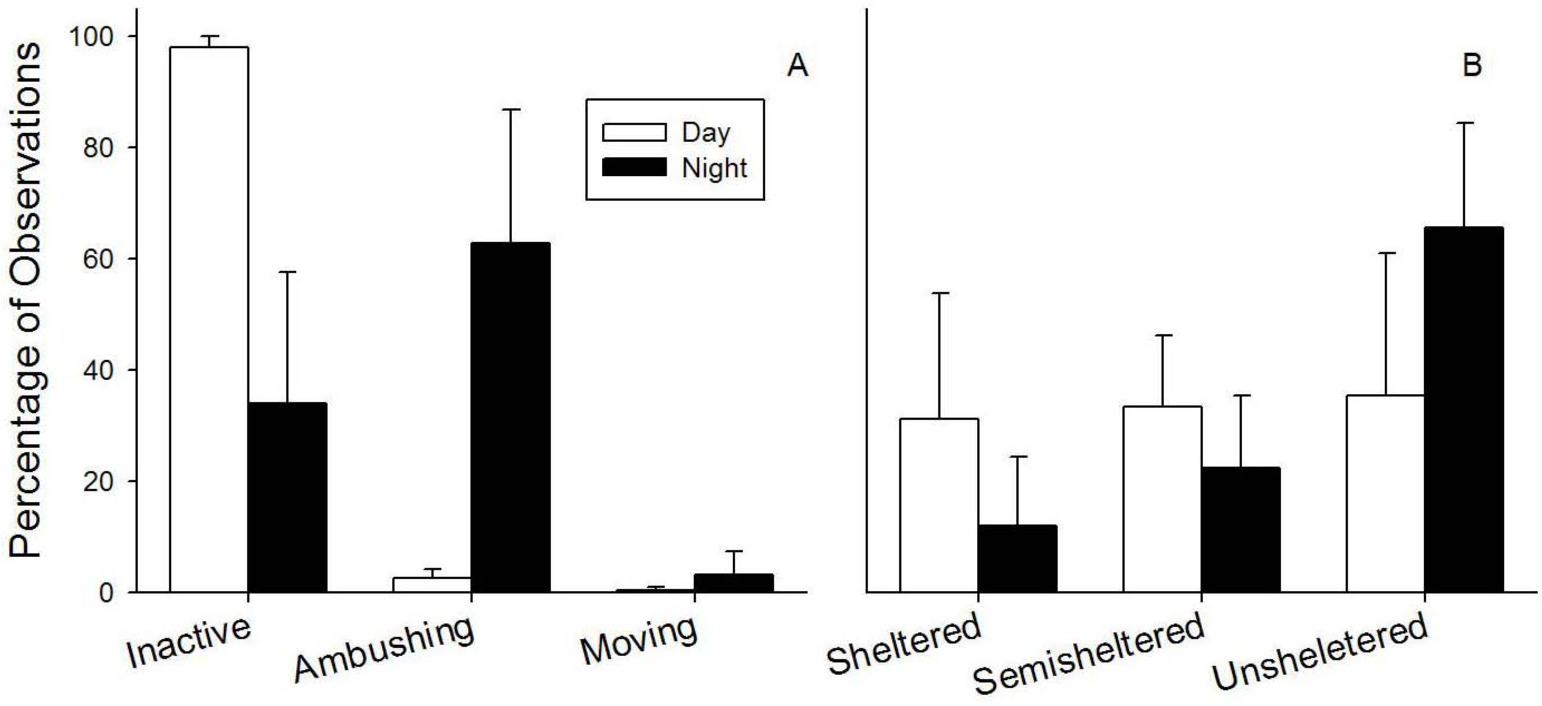

Figure 2.1. Frequency (+1SD) of daytime and nighttime observations of snake A) activity and B) shelter usage. All day/night pairs were significant at $p<0.05$.

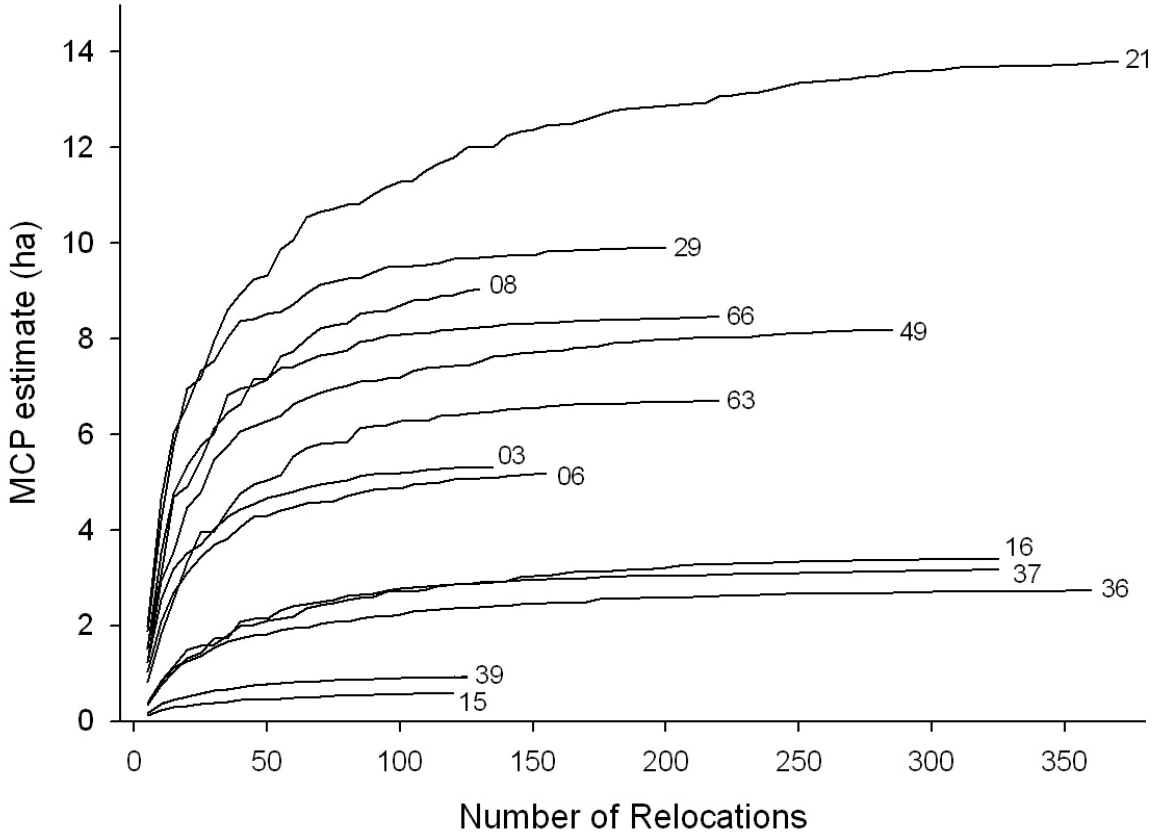

Figure 2.2. Mean MCP home range estimate of each snake based on 1000 bootstrap replications at each number of relocations. Numbers following each line are the identification number for that individual (Table 2.1).

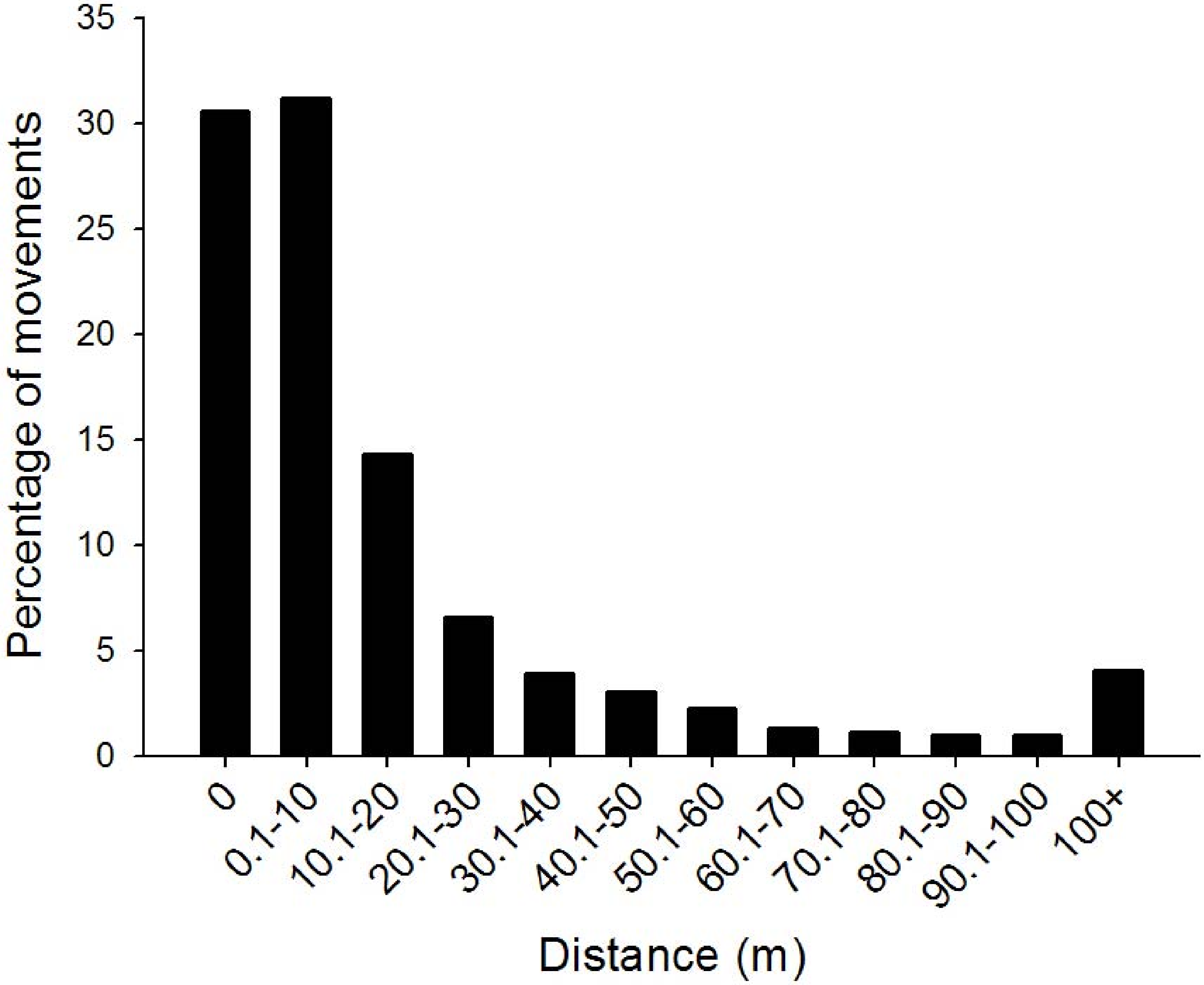

Figure 2.3. Frequencies of straight-line displacement distances between successive relocations, determined as actual displacement divided by the number of days between relocations. Data are compiled from all individuals and years.

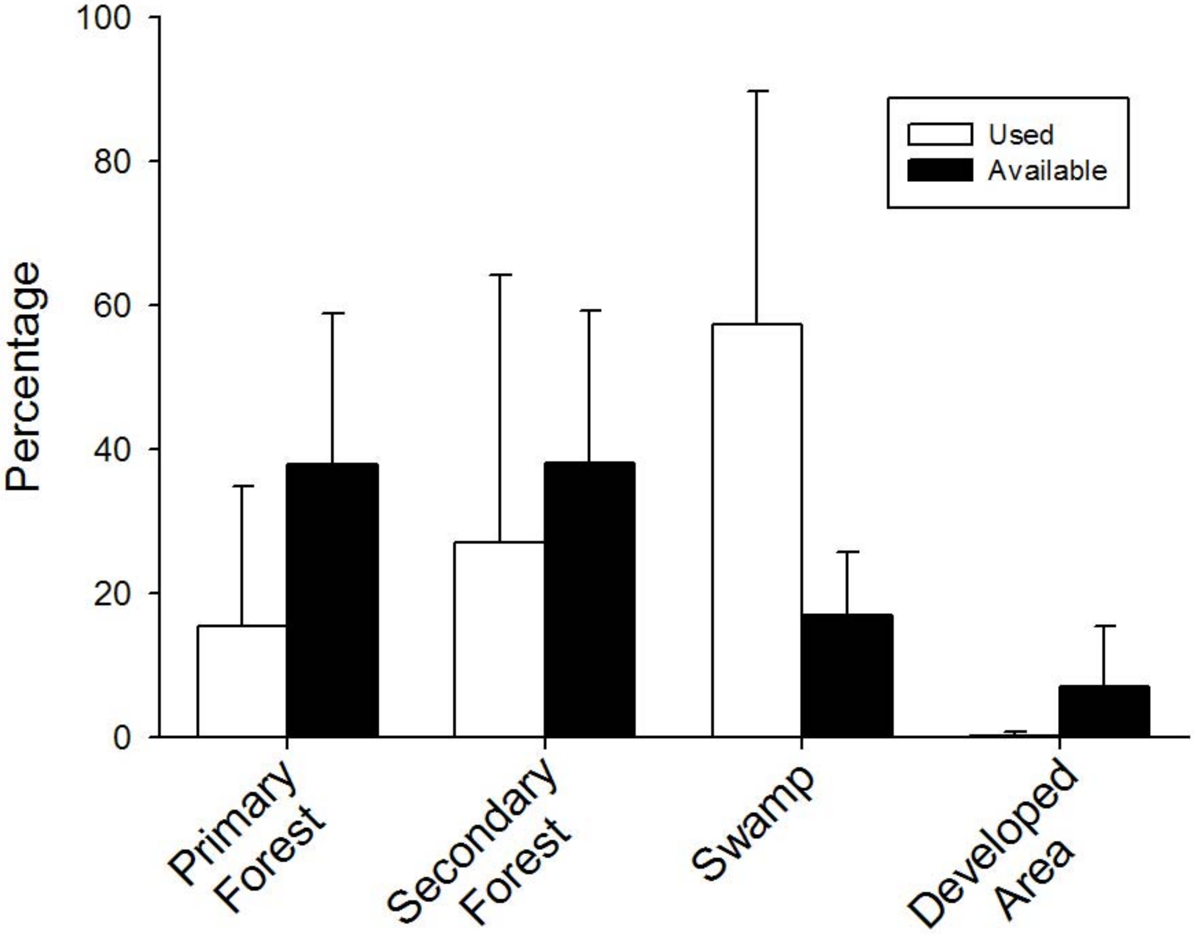

Figure 2.4. Mean percentage y (+1 SD) of habitats available to and utilized by all snakes over the study period. Units are land coverage (ha) for Used, number of observations for Available.

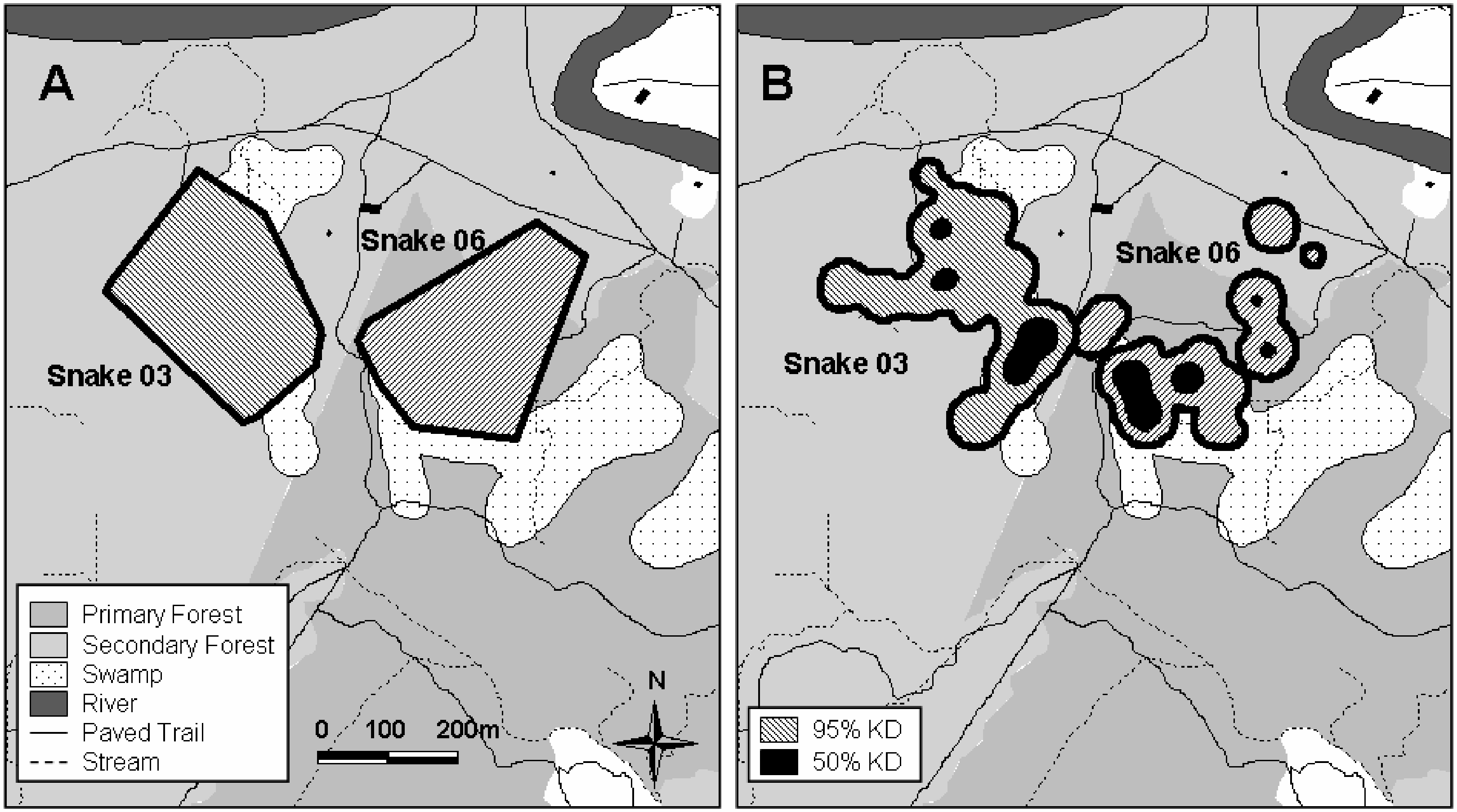

Figure 2.5. Home ranges of two *B. asper*, #3 (female) and #6 (male), as estimated by A) minimum convex polygon and B) kernel density methods. MCP areas are 5.33 and 5.18ha respectively; 95% KDs are 4.82 and 3.78ha, and 50% KDs cumulatively for each individual 0.53 and 0.57ha.

