SNAKES IN FRAGMENTING LANDSCAPES: AN INVESTIGATION OF LINEAR BARRIERS AND LANDSCAPE ALTERATIONS

by

KIMBERLY M. ANDREWS

(Under the Direction of J. Whitfield Gibbons)

ABSTRACT

Development and habitat loss pose the most serious threats to reptile persistence. The overall objective of this study was to provide initial assessments of snake behaviors around landscape fragmentation features, in particular the initial stages of residential and recreational development and roads. I used data from three studies in South Carolina to examine: 1) the variation within and among snake species recorded on roads using a 50-year database; 2) home range and spatial use patterns of timber rattlesnakes (*Crotalus horridus*) in a developing coastal landscape; and 3) variation in overwintering ecology among populations of *C. horridus*. In an investigation of road captures, 15 of 29 species exhibited male-biased road captures. I also noted that longer and heavier individuals were more susceptible to road mortality. Secondly, I analyzed home range sizes for *C. horridus* using multiple home range estimators (minimum convex polygons (MCP), fixed kernel distributions, and LoCoH nearest neighbor convex hulls (NNCH)). Males exhibited larger home ranges than females. Home ranges in developing areas were significantly larger than in undeveloped areas for MCPs and 95% fixed kernel estimations. The NNCH analyses revealed that snakes were not necessarily using more space in developed areas, but that ranges were more sprawling and fragmented. Sex influenced the size of breeding and foraging areas, but development only affected foraging ranges. Lastly, I assessed variation in winter surface activity, number of hibernacula used, body posture, and hibernacula structure types between a coastal and an inland population of *C. horridus* at different temporal scales. At seasonal and monthly scales, average air temperature and snake body condition significantly influenced surface activity and the number of hibernacula used. Average temperatures were significant in individual daily models, and precipitation and photoperiod also accounted for some of the variation. Coastal and inland sites were significantly different in terms of dominant hibernacula and structure types used during the winter. This assessment of initial landscape development is important to understanding the process of urbanization and wildlife population declines. These data facilitate the production of wildlife conservation plans for developing landscapes.

INDEX WORDS: Alive on Road, amphibian, body condition, body size, climate, coastal, community, Dead on Road, development, direct, ecology, education, effects, fragmentation, habitat management, hibernation, highway, indirect, kernel, LoCoH, MCP, mitigation, mortality, population, reptile, road, sex ratio, South Carolina, structure, suburban, thermal, urban

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DEDICATION

The achievement of this goal has been fueled by many who have touched my life and inspired me along the way, and therefore, I need to provide a special tip of the hat to several key players:

To my undergraduate advisor, the late Frank Golley, who taught me what being an ecologist was all about, and who believed in me from the first day I walked into his office at 18 years old to his last days. I miss you greatly Dr. Golley.

To My Family:

Papa, who taught me to be tough, and how to play "no down"

Nana, who showed me you never stop fighting for what you want to hang on to

Brent, my big brother, my friend, my childhood woods buddy who taught me to hang with the boys, and who first said the words "Whit Gibbons" to me

Mom and Dad, for bringing me into this world and raising me to never settle for anything less than everything that I wanted to be

To the canebrake rattlesnakes, an underappreciated evolutionary wonder, who also inspired Benjamin Franklin (*Pennsylvania Journal*, December 1775):

> She never begins an attack, nor, when once engaged, ever surrenders. She is therefore an emblem of magnanimity and true courage…Conscious of this, she never wounds till she has generously given notice, even to her enemy, and cautioned him against the danger of treading on her.

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CHAPTER 1

INTRODUCTION

Earth's ecosystems are experiencing more anthropogenic pressures than ever before. Conservation biologists are reacting with concern as we are increasingly documenting the alarming rate of change in natural systems, such as the loss of biodiversity or alterations in temperatures and precipitation rates. These rates of changes are causing concern as to whether we can sustainably maintain this pace of technology and natural resource consumption without irreversible effects. Habitat loss is the most substantial threat to global ecosystems, and an estimated one-third to one-half of the land surface is considered to have been transformed by human activity (Vitousek et al. 1997). However, in an exercise to calculate the "human footprint," Sanderson et al. (2002) estimated that 83% of land surface has been affected by humans, and specifically, 98% of arable land. Rates of consumption of natural resources are disproportionate for the United States; Wilson (2002) claims that if every human consumed at the level of the average American, it would take four Earths to meet the demand. One of our greatest challenges as ecologists is how to distill this information to the general public without the portrayal of the "chicken little" perception often imposed by the media or powerful entities with alternative goals.

Human populations are increasing rapidly in many ecologically-sensitive areas. Cincotta and authors (2000) calculated that 20% of the world's population was living within 25 of the world's biodiversity hotspots that were targeted by biologists as high priority locations for conservation agendas. The subsequent pressures of landscape transformation and alteration are disproportionately apparent in coastal habitats; more than 60% of the world's population resides within 100 km of a coastline (Vitousek et al. 1997). Vitousek et al. (1997) further state that as of 1995, 22% of marine fisheries were overexploited and an additional 44% were at their limit of exploitation.

Not surprisingly, the cumulative impacts of human activity are becoming apparent at all levels of ecological organization. However, due to the complexity of natural systems, it is quite difficult to design studies that can rigorously quantify and interpret these alterations. The process of urbanization occurs rapidly, and while the effects of direct habitat loss are more readily apparent than secondary effects, population and community-level consequences often experience a time lag before the effects are truly detectable. While data are lacking, and many that have been collected are problematic, the trend is clear – wildlife species cannot persist when their resident landscapes become uninhabitable.

In addition to expanding development, many regions are also experiencing the phenomenon referred to as "urban sprawl." Instead of concentrating activity surrounding metropolitan centers, rural areas are being increasingly populated, ultimately resulting in larger degrees of land transformation and development. Between 1970-2000, the distance of residential development from metropolitan centers increased and household size decreased (Brown et al. 2005). By 2000, this sprawl, or exurban development (~6-25 homes/km^2), occupied nearly 15 times the area of high-density urbanized development. Not only does this trend result in increased residential and home construction expansion, it subsequently causes increased traffic from commuter travel and the transportation of supplies to peripheral grocery stores and markets. It subsequently encourages exportation as opposed to "buying locally" at the mom and pop store that you can walk to.

Urban and suburban expansion into rural areas surrounding cities also means that natural areas are being developed, and backyard wildlife species that remain are not necessarily welcome. Huston (2005) identifies three phases of land-use change: agricultural, industrial, and information/communications. The initial agricultural phase tends to eliminate species that cannot survive on marginal disturbed lands. The requirements for industrialization tend to amplify these effects through an increased development footprint. The information/communication stage tends to then affect parts of the landscape that neither of the first stages did, and represents the true linkage break of human society with the philosophy of the land ethic (Leopold 1949). Exurbanization has been shown to reduce survival, reproduction, and richness of native species, although exotic and early successional species tend to increase (Hansen et al. 2005). Hansen and colleagues (2005) found these responses to be nonlinear and that they could take several decades to manifest, such that current responses could be expressions of development patterns from the mid-20th century.