CHAPTER 3

HABITAT SELECTION OF THE FER-DE-LANCE (*BOTHROPS ASPER*, SERPENTES: VIPERIDAE) IN A LOWLAND RAINFOREST IN COSTA RICA

SUMMARY

Despite their high diversity and importance as top predators in many ecosystems, the ecology of many snakes remains poorly understood. This situation is especially true at low latitudes, as few attempts have been made to quantify patterns of space usage by tropical snake species. Here, we describe macro- and microhabitat use by the abundant pitviper *Bothrops asper* in lowlands of Costa Rica. Specifically, we used radiotelemetry to monitor nine female and four male adult snakes at La Selva Biological Station between 2004 and 2006. We determined macrohabitat usage and availability based on the movements of individual snakes and analyzed selection using compositional analysis. Microhabitat was quantified by a series of structural characteristics, and groups of locations compared using MANOVA. Fer-de-lance demonstrated a positive selection for swamp habitat and avoidance of human-disturbed areas by both male and female snakes. Microhabitat usage did not differ between males and females, but did differ for all individuals between daytime observations, when snakes were typically inactive, and nocturnal observations, when snakes moved to more exposed areas and foraged using ambush tactics. Microhabitat characteristics were significantly nonrandom at both times, suggesting that *B. asper* actively select particular sites for both diurnal retreat and nocturnal foraging sites. These data emphasize that the contrasting ways in which animals may utilize resources at separate times or for different activities should be considered in studies of overall habitat selection.

BACKGROUND

Patterns of habitat selection and utilization are a central component of any species' ecology and natural history. Among snakes, both large- and small-scale habitat characteristics may directly influence demographic parameters such as reproduction (Reinert 1993; Reinert and Zappalorti 1988; Shine 2003) and survivorship (Bonnett et al. 1998; Elick and Sealander 1972; Madsen and Shine 1998), as well as behaviors related to foraging (Chandler and Tolson 1990; Lind and Welsh 1994; Reinert et al. 1984) and thermoregulation (Beaupre 1995; Blouin-Demers and Weatherhead 2002). However, perhaps due largely to their cryptic nature and historical difficulty of study prior to the development of implantable radiotransmitters (Reinert and Cundall 1982; Weatherhead and Anderka 1984), many snakes are poorly represented in studies of habitat selection, especially species occurring in the tropics. Consequently, much additional information must be collected before meaningful comparisons can be drawn between snake species occurring in tropical regions and those from the highly-dissimilar temperate zones from which more information is available.

Among tropical species, habitat usage by species that exhibit high sexual dimorphism are of particular interest, as intraspecific variation might suggest variation in ecological strategies. Sexual size dimorphism exists in many animal groups including snakes, driven by interactions of both ecological (Bolnick and Doebli 2003; Camilleri and Shine 1990; Shine 1989) and sexual selective pressures (Bonnett et al. 1998; Shine 1978, 1991). Such differences in body size can lead to divergent trophic habits (Camilleri and Shine 1990; Pearson et al. 2003; Shine 1991; Vincent et al. 2004) which may in turn influence differential habitat usage of males and females (Durner and Gates

1993; Shine 1986; Shine et al. 2003). In addition to intersexual differences, habitat usage may also vary temporally, as individual animals select specific habitats for various activities such as foraging, reproduction, thermoregulation, or ecdysis (Blouin-Demers and Weatherhead 2002; Chandler and Tolson 1990; Reinert 1993).

Lancehead pitvipers (genus *Bothrops,* Serpentes: Viperidae) may present an ideal opportunity to study variation in spatial ecology and the factors that might influence it. These snakes are widely distributed across southern Mexico and Central and South America and exhibit strong sexual dimorphisms (Sasa 2002). Here we report on the habitat associations of the tropical snake *Bothrops asper* (fer-de-lance) in lowland rainforests of Costa Rica. *B. asper* is a large snake (maximum total length 2.5m, Savage 2002) that is abundant in a variety of ecosystems from southern Mexico through northern South America (Campbell and Lamar 2004). The fer-de-lance is a highly venomous nocturnal ambush predator, and is one of the most medically-important species in the New World, being responsible for the majority of human snakebites and snakebite fatalities within its range (Hardy 1994*a,b*; Saborío et al. 1998). Its ecology and natural history under field conditions is, however, very poorly documented (but see Nickerson et al. 1978, Solórzano and Cerdas 1989, Talley et al. 2005). Although the species is generally described as primarily a terrestrial denizen of tropical forest habitats, such depictions are often based on collections of museum specimens or incidental field observations (Cisneros-Heredia and Touzet 2004, Martins et al. 2002).

We used radiotelemetry to study the ecology and behavior of *Bothrops asper* in lowland rainforest of Costa Rica. Here we report on patterns of habitat usage by thirteen free-ranging individuals over two years. Specifically, we determined macrohabitat selection using compositional analysis and characterized microhabitat by a series of structural variables. We also investigated whether habitat was utilized differently between males and females, or by all individuals for diurnal versus nocturnal activities. These data present insight into the natural history and distribution of a poorly-understood snake species, and information regarding habitat selection, particularly of areas disturbed or frequented by people, may prove useful for avoiding its bite.

MATERIALS AND METHODS

Study Site. – Field research was conducted from 30 November 2004 through 10 December 2006 at La Selva Biological Station (LSBS) in Puerto Viejo de Sarapiquí, Heredia Province, northeastern Costa Rica (84˚00'12.959 W, 10˚25'52.513 N). LSBS is a 1700ha reserve consisting of primary and secondary lowland tropical rainforest, with numerous small forested swamps, and some areas developed for human usage. The region is fairly aseasonal in temperature, but does typically experience periods of reduced rainfall from January through April and in September; rainfall is abundant throughout the remainder of the year, averaging 4300 mm/year. More extensive descriptions are provided elsewhere of climate (Fetcher et al. 1985; Guyer 1988) and vegetation cover (Frankie et al. 1974; Holdridge et al. 1971).

Field and Telemetry Methods. – Adult snakes were located by active search at night, since *B. asper* are nocturnal ambush predators that are more exposed while hunting but highly cryptic during the day. Although search efforts were not strictly controlled, we attempted to spend roughly equal time searching for animals in primary forest, secondary forest, and swamps to minimize bias due to habitat in which the snakes were initially caught. Captured animals were taken to the laboratory, measured, anesthetized and implanted with radiotransmitters (Holohil 5g model SI-2 or 9g model SB-2, depending on size of the animal) following the methods of Hardy and Greene (1999). All transmitters weighed less than 5% of the snake's body mass. Snakes were retained in the laboratory for 48hrs post-surgery to monitor for adverse reactions, then released at point of capture. We located snakes using receivers from Communications Specialists Inc. (R-1000) and Habit Research (HR2600 Osprey), and 3-element directional antennae from Wildlife Materials. We attempted to locate snakes daily, alternating daytime and nighttime observations. Macrohabitat coverage at each location was determined using ArcView 3.2 with Animal Movement Extension (Hooge and Eichenlaub 2000) and current GIS maps of LSBS which are based on vegetation structure and history of usage. In addition to existing habitat classifications, we defined four broad macrohabitat categories by aggregating similar sub-types. Primary Forests were any historically undisturbed forest, and included only LSBS-defined old-growth forest. Secondary Forests (including abandoned agroforestry, abandoned plantation, current tree plantation, secondary-growth forest, and selectively-logged forest) were defined as currently heavily forested areas which had experienced modification by humans. Swamps (forested swamp, swamp edge) were areas characterized by frequent retention of standing water and distinct vegetation profiles, and included the areas immediately surrounding them (within 20m). Developed Areas (lab clearing, open pasture, shaded pasture) were habitats heavily modified by human activity, typically featuring reduced canopy closure, relatively sparse vegetation, and little structural ground cover.

At each snake location we recorded a series of microhabitat characteristics: substrate type, height above the ground (for example, if on a log or branch), percent canopy closure (using a spherical densiometer), and distance from the snake's body to the nearest large canopy tree (≥25cm diameter at breast height), small understory tree (<25cm dbh), log (fallen branch ≥20cm diameter), and body of water. A habitat component was considered "unavailable" at that site if none were present within 25m of the snake. Microhabitat data were also collected from 500 points selected randomly from within the area enclosed by all individuals' home ranges.

During daytime observations, fer-de-lance usually remained in a cryptic resting posture and did not attempt to move away from observers, allowing us to record distance and height data to the nearest 0.1m using a tape measure. At night, snakes were more alert and tended to flee if approached, so we often noted their exact location and recorded microhabitat data the following day to minimize disruption of their natural movement pattern.

Analysis. – Macrohabitat type (primary forest, secondary forest, swamp, or developed area) at each snake relocation point was determined from available GIS maps of LSBS using ArcView 3.2 with Animal Movement Extension (Hooge and Eichenlaub 2000). Compositional analysis (CA) (Aebischer et al. 1993) was performed with the program Resource Selection (Leban 1999) and used to determine whether proportional usage of each macrohabitat type varied from its availability. CA expresses habitat usage and availability as a unique vector of proportional usage of each habitat type, and analyzes the log-ratios of these proportions using MANOVA (Aitchinson 1986). This method is useful for the analysis of data from multiple individuals with several relocations per individual, and is not affected by the habitat type in which an individual “began”. For analytical purposes, complications arise only in arriving at the most appropriate definition of “available” habitat.

There is no universal approach to determining habitat availability (Johnson 1980; McClean 1998), but for snakes it is often based on either the animal’s home range or the entire study site (e.g., Johnson et al. 2007; Marshall et al. 2006; Moore et al. 2006). Because study sites may be overestimates of availability by including regions not actually reachable by the snake, and home ranges underestimates by treating outer edges of the home ranges as absolute boundaries, we used an individualized approach to habitat availability. Each snake relocation point was buffered with a radius equal to that individual’s maximum observed single-day movement distance, creating a circle representing the total area to which that snake *could* have traveled from its current location, based on its actual movement pattern. The cumulative area covered by the resulting overlapping circles was considered the area “available” to each snake over the course of the study. Areas covered by rivers were excluded from analysis, as snakes rarely crossed and were never actually observed in or around moving water. We conducted compositional analysis on both our broad categories and the full set of habitat sub-types.

We determined whether snakes demonstrated active selection for structural microhabitat (as defined by percent canopy closure and distance to large tree, small tree, log and water) by comparing sites actually used by snakes to randomly-selected unused points, with data from day and night observations analyzed separately. We also compared microhabitat usage between males and females, and between all snakes for day and night observations. Because microhabitat features (small and large tree, log, water) at distances greater than 25.0m were considered "not available", we transformed distance data by subtracting from 26, resulting in a range of possible values from 26 (adjacent) to 1 (25m distant), with "unavailable" scored as 0. We then took the mean value of each microhabitat variable for each snake, and compared the resulting values using one-way MANOVA conducted with Systat 12.0.

RESULTS

Telemetry data were collected from 9 female and 4 male fer-de-lance, with the number of relocations ranging from 97 to 370 per individual. As *B. asper* is highly nocturnal, animals typically foraged in the evening using sit-and-wait tactics, and were typically completely inactive during the day. Movement between successive relocations thus occurred exclusively at night. All snakes demonstrated true home ranging behavior, with a mean 95% Kernel Density size of 3.71±2.56ha (see Chapter 2).

Macrohabitat. – Overall macrohabitat cover at the study site consisted of 37.9% Primary Forest, 38.0% Secondary Forest, 17.0% Swamp, and 7.1% Developed Area. CA based on the full suite of LSBS habitat descriptions produced identical results across all subcategories of each broad habitat type, with the exception of Developed Areas. Within Developed Areas, the laboratory clearing was the most-avoided of any habitat in the study and was utilized significantly less than open or shaded pastures. Because analyzing finer-resolution macrohabitat data yielded no additional information regarding relative preference for each habitat type, we present results here using only the broader habitat categories.

Overall habitat utilization was significantly nonrandom relative to availability (Wilk's λ= 0.232, χ^2=18.977, df=3, p<0.001). Swamps were used significantly more than Primary Forest or Developed Areas, while usage of Primary and Secondary Forests did not differ from one another (Table 2.1). Developed Areas were used significantly less than any other habitat type, and were completely avoided by most snakes, even when their home ranges contained a substantial proportion (up to 28.8%) of such areas. Swamps were also the only habitat with proportionally greater usage than availability, being utilized about three times more often than predicted by random movement (Fig. 3.2).

Microhabitat. – B. asper in this study were highly terrestrial and usually remained on leaf litter on the ground, using slightly elevated perches (such as sitting atop a log or inside the root system of a tree) during 5.23% of relocations, split evenly between day and night observations. Mean height of these perches was 0.49±0.03m, to a maximum height of 2.1m for a snake observed on the exposed roots of a fallen tree. No study animals were ever found in trees or on tree branches, as has been reported previously by Greene (1997).

During the day, snakes typically were inactive and often utilized logs or other structures as daytime refugia. At night, snakes were more exposed on open leaf litter, and activity consisted mainly of sitting stationary in ambush position (coiled and alert with the head raised). Based on the recorded structural characteristics, we found no difference between male and female microhabitat usage during the day (λ=0.871, F=0.207, df=5,7, p=0.949) or at night (λ=0.876, F=0.198, df=5,7, p=0.953 revealed by MANOVA. Pooling data for males and females, overall microhabitat usage differed significantly between daytime and nighttime observations (λ=0.282, F=4.080, df=5,7, p=0.039). Two of the five recorded variables, distance to nearest log and to nearest water, differed significantly (Table 3.1).

Structural microhabitat characteristics of randomly-selected, unused sites differed significantly from those of sites actually used by snakes during both day (λ=0.968, F=3.303, df=5,507, p=0.006) and night (λ=0.965, F=3.626, p=0.003), implying overall non-random microhabitat usage. During both times, distance to nearest log and nearest body of water differed from random availability, with percent canopy coverage approaching statistical significance (Table 3.1).

DISCUSSION

Any analysis of habitat preference depends highly on the definitions of "used" and "available" (Johnson 1980, Rettie and McLoughlin 1999, Rosenberg and McKelvey 1999). McClean et al. (1998) found that excluding areas which were actually used by study animals (by the use of buffered animal relocations) increased the chances of committing a Type II error and failing to correctly determine significant selection, while including areas not actually so used (by including the entire study area) increased the chances of committing a Type I error and falsely determining significant selection, but allowed for an overall more sensitive test. However, most authors suggest tailoring analytical methodology to the goals of the study and biology of the species in question.

When studies focus on highly-mobile species or when relocations are infrequent, collected data may reflect only a snapshot of habitat use, providing little insight into the range of areas actually encountered by or available to focal animals. For animals that move little or studies with little elapsed time between successive relocations, animal relocation points may be a more biologically-meaningful basis for determining availability.

We used an individualized approach based on the movements of each snake in order to generate biologically realistic estimates of habitat availability and usage. Although we relocated snakes only once per day, based on 24-hour observations we found *B. asper* to be highly sedentary on a daily basis, with animals often remaining in the same location for several days at a time and moving only briefly and directly between subsequent relocation sites (see Chapter 2). Each relocation point therefore reflects the entirety of an individual's activity for a period of several hours to several days, suggesting that our data present a reasonable depiction of study animals' overall habitat usage. For habitat availability, we determined the maximum observed single-day movement of each individual, and considered that distance as the radius from within which a snake could potentially select its next location. This also provided a biological, individual-based criterion for defining availability, rather than relying on extrinsic standards such as the study area or arbitrary buffer distances.

Though typically described as a forest-dwelling species (Martins et al. 2002), *B. asper* at LSBS demonstrated a significant preference for swamps over other habitat types (Table 2.1). Study snakes were initially captured in a variety of habitats, but the home range of most individuals was centered in or around swamps (Fig. 3.1), even though such areas constituted only a small percentage (17.02%) of the overall available area (Fig. 3.2). Our observations suggest that this may be due to foraging habits. When snakes were near swamps, they often ambushed at night along the water's edge, but sheltered during the day ~5-10m away. Fer-de-lance are considered dietary generalists that specialize primarily on small mammals as adults (Martins et al. 2002), but small mammals such as rodents were found to be very uncommon at LSBS during the study period based on a trapping survey and field observations. However, many species of frogs were abundant in swamp areas, and adult *B. asper* attempted to feed on the larger-bodied frog species *Rana vaillanti* and *Leptodactlyus pentadactylus* on several occasions (pers. obs.). Thus the disproportionate utilization of swamp habitat by study animals may reflect attempts to exploit amphibians as a food source at LSBS. It is unknown whether this pattern holds true for other populations of *B. asper*.

Contrary to popular perception (Chaves et al. 1996), *B. asper* in this study showed an avoidance of sites heavily disturbed by human activity. Pastures and areas cleared for human usage featured reduced canopy closure, reduced ground vegetation, and little structural cover. These factors may expose snakes to increased predation risk (Bonnett et al. 1999) or increase their likelihood of detection by potential prey (Bouskila 1995, Kotler et al. 1993). The home ranges of several individuals were adjacent to the laboratory clearing at LSBS, and they often circled but were never found to actually enter the area. However, it should be noted that during the study several non-telemetered juvenile and adult *B. asper* were found within the residential areas, including some that ventured around or even into buildings. While this reinforces the idea of *B. asper* as somewhat of a habitat opportunist, the circumstances surrounding these occasions (e.g. dispersal movements, mate-searching, prey scent-trailing) are unknown.