Development and habitat loss pose the most serious threats to vertebrate populations (e.g., Gibbons et al. 2000; Cushman 2006; Todd et al. 2010). Approximately 25% of the world's bird species have been driven to extinction (Vitousek et al. 1997), and two-thirds of turtle species are threatened with extinction (IUCN 2008). A concerning aspect is that these wildlife species are taxa that people tend to attach to and enjoy. The lesser-respected species, such as squamates (lizards and snakes), receive far less attention and thereby, less research funding; subsequently, we know little about the status of most squamate species (e.g., Mullin and Seigel 2009). According to the 2004 IUCN Global Species assessment, 100% of described bird species, 100% of amphibians, 90% of mammals, and 67% of turtles had been evaluated while only 3.4% of squamates had been reviewed (Baillie et al. 2004). Among squamates, large venomous snakes, which are susceptible to both incidental and intentional mortality as human densities and encounter probabilities increase, have been particularly neglected in ecological research and conservation.

URBANIZATION AND HABITAT FRAGMENTATION

The process of urbanization has demonstrated deleterious and irreversible effects on biodiversity and ecosystem-level trophic dynamics (e.g., McKinney 2002, Faeth et al. 2005). Aside from direct mortality and habitat loss, wildlife ecology can be altered due to responses to landscape change, such as habitat fragmentation. The propensity for avoidance behaviors of roads, open spaces, and human-dominated areas, and reduced home ranges in the presence of urbanization is being increasingly documented for snakes, turtles, and mammals among others (e.g., Sealy 2002, Riley et al. 2003, Andrews and Gibbons 2005, Grgurovic and Sievert 2005, Andrews et al. 2008). Some amphibian and reptile species readily reside in areas experiencing anthropogenic disturbance (e.g., Neill 1950; Zappalorti and Burger 1985). However, some species that appear to occur in healthy numbers in suburban areas may decline in numbers with increased urbanization (Minton 1968).

Haila (2002) framed island biogeography theory (MacArthur and Wilson 1963, 1967) as the "intellectual attractor" for fragmentation studies, but encouraged the furthered perspective of fragmentation as a particular form of human-induced environmental degradation in heterogeneous landscapes. Aside from the biogeographic elements of fragmentation, there are also incredible alterations to physical processes influencing forest remnants (e.g., wind, temperature, degree of connectivity; Saunders et al. 1991) that warranted the evolution of this field of study.

Fragmentation refers to both habitat loss and the breaking apart of intact habitat as it pertains to wildlife's ability to move among remaining habitat pieces. Fragmentation can be differentiated from habitat patchiness in that fragmented landscapes are those "that were formerly forested but now consist of forested tracts that are segregated and sometimes isolated in a matrix of non-forested habitat" (Harris and Silvia-Lopez 1992). Fragmentation and the interpretation of effects are scale-dependent, and the mechanism of fragmentation can vary greatly among organisms and within a landscape. Further, fragmentation can be largely differentiated from habitat loss because there is retention of edge habitat (usually in increased percentages relative to interior habitat); therefore, it is important to recognize how the semantics of fragmentation relate to real ecological mechanisms to understand how wildlife respond to spatial shifting from increased edge and reduced insular forest.

There are five types of fragmentation as identified by Harris and Silvia-Lopez (1992): 1) *regressive* (clearing from single direction and frontal edge of forest is pushed back by successive bouts of cutting); 2) *enveloping* (clearing from all directions); 3) divisive (linear barrier bisects); 4) *intrusive* (clearing occurs from within patch); and 5) *encroaching* (clearing from either side of linear forest but connectivity to larger patches remains). In this study, I was able to observe all five types of fragmentation. However, my objectives for this dissertation did not permit quantification or comparison of the different processes.

Fragmentation additionally occurs in stages, and in many instances, can be a gradual progression although there are many examples of these stages (dissection, perforation, fragmentation, attrition) occurring in rapid succession (Hunter 1997). The initial stage is *dissection*, which usually represents the installation of linear barriers and roads that provide accessibility to the landscape that enables further development. Secondly, *perforation* involves the construction of small patches, generally of sizes that do not present true barriers to animal movement. In some instances, this stage benefits many edge-attracted species similar to a wildlife food plot. Next, *fragmentation* represents the progression of perforation where patches become more prominent and begin influencing movement of particular species (e.g., disturbance avoiders and wide-rangers). *Attrition* is the ultimate stage where only small, isolated patches remain that are inadequate for the persistence of most species, and which are so isolated that recolonization and metapopulation dynamics are highly disrupted. The probability of recolonization is the ultimate determinant for long-term population viability. This probability is dependent upon: 1) spatial relationships among landscape elements (configuration); 2) dispersal characteristics of the organism; and 3) temporal changes in the landscape structure (Fahrig and Merriam 1994).

While conceptually easy to grasp, the complications of studying these mechanisms have challenged landscape and wildlife biologists immensely. The effects of habitat loss and fragmentation are ideally measured independently, and most empirical studies are unable to partition these mechanisms (Fahrig 2003). Further, most fragmentation is measured at the patch scale instead of the landscape scale (Fahrig 2003). These hurdles are not downfalls to the research provided that researchers are aware of the limitations of their scopes. While this dissertation does not quantify the mechanisms of fragmentation, these data serve as a needed baseline assessment of initial responses in the dissection and perforation stages of the process in order to better gauge responses in the later stages of fragmentation of this field site.

ROADS ARE THE FIRST STEP OF URBANIZATION AND FRAGMENTATION

Urbanization occurs at multiple spatial scales from the opening of a store, construction of a residential neighborhood, or development of a city. Between 1950 and 1990, urban land area increased more than twice as fast as human population growth (White and Ernst 2003). Roads enhance connectivity between rural and heavily populated areas, and consequently are the ultimate manifestation of urbanization, which occurs in progressive stages across multiple temporal and spatial scales. Human societies, whether urban or rural in population density, depend on transportation networks to establish conduits for people and products. Mass production of vehicles in the 1900s created demand for expansion and efficiency of the road network, particularly in the United States (U.S., Forman et al. 2003). Approximately 6.4 million km of public roads spanned the U.S. by the mid-1990s; between 1998 and 2003, the total increased by 112,654 km (U.S. Bureau of Transportation Statistics [USBTS] 2004).

As development sprawls outward from the city core, existing transportation corridors are supplemented to support increased traffic volumes (Forman et al. 2003). The extension of the U.S. road system permits vehicle access to most areas, as evidenced by the fact that 82% of all land lies within only 1 km of a road (Riitters and Wickham 2003). Based on a conservative assumption that effects permeate 100-150 m from the road edge, an estimated 15-22% of the nation’s land area is projected to be ecologically impacted by roads (Forman and Alexander 1998), an area about 10 times the size of Florida (Smith et al. 2005). However, some effects appear to extend to 810 m (i.e., 0.5 mi), resulting in 73% of U.S. land area that would be susceptible to impacts (Riitters and Wickham 2003).

The USBTS (2004) defines an urban area as "a municipality . . . with a population of 5,000 or more.” By this definition, many national parks and wildlife refuges have daily visitation levels equivalent to populations of small urban areas and during months of peak visitation, have traffic volumes comparable to some cities (National Park Service 2004). Therefore, recreational activities in these natural areas may detrimentally affect species that should otherwise be protected (Seigel 1986). The area affected by roads due to strong edge effects can be 2.5-3.5 times greater than that of clearcuts; therefore, road fragmentation can also be apparent in these remote "protected" locations (Reed et al. 1996), urbanizing even parks and refuges. These roads may subsequently facilitate future development of an area, increasing use of surrounding habitats by humans for hunting, collecting, and observing of wildlife (Andrews 1990; White and Ernst 2003).

Conflicts continually arise due to the interconnectedness of issues related to roads, wildlife, and adjacent habitats. These conflicts have led experts from multiple fields (e.g., transportation planners, landscape and wildlife ecologists, and engineers) to contribute their knowledge in an effort to explain the "complex interactions between organisms and the environment linked to roads and vehicles" in the field of road ecology (Forman et al. 2003). Reviews, bibliographies, and books have focused on the general effects of roads on natural systems (e.g., Andrews 1990; Trombulak and Frissell 2000; Forman et al. 2003; White and Ernst 2003). However, little attention has been given to amphibians and reptiles, with the exception of Jochimsen et al. (2004) and Andrews et al. (2006) who present comprehensive syntheses of road literature pertaining to these taxa with emphasis on direct effects and mitigation efforts.

The extent to which roads are linked to the widespread decline of amphibian and reptile populations (Gibbons et al. 2000; Stuart et al. 2004) is unresolved. Nonetheless, the prospect of mitigating and, even more ideally, reducing the adverse effects that can be attributed to roads seems attainable. A better understanding of how roads affect herpetofauna and the subsequent application of this knowledge will minimize detrimental effects on these taxa.

DEMOGRAPHIC BIASES IN RESPONSE TO URBANIZING FEATURES

Reptiles, as part of the world's hidden biodiversity (Gibbons et al. 2000), are often challenging to study because of difficulties in obtaining adequate sample sizes, in particular, due to their secretive nature and low abundance. Road cruising, the common technique of searching for animals on roads from vehicles, has been used effectively with many snake species (e.g., Klauber 1939; Fitch 1949; Campbell 1953; Pough 1966; Dodd et al. 1989; Krivda 1993; Seigel and Pilgrim 2002). Ironically, one value of road cruising is to collect dead-on-road (DOR) snakes, which serve as indicators of the extent to which particular roads can be lethal transects (e.g., Andrews and Gibbons 2008).

As the number of roads that fragment the landscape increase (Andrews 1990, Clark et al. 2010a), higher mortality is assured for many vertebrate groups, including snakes. Many intrinsic (e.g., reproductive state, home-range size, daily activity patterns) and extrinsic (e.g., season, weather, and proximity of a road to particular habitats) variables influence whether a snake will cross a road successfully (e.g., Dodd et al. 1989; Andrews and Gibbons 2005), some of which have been considered quantitatively (e.g., Rosen and Lowe 1994; Bonnet et al. 1999; Enge and Wood 2002). Few studies have had adequate sample sizes to evaluate the interspecific and intraspecific relationships of sex ratios, mortality levels, and body sizes of snakes on roads in areas with high species diversity. Ascertaining why certain species or individuals exhibit differential patterns of road use or crossings is critical for development of effective management strategies.

RESPONSES TO VARIATION IN ENVIRONMENTAL CONDITIONS

The effects of temperature and other abiotic conditions on ectotherms are strong drivers of behaviors of ectotherms (e.g., Huey et al. 1989). Bound by an inability to control their temperature other than through behavioral thermoregulation (e.g., Pough 1983), environmental conditions limit these animals in some aspects, while making them so productive in others. Thermoregulation is a key feature of their behaviors in both active and inactive periods, and in particular, through microhabitat selection of retreats, and positioning within retreats (e.g., Huey et al. 1989). Therefore, an assessment of these retreating behaviors during the coldest part of the year can be quite revealing of their overall strategies for surviving the winter. Snakes are ideal models for these investigations due to their elongate bodies and high surface-to-body area and a resulting ability to maximize spatial and temporal thermal variability through microhabitat selection and body posturing (e.g., Lillywhite 1987; Peterson et al. 1993).

The geographic range of timber rattlesnakes (*Crotalus horridus*) spans the broadest diversity of ecological habitats of any North American rattlesnake. Hence, the level of variability within the species is extensive (e.g., Allsteadt et al. 2006; Sexton et al. 1992). Despite a relatively abundant amount of literature on this particular species, we still know little about how to apply our understanding of this variability into species-level conservation plans. Specifically, *C. horridus* in the southern part of their range, where they are often referred to as canebrake rattlesnakes, remain under-studied relative to their northern populations. Baseline data on habitat-use patterns and phenology in *C. horridus* in these warmer climates are needed, a need that is becoming increasingly urgent due to rapid and large-scale residential and commercial development pressure in warm, coastal environments. Further, southern conspecifics are larger

(SC, Cale and Gibbons 1972; Gibbons 1972) relative to those in cooler regions (e.g., NY, Brown 1993), which implicates larger body sizes to maintain in terms of foraging, reproduction, and overwintering physiology.

Hibernacula of *C. horridus* have been fairly well-characterized in the northern part of their range where *C. horridus* exhibit site fidelity to communal dens (e.g., Cobb et al. 2005; Anderson 2010; Clark et al. 2010b). However, overwintering habitat and activity characterization for southern *C. horridus* have not been published. Simply and firstly, less research has been conducted on these populations than at northern sites, and secondly, the detectability of southern *C. horridus* is lower as they are more spatially dispersed and cannot be as easily surveyed and captured *en masse* as at denning-site aggregations upon spring emergence. Their reliance on these denning locations strongly influences home range configuration through habitat use patterns prior to and following inactive seasons (Galligan and Dunson 1979; Brown et al. 1982; Reinert and Zappalorti 1988; Brown 1993; Laidig and Golden 2004; Adams 2005; Browning et al. 2005).

Climate change may also have consequences for ectotherms. Current models for the southeastern U.S. predict increases in temperature ranging from 2.5ºC to 5ºC, as well as changes in patterns and quantities of precipitation and increased flooding from sea-level rise (e.g., Karl et al. 2009). Wildlife biologists are in a state of rapid assessment of climate change effects that can have global consequences on ectotherms, which could influence predator-prey dynamics (e.g., Bickford et al. 2010, Sperry et al. 2010) or disproportionately affect species richness of ectotherms (Moreno-Rueda and Pizarro 2007). Temperature is the most frequently studied variable used in investigating potential shifts over time or animals' adaptability to rapid and slight environmental changes (Visser 2008). Hence, field assessment of the influence of abiotic conditions on surface activity and hibernacula use in *C. horridus* is a timely exercise.