We quantified microhabitat on the basis of several physical characteristics of the environment that are often used to define snake habitat usage (Reinert 1993). It is also important to note that many other factors may be equally important in describing habitat as it is actually experienced by snakes. Pitvipers' unique suite of sensory organs implies that they exist in a world of visual, tactile, olfactory, and thermal cues that are largely invisible to human observers (Ford and Burghardt 1993). Restricting our characterization to the recorded structural features, however, proved sufficient for the goals of this study.

Microhabitat use was significantly different between diurnal and nocturnal observations, and both differed from random unused sites, suggesting active microhabitat selection during both day and night. This pattern may also be largely explained by foraging behavior. During the day, snakes were almost completely inactive and tended to be closer to logs, under or next to which they often sheltered (Fig. 3.3). At night, snakes typically moved a short distance from daytime refugia to more exposed areas and settled in an ambush posture. *B. asper* was not found to incorporate logs or other structural features of the environment into their ambush tactics, as has been described for other pitviper species (Reinert et al. 1984). If standing water was available (such as in a swamp), snakes often moved closer to its edge; however, no snake was ever observed actually in any body of water. All observed frog-predation attempts were recorded when the snake was positioned less than 1m from the water's edge. These results suggest that studies of habitat selection should carefully consider the times and circumstances of data collection, as animals may utilize habitat in subtly different ways for various activities.

Our results also emphasize that due to the highly cryptic nature of many snakes, the places and circumstances in which they are encountered by people may differ greatly from those in which they actually spend the majority of their time. For example, many visitors to LSBS primarily encounter *B. asper* that have entered human-inhabited areas or that are crossing paved forest paths, even though such events were rare and even avoided by the majority of study snakes. Misconceptions may hold even among experienced naturalists; many researchers and field workers in discussion with the authors echoed the common “knowledge” that fer-de-lance are most often encountered sheltering in the buttresses of large trees, as do some other herpetofauna (Whitfield and Pierce 2005). In reality, telemetered snakes were found in such places during fewer than 1% of observations. Finally, the observed habitat specificity and avoidance of human-altered areas might indicate that *B. asper*, contrary to popular belief, is threatened by severe habitat modification in rural areas, an expectation that is supported by the species’ relatively low abundance in grasslands and semi-urban environments.

	MALE VS. FEMALE		DAY VS. NIGHT		USED (DAY) VS. RANDOM		USED (NIGHT) VS. RANDOM	
	F	p	F	p	F	p	F	p
Overall	**0.196**	**0.954**	**4.080**	**0.039***	**3.303**	**0.006***	**3.626**	**0.003***
Large Tree	0.052	0.824	0.746	0.405	2.442	0.119	2.297	0.130
Small Tree	0.010	0.923	2.117	0.171	0.014	0.904	0.047	0.829
Log	0.195	0.667	5.689	0.034*	4.708	0.030*	4.383	0.037*
Water	0.748	0.406	5.840	0.033*	5.126	0.024*	6.338	0.012*
Canopy Closure	0.164	0.693	0.868	0.370	3.061	0.081	3.843	0.051

Table 3.1. – Results of microhabitat comparisons between groups using MANOVA. Data for Male vs. Female were pooled from both day and night observations; data for all other comparisons were pooled from both males and females. Statistically significant differences are denoted by an asterisk (*). See Fig. 3.3 for actual values of each variable.

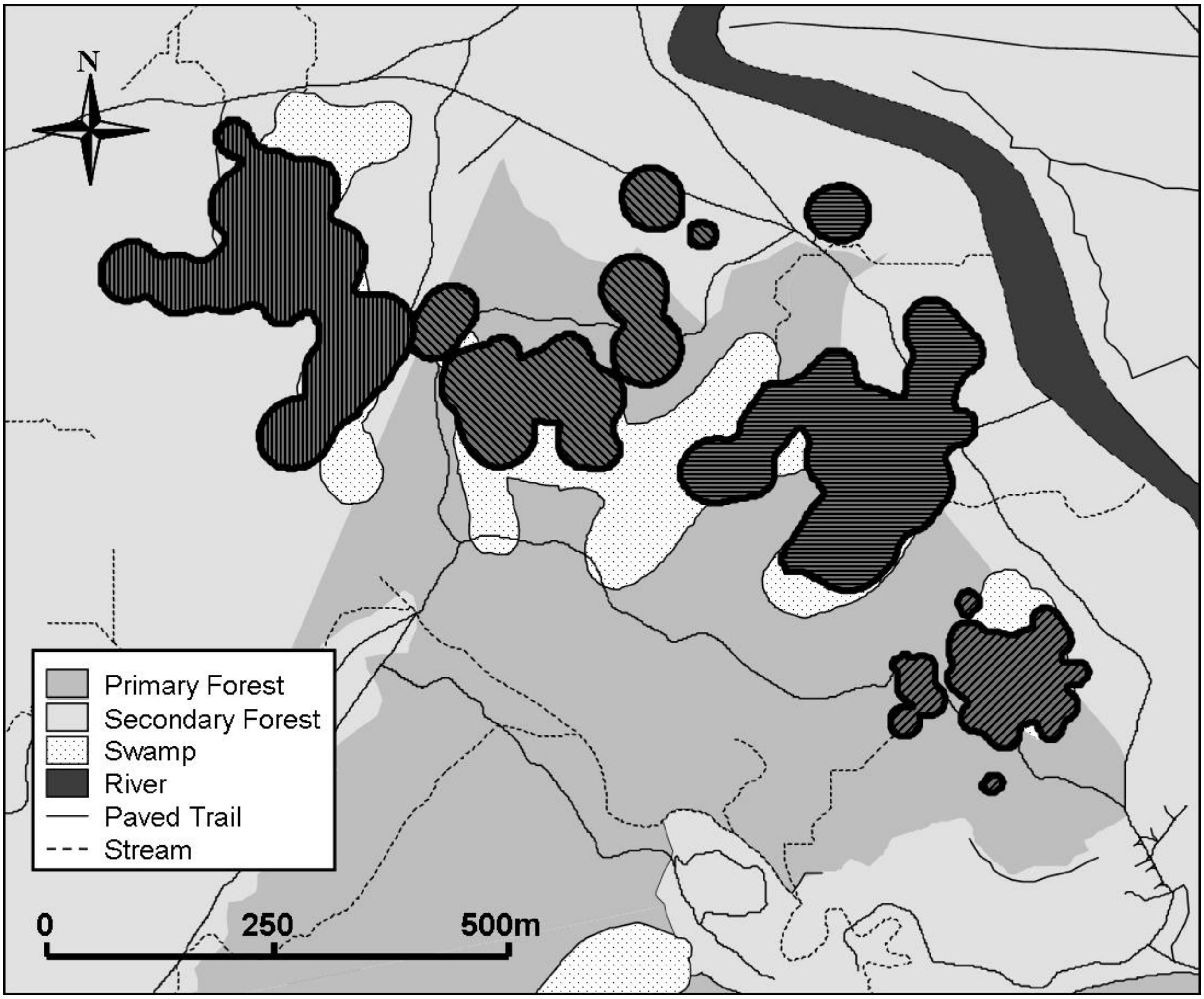

Figure 3.1. – Partial study-site map showing the 95% kernel-density home ranges of four adult *B. asper*, each shaded in a different cross-hatch pattern. These individuals were selected for illustrative purposes; home ranges overlap extensively with those of other snakes.

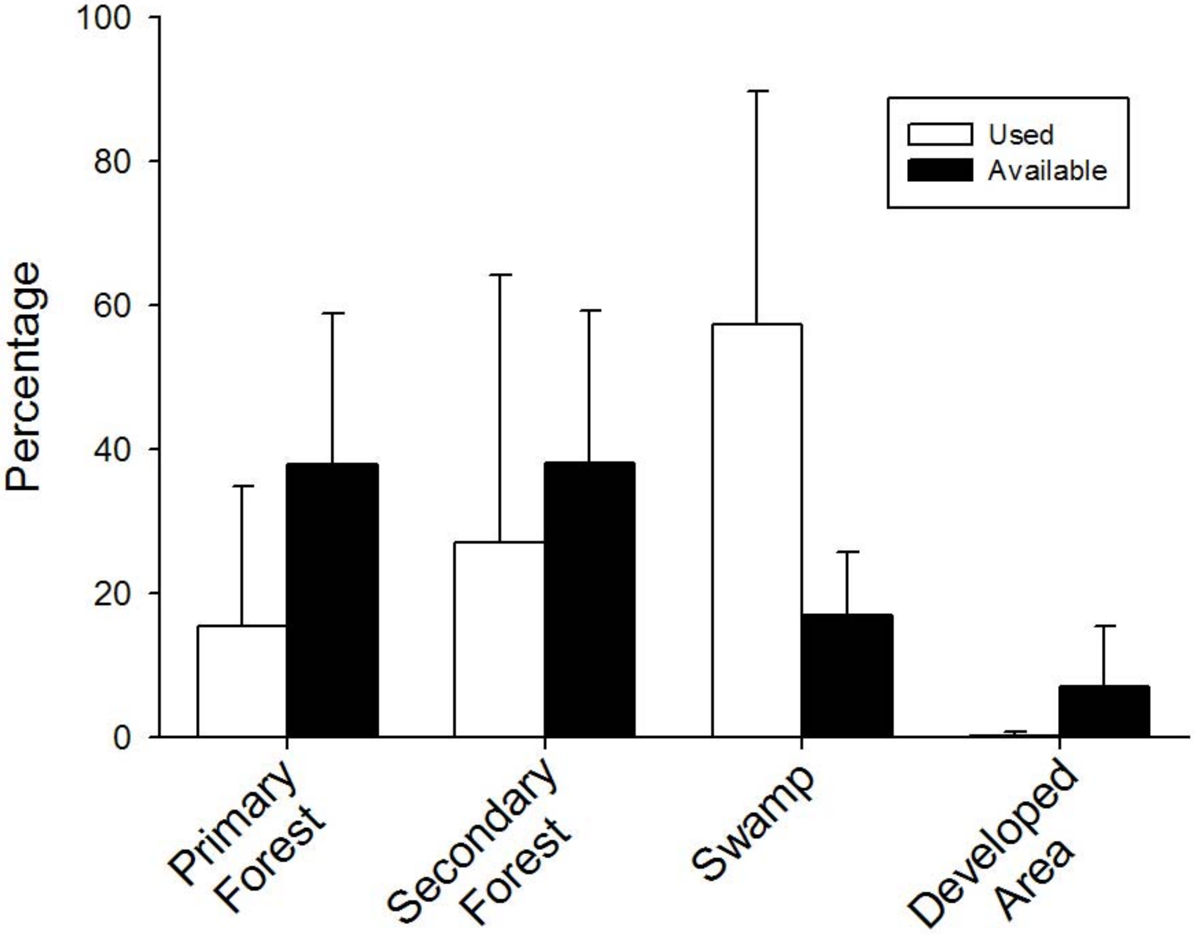

Figure 3.2. – Mean proportional distribution (+1 SD) of habitats available to and utilized by all snakes over the study period. Percentages were determined from area (ha) for Used, number of observations for Available.

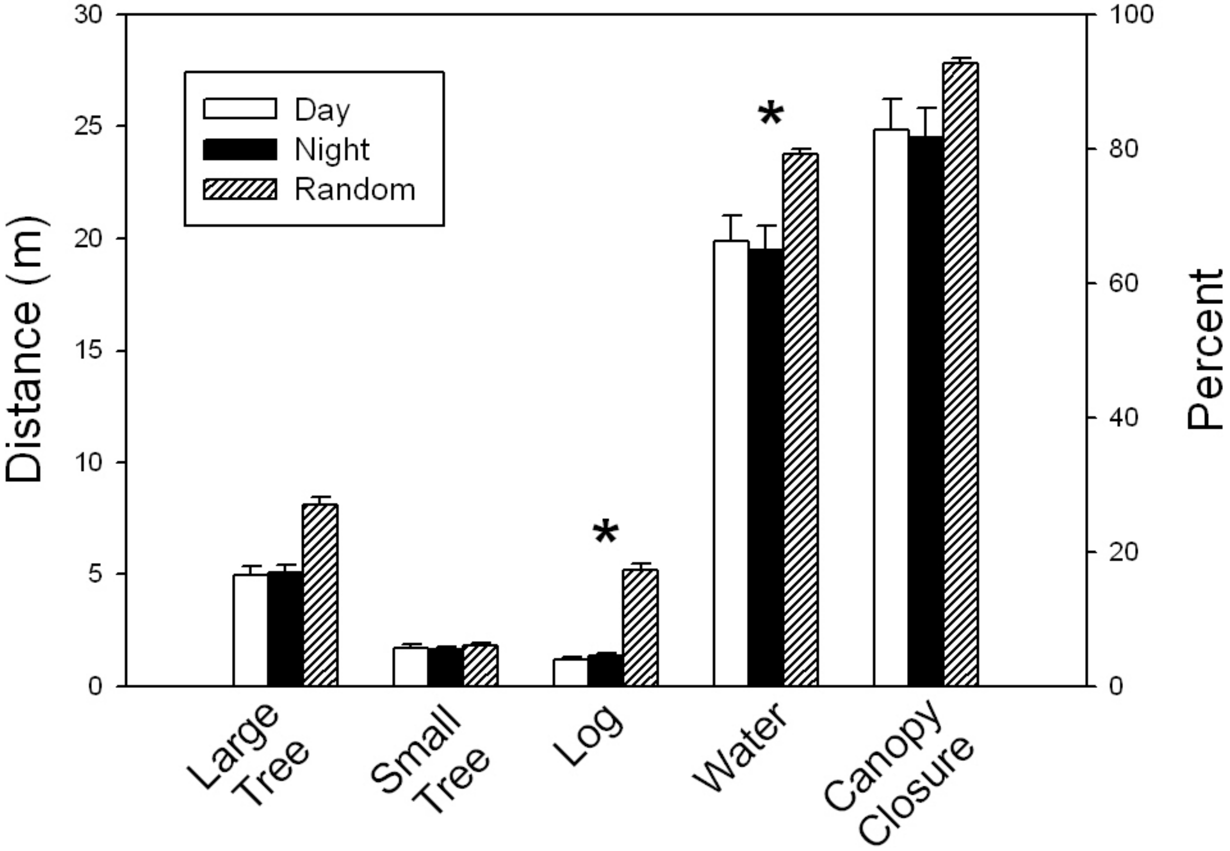

Figure 3.3. – Mean distance (+ 1 SD) to nearest microhabitat features (left axis) and percent canopy closure (right axis) of sites used by all *Bothrops asper* during the day and at night, and of randomly-selected unused points. Variables marked with an asterisk (*) differed across all three categories at p≤0.05; unmarked variables did not differ between any groups.

CHAPTER 4

BEHAVIORAL AND ECOLOGICAL CONSEQUENCES OF PREY AVAILABILITY IN A NEOTROPICAL AMBUSH PREDATOR

SUMMARY

Artificially manipulating food availability under field conditions has proven a useful tool for investigating the resource dependencies and limitations of animal species in a variety of contexts. However, both ectothermic vertebrates (such as reptiles) and species occurring in tropical systems remain underrepresented in existing studies, and potential differences in their responses to fluctuating resource levels largely undocumented. To this end, we experimentally investigated the relationship between food intake and spatial ecology in a population of the snake *Bothrops asper* in a lowland rainforest of Costa Rica. Six adult snakes were allowed to forage naturally while six were offered supplemental food in the field, and both groups monitored using radiotelemetry. Mean home range size did not differ statistically between groups, but supplementally fed snakes demonstrated increased mass acquisition, and shorter and less frequent movement than control snakes, as well as altered patterns of macro- and microhabitat selection. Shifts in habitat usage may be due to *B. asper* utilizing swamps in order to feed on amphibians, but remaining in preferred forest habitat when food is otherwise abundant. Fed snakes also devoted less time to foraging efforts, and were more frequently observed inactive and utilizing shelter. The strong behavioral and ecological responses of snakes in this population to increased feeding regime may be influenced by an apparent overall scarcity of prey at the study site.

BACKGROUND

The availability of food is one of the most important factors affecting the life history, ecology, and behavior of animals. Although determining the food resources actually available to wild populations is difficult, experimentally manipulating food availability has proven a useful alternative. Among terrestrial vertebrates, the majority of food-supplementation studies have been applied to small seed-eating birds and mammals in temperate regions (see review in Boutin 1990), most often in the context of population demography (i.e. Kenner and Krebs 1991, Doonan and Slade 1995, Huitu et al. 2003) or physiological effects such as reproductive output or growth and development (O'Donoghue and Krebs 1992, Styrsky et al. 2001, Schoech and Hahn 2007). Studies involving ectothermic vertebrates remain relatively scarce, although their responses to food availability may be quite different from those of endotherms as they have dissimilar energetic requirements, life histories, and social organization. Tropical regions are similarly underrepresented in existing literature, despite the highly divergent patterns of resource availability presented by aseasonal environments.

Studies using food supplementation to address questions of spatial ecology have often found home range size to be inversely correlated with food availability, but cases are reported in which home range is resource-independent (Boutin 1990, Adams 2001). Most studies applying supplementation to ectothermic vertebrates involve lizards; conflicting results have been reported for species that decrease space usage with augmented resources (Simon 1975, Ferguson *et al*. 1983, Eifler 1996) and those with home range sizes independent of food level (Stamps and Tanaka 1981, Waldschmidt 1983, Guyer 1988). The high degree of territoriality among many lizards, as well as mammals and birds, however, may allow effects of competitor pressure, mate distribution, and energetic costs of defense to obfuscate the influence of prey availability (Adams 2001). Snakes are not generally considered territorial (Gregory *et al*. 1987), so their space usage may be more directly tied to resource availability. We are aware of no studies, however, that have investigated this question experimentally.

Snakes may represent ideal model organisms for such examination of the linkage between spatial and feeding ecology. While the proximate and ultimate factors influencing snake movements and activities are not fully understood, they have been found to be associated with prey abundance (Gregory *et al*. 1987, Macartney et al. 1988). Strong selective pressures may exist for snakes to behaviorally maximize their energy acquisition, as many of their traits are fairly plastic and strongly dependent upon food intake, including growth and maturation (Ford and Seigel 1994), frequency of reproduction (Macartney and Gregory 1988), offspring number or size (Seigel and Ford 1991), and morphology (Bonnet et al. 2001). Pitvipers (family Viperidae, subfamily Crotalinae) are especially appropriate as they are a diverse, widespread group of predators that have low energetic requirements (Secor and Nagy 1994, Beaupre 1996), feed infrequently (Mushinsky 1987), reduced movement rate and home range size in comparison to other vertebrate predators (Macartney et al. 1988, Beck 1995, Marshall et al. 2006), and are easily identified and approached in the field with minimal disturbance using radiotelemetry. Most pitvipers also hunt by ambush rather than active foraging (Chiszar et al. 1982) and tend to select ambush sites based on prey availability (Reinert *et al*. 1984, Shine *et al*. 2002), but they may increase movement rates in search of optimal ambushing habitat or resort to occasional active foraging when prey are scarce (Duvall *et* *al*. 1985, Sazima 1992). Finally, species occurring in tropical regions are additionally desirable as study organisms in that they are largely free of constraints imposed by dependence upon daily thermal refugia or overwintering hibernacula (Shine and Madsen 1996, Luiselli and Akani 2002).

We investigated the effect of experimentally-supplemented food on the behavior and spatial patterns of free-ranging fer-de-lance (*Bothrops asper*), an abundant predator found throughout southern Mexico and most of Central America. Specifically, we tested the hypotheses that supplementally-fed individuals would exhibit greater mass acquisition and survivorship, and decreased foraging activity, movement rate, and home range size than control snakes. In addition, based on an observed scarcity of small mammals at the study site, we believed the population to be strongly food-limited and dependent upon amphibian prey, and we therefore predicted that fed snakes would demonstrate an altered pattern of selection from swamp towards forest habitat.

METHODS AND MATERIALS

TELEMETRY AND FEEDING METHODS. – This experiment was conducted from 5 January through 10 December 2006 at La Selva Biological Station (LSBS) in Puerto Viejo de Sarapiquí, Heredia Province, northeastern Costa Rica (84˚00’12.959 W, 10˚25’52.513 N). LSBS is a 1700ha reserve consisting of primary and secondary lowland tropical wet forest, with numerous small forested swamps, and some developed areas and disturbed sites (see McDade and Hartshorn 1994 for detailed description and history of the site). The region is fairly aseasonal in temperature, but does experience periods of reduced precipitation from January through April and in September; rainfall is abundant throughout the remainder of the year. Comprehensive descriptions for LSBS are provided elsewhere of climate (Fetcher et al. 1985, Sanford *et al*. 1994) and vegetation cover (Frankie et al. 1974, Holdridge et al. 1971).

Adult *B. asper* were located by active search at night; although search efforts were not strictly controlled, we attempted to spend roughly equal time searching for animals in primary forest, secondary forest, and swamps. Captured snakes were returned to the laboratory, measured to the nearest 0.1cm and 1g to assess body condition, and anesthetized and implanted with radiotransmitters (Holohil 5g model SI-2 or 9g model SB-2, depending on size of the animal) following the methods of Hardy and Greene (1999). All transmitters weighed less than 5% of the snake's body mass; transmitters were removed and snakes re-measured at the conclusion of the study period. From each individual, we also collected a fecal sample either by normal defecation or manual palpation in order to investigate diet. Snakes were tracked using receivers from Communications Specialists Inc. (R-1000) and Habit Research (HR2600 Osprey), and 3-element directional antennae from Wildlife Materials. We attempted to locate snakes daily, alternating daytime and nighttime observations.

Using a random design stratified by sex, we assigned five male and nine female adult snakes to either a "fed" or "control" group. Control snakes foraged normally, while fed snakes were offered a pre-killed rat in the field once every two weeks in addition to any food obtained on their own. This feeding regime was designed to simulate increased but not unrealistically high prey abundance. Food was offered at night, as *B. asper* is a nocturnal ambush hunter and we attempted to simulate normal rodent-predation events. To supplementally feed snakes, a 200-250g dead rat (*Rattus norvegicus*) was raised to approximately 37°C by submersion in hot water and tied using a slipknot to the end of a collapsible 5m pole. From an observer distance of 4-5m, the rat was moved along the ground in front of the snake until struck; envenomated prey was then dragged a short distance (0.5m) away and released from the slipknot, and the snake observed to ensure that ingestion actually occurred. Snakes were fed *in situ*, regardless of where they were within the total home range.

At each snake relocation, microhabitat was characterized using a series of structural variables often used to measure microhabitat of snakes (Reinert 1993): distance from the snake's body to the nearest large canopy tree (≥25cm diameter at breast height), small understory tree (<25cm dbh), log (fallen branch ≥20cm diameter), and body of water, as well as percent canopy closure (determined using a spherical densiometer). A microhabitat component was considered "unavailable" at that site if none were present within 25m of the snake. Snake activity was scored as *inactive* if the animal was lying coiled with its head resting when first located, *active* if it was moving, and *ambushing* if it was lying coiled and alert with the head raised. To characterize shelter usage, a snake was considered *sheltered* if it was completely within structural cover (*e.g.* hollow log or root system of a tree), *semisheltered* if it was partially covered (*e.g.* in dense herbaceous vegetation, adjacent to the base of a tree, or below but not concealed by a raised log), and *unsheltered* if it was in the open.

ANALYSES. – We expressed body size as snout-vent length (SVL) to the nearest 0.1cm and body condition as grams body mass per centimeter. Change in length and body condition were calculated by subtracting initial from final values, divided by the number of days in the study period because starting and ending dates varied among snakes. Snakes were not remeasured during the study period, to avoid influencing their behavior or space usage due to capture. Mean changes in length and condition per day were compared between fed and control snakes using Mann-Whitney *U*-tests. Unless otherwise noted, all statistical analyses were conducted using Systat 12.0.

We estimated home range size using both Minimum Convex Polygon (MCP) and 95% and 50% Kernel Density (KD) (Worton 1989) methods using ArcView 3.2 with Animal Movement Extension (Hooge and Eichenlaub 2000). For kernel estimates, the least-squares crossed validation recommended by Seaman and Powell (1996) was used to determine smoothing parameter *h*. Home range sizes of fed and control snakes were compared separately for each estimation method using Mann-Whitney *U*-tests.

Daily movement was determined as straight-line displacement between relocations on consecutive days. Where data were unavailable for one or more days, we calculated a daily mean by dividing the total movement by the number of days between relocations, but excluded from analysis periods with more than 4 days between fixes. To determine whether the frequency of movement (days with displacements greater than zero) was associated with feeding treatment, we calculated the number of zero and nonzero movements within each group, and compared treatments using a log-likelihood ratio test (*G*-test). To determine whether the magnitude of distances moved by fed and control snakes differed, we pooled all single-day movements of all individuals (excluding movements of 0m) and compared treatments using a Mann-Whitney *U*-test.

We analyzed macrohabitat selection of fed and control snakes separately using Compositional Analysis (Aebischer 1993) in the program Resource Selection (Leban

1999). CA expresses habitat usage and availability as a unique vector of proportions for each individual, and analyzes the log-ratios of these proportions using MANOVA (Aitchinson 1986), making it for the analysis of data from several individuals with multiple relocations per individual. Habitat usage was calculated by determining habitat coverage (primary forest, secondary forest, swamp, or developed area) at each snake relocation from existing GIS maps of LSBS. Habitat availability was calculated by buffering each snake relocation with a radius equal to that individual's maximum observed single-night movement, and the cumulative area encompassed by these radii considered "available" to that individual over the course of the study.

To determine whether microhabitat usage of fed and control snakes varied, we calculated a mean value for each recorded microhabitat variable for each snake and compared groups using one-way MANOVA. Microhabitat usage was compared separately for day and night observations to control for temporal differences in habitat usage, as *B. asper* typically forages in the evening but is inactive during the day. We used *G*-tests to determine whether patterns of activity and shelter usage were associated with feeding treatment, with data from day and night observations again analyzed separately.

♂♀

RESULTS

Data here are reported from six fed (three male, three female) and six control (one male, five female) *B. asper*. Two additional snakes that were implanted provided only minimal data (fewer than 15 relocations) before loss due to equipment malfunction or failure to relocate the animal, so were excluded from analysis. Snakes ranged in size from 89.7 to 145.0cm SVL and 288 to 1522g body weight; body size was not found to affect *B. asper* home range or movement patterns in an earlier study (Chapter 2). The method of food supplementation proved highly successful, with no snakes ever refusing to accept or ingest food when it was offered.

Fed and control snakes differed in change in body condition ($U<0.001$, df=1, $p=0.014$) but not body length ($U=5.000$, df=1, $p=0.221$) during the study period. Body condition of fed snakes increased at a mean of 0.010±0.004g/cm/day, while control snakes demonstrated a mean decrease in mass at -0.001±0.003g/cm/day. Increase in body length was not significantly greater for fed than control snakes (0.027±0.023cm/day and 0.008±0.006cm/day respectively). Morphology data are not available from all individuals because some animals (one fed, two control) were lost or died before the end of the study; carcasses of snakes that died in the field were quickly destroyed by scavengers.

Mean home range of fed snakes was smaller than that of control snakes as estimated by MCP and 95% KD (Fig. 4.1), but did not differ significantly by any estimation method (MCP $U=15.000$, df=1, $p=0.522$; 95% KD $U=16.000$, df=1, $p=0.394$; 50% KD $U=11.000$, df=1, $p=0.831$). Mean estimate size (ha) for fed and control snakes respectively by MCP was 3.96±2.22 and 6.07±3.45; for 95% KD 2.61±0.53 and 4.40±3.01, and for 50% KD 0.44±0.28 and 0.39±0.21ha. Two fed snakes were omitted from home range analyses due to insufficient data (<100 relocations).

Movement patterns of fed and control snakes differed in terms of both frequency of movement and movement distance. Frequency of movement was significantly associated with feeding treatment ($G= 57.667$, df=1, $p<0.001$); fed snakes did not move at all on 38.81% of observations, while control remained stationary between only 25.14%. When snakes did move, the magnitude of displacement was smaller for fed than control snakes (U=1152852.500, df=1, $p<0.001$; Fig. 4.2).

We found different patterns of macrohabitat selection for fed and control snakes. Overall habitat selection was significantly nonrandom for control snakes ($\lambda=0.121$, $\chi^2=12.669$, df=3, $p<0.05$), with animals selecting for swamp habitat and avoiding developed areas (Fig. 4.3). No such selectivity was detected among fed snakes, whose habitat usage did not differ from random availability ($\lambda=0.845$, $\chi^2=1.009$, df=3, $p<0.799$).

Microhabitat usage differed between treatment groups both during the day ($\lambda = 0.940$, F=30.504, df=5,2379, $p<0.001$) and at night ($\lambda = 0.935$, F=16.134, df=5,1167, $p<0.001$). During daytime observations, fed snakes were usually further from water and closer to small trees (Fig. 4.4). At night, the pattern was identical except that fed snakes also tended to be closer to large trees. Distances to the nearest log and percent canopy closure did not differ between groups at any time.

Ambushing activity of fed and control snakes differed at night (mean percent of nights ambushing= 61.7% fed, 75.8% control; G=46.108, df=2, p=0.000) but not during the day (2.2% fed, 4.1% control; G=5.313, df=2, p=0.070). At night, fed snakes were less likely to ambush, while little activity of any kind was seen by either group during the day (Fig. 4.5). Shelter usage differed both during the day (G =99.694, df=2, p=0.000) and at night (G=78.368, df=2, p=0.000), with fed snakes making greater use of shelter and control snakes more often Semisheltered or Unsheltered during both times (Fig. 4.5).

DISCUSSION

This experiment was dependent upon the requirement that fed snakes ingest more food than do control snakes, but actual feeding rates could not be determined. Given that fed snakes received experimentally-offered food in addition to that obtained naturally by both groups, it is very likely that fed snakes ingested greater prey mass and number of prey items during the study. Our results also support this assumption; fed snakes demonstrated significant differences from control snakes in terms of growth, spatial ecology and behavior.

During an initial radiotelemetry study of fer-de-lance at LSBS (Chapter 2), several observations suggested that the population was strongly affected by limited food availability. *B. asper* has been reported to feed primarily on small mammals, particularly rodents, as adults (Martins et al. 2002). A trapping survey conducted to assess prey availability at LSBS, however, captured no rodents in more than 9000 trap-nights, although the same equipment and methodology was used successfully elsewhere to trap forest rodents. Very few rodents (<12) were ever observed during more than two years of fieldwork at the study site. This is in contrast to previous studies of rodents at LSBS (Fleming 1974, Rivas and Colton 1999), suggesting that a decrease in rodent abundance may be a recent local phenomenon. *B. asper* is also typically described as a forest-dwelling species that is not tied to bodies of water in humid regions (Campbell and Lamar 2004), but most individuals at LSBS demonstrated greater selection of swamp habitat (Chapter 3), where they were observed to attempt predation upon the larger-bodied, water-associated (Savage 2002) frog species *Lithobates vaillanti* (Ranidae) and *Leptodactylus savagei* (Leptodactylidae). Inspection of fecal samples collected during both the earlier and current studies revealed that few (29%) contained hairs, which are normally passed by snakes following ingestion of a mammal. Further analyses of samples are required to determine whether focal snakes did feed largely on amphibians.

Three snakes (one male and two females) are believed to have starved to death while being monitored in the previous study. These individuals were seen to behave normally for several weeks to months before beginning to appear thinner with the vertebrae clearly protruding; locomotion soon ceased and the animals died within 1-2 weeks. In the current experiment, two control snakes (one male and one female) but no fed snakes died in a similar manner. Necropsies of these carcasses when available revealed virtually no stored body fat, though none of the females recently gave birth, which can similarly deplete energy stores (Naulleu and Bonnet 1996). Many additional, non-telemetered fer-de-lance encountered during the study period exhibited similar emaciation. These data could be interpreted to suggest that *B. asper* at the study site are strongly food-limited; animals from such a population may be especially responsive to augmented food acquisition.

Growth and feeding rates are positively associated among many animals, but may be especially so for ambush-foraging vipers, whose low metabolic demands allow them to utilize a high proportion of energy obtained from ingested food (Secor and Nagy 1994). Fed *B. asper* gained significantly more mass (g/cm/day) than control individuals but did not show a greater increase in body length (cm/day). Although variation between individuals was high, mean change in body mass for control snakes was negative, with two of the four control individuals analyzed losing mass over the study period; such inability to maintain constant body mass is expected when little food is available.

Reproductive output of *B. asper* is correlated with female body size (Solórzano and Cerdas 1989), but minimum energy reserves also present a threshold for reproduction (Naulleau and Bonnett 1996). As in other vipers, *B. asper* may allocate more energy to storage than to growth when food is limited (Forsman and Lindell 1991), as fat reserves can be later metabolized as necessary to meet basic maintenance, reproductive, or other costs.

We estimated home range by three different methods, MCP, 95% KD, and 50% KD. Minimum convex polygons are a historically widely-used estimate, consisting of the smallest area enclosing all relocation points; kernel densities are based on the distribution of points and represent the probability of a snake being in a given area at any time. For *B. asper*, MCPs represent the absolute outer boundaries of home ranges, but we believe 95% KD to be the most biologically-meaningful estimation method for *B. asper*, as it minimizes inclusion of areas crossed but not actually utilized by individuals (Chapter 2). 50% KDs are the "core area" of home ranges (Hooge *et al*. 2001), which represent the most frequently-used foraging areas to which snakes returned repeatedly over time. We predicted that home ranges of fed snakes would be smaller than those of control snakes if fer-de-lance assess a particular area as more "suitable" due to higher incidence of prey capture. Home range estimates were smaller for fed than control snakes by both MCP and 95% KD, but feeding groups did not differ statistically (Fig. 4.1). These statistical results may be largely due to high variation between individuals and the relatively small number of animals (4 fed, 6 control) available for home range analysis. It is also notable that variation in 95% KD size was much lower among fed snakes (1.918 to 3.195ha) than control snakes (from 1.034 to 8.825), which may further suggest that food augmentation did influence home range size. For example, this phenomenon might be explained by some control snakes being able to successfully obtain food and therefore having home ranges similar to those of supplementally-fed snakes, while others were less successful and consequently utilized more space while searching for food.

We also hypothesized that fed snakes would move less frequently and for shorter distances in search of prey, although the overall movement pattern exhibited by both groups was similar. Fer-de-lance were largely sedentary, with most movements consisting of short (<10m) movements between nocturnal ambush sites and diurnal refugia. This pattern was interspersed with occasional longer-distance movements (to a maximum observed single-night distance of 278.48m, by a fed snake) to a new foraging area where the pattern repeated. Frequency of such movements was significantly lower for fed snakes, with animals more often remaining stationary (movement =0.0m) between subsequent days. This result may again be explained by snakes' assessment of habitat suitability, though it may be partially attributable to postprandial inactivity. Following feeding, *B. asper* typically moved to a nearby shelter and did not emerge for 3-6 days. Higher feeding rate by fed snakes may lead to higher incidence of such inactivity, thus to a greater proportion of zero-movement days. Despite presumably having more energy to allocate to locomotion, fed animals tended to move shorter distances than unfed ones when movement did occur (Fig. 4.2). This phenomenon may again reflect an assessment by fed snakes of higher prey density areas, while unfed snakes moved further in search of food.

Habitat usage by fed and control snakes differed on both the landscape and microhabitat scales. *B. asper* at the study site have previously been found to demonstrate nonrandom habitat usage and a strong preference for swamps (see Chapter 3), patterns identical to those of control snakes here. Fed snakes deviated from this pattern, with macrohabitat types being used roughly in proportion to their availability (Fig. 4.3). Selection of swamp habitat constituted the most pronounced difference between groups, supporting the idea that *B. asper* at LSBS disproportionately utilized swamps in order to exploit frogs as a food source, with fed animals freed from this dependency and returning to otherwise-preferred forest areas. Altered habitat usage by snakes in response to experimentally-increased feeding has been previously reported for temperate, actively-foraging ratsnakes *Elaphe obsoleta* (Blouin-Demers and Weatherhead 2001), but was attributed to snakes moving from forest interior to edge in order to facilitate thermoregulation rather than in direct response to food availability.