HERPETOFAUNA

Reptiles and amphibians are a difficult group of wildlife to study not only because they tend to be covert and secretive and therefore can be hard to detect, but because there is a reduced ability to reasonably generalize among taxa. While some species are sensitive to the slightest alterations and are among the first to disappear from urbanizing settings, others are quite cosmopolitan and may even benefit from disturbance. Therefore, select species have a tremendous potential to serve as indicator species for very different objectives that seek to categorize both vulnerabilities and resiliencies (e.g., Hager 1998).

For instance, amphibians can be particularly desirable for assessing wetland conditions in urbanizing landscapes due to their sensitivity to increased run-off from impervious surface that results in altered hydroperiods (e.g., Rubbo and Kiesecker 2005), and loss of ground cover that increases soil erosion and reduces water quality (e.g., Orser and Shure 1972). Amphibians can simply be easier to study as they are not only more charismatic from the societal eye, but they have shorter life spans and tend to be more concentrated due to their close affiliation with aquatic habitats.

However, reptiles, and snakes in particular should not be underestimated for what they can reveal about ecosystem health (e.g., Beaupre and Douglas 2009). Typically, mammalian predators have received much of the focus in studies on effects of fragmentation not only because of their charisma, but because they are one of the first and most noticeable groups to exhibit altered spatial patterns in fragmenting landscapes and eventually, disappear (e.g., bobcats and coyotes, Riley et al. 2003). However, some of the larger snake species tend to serve important predator roles as well and have the potential to be equally sensitive to fragmentation due to wide-ranging space use and vulnerability to roads and genetic disruption (e.g., Clark et al. 2010a).

TIMBER RATTLESNAKES

Crotalus horridus is the only wide-ranging woodland rattlesnake species (e.g., Brown 1993). This species is still thought of as broadly ubiquitous in North America, including in southern regions of the U.S. (Gibbons 1972, Tennant and Bartlett 2000). However, there are apparent declines noted for populations throughout its range due to a suite of pressures attributable to habitat loss, habitat degradation, road mortality, and both intentional and incidental mortality (e.g., Brown 1993). Although *C. horridus* receives no listing in South Carolina where this study was conducted, it is listed as vulnerable, critically imperiled, or imperiled in 20 of the 31 states in which it occurs, and has been extirpated from Maine, Rhode Island, and Ontario, Canada (CITES 2000). This species is an ideal candidate for this investigation as it is still considered more common than the eastern diamondback rattlesnake (*Crotalus adamanteus*, Waldron et al. 2008) but is susceptible to conservation pressures that warrant both immediate and long-term concerns. Further, it serves as an excellent model to examine fragmentation effects and human-wildlife coexistence because it: 1) exhibits large home range sizes (e.g., Reinert and Zappalorti 1988) and therefore, is more likely to respond to fragmentation and road effects (e.g., Clark et al. 2010a); 2) is a predator with high adult survivorship (e.g., Brown et al. 2007) and therefore, is a good model for urban effects on key species in ecosystems; 3) exhibits high interannual site fidelity (e.g., Brown et al. 1982, this study (Chapter 5)) and therefore, is likely to implicate levels of spatial adaptability in response to habitat loss; and 4) is a large, venomous snake and therefore, is a good model for outreach and education efforts with developers and property owners.

OBJECTIVES

In Chapter 2, we elaborate on how roads in urban areas may cause numerous subtle yet pervasive effects through indirect processes, and provide an ecological framework for future research on herpetofaunal road ecology (see also Andrews et al. 2006; www.parcplace.org). Our objective here was threefold: 1) identify biological characteristics of herpetofauna that increase their susceptibility to roads; 2) discuss how roads and vehicles directly and indirectly affect amphibian and reptile individuals, populations, and communities through direct mortality, habitat loss, fragmentation, and ecosystem alterations; and 3) provide examples of post-construction mitigation and long-term solutions of pre-construction transportation planning and public awareness.

In Chapter 3, we examined differential capture rates of snake species in a prescribed region of the southeastern U.S. based on records collected over a 54-year period. Our primary goal was to evaluate inter- and intraspecific differences in sex and status [DOR or alive-on-road (AOR)] of on-road captures. A secondary goal was to assess differences in species richness, sex, and body size between on-road and off-road captures. Lastly, we discuss how these trends apply to snakes on roads in urban and suburban areas.

In Chapter 4, I investigated influences of the initial stages of residential and recreational development on home range sizes of *C. Horridus* in South Carolina. The objectives of this study were to assess the potential effects on home range size (overall, within-season activity ranges, and interannual ranges) of sex, body condition, development phase, road density, and distance to nearest manmade open space. I hypothesized that: 1) body condition would be positively correlated with home range size; 2) males would use larger home ranges than females; 3) home range size would be affected by development phase through increased overlap in activity ranges and decreased overlap in home range fidelity; 4) road density would be inversely related to home range size; and 5) distance to nearest open space would be positively related to home range size.

Lastly, in Chapter 5, we compared data from a coastal and an inland population of *C. horridus* in South Carolina. We used radiotelemetry data collected between 2002 and 2010 to quantify winter activity at three temporal scales: seasonal (i.e., annual), monthly, and daily (i.e., snake locations). We predicted that: 1) coastal and inland field sites would vary significantly in their level of surface and hibernacula activity; 2) temperature would have a positive relationship with surface activity; 3) snakes with lower body condition would bask more (greater surface activity); and 4) snakes with higher body condition would move more frequently during winter (use greater numbers of hibernacula).

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CHAPTER 2

ECOLOGICAL EFFECTS OF ROADS ON AMPHIBIANS AND REPTILES: A LITERATURE REVIEW[1]

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[1] Andrews, K. M., J. W. Gibbons, and D. M. Jochimsen. 2008. *In* J. C. Mitchell, R. E. Jung Brown, and B. Bartholomew (eds.), Urban Herpetology, pp. 121-143. Herpetological Conservation vol. 3, Society for the Study of Amphibians and Reptiles, Salt Lake City, UT. Reprinted with permission of the publisher.

ABSTRACT

Roads are the ultimate manifestation of urbanization, providing an essential connectivity within and between rural and heavily populated areas. The ecological impacts roads have on herpetofauna across temporal and spatial scales are profound, beginning during the early stages of construction and progressing through to completion and daily use. We provide examples of physiological, ecological, and behavioral traits inherent among herpetofauna that enhance their susceptibility to habitat alterations and environmental changes that can result from the development as well as the use of roads. We emphasize areas in which impacts on herpetofauna have not yet been documented, but are likely. We also identify potential threats to amphibians and reptiles by noting and discussing previous research in road ecology that is applicable. The most obvious impacts of roads are direct effects, which result in injury or death as a consequence of road construction followed by on-road mortality (roadkills) from contact with vehicles. In addition to the more measurable direct effects, road impacts are compounded further by a variety of indirect effects of roads on herpetofauna that can be pervasive through habitat fragmentation and alteration that extend to population and community level impacts. By identifying herpetofaunal susceptibilities and providing concrete examples of road impacts, we offer an ecological framework that can serve to suggest research questions and encourage investigators to pursue goals that relate to both direct and indirect effects of road development and subsequent urbanization on herpetofauna. Lastly, we present current and possible approaches for resolving and preventing conflicts between wildlife and roads.