Microhabitat was quantified on the basis of several structural variables, though many other factors may be equally important in describing an environment as it is actually experienced by snakes. Pitvipers' unique suite of sensory organs implies that they exist in a world of visual, tactile, olfactory, and thermal cues which are largely invisible to human observers (Ford and Burghardt 1993). However, even our simplified methodology was sufficient to detect differences in microhabitat usage between fed and control snakes. During the day, *B. asper* typically rested in shelter or open leaf litter, and fed snakes were further from water and closer to small trees (Fig. 4.4). At night, the animals usually moved short distances away from daytime refugia and ambushed in more exposed areas; fed snakes were again further from water and closer to small and also large trees. However, it is important to note that few bodies of water are present at LSBS other than swamps and streams, that density of large and small trees is higher in forests than swamps, and that the root systems of large trees often served as daytime refugia. Thus microhabitat results may be attributable more to fed snakes' decreased usage of swamps and greater levels of inactivity than to differences between groups in actual selectivity. It is likely that similar structural conditions will prove advantageous as shelter or ambush sites regardless of feeding treatment.

Finally, we predicted that fed snakes would spend significantly less time ambushing and would make greater use of shelter. Little difference in activity was seen during the day, as both fed and control snakes were inactive on over 95% of observations (Fig. 4.5). At night, fed snakes were significantly more likely to be inactive, as control snakes allocated a greater proportion of time to foraging using sit-and-wait tactics. Fed snakes made greater use of shelter during both day and night, while control snakes were more often in exposed or semisheltered (such as adjacent to an overhanging log or in dense vegetation) sites. Activity and shelter usage are likely correlated, as shelters were often as daytime retreats, but exposed or semisheltered conditions more suitable for nocturnal ambush. These results are not surprising for a highly nocturnal pitviper such as *B. asper*, and would be expected if control animals devote more time to foraging for prey but are constrained by innate nocturnality. Postprandial inactivity may again play a role, but considering the relative infrequency of supplemental feeding (once per two weeks), seems less likely to explain the observed patterns than does greater effort by control snakes to obtain food.

Despite the relatively small sample size used in this study, the consistency of differences between feeding treatments suggests that *B. asper* activity and space usage are strongly affected by food availability. Furthermore, one fed male and two control females were radio-tracked for approximately one year in an earlier, non-experimental study (snakes #16, 21 and 26 in Chapter 2). Upon initiation of supplemental feeding, the fed snake demonstrated reduction in home range size, movement frequency, movement distance, and level of foraging activity, and shifted its habitat preference from swamp to forest habitat (Table 4.1). Control snakes showed increased or only slightly decreased home range size, increased movement frequency and distance, greater foraging activity, and no change in habitat preference for swamps between the previous and current studies. These results may be indicative of an increasingly food-stressed population, and reinforce the idea that *B. asper* alter their behavior and movements in response to increased feeding.

Because of their lack of territoriality or other strong social associations, space usage by snakes may be largely determined by the distribution of resources including food, mates, and shelter (Madsen and Shine 1996, Duvall and Schuett 1997, Beck 1995). It is important to note that such distributions, and thus their effect on snake movements, may be very different between tropical and temperate systems. In the only other study of which we are aware using food supplementation to explicitly address snake movements, Taylor *et al*. (2005) focused on western diamondback rattlesnakes (*Crotalus atrox*), a desert species related and similar in size to *B. asper*. Fed rattlesnakes in that study acquired greater mass and reproduced more often, but did not have altered home ranges or activity levels, despite a much more frequent feeding regime (1-4 times per week) than our own. That feeding did so affect *B. asper* may reflect that spatial patterns are more constrained by factors other than food (e.g. reliance upon daily or annual thermal refugia) in predictable seasonal environments, or that responses differ when food is patchily distributed across a mosaic of habitats (e.g. amphibian prey in swamps). Additional field studies from a variety of systems are necessary to further elucidate the ways in which temperate and tropical species differ in their resource dependencies and responses to fluctuating prey availability.

	MCP (ha)	95% KD (ha)	50% KD (ha)	Mean Distance (m)	Movement Frequency	Most-used Habitat	% of Nights Ambushing
#16 (♂, fed)	-1.26	-0.18ha	-0.05ha	-6.55	-9%	Swamp → Forest	-7%
#21 (♀, control)	-0.29	+0.36ha	-0.17ha	+0.13	+12%	Swamp → Swamp	+20%
#36 (♀, control)	+1.53	+1.61ha	+0.24ha	+8.81	+13%	Swamp → Swamp	+25%

Table 4.1. Comparisons for three snakes monitored during both the current feeding experiment and an earlier non-manipulative study (Chapter 2). Each value represents the change from the previous to the current study.

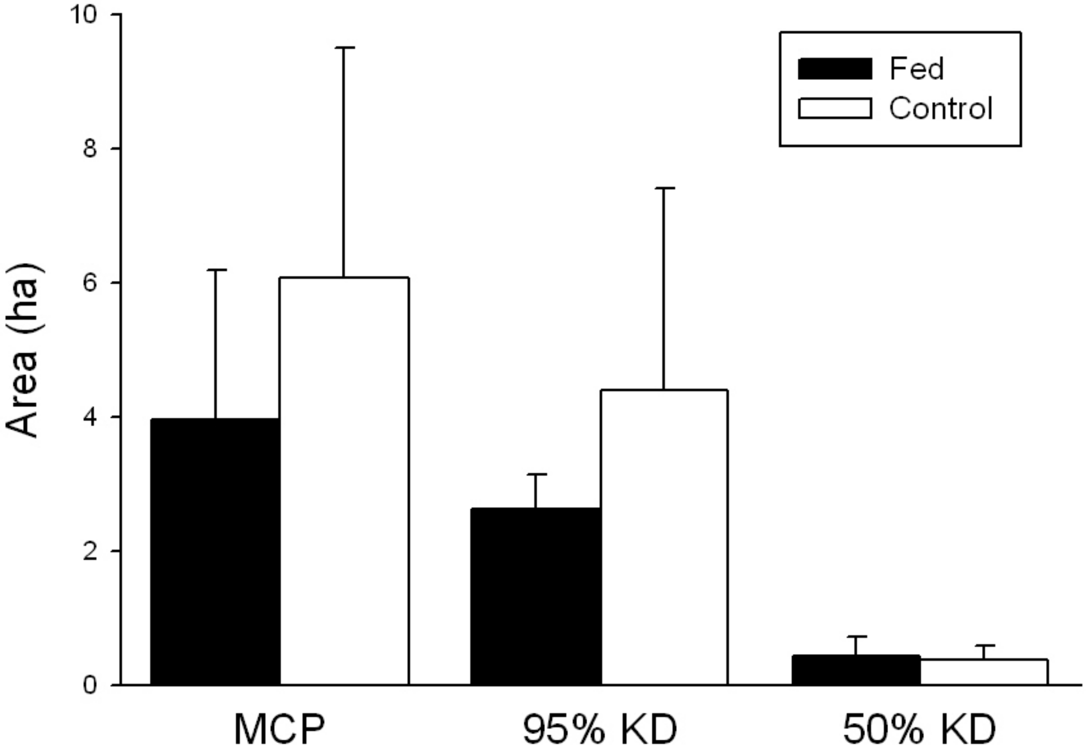

Figure 4.1. Mean home range size of fed (n=4) and control snakes (n=6) by three estimation methods. Home range size did not differ significantly between groups by any estimation ($p \geq 0.05$). Individuals with <100 relocations (n=2, both fed) were excluded from analysis.

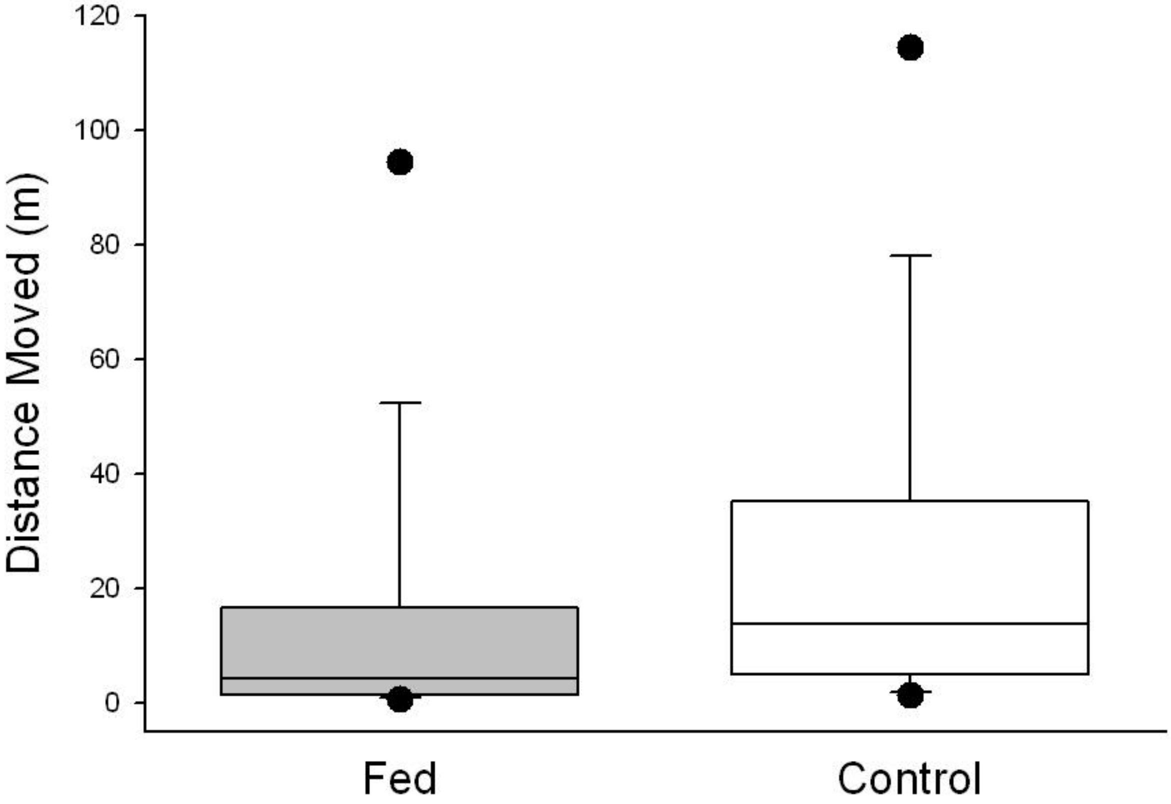

Figure 4.2. Box plot of all distances moved by fed (n=697) and control snakes (n=1173) during the study period, excluding movements of zero. Lines within box plots represent median values, upper and lower boundaries of boxes are the 75th and 25th percentiles, whiskers are the 90th and 10th percentiles, and closed circles are the 95th and 5th percentiles. Outliers above the 95th percentile (fed n=34, control n=59) are not displayed. Difference in movement between groups was significant at $p<0.001$.

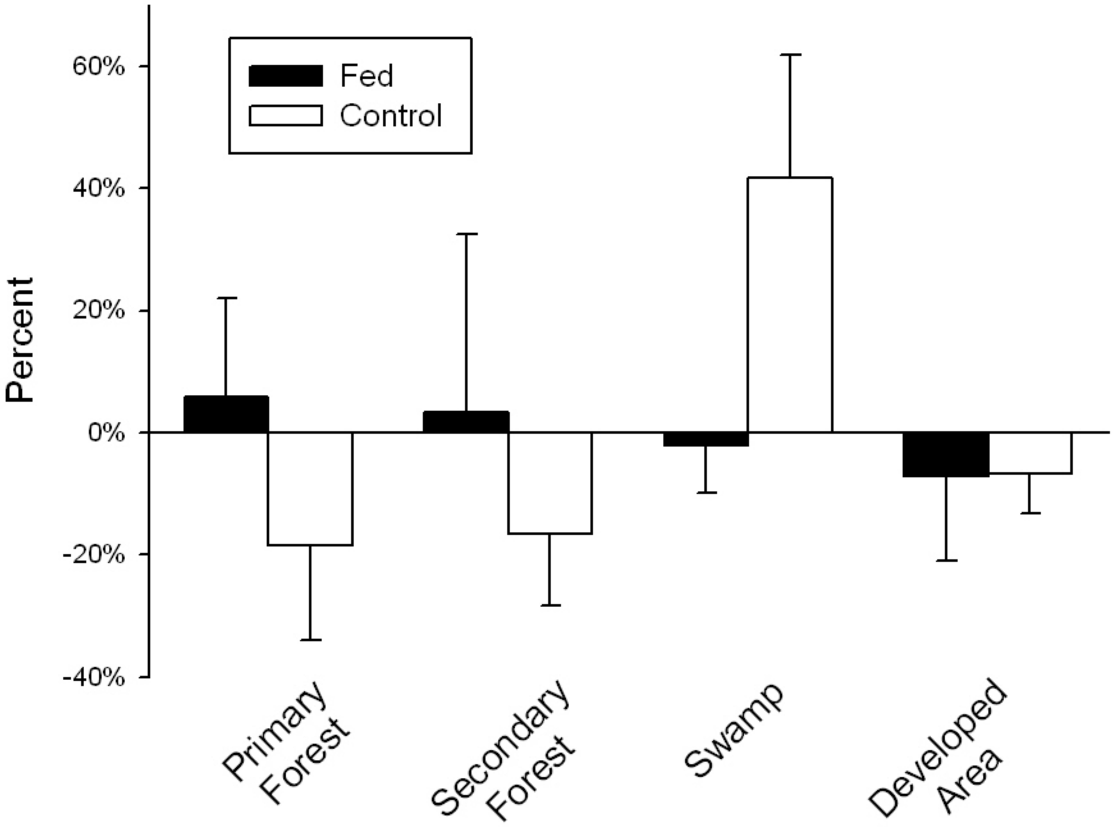

Figure 4.3. Increase or decrease (+1 SD) in usage relative to availability of four habitat types by fed and control snakes.

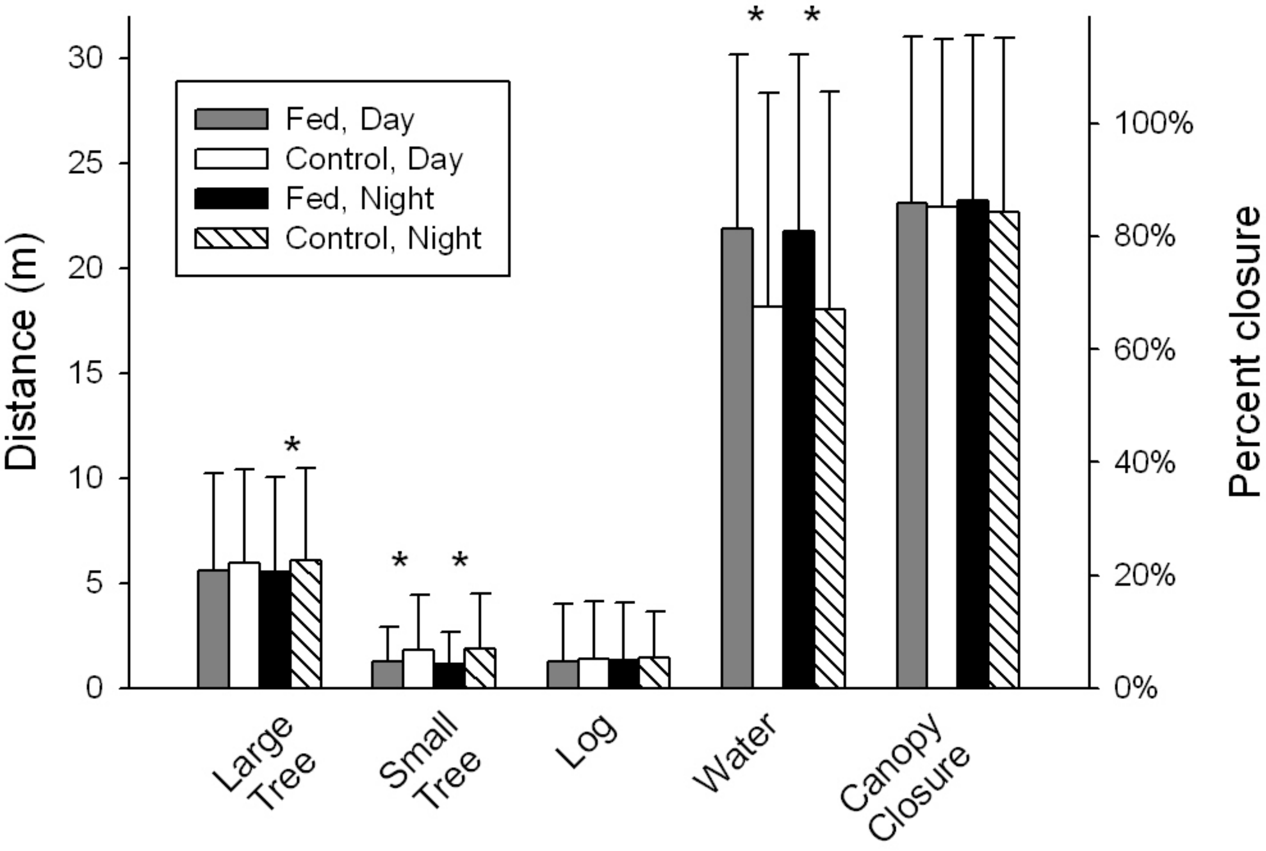

Figure 4.4. Mean distance to nearest microhabitat features (left axis) and percent canopy closure (right axis) of sites used by fed and control snakes. Feeding treatments were analyzed separately for day and night observations; fed/control pairings marked with an asterisk (*) differed at p<0.05.