Key words: Amphibian, Community, Direct, Education, Effects, Fragmentation, Highway, Indirect, Mitigation, Mortality, Population, Reptile, Road

INTRODUCTION

Human societies, whether urban or rural in population density, depend on transportation networks to establish conduits for people and products. Mass production of vehicles in the 1900s created demand for expansion and efficiency of the road network, particularly in the United States (Forman et al. 2003). Approximately 6.4 million km of public roads spanned the U.S. by the mid-1990s (Fig. 2.1); between 1998 and 2003 the total increased by 112,654 km (U.S. Bureau of Transportation Statistics [USBTS] 2004). Roads generate an array of ecological effects that disrupt ecosystem processes and wildlife movement. Road variables that potentially affect wildlife, both directly and indirectly, include size, substrate, age, accessibility, and density. Road placement within the surrounding landscape is possibly the most important factor determining the severity of road impacts on wildlife because it influences roadkill locations and rates and the observed presence or absence of species.

The combined environmental effects generated by roads (e.g., thermal, hydrological, pollutants, noise, light, invasive species, human access), referred to as the "road-effect zone" (Forman 2000), extend outward from 100 m to 800 m beyond the road edge (e.g., Reijnen et al. 1995). Considered independently, each factor influences the surrounding ecosystem to varying extents and is further augmented by road type and environmental processes, including wind, water, and behavior (Forman et al. 2003). Based on a conservative assumption that effects permeate 100-150 m from the road edge, an estimated 15-22% of the nation's land area is projected to be ecologically impacted by roads (Forman and Alexander 1998), an area about 10 times the size of Florida (Smith et al. 2005). However, some effects appear to extend to 810 m (i.e., 0.5 mi), resulting in 73% of U.S. land area that would be susceptible to impacts (Riitters and Wickham 2003).

Roads enhance connectivity between rural and heavily populated areas, and consequently are the ultimate manifestation of urbanization, which occurs in progressive stages across multiple temporal and spatial scales. Between 1950 and 1990, urban land area increased more than twice as fast as population growth (White and Ernst 2003). As development sprawls outward from the city core, existing transportation corridors are supplemented to support increased traffic volumes (Forman et al. 2003). Alternatively, roads may facilitate future development of an area, increasing use of surrounding habitats by humans for hunting, collection, and observation of wildlife (Andrews 1990; White and Ernst 2003). The extension of the U.S. road system permits vehicle access to most areas, as evidenced by the fact that 82% of all land lies within only 1 km of a road (Riitters and Wickham 2003).

The USBTS (2004) defines an urban area as "a municipality . . . with a population of 5,000 or more.” By this definition, many national parks and wildlife refuges have daily visitation levels equivalent to populations of small urban areas and during months of peak visitation have traffic volumes comparable to some cities (National Park Service 2004). Therefore, recreational activities in these natural areas may detrimentally impact species that should otherwise be protected (Seigel 1986).

Conflicts continually arise due to the interconnectedness of issues related to roads, wildlife, and adjacent habitats. These conflicts have led experts from multiple fields (e.g., transportation planners, landscape and wildlife ecologists, engineers) to contribute their knowledge in an effort to explain the “complex interactions between organisms and the environment linked to roads and vehicles” in the field of road ecology (Forman et al. 2003). Reviews, bibliographies, and books have focused on the general effects of roads on natural systems (e.g., Andrews 1990; Trombulak and Frissell 2000; Forman et al. 2003; White and Ernst

2003). However, little attention has been given to amphibians and reptiles, with the exception of Jochimsen et al. (2004) who presented a comprehensive synthesis of roads literature pertaining to these taxa with emphasis on direct effects and mitigation efforts. Here we elaborate on how roads in urban areas may cause numerous subtle yet pervasive effects through indirect processes, and provide an ecological framework for future research on herpetofaunal road ecology (see also Andrews et al. 2006; www.parcplace.org)

The extent to which roads are linked to the widespread decline of amphibian and reptile populations (Gibbons et al. 2000; Stuart et al. 2004) is unresolved. Nonetheless, the prospect of mitigating and, even more ideally, reducing the adverse effects that can be attributed to roads seems attainable. A better understanding of how roads affect herpetofauna and the subsequent application of this knowledge will minimize detrimental effects on these taxa. Our objective here is threefold: 1) identify biological characteristics of herpetofauna that increase their susceptibility to roads; 2) discuss how roads and vehicles directly and indirectly affect amphibian and reptile individuals, populations, and communities through direct mortality, habitat loss, fragmentation, and ecosystem alterations; and 3) provide examples of post-construction mitigation and long-term solutions of pre-construction transportation planning and public awareness.

ECOLOGICAL SUSCEPTIBILITIES OF HERPETOFAUNA TO ROAD IMPACTS

Amphibians and reptiles possess physiological, ecological, and behavioral traits that make them vulnerable to environmental changes associated with road impacts. As the degree to which the suite of road impacts affect herpetofauna has yet to be documented, we provide an ecological framework that can help drive research questions in areas where little or no data exist, but where road development and subsequent urbanization will incur obvious consequences.

Physiological Vulnerabilities.— High skin permeability exacerbates the susceptibility of amphibians to alteration of microhabitat conditions on roads and in adjacent habitats. Toxic chemicals emitted from vehicles and compounds used for road maintenance may act as endocrine disruptors in amphibians that reduce reproductive abilities and survivorship (e.g., Hayes et al. 2006; Rohr et al. 2006). Skin permeability and vulnerability to water loss also makes it difficult for organisms, such as amphibians, to maintain optimal moisture levels. Desiccation rates increase during dispersal, particularly in altered environments that do not retain natural moisture levels (e.g., Rothermel and Semlitsch 2002) and may also be accelerated for some species when they must traverse roads in urban areas.

Research suggests that roadsides and road surfaces attract some reptiles for thermoregulatory purposes. Amazonian lizards may benefit from open patches created by roads, due to increased access to basking sites, which consequently improves foraging efficiency (e.g., Sartorius et al. 1999), and some snakes may be attracted to roads that serve as basking sites (e.g., Klauber 1939; Brattstrom 1965; Sullivan 1981a; but see Andrews and Gibbons 2005). Further research is needed to explore variables (e.g., species, season, and environmental conditions) that would likely be involved if thermal conditions serve to attract reptile species to roadsides and road surfaces.

Finally, microhabitat changes may obscure olfactory or pheromonal cues. Olfaction plays a primary role in amphibian migration and orientation (e.g., Duellman and Trueb 1986), and some snakes rely extensively on scent for directional movement cues to locate mates (e.g., LeMaster et al. 2001), prey items (e.g., Chiszar et al. 1990), and ambush sites (e.g., Clark 2004). Some naïve neonate snakes trail conspecific adults to hibernacula (e.g., Cobb et al. 2005). Pheromone scent trailing, observed in a variety of species, could conceivably be altered by some contaminants, such as oil residues on roads (Klauber 1931) or road substrate type (Shine et al. 2004).

Spatial Complexity.— As road density increases, the probability also increases that individuals reliant on landscape complementation (i.e., spatial arrangement of necessary habitat types) will be killed or injured by traffic during movements in search of resources. Species that depend on a non-fragmented landscape to complete their life cycles (e.g., Pope et al. 2000) will be in greatest jeopardy. In a modeling assessment by Jaeger and colleagues (2006), population persistence was higher if roads were spatially clustered as opposed to evenly distributed across the landscape.

Resources associated with refugia, mates, and prey tend to be concentrated in distinct habitats that are patchily distributed and seasonally available. When roads bisect these habitats, mortality may become concentrated spatially and seasonally. Some amphibians make repetitive, within-season forays to breeding ponds before final migration to an overwintering site (Lamoureux et al. 2002), and many others migrate *en masse* between breeding ponds and terrestrial habitats (e.g., Semlitsch 2002). Seasonal aggregations of females within nesting habitat occur in some snake species that are widely spaced for the remainder of the year (e.g. Parker and Brown 1980). In northern latitudes, snakes make loop-like migrations from communal hibernacula to summer foraging habitats across relatively long distances (e.g., Gregory and Stewart 1975).

An individual's vulnerability to road mortality is influenced by dispersal tendencies as well as the spatial scale and frequency of movements. Carr and Fahrig (2001) demonstrated that vagile amphibian species are more likely to encounter roads, resulting in greater risk of mortality. Conversely, amphibians with lower mobility are more likely to persist in landscapes with low habitat cover, such as roadside areas (Gibbs 1998a). Bonnet et al. (1999) documented that snake species that move frequently over long distances experience higher mortality than sedentary foragers. Roe et al. (2006) detected a higher probability (14-20% of annual population mortality) of road mortality in a model comparing the wide-ranging Copperbellied Watersnake (*Nerodia erythrogaster neglecta*) with the more sedentary Northern Watersnake (*Nerodia sipedon*; 3-5% mortality). Some long-distance movers, such as Eastern Indigo Snakes (*Drymarchon couperi*) are particularly sensitive to edge effects and therefore could be an ideal umbrella species to look at the effects of landscape fragmentation (Breininger et al. 2004).

Landscape permeability and maintenance of movement corridors are critical to ensure metapopulation dynamics (Pulliam 1988) of amphibians and reptiles in urbanized environments (Marsh and Trenham 2001). Many herpetofaunal species require not only the terrestrial habitat peripheral to wetlands, but corridor linkages with other isolated water bodies (Gibbons 2003). Radiotelemetry data suggest that some reptile species are philopatric to migratory routes in successive years (e.g., Burger and Zappalorti 1992; Buhlmann and Gibbons 2001). These dynamics are often sacrificed by ill-conceived planning of landscape development and road placement, which likely contributes to resistance (i.e., reduced permeability) between patches (Bennett 1991), thereby catalyzing population isolation. Depending on the mechanisms driving migratory patterns (e.g., genetic, behavioral), an individual's ability to readily adapt to a road that interferes with the animal's migratory route may be limited. Deterministic movements by wildlife complicate the ecological provisions that must be retained when managing an area, a process for which ecological understanding is essential (Gibbons and Semlitsch 1987).

Behavioral Variation.— Behaviors such as movement speed and predator responses influence responses and susceptibility to road mortality and fragmentation. Slow-moving animals, or those that cross the road at a wide angle, increase their mortality risk. Slow movements of amphibians (Hels and Buchwald 2001), turtles (Gibbs and Shriver 2002; Aresco 2005a), and snakes (Andrews and Gibbons 2005) while crossing roads have been documented. While road-crossing speeds of amphibians and turtles may be fairly consistent within and among species in each group (but see Finkler et al. 2003 where gravid female Spotted Salamanders (*Ambystoma maculatum*) show reduced speed relative to males), crossing speeds of snakes vary significantly among species, suggesting that snakes may suffer a greater range of road mortality rates than other taxa (Andrews and Gibbons 2005). Although correlations of age, reproductive condition, or sex with road crossing speed have not been documented or studied, natural differences in speed exist (Plummer 1997). Lastly, little is published regarding crossing angles for herpetofauna. Two studies on snakes found that individuals consistently move perpendicularly across the road, taking the shortest route possible (Shine et al. 2004; Andrews and Gibbons 2005) suggesting that the road is an area that animals are simply passing through and not a selected habitat.

Immobilization behaviors that are likely derived from predator responses (Andrews and Gibbons 2005) may lead to responses to oncoming or passing vehicles that could significantly influence crossing time. Mazerolle et al. (2005) found that the strongest stimuli for immobilization behavior across six amphibian species were a combination of headlights and vibration. Andrews and Gibbons (2005) found high rates of immobilization in response to a passing vehicle among three snake species at levels that would greatly jeopardize some from crossing a busy highway.

DIRECT MORTALITY

Researchers have conducted surveys along roads in an effort to quantify the most conspicuous effect that roads impose on wildlife--mortality inflicted by vehicles. Direct effects involve injury or mortality that occurs during road construction (e.g., inadvertent burial or death from blasting and earth moving), or subsequent contact with vehicles associated with increased urban development. Direct mortality on roads is prevalent throughout the world on public and private lands. Further, while urban areas present obvious concerns for roadkills, road mortality has been considered the greatest non-natural source of vertebrate death in protected areas (e.g., parks and reserves; Bernardino and Dalrymple 1992; Kline and Swann 1998). Many studies have been designed to document all vertebrate mortalities across a given survey area and include the proportion of herpetofauna observed (Fig. 2.2). While direct mortality of herpetofauna has been documented since the beginning of the 20th century, the effects of roadkill were not observed until decades later (e.g., amphibians, Puky 2006; snakes, Fitch 1999). Studies investigating road effects specifically on amphibians have been conducted in Europe perhaps longer than in any other region, and mitigation efforts have been in place since the 1960s (Puky 2003; Schmidt and Zumbach 2008).

Since the 1930s, herpetologists have driven U.S. roads to document snake occurrence and collect specimens (e.g., Klauber 1931; Scott 1938), and many herpetologists still consider road surveys valuable for monitoring amphibian and reptile occurrence despite obvious biases with this survey method (e.g., Case 1978; Enge and Wood 2002; Steen and Smith 2006). Road surveys are occasionally used to monitor the status of populations (Seigel et al. 2002; Weir and Mossman 2005); however, we urge caution in the interpretation of these data as status cannot be considered independent of the myriad impacts of roads on herpetofauna.