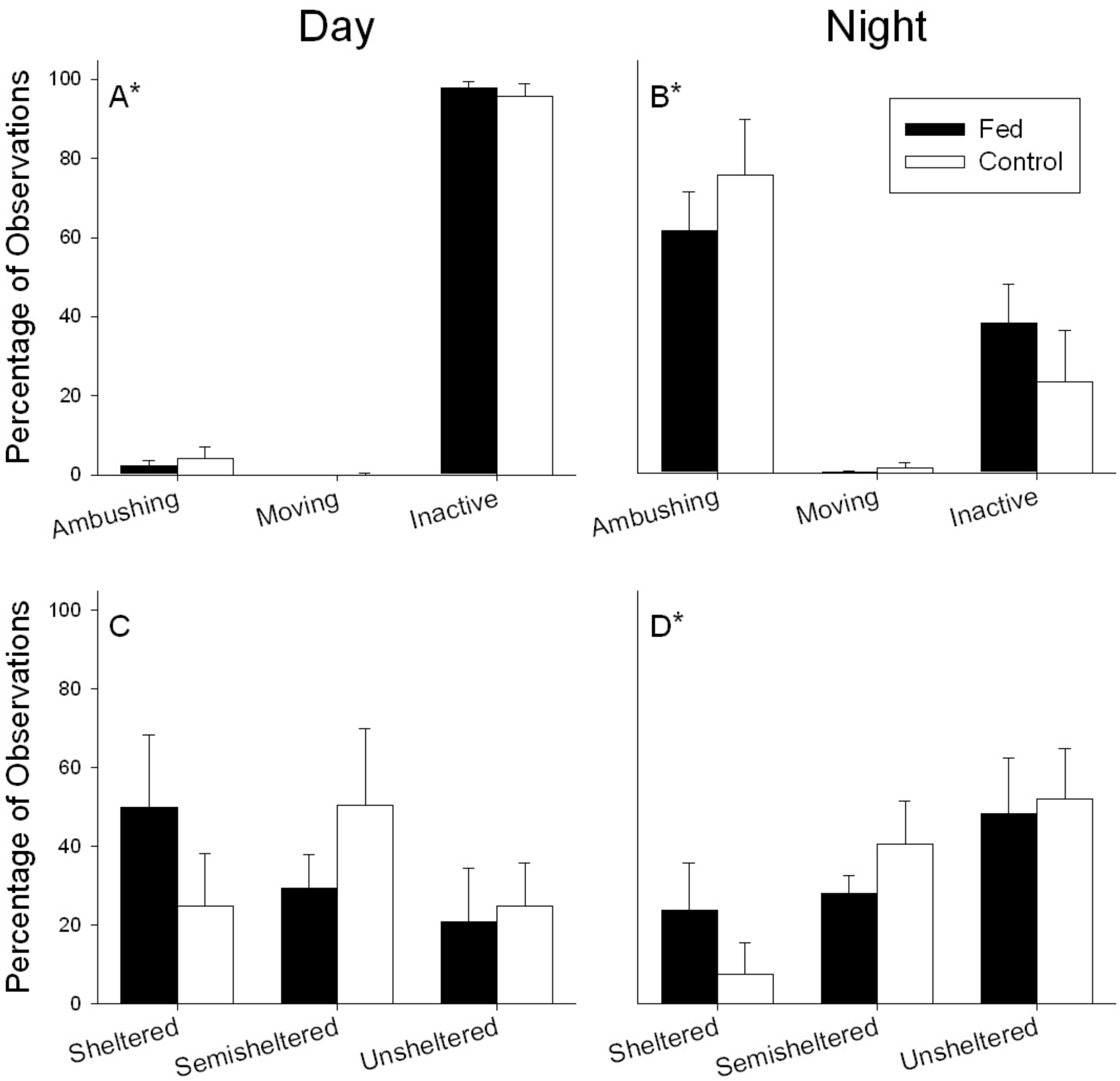

Figure 4.5. Proportional distribution (±1 SD) of shelter usage (A,B) and activity (C,D) by fed and control snakes. Plots with an asterisk (*) indicate a significant (p<0.05) association between proportion and feeding treatment.

CHAPTER 5

BEHAVIORAL EFFECTS OF DIRECT AND INDIRECT PREDATOR CUES ON THREE SPECIES OF NEOTROPICAL RODENTS

SUMMARY

Small mammals from temperate and desert ecosystems are frequently reported to assess predation risk using various sensory cues, and to avoid “dangerous” habitats and reduce foraging efforts in response to increased risk; similar data from tropical regions are scarce. We assessed predator-avoidance and foraging-reduction responses of three Neotropical rodents (*Heteromys desmarestianus*, *Peromyscus mexicanus*, and *Melanomys caliginosus*) when exposed to feces or actual presence of a sympatric snake predator, *Bothrops asper*. For each species we compared habitat selection of snake-cued and -uncued treatments in an experimental arena, and compared giving-up densities as a measure of foraging effort under arena, semi-natural, and field conditions. One species (*H. desmarestianus*) demonstrated snake avoidance and reduced foraging under some conditions, but these limited responses are not likely to be significant in an ecological context. Other species showed no response to the presence of predators or predator cues in any experiments. Our results contrast with the majority of existing studies, possibly due to inherent differences between temperate and more speciose tropical systems or adaptations towards extreme crypticity by an ambush-hunting snake.

BACKGROUND

Predation is a strong selective pressure among small mammals. Many species regulate behaviors that may affect their vulnerability to predators, such as foraging and habitat selection, in response to perceived predation risk (Krebs 1980, Gilliam and Fraser 1987, Lima and Dill 1990). Because direct observation of potential predators can be in itself highly risky and not always possible, a wide range of animals use olfactory cues in order to assess such risk indirectly, including insects, mollusks, arthropods, echinoderms, fishes, amphibians, reptiles, birds, and mammals (Petranka et al. 1987, Schwenk 1995, Kats and Dill 1998, Wisenden 2000, Apfelbach et al. 2005).

Small mammals in particular seem readily able to detect predator odors, assess corresponding predation risk, and respond accordingly. Among various rodent and sciurid species, responses may include avoidance of cued areas, reduced foraging, altered microhabitat usage, decreased home range, reduced locomotion, and reduced sensitivity to pain (Dickman 1992, Saksida et al. 1993, Perrot-Sinal and Petersen, 1997, Borowski 1998, Herman and Valone 2000, Orrock et al. 2004, Hayes et al. 2006). These responses may be elicited by scents of actual predators, or from secondary sources such as urine or feces. In addition, some rodents appear to have a fine level of olfactory resolution, able to discriminate between odors of threatening and non-threatening species (Epple et al. 1993, Jedrzejewski et al. 1993).

The majority of studies investigating olfactory predator avoidance by rodents, however, have focused on mammalian carnivores (Apfelbach et al. 2005) despite the fact that snakes are also important and often more abundant terrestrial predators. Small mammals are known to respond to the presence of live snakes (Kotler et al. 1993, Bouskila 1995, Randall and King 2001), again with precision sufficient to distinguish between snake species (Hennessy and Owings 1978, Rundus et al. 2007). If small mammals face a substantial mortality risk imposed by snake predation, they should also assess and respond to olfactory cues of snakes. A growing number of studies support this idea, and responses by small mammals to snake cues appear similar in nature and magnitude to cues from mammalian predators (Webster 1973, Weldon et al. 1996, Dell'omo and Alleva 1994, Carere et al. 1999), and even specific enough to distinguish between cues from snakes that have and those that have not fed on study species' conspecifics (Pillay et al. 2003). Studies dealing with snake detection and avoidance, however, have so far been conducted primarily under laboratory conditions, or in natural systems with relatively simple food webs, such as deserts. Antipredator responses may differ in speciose ecosystems featuring a diverse suite of potential predators (Sih et al. 1985).

We investigated snake-avoidance behavior by three abundant Neotropical rodents, Desmarest's spiny pocket mouse (*Heteromys desmarestianus*, family Heteromyidae), Mexican deer mouse (*Peromyscus mexicanus*, family Cricetidae), and dusky rice rat (*Melanomys caliginosus*, family Cricetidae), when confronted by cues of the fer-de-lance *Bothrops asper* (Serpentes: Viperidae) in montane forests of Costa Rica. *B. asper* is widespread throughout Central America, feeds primarily on rodent and other small mammals on adults (Martins et al. 2002), and is among the most abundant snake species in many systems (Campbell and Lamar 2004). It is therefore likely to be among the most important reptilian predators of small mammals in the region. Also, because *B. asper* is a highly cryptic ambush predator (Chapter 2), it presents an opportunity to investigate whether rodents can detect predators from olfactory as well as visual cues. Specifically, we tested 1) whether rodents selected snake-free areas over those featuring snakes or snake cues, 2) whether they reduced foraging efforts in the presence of snakes or snake cues, and 3) whether rodents respond similarly in a controlled laboratory environment and under natural field conditions.

METHODS AND MATERIALS

Work was conducted on private property in Jicotea de Turrialba, Costa Rica (83°32′59.94 W, 94°85′9.95 N). The area consists of primary and secondary montane forest with surrounding agricultural areas. We captured rodents using live-catch traps baited with oats and peanut butter; we did not target particular species, but used the three most frequently-captured species (*H. desmarestianus*, *P. mexicanus*, and *M. caliginosus*) for experiments. Fer-de-lance were collected using visual-encounter surveys and manual capture.

Each rodent was maintained in captivity for no more than 3 days, and was not fed for 12 hours prior to use in experimental trials. Individual rodents were used for both treatments (cued and uncued) of paired experiments, with treatment order randomized for each individual. Each *B. asper* was used as a stimulus in multiple trials. All trials were conducted at night under roofed but open-air conditions and using only ambient lighting, as the three focal rodent species are primarily nocturnal (Reid 1997). Trials were recorded with a night-vision video camera, and data later collected from tapes after digital manipulation for ease of viewing.

Snake Avoidance. – Using a choice arena (Figure 5.1), we tested whether rodents selected against areas featuring snakes or snake cues. Arenas consisted of a 1m x 1m paper-lined wooden box divided lengthwise by a vertical wall into identical left and right halves, with a 0.1 x 0.1m entrance portal from which rodents could move into either side. Entrance portals could be closed so that a rodent was still free to move between sides but could not re-enter the portal. For each trial, we randomly designated cued and uncued sides, and placed the appropriate experimental and control stimuli at the terminal end of each. For snake-avoidance trials, we used a live *B. asper* in a 0.2m x 0.4m wire-mesh cage; for snake-cue avoidance, we used a Petri dish containing *B. asper* feces consisting of a conspecific of the rodent being tested. Control stimuli were an empty cage or Petri dish, respectively.

A rodent was introduced into the entrance portal and allowed to acclimate for 5 minutes before the arena entrance was opened. Trials ran for 20 minutes, beginning once the rodent entered the arena of its own volition, at which point the portal was again closed. Because there may be a threshold effect of distance from a cue, a rodent was considered to be *neutral* if it was in the undivided area near the entrance, *on a side* if it was between the neutral area and the stimulus, and *close* to the stimulus if it was within 20cm. We continuously scored the occupancy time spent by the animal on each side in total and at close distance, as well as the number of crosses it made into that side and into close distance during each trial. Between trials, the arena's paper lining was replaced in order to minimize lingering scent cues.

We statistically compared whether each species' selection for cued and uncued sides differed in terms of the total number of crosses into a side, the number of crosses into close distance, the amount of time spent on each side, and the amount of time spent in close distance. For each comparison, we took the proportion (of time or number of crosses) on the cued side for each individual, and analyzed all of these proportions using a one-sample t-test with a null mean of 0.5 (equal proportion on each side). All statistical analyses were conducted using Systat 12.0.

Foraging Reduction. – We tested whether rodent foraging behavior was influenced by the presence of snakes or snake cues, using the giving-up density (GUD) of Brown (1988) as an indicator of foraging effort. Foraging experiments were conducted in the same arena, with a tray containing 20 maize (*Zea mays*) kernels placed adjacent to the stimulus. All rodents collected readily ate maize in captivity. For all experiments, maize kernels were loosely mixed with soil, in order to increase the time and energetic costs of food acquisition and more closely replicate natural foraging activity. We utilized the same snake and snake feces as stimuli, but also conducted trials using feces from opossum (*Didelphis virginiana*) as a cue, to assess whether study rodents responded to scent cues from an active mammalian predator in addition to a sit-and-wait reptilian predator. Arena foraging trials were initiated following the procedure described above, but ran for a total of 10 minutes, after which we scored the number of kernels remaining on each side as the GUD.

We also conducted foraging trials in a larger semi-natural enclosure and under field conditions, both using live snakes as a stimulus. Semi-natural enclosures consisted of a 3m x 3m open-air, soil-floored room, with a 35cm-diameter cage (containing either a fer-de-lance or as an empty control) situated in one corner, and a seed tray containing 20 maize kernels placed 0.5m from the cage. We used each rodent for two trials (with one snake and one empty control), randomizing the treatment order as well as the corner into which the cages were placed. Rodents were placed under a box in the center of the room and allowed to acclimate for 5 minutes, at which point the box was raised by means of a pulley suspended from the ceiling to initiate the trial. Trials were ended after 10 minutes, GUD recorded, and dirt scattered to homogenize any remaining snake odors.

In field experiments, two empty cages and two containing snakes were placed at least 50m from each other near the border of forested and agricultural areas just prior to sunset, and allowed to remain overnight. Because we anticipated encounter by a larger number of rodents and therefore a higher seed-predation rate, we increased the number of maize kernels per tray to 30, and used two seed trays per cage: one at 0.5m distance, and one at 1.5m distance. In the morning, we recorded the number of maize kernels remaining in each tray.

We used Wilcoxon matched-pairs signed ranks tests to determine whether GUD differed between cued and uncued treatments for each rodent species and cue type, as well as between GUDs at 0.5m and 1.5m seed trays. For field experiments, we compared cued and uncued treatments using a Mann-Whitney U-test because cages represented independent, unpaired samples.

RESULTS

The total number of trials conducted for each experiment is shown in Table 5.1. In both selection and foraging experiments, behavioral differences between rodent species were observed. *H. desmarestianus* tended to wander constantly, investigating experimental enclosures. *P. mexicanus* and *M. caliginosus* tended to dart quickly from place to place rather than slowly exploring enclosures, though *M. caliginosus* was more likely than *P. mexicanus* to remain in one place for several minutes. In foraging experiments, *H. desmarestianus* tended to consume more maize kernels than did other species, and was more likely to remove food from trays to store or consume elsewhere in the enclosure; *P. mexicanus* and *M. caliginosus* more often fed *in situ*.

No rodent species, however, demonstrated obvious avoidance of any cues. Snake and opossum feces were often closely investigated and sniffed by all three species, and one *H. desmarestianus* briefly picked up a piece of snake feces. On two occasions, caged *B. asper* were seen to strike at rodents (one *H. desmarestianus* and one *P. mexicanus*), both of which recoiled but then immediately resumed their previous activity. On several occasions (but fewer than 10% of observations), caged snakes moved towards rodents or about their cage, but no rodent reaction was observed. Both empty cages and cages containing a fer-de-lance were regularly investigated by rodents. During selection experiments, four *P. mexicanus* and two *M. caliginosus* actually entered cages containing snakes; one *P. mexicanus* and both *M. caliginosus* were killed and consumed. Cages were altered for foraging experiments using a finer mesh that rodents could not enter.

Snake Avoidance. – In arena experiments testing response to a live *B. asper*, no selective preference was demonstrated in the number of crosses made into cued and uncued areas (proportion of entries onto cued side did not differ from 0.5) by *H. desmarestianus* (abbreviated hereafter as *Hd*; mean proportion= 0.49±0.20, t = -0.141, p= 0.889), *P. mexicanus* (*Pm*; mean= 0.45±0.24, t= -1.121, p= 0.277), or *M. caliginosus* (*Mc*; mean= 0.55±0.27, t= 1.191, p= 0.252), or in the number of crosses made into close distance on cued and uncued sides (*Hd* mean= 0.50±0.26, t= -0.087, p= 0.932; *Pm* mean= 0.43±0.26, t= -0.867, p= 0.397; *Mc* mean= 0.58±0.27, t= 1.207, p= 0.246). No species differed in the total amount of time spent on cued and uncued sides (proportion of time spent on cued side did not differ from 0.5) (*Hd* mean= 0.44±0.27, t= -1.030, p= 0.314; *Pm* mean= 0.46±0.28, t= -0.743, p= 0.467; *Mc* mean= 0.56±0.31, t= 1.125, p= 0.278), but *H. desmarestianus* spent significantly less time at close distance on cued sides than at close distance on uncued sides (mean= 0.38±0.28, t= -2.127, p= 0.045). Time at close distance by the other two species did not differ between treatments (*Pm* mean= 0.50±0.3, t= 0.153, p= 0.880; *Mc* mean= 0.51±0.28, t= -0.033, p= 0.974).

In arena experiments using *B. asper* feces, no selective preference for cued or uncued sides was demonstrated by any species in terms of number of crosses into each side (*Hd* mean= 0.46±0.16, t= -0.476, p= 0.645; *Pm* mean= 0.42±0.19, t= 0.713, p= 0.494; *Mc* mean= 0.44±0.14, t= 0.229, p= 0.826), number of crosses into close distance (*Hd* mean= 0.47±0.24, t= -0.321, p= 0.755; *Pm* mean= 0.42±0.18, t= 0.700, p= 0.507; *Mc* mean= 0.54±0.14, t= 0.473, p= 0.650), total amount of time spent on a side (*Hd* mean =0.39±0.08, t= -0.737, p= 0.480; *Pm* mean= 0.41±0.17, t= -0.056, p= 0.957; *Mc* mean= 0.41±0.16, t= 0.514, p= 0.623), or amount of time spent at close distance (*Pm* mean= 0.41±0.16, t= -0.072, p= 0.944; *Mc* mean= 0.45±0.15, t= 0.484, p= 0.643), though amount of time spent at close distance by *H. desmarestianus* approached statistical significance (*Hd* mean= 0.39±0.12, t= -1.969, p= 0.080).