Amphibians (Salamanders and Anurans).— The highest rates of road mortality for amphibians occur where roads located in the vicinity of a wetland or pond disrupt the spatial connectivity of essential resources and habitats across the landscape (e.g., Ashley and Robinson 1996; Smith and Dodd 2003). Many species fall victim to roads in great numbers during mass migrations of breeding adults and later as emerging metamorphs. Road mortality is likely substantially higher for some species of anurans relative to most salamanders due to higher reproductive output and tendency to breed in roadside habitats. In addition, anurans possess a delicate body structure that may make them more vulnerable to the high pressure wave created by a passing vehicle, which researcher Dietrich Hummel found can create enough force to cause the animal to expel its internal organs without experiencing a direct hit from a vehicle (Holden 2002).

Mass movements triggered by rainfall and warm weather may result in excessive rates of road mortality for salamanders and anurans (e.g., Turner 1955). In Michigan, Duellman (1954) reported that heavy rains initiated a mass migration of Tiger Salamanders (*Ambystoma tigrinum*) across a stretch of road where 83% of observed individuals were dead (n=274; 3.5 km; 30 hours). Clevenger et al. (2001) documented *A. tigrinum* movement across the Trans-Canada highway that occurred during heavy rainfall and warm temperatures (n>180 dead; 1.05 km; 5 days). In southern California, Ervin et al. (2001) suggested that wet roadways with high traffic volumes pose the greatest risk to amphibians in terms of road mortality; 93 nights of surveys conducted under wet conditions yielded a mortality rate of 48% (465 dead individuals) compared to a 19% (25 dead individuals) mortality rate measured during dry conditions. Several studies have focused strictly on the probability of individual amphibians being killed on the road. The estimated survival rate of toads crossing roads in Germany with traffic densities of 24-40 cars per hour varied from zero (Heine 1987) to 50% (Kuhn 1987). Hels and Buchwald (2001) calculated that the probability of individual mortality while crossing a road ranged from 0.34 to 0.98 across traffic volumes, depending on various attributes of a given species. Their model has been adapted to assess mortality probabilities for turtles (Gibbs and Shriver 2002; Aresco 2005a) and snakes (Andrews and Gibbons 2005) but has yet to be applied to lizards or salamanders. However, all are based on individual deaths presented as proportions, so the extrapolations to true population levels are equivocal.

Reptiles (Crocodilians, Lizards, Turtles, and Snakes).— Few road surveys have documented mortality of crocodilians and lizards, and most observations have been recorded incidentally (e.g., Klauber 1939; Fitch 1949; Dodd et al. 1989). Traffic deaths have been suggested as the major known source of mortality for some large, endangered species, including the American Crocodile (*Crocodylus acutus*; Kushlan 1988; Harris and Gallagher 1989); automobile collisions accounted for 46% of human-related mortality of this species in southern Florida (Gaby 1987). Crocodilians also present a human safety concern for drivers as evidenced by the death of a woman when her car flipped after a collision with an Alligator crossing Highway 17 in Jasper County, South Carolina (Associated Press 2005). A one-year survey conducted in the llanos of Venezuela reported a total of 65 Green Iguanas (*Iguana iguana*) discovered dead on the road (Rodda 1990). Lack of evidence for high mortality of lizards could be a detection issue due to small size and rapid deterioration of road-killed specimens of many species (e.g., Kline and Swann 1998), or a lower mortality rate due to their ability to cross roads faster than other reptiles (but see Kline et al. 2001 for a model predicting higher mortality rates in lizards than snakes). Also, most species of lizards do not migrate seasonally and exhibit high site-fidelity within small home ranges, potentially limiting their encounters with roads (Rutherford and Gregory 2003).

Slow-moving turtles, especially species that retreat into their shells when vehicles pass, are long-lived species that likely experience irreparable population impacts when adult females are killed (Congdon et al. 1993). Studies report seasonal peaks in road mortality correlated with the migration of nesting females and hatchling dispersal (e.g., Ashley and Robinson 1996; Gibson and Merkle 2004). Fowle (1996) found a major pulse of road mortality during the nesting season of Western Painted Turtles (*Chrysemys picta*) in Montana. In central Ontario, road mortality of Snapping Turtles (*Chelydra serpentina*) peaked during the nesting season with 30.5% of all turtles observed during roadside surveys discovered DOR (dead-on-road); only three individuals were encountered on roads during the post-nesting season (Haxton 2000).

Concentrations of turtle mortalities tend to be associated with movement between wetland habitats. In a summer survey in northern Alabama, Dodd et al. (1989) found that 85% of roadkills were Eastern Box Turtles (*Terrapene carolina*; n=119; 19,045 km; 5 mos.). In a seven-year census (1989-1995), Wood and Herlands (1997) reported the roadkill deaths of 4,020 Diamond-backed Terrapins (*Malaclemys terrapin)* along a road that bisects a marsh in coastal New Jersey. Along a highway dividing Lake Jackson in Tallahassee, FL, Aresco (2005a) never observed a single individual survive a road crossing, and subsequently has documented the highest turtle road mortality rate yet reported (pre-fence data; n=343; 95% killed when entering highway, remaining 5% killed in first two lanes).

The most thorough, long-term records of direct road mortality have been provided for snakes, with documentation of traffic fatalities since the 1930s (Fig. 2.3). Reports in which the majority of specimens are already dead are not uncommon (Fig. 2.4). The highest road mortality of snakes has been documented along U.S. Highway 441 in Paynes Prairie State Preserve in Florida (1.854 individuals/km surveyed, 623 snakes killed, 336 km surveyed, Smith and Dodd

2003). Franz and Scudder (1977) reported a mortality rate of 90.4% along a 3 km segment of the highway and surveys conducted from 1987-1990 along a 4.64 km section revealed that 13,000 snakes were killed (Harris and Scheck 1991).

Episodic weather events may trigger mass movements of snakes that result in high levels of mortality over fine spatial and temporal scales. Hellman and Telford (1956) observed 478 juvenile Mud Snakes (*Farancia abacura*; 47% DOR) concentrated within a 2-mile stretch along Highway 441 following a period of extended rainfall, and Carr (1974) observed more than 700 snakes (67% DOR) following a hurricane. Movement patterns influenced by weather are not always exhibited immediately as evidenced by the summer flooding of the Mississippi River that later triggered a pulse in snake movement across a bordering highway in October (Tucker 1995).

Ample evidence exists that road mortality of herpetofauna results in significant loss of individuals and in some situations threatens the sustainability of populations. Reed et al. (2004) concluded that road mortality is substantial, exceeding the damage incurred by other anthropogenic sources such as illegal collection for trade. Quantitative effects on populations have mainly been estimated using models or based on mean mortality rates determined by surveys (e.g., Rosen and Lowe 1994), estimates that must be interpreted with caution due to biases associated with road sampling (Table 2.1). As the research on road impacts has been disproportionately focused on mammals and birds, we are still learning about some of the more straightforward direct effects of roads on herpetofauna. However, it is apparent that roads are unequivocally a major source of mortality for many amphibians and reptiles in many areas, and likely pose risks to population viability.