Foraging Reduction. – In experiments conducted in the small arena, GUD did not differ for any rodent species between cued and uncued treatments in response to live snakes (*Hd* mean GUD= 14.9±6.3 cued, 16.4±3.0 uncued, z= 0.213, p= 0.832; *Pm* mean= 17.4±4.2 cued, 17.1±5.1 uncued, z= -0.135, p= 0.832; *Mc* mean= 18±2.4 cued, 17.5±4.1

uncued, z= 0.059, p= 0.953), snake feces (*Hd* mean= 16.1±6.0 cued, 16.3±5.0 uncued, z= -0.101, p= 0.919; *Pm* mean= 18.9±1.5 cued, 18.4±3.0 uncued, z= 0.514, p= 0.607; *Mc* mean= 17.7±2.3 cued, 19.1±1.6 uncued, z= 1.519, p = 0.129), or opossum feces (*Hd* mean= 16.4±5.9 cued, 17.1±4.1 uncued, z= -0.119, p= 0.906; *Pm* mean= 18.5±2.1 cued, 17.2±3.8 uncued, z= 1.467, p= 0.140; *Mc* mean= 16.3±6 cued, 18.3±2.9 uncued, z= 0.530, p = 0.596). When the same experiment was conducted in a semi-natural enclosure using live *B. asper* as a cue, *H. desmarestianus* GUD differed significantly between treatments, with GUD being higher (fewer seeds eaten) when snakes were present (mean= 14.1±6.6 cued, 11±7.6 uncued, z= -2.581, p= 0.010). Foraging in semi-natural enclosures did not differ between treatments for the other two rodents (*Pm* mean= 18.2±5.5 cued, 18.5±4.7 uncued, z= 0.962, p= 0.336; *Mc* mean= 19.5±0.9 cued, 19±1.8 uncued, z= -0.954, p = 0.340).

In field experiments, GUD did not differ between empty cages and those containing snakes for seed trays at distances of 0.5m (mean GUD= 7.2±8.3 cued, 7.2±8.9 uncued, U= 1054.500, p= 0.704) or 1.5m (mean= 9.0±10.0 cued, 9.3±9.9 uncued, U= 1162.000, p= 0.663). GUD also did not differ between seed trays at 0.5m and 1.5m distance from the same cage for either cued (z= 0.493, p= 0.640) or uncued treatments (z= 0.866, p= 0.386).

DISCUSSION

Our results suggest that the three focal rodent species do not respond strongly to actual predator presence or predator cues, that responses may be elicited only under certain conditions, and that species differ in their responsiveness. Our results conflict with those reported by the majority of studies of small mammal-predator interactions. While this may be due in part to under-reporting of negative results (Csada 1996), explanations for previous cases which similarly reported no predator avoidance have included low likelihood of actual contact between predators and prey (Dickman and Doncaster 1984), assessment by prey of stimulus carnivore species as a negligible predation threat (Jones and Dayan 2000), or predator-naïve prey (Chiszar 1975). We reject these possibilities for the study system, as *B. asper* does overlap in habitat usage with all three rodent species (Chapter 3) and feeds extensively on small mammals, and all rodents used were adults captured under field conditions. It has also been suggested that predator avoidance may be largely an artefact of laboratory experimental conditions (Lima 1998, Jonsson et al. 2000), and not actually exhibited in the field; however we found no avoidance regardless of experimental setup or scale.

A greater number of entries by an animal into one area relative to another might indicate its assessment of a more suitable area, or could reflect a heightened attempt to assess a potentially dangerous stimulus. Although the actual number of entries varied across species, the ratio of crosses into cued and uncued areas did not differ for any species in response to the presence of a live snake or snake feces, regardless of distance from the cue (Figure 5.2). Time spent within a given area may better reflect an animal's eventual decision regarding its suitability. However, only one species (*H. desmarestianus*) spent less time in areas featuring a live snake, and even this effect was undetectable at distances greater than 20cm (Figure 5.3). This is considerably less than the striking distance of adult *B. asper* (pers. obs.), therefore may not reflect a biologically-meaningful level of avoidance.

Even where statistically significant, our results may not necessarily indicate reduced predation risk to individuals in an ecological context. This suggestion is reinforced by the fact that most rodents repeatedly approached and investigated live *B. asper*, including several *P. mexicanus* and *M. caliginosus* that entered snake cages, sniffed and climbed on snakes, and in a few cases were actually eaten as a result. Although no *H. desmarestianus* entered snake cages, they nevertheless often approached, sniffed, and occasionally stuck their head into the cage. In the wild, such activity would almost certainly lead to a high likelihood of being eaten.

No significant avoidance was observed in response to predator feces by any rodent species, though spiny pocket mice spent slightly less time at close distance to cued areas (Figure 5.3b). These results are in contrast to numerous studies illustrating that indirect cues such as predator scats can be more powerful olfactory stimuli than predators themselves and convey information regarding the general level of predation risk in an area (Müller-Schwarze 1983, Dickman and Doncaster 1984, Jones and Dayan 2000). Although live snakes do present visual in addition to olfactory stimuli, it is likely that predator scats were still detectable by rodents, as both snake and opossum feces produced odors easily noticeable even to human observers.

Results of foraging-reduction experiments largely followed the same pattern. In experimental arenas, GUD was not higher in the presence of any predator cue for any rodent species (Figure 5.4). According to optimal-foraging theory, GUD in this context addresses the assumption that animals stop foraging sooner (leaving a higher GUD) in areas that are assessed as having a greater risk of predation (Brown 1988). No significant difference might be observed between treatments if rodents reached a satiation point after feeding on very few seeds; however, between both cued and uncued seed trays individual *H. desmarestianus*, *P. mexicanus*, and *M. caliginosus* were found to consume or remove a maximum of 40, 19, and 15 seeds respectively. In addition, repeating the experiment in a semi-natural enclosure produced significantly reduced foraging by *H. desmarestianus* but not *P. mexicanus* or *M. caliginosus* (Figure 5.5). Assuming that the effect of predator cues is constant, this may suggest that larger semi-natural enclosures better replicated normal rodent foraging under field conditions, with focal animals more stressed in a smaller arena.

Given the high species diversity of rodents and other small mammals at the study site, that only one of three study species demonstrated foraging response to snakes, and the high behavioral variability across individuals, it is not surprising that GUD did not differ between cued and uncued treatments under field conditions regardless of distance to the cue (Figure 5.6). Any effects of rodents that avoided foraging near snakes would likely be swamped out by those that did not. The presence of a sedentary predator such as *B. asper* therefore likely has little effect on local seed-predation rates or other effects of small mammals.

It is unclear why one rodent species might respond to predator cues while another would not. The three rodent species used here are similar in size and well within the normal size range of prey for *B. asper* and other snakes. In considering foraging experiments, it is notable that *H. desmarestianus* is more granivorous than *P. mexicanus* or *M. caliginosus*, both of which also feed heavily on arthropods (Reid 1997). All three readily ate maize in captivity, however, and most individuals did forage to some extent during experimental trials. Furthermore, rodent species should face a comparable threat of snake predation regardless of dietary preference. The failure of *P. mexicanus* and *M. caliginosus* to respond to predator cues in selection studies, and the questionable relevance of the limited avoidance behaviors as exhibited by *H. desmarestianus*, suggests that these rodent species do not detect predator cues, do not associate these cues with increased predation risk, or do not respond to predation risk in ways addressed here.

There are a number of possible reasons why little predator avoidance overall was observed in this study. If food resources are scarce or rarely encountered, it may be advantageous for an animal to feed to satiation whenever possible regardless of predation risk. Although we did not determine actual food availability at the study site, both native and agricultural plants were abundant, and resource availability was presumed high. Furthermore, predator-induced foraging reduction has been documented in desert ecosystems where food resources should be markedly rarer (Bouskila 1995).

The complexity of a tropical forest system itself may also play a role. Increased floral and faunal diversities and abundances, as well as high structural complexity may contribute to an overabundance of sensory cues. It is unlikely that rodents' acute sensory capabilities were unable to detect olfactory signals that were obvious even to human observers, but under natural conditions such cues may be mediated by the presence of numerous conflicting cues from food resources, predators, prey, competitors, and other sources. Alternatively, behaviors that contribute to reducing risk from one predator type may serve to increase vulnerability to another (Kotler and Brown 1991, Korpimäki et al. 1996). For animals adapted to a speciose tropical system featuring a large suite of potential predators, there may not be a strong selective advantage in responding to any one predator type, such as ambushing snakes.

Finally, although *B. asper* feeds heavily on small mammals (Martins et al. 2002), the risk of encounter by any individual rodent may be low. In addition, because fer-de-lance forage almost exclusively by ambush rather than active hunting (Chapter 2), they therefore require prey animals to pass within close distance in order to feed. For such a species, there should be a strong selective pressure to avoid detection and subsequent avoidance by prey.

	Response	Cue	*Heteromys desmarestianus*	*Peromyscus mexicanus*	*Melanomys caliginosus*
Arena	Selection	Snake	23	16	19
		Snake Feces	10	8	10
	Foraging	Snake	9	9	11
		Snake Feces	27	13	17
		Opossum Feces	13	11	8
Room	Foraging	Snake	27	13	12
Field	Foraging	Snake	47 cued (live snake), 47 control		

Table 5.1. Sample sizes for each experiment used in the study. For Arena and Room experiments, figures represent the number of individuals. For Field experiments, figures represent the number of cage-nights.

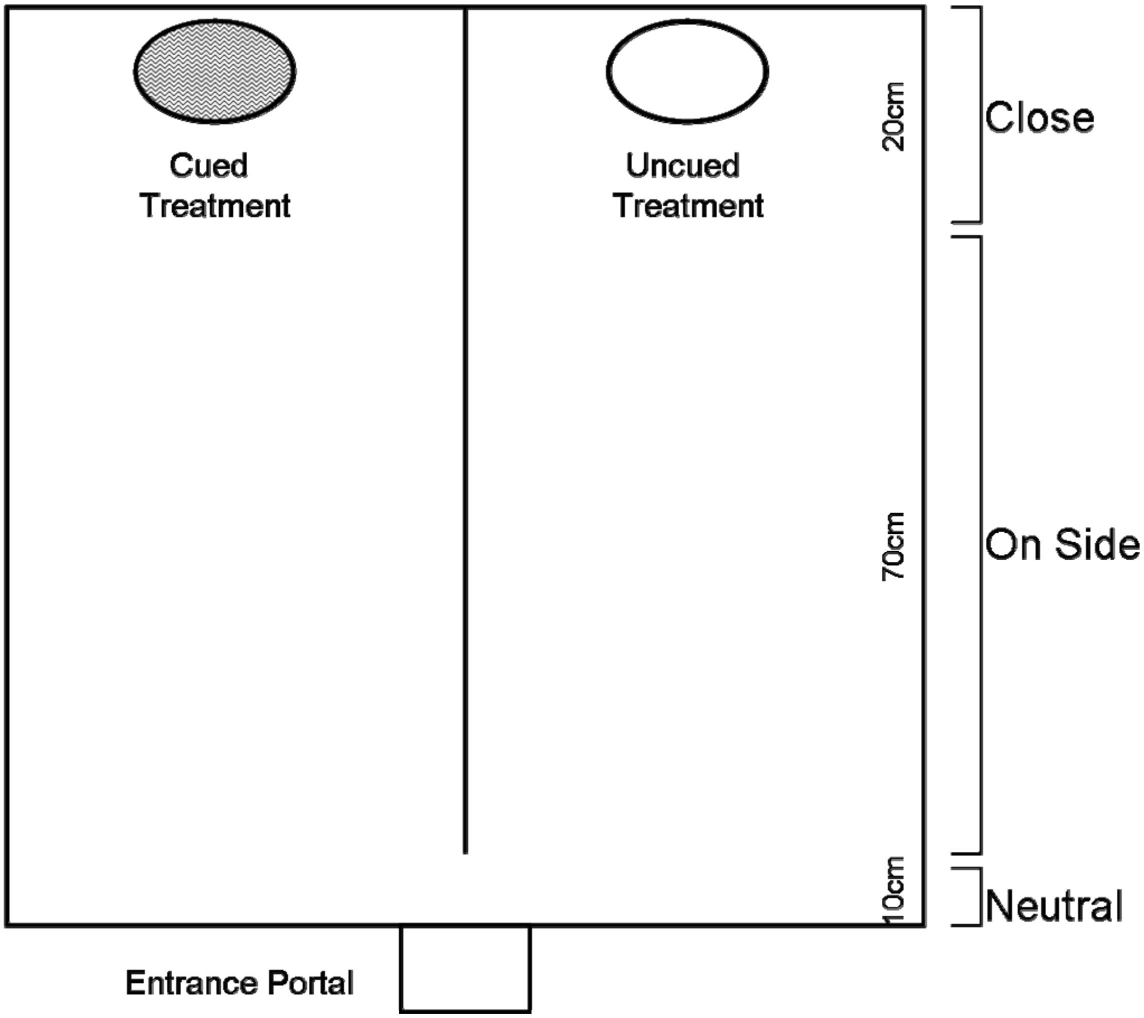

Figure 5.1. Experimental setup used in Arena experiments. Cued and Uncued sides were randomly assigned for each trial.

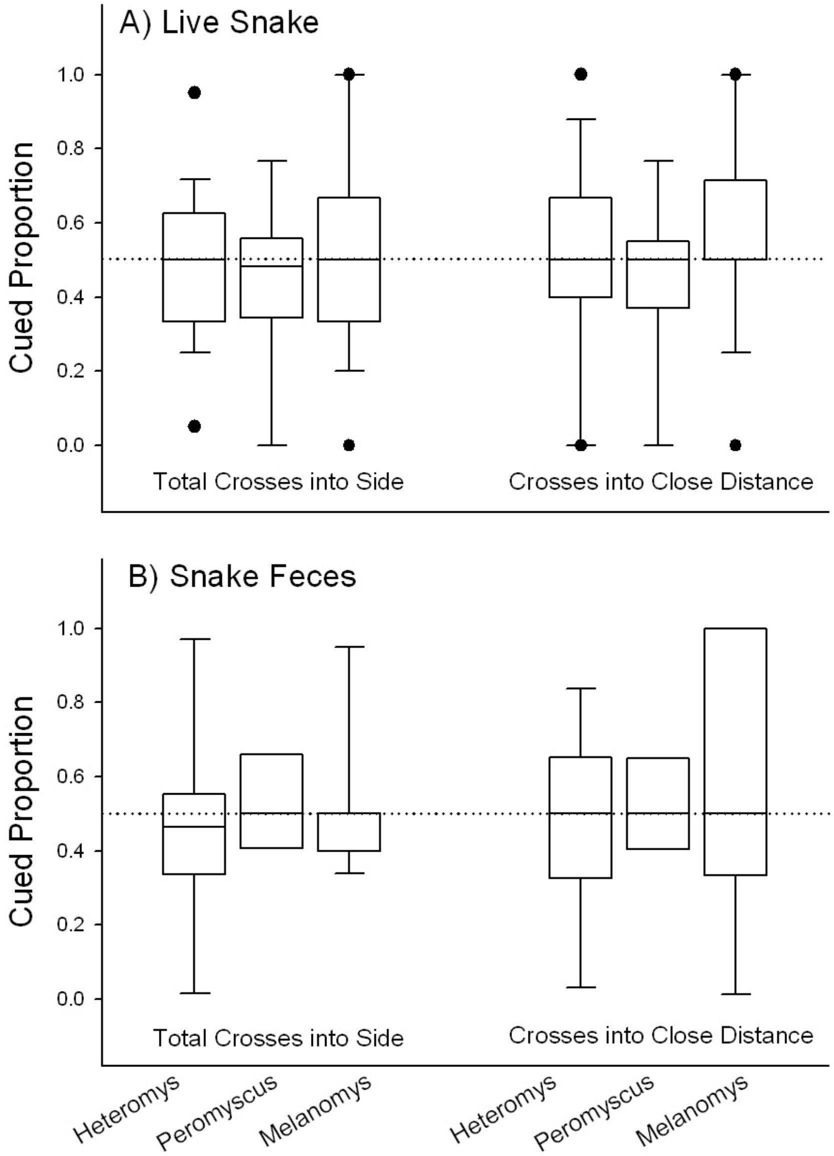

Figure 5.2. Ratios of cued to uncued total and close-distance entries made by three rodent species in response to A) live *B. asper* and B) *B. asper* feces containing a conspecific during snake-avoidance experiments. Lines within box plots represent median values, upper and lower boundaries of boxes are 75th and 25th percentiles, whiskers are 90th and 10th percentiles, and closed circles are 95th and 5th percentiles. Dashed center line represents a ratio of 0.5, or equal proportions on each side. Ratios did not vary from 0.5 for any group ($p \geq 0.05$).

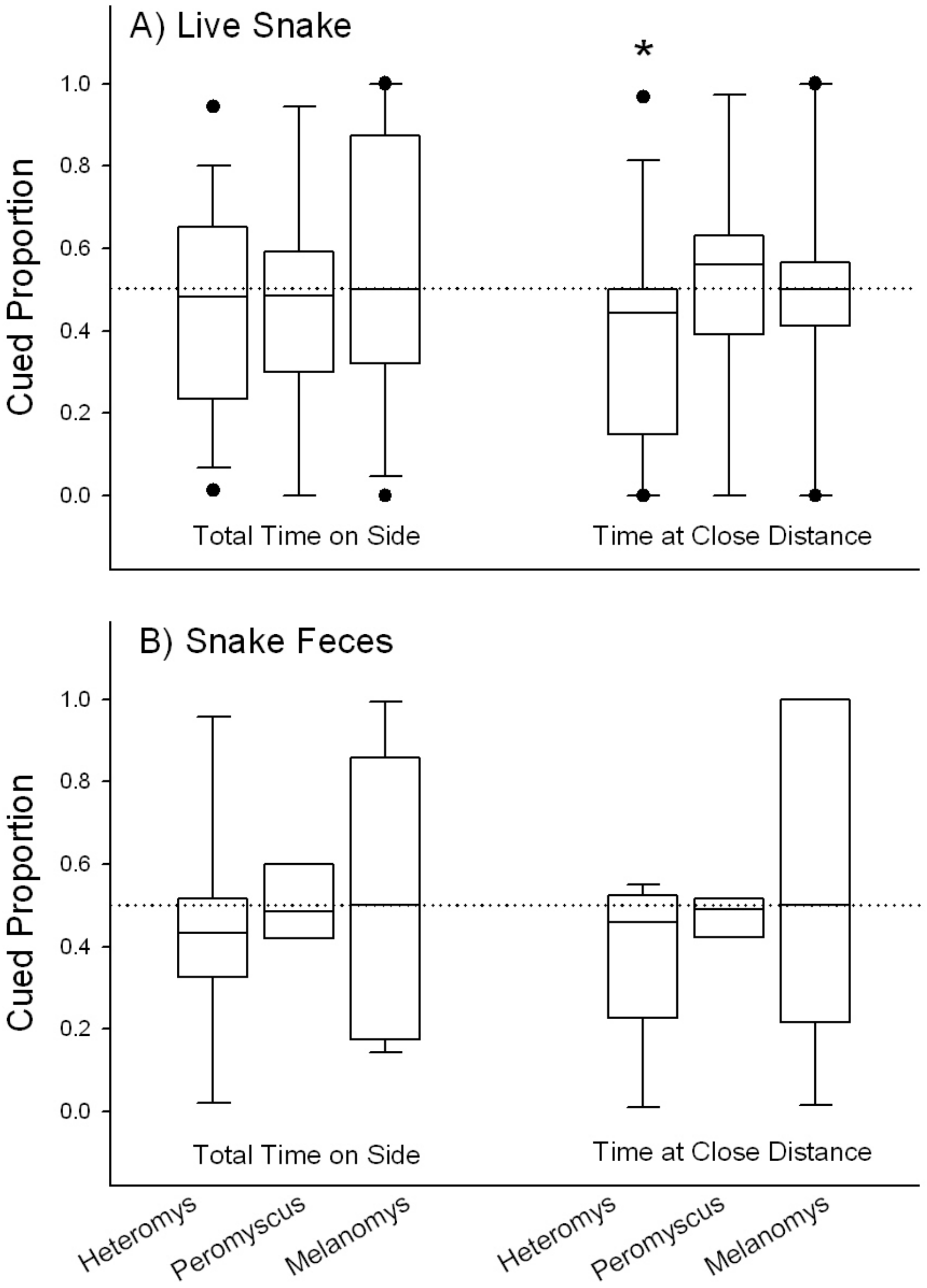

Figure 5.3. Ratios of cued to uncued total time and close-distance time spent by three rodent species in response to A) live *B. asper* and B) *B. asper* feces containing a conspecific during snake-avoidance experiments. Dashed center line represents a ratio of 0.5, equal proportions on each side. Groups marked with an asterisk (*) differed significantly from 0.5 ($p<0.05$).

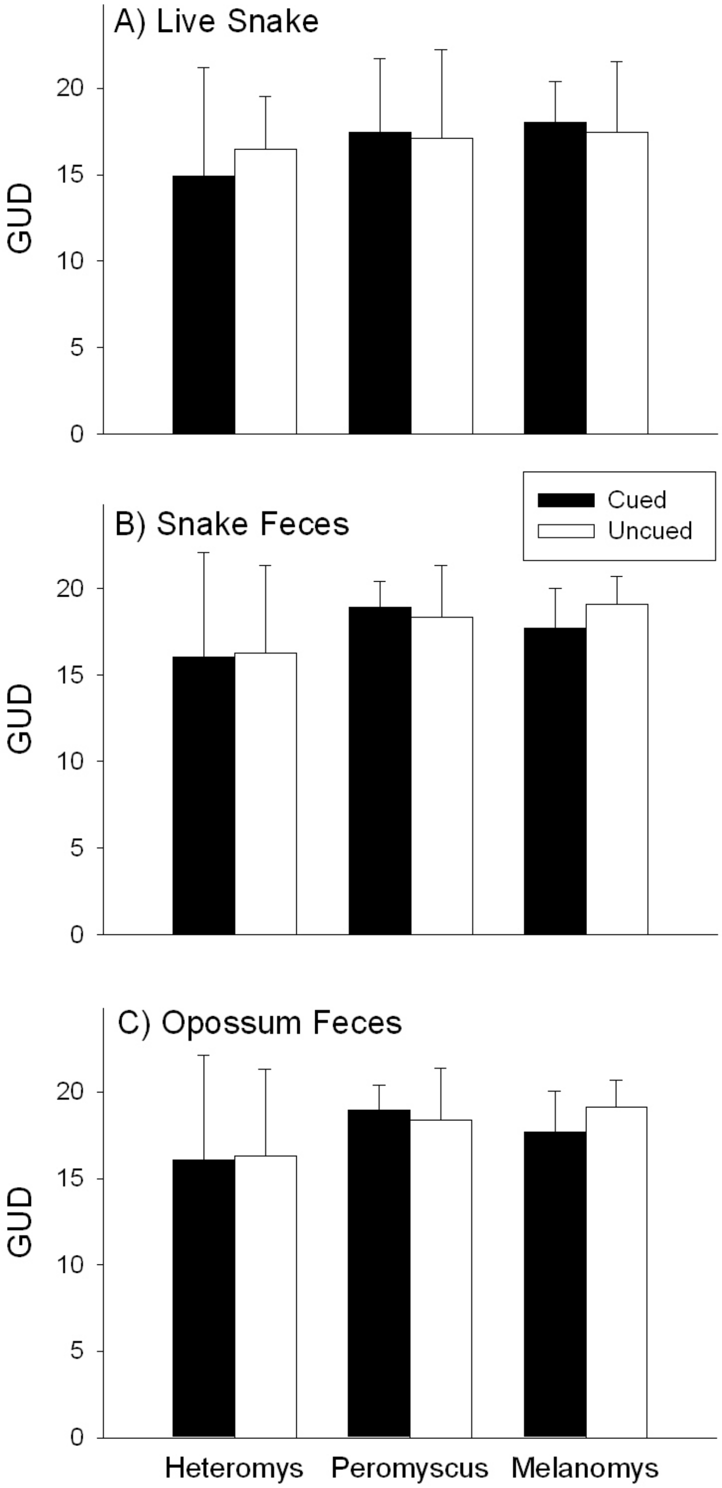

Figure 5.4. Mean (+1SD) giving-up density (GUD) by three rodent species on cued and uncued sides of arena foraging-reduction experiments using A) live *B. asper*, B) *B. asper* feces containing a conspecific, and C) opossum feces. Cued and uncued treatments did not differ for any group ($p \geq 0.05$).

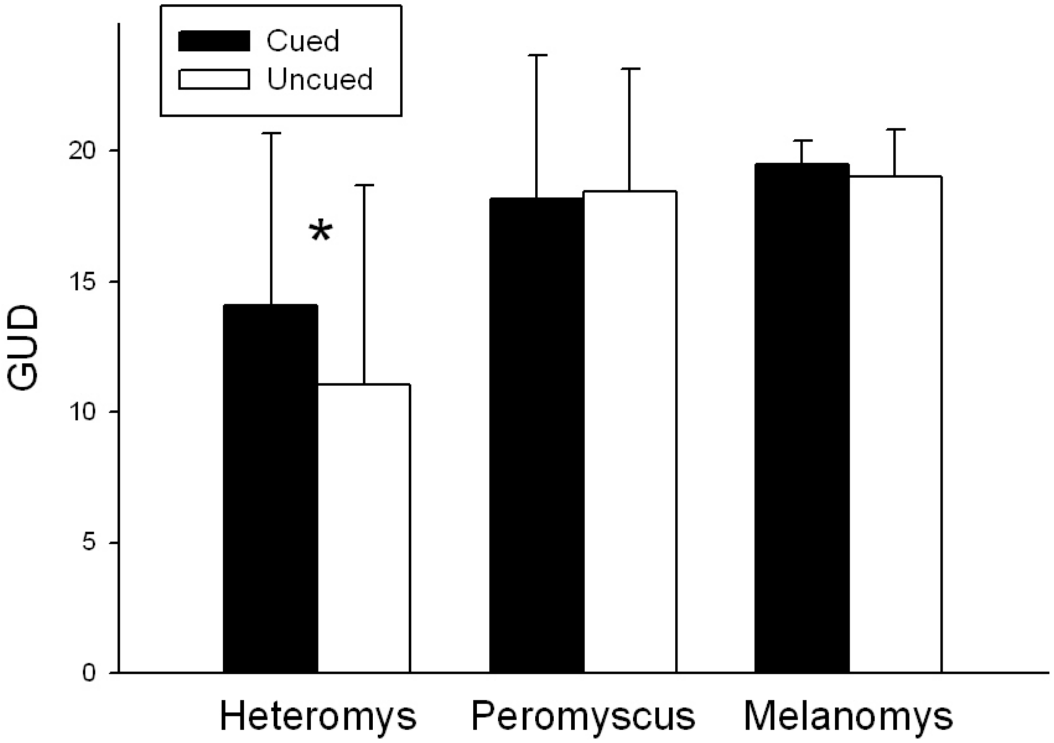

Figure 5.5. Mean (+1SD) giving-up density (GUD) by three rodent species on cued and uncued sides of seminatural-enclosure foraging-reduction experiments using live *B. asper*. Groups marked with an asterisk (*) differed significantly between Cued and Uncued treatments ($p<0.05$).

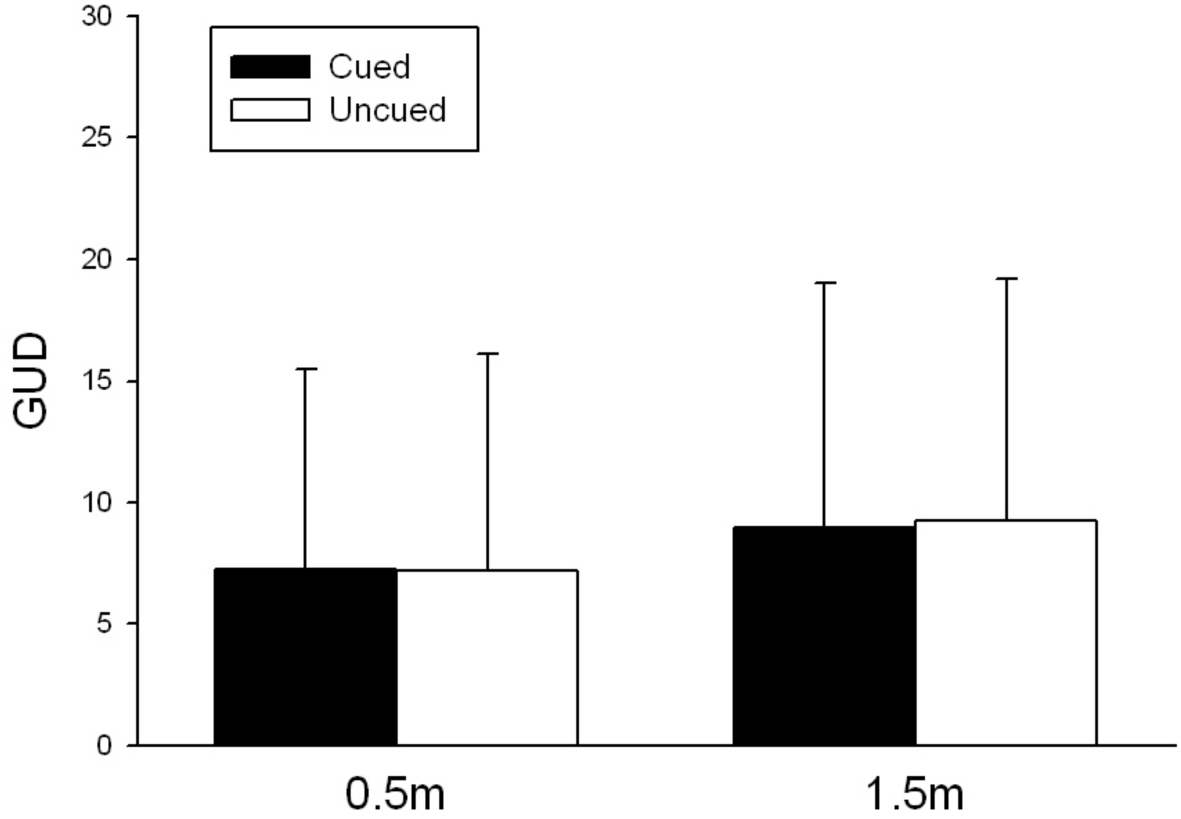

Figure 5.6. Mean (+1SD) giving-up density (GUD) remaining after 12 hours in bait stations at 0.5m and 1.5m distance from cued and uncued treatments in field foraging-reduction experiments using live B. asper. Cued and uncued treatments did not differ for any group ($p \geq 0.05$).

CHAPTER 6

CONCLUSIONS

The results of this study demonstrate that spatial biology and feeding habits are closely correlated for *Bothrops asper*. In general, fer-de-lance were found to be highly nocturnal ambush hunters. *B. asper* utilize less space and have reduced movement rates relative to many similarly-sized pitvipers in temperate areas (Macartney 1985, Reinert and Zappalorti 1988, Secor 1994), but similar patterns are seen among those occurring in aseasonal environments (Beck 1995, Angelici et al. 2000). The extreme differences in home range between tropical and temperate species may largely be due to the latter's dependence upon overwintering hibernacula. Because these sites are often separated from summer feeding grounds by distances of up to several kilometers, home ranges in such cases must include both areas, and depending on estimation method may include the intermediate regions as well. Tropical species need not make such seasonal migrations, instead remaining in the same feeding habitat year-round.

Movement rates were similarly reduced among *B. asper*, which my study suggests is related to an extreme reliance upon sit-and-wait foraging tactics. Many pitvipers are primarily ambush hunters, but occasional active foraging is also reported for many species (Mushinsky 1987). *B. asper*, however, was observed actively moving during less than 1% of all observations, none of which could be conclusively ascertained as foraging events. All fer-de-lance were regularly located in the same area for periods of several days to several weeks, moving only very short distances (<10m) between nocturnal ambush sites, if they moved at all. This pattern was occasionally interspersed by longer-distance movements to new feeding habitats, where the pattern was repeated. I propose that this pattern is similar to the "traplining" behavior seen among various nectarivores (Janzen 1971, Stiles 1975, Janson *et al*. 1981) which regularly monitor a series of known feeding areas in order to maximize foraging efficiency. Such behavior has not been previously described among snakes.

I also demonstrated experimentally that food resources directly influence spacing, movement, and habitat selection. During the initial stages of this project, several factors suggested that *B. asper* at La Selva Biological Station were strongly food-limited. Many fer-de-lance captured during the study were unusually thin, with no stored body fat; several telemetered animals are believed to have died of starvation. Small mammals normally constitute the bulk of *B. asper*'s diet (Martins et al. 2002), but were rarely encountered at the study site, and a trapping survey conducted to assess prey base captured no rodents or other small mammals in over 9000 trap-nights. Nearly all individuals utilized swamp habitat to a much greater degree than predicted by random availability, which I suggest reflects their efforts to exploit frogs as a food source. These observations directly inspired my supplemental-feeding experiment investigating the resource dependence of spatial patterns.

I hypothesized that if *B. asper* were limited by food availability, supplementally-fed individuals should have smaller home ranges, reduced movement rates, and reduced utilization of swamp habitat. My results supported all three of these predictions; the only other study investigating the spatial effects of increased food on snakes (Taylor 2005) was conducted in a desert, and found no such reduction. Fed individuals tended to remain in the same area for longer periods, and usually remained in shelter without emerging at all for several days to more than a week immediately after eating. Fed snakes also made fewer movements between ambushing sites, and traveled shorter distances when they did move. Increased site fidelity may indicate snakes' assessment of a given area as more "suitable" due to higher incidence of prey capture. Previous studies have usually proposed prey odors and densities rather than actual feeding success rate as indicators used by snakes to determine food availability (Downes 1999, Clark 2004, Tsairi and Bouskila 2004). The marked shifts by fed snakes from swamp to forest habitat may be explained by fed animals' returning to preferred habitat once freed from dependence upon swamp-dwelling frogs as a primary food source. I am unaware of other studies demonstrating shifts in habitat selection as a direct consequence of augmented food availability.

Finally, I investigated the role of *B. asper* in ecosystem dynamics by addressing the hypothesis that snakes affect the habitat usage and foraging efforts of their rodent prey. Because small mammals are known to avoid snakes (Dickman 1992, Kotler et al. 1993), and many tropical rodents are granivores (Reid 1997), an abundant, widespread, and relatively sedentary predator of small mammal such as *B. asper* could influence seed predation and dispersal rates on a local scale. Experiments conducted with three species, several types of stimuli, and at multiple scales, however, revealed very little snake avoidance of any kind by study species, and none of likely ecological relevance. Interestingly, these results contrast sharply with most existing data, which generally report marked snake avoidance and foraging reduction among rodents from temperate and desert ecosystems. In speciose tropical systems, snake predation may present a relatively minor survival threat, avoidance of snakes may increase vulnerability to other predators, or effective foraging strategies may differ fundamentally in seasonal and aseasonal environments. Alternatively, extreme ambush hunters such as *B. asper* may face a strong selective pressure to avoid detection by potential prey.

This dissertation represents the first long-term ecological study of *Bothrops asper*, and is among the first for any tropical snake. My results differ sharply from the existing body of literature regarding temperate snake species in terms of spatial ecology, resource dependence, and influence on prey. It is not yet clear whether this discrepancy signifies fundamental differences between temperate and tropical species, consequences of adapting to seasonal and aseasonal environments, or the idiosyncrasies of a unique snake predator. Because much of this study was conducted on a single population, it may also represent phenomena exclusive to the La Selva study site. Additional studies on *B. asper* in other regions and ecosystems would help clarify whether the results of this study are replicable across its range. Further work is also required to more fully elucidate the natural history, ecology, and ecosystem role of a beautiful, fascinating, and clearly ecologically-important predator in the fer-de-lance, which I have been able to only begin here.

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