INDIRECT EFFECTS

The manifold effects of roads extend far beyond encounters between wildlife and vehicles. Roads affect wildlife indirectly, including landscape fragmentation and alteration of physical conditions in the vicinity of roads (Andrews 1990; Forman et al. 2003). Multiple effects occur across various spatial scales that extend beyond the road, most of which are increased in urban areas. When discussing indirect road effects on herpetofauna, the information base becomes sparse because indirect effects are more pervasive and more difficult to quantify than direct effects, and documenting indirect effects due to roads often requires extensive and long-term monitoring.

Roads are designed to serve as travel corridors for humans, usually without regard for the environmental needs of wildlife. Therefore, problems may arise when wildlife use road systems for their own movement. Unlike natural corridors, roads frequently cross topographic and environmental contours, thereby fragmenting a range of habitat types (Bennett 1991) and affecting many wildlife groups that possess a diversity of ecological and life history strategies. The transformation of physical conditions on and adjacent to roads eliminates areas of continuous habitat while simultaneously creating long-lasting edge effects (Forman and Alexander 1998).

The Road Zone as Habitat: for Better or Worse.— Roads and roadside areas can provide habitat for amphibian reproduction. Amphibians, especially frogs, are known to breed in roadside ditches, but successful egg and larval development may be rare (Richter 1997), as ditches often dry before larvae can metamorphose. Some anurans use water-filled tire ruts for breeding and moisture when traversing long distances (e.g., Reh and Seitz 1990), which can lead to adult and larval mortality (D. M. Jochimsen, pers. obs.).

The road zone can also serve as an attractant for reproductive behaviors for reptiles. Hódar et al. (2000) reported that Common Chameleons (*Chamaeleo chamaeleon*) in southern Spain selectively used habitats adjacent to roads and orchards for nesting habitat. Reproductive activity coincided with increased traffic densities during the summer?, resulting in a high susceptibility to road mortality (Caletrio et al. 1996). This temporal coincidence is compounded because this species also suffers from illegal collection along roadsides (Caletrio et al. 1996). Roadside nesting by turtles in urban areas may result in reduced survivorship of both adult females and hatchlings. Aresco (2005b) noted that road shoulders serving as nesting habitat attracted 6-29% of all observed gravid female turtles of three species annually, an occurrence also believed to be a primary source of female road mortality in *M. terrapin* in New Jersey (Szerlag and McRobert 2006). Female *T. carolina* were observed crossing roads in suburban areas in Aiken, South Carolina, at a higher frequency than males (Brisbin et al. 2008). A similar pattern was detected in the suburbs of Perth, Australia, where female Oblong Turtles (*Chelodina oblonga*) experienced differential mortality rates from crossing roads while attempting to nest in residential gardens (Guyot and Kuchling 1998).

Secondary impacts of roads on herpetofauna can occur when roads attract prey or predators (e.g., small mammals, Getz et al. 1978; nesting birds, Ortega and Capen 2002). Roadsides in Great Britain were recognized more than a century ago for harboring lizards and snakes (Leighton 1903; Smith 1969) and the greatest numbers of snakes observed across Paynes Prairie in Florida were associated with road sections bordered by permanent water in ditches (Franz and Scudder 1977), correlations that were attributed to prey concentrations. Slow Worms

(*Anguis fragilis*) were more common in roadside habitats where invertebrate prey was abundant (Wells et al. 1996). A higher density of snake species was observed in the ecotonal area of a road-cruising route in California, presumably resulting from increased prey diversity in the edge habitat (Sullivan 1981b). Small mammal species residing along road borders in Australia were the most common prey items in road-killed Carpet Pythons (*Morelia spilota*; Freeman and Bruce 2006). Terrestrial Garter Snakes (*Thamnophis elegans*) were observed foraging on Western Toad (*Bufo boreas*) tadpoles in ruts on a road in Idaho (D. M. Jochimsen, pers. obs.). Roads also provide simplified foraging opportunities for predators as they increase exposure to animals crossing the road (e.g., Red-tailed Hawk [*Buteo jamaicensis*] attempting predation of an Eastern Ratsnake [*Elaphe alleghaniensis*] crossing highway; Vandermast, 1999). Also, dead animals attract scavengers (e.g., Gopher Tortoise [*Gopherus polyphemus*] scavenging on road-killed Great-horned Owl [*Bubo virginianus*], Jackson and Ostertag 1999; *T. carolina* scavenging on road-killed Copperhead [*Agkistrodon contortrix*], Jensen 1999). Clearly, some species benefit from roadside edge habitat under certain circumstances and the disturbance of urbanization in general (Faeth et al. 2005), but ultimately this may incur increased risks. Perhaps more commonly, many herpetofaunal populations are intolerant of edge conditions generated by roads and may decrease directly, or indirectly, because of reduced prey levels resulting from reduced habitat quality surrounding roads (e.g., Haskell 2000). Therefore, assessments of indirect road impacts as a consequence of predator-prey relationships must be conducted in the context of individual species and the ecological requirements of predators and prey.

Lastly, roads can serve as dispersal corridors, facilitating species expansion, an occurrence that is particularly problematic with invasive species which can ultimately have detrimental effects on native amphibian and reptile populations. Roads and trail systems facilitated the expansion across Australia of introduced Cane Toads (*Bufo marinus*, Seabrook and Dettmann 1996), which have been estimated to invade new areas at a rate of over 50 km a year (Phillips et al. 2006). Tracked individuals actively used roads as dispersal corridors and toad density significantly increased along roads and vehicle tracks. Phillips et al. (2003) estimated that *B. marinus* could pose a threat to as many as 30% of terrestrial Australian snake species. Additionally, Fire Ants (*Solenopsis invicta*) proliferate in roadside areas in the United States (Stiles and Jones 1998) and have been identified as a problematic predator on egg-laying reptiles (e.g., Allen et al. 1997; Buhlmann and Coffman 2001; Parris et al. 2002), reducing reproductive output and hatchling survivorship. Lastly, roads enable the spread of exotic plant species that subsequently eliminate native flora and fauna (Parendes and Jones 2000). Introduced species comprised 74% of the roadside flora in Hawaii, a trend that was not observed on adjacent substrates (Wester and Juvik 1983). Invasive species dominance could also compromise the quality and availability of habitat and prey bases (e.g., Maerz et al. 2005). Jochimsen (2006) found a correlation between Gophersnake (*Pituophis catenifer*) mortality and cover of an invasive grass species along roadsides in Idaho. Finally, invasive species have the potential to alter mineralization processes and soil organic matter (Zink et al. 1995), which could have repercussions on invertebrate communities and their vertebrate predators.

Landscape Pollution.— Hydrological changes occur beyond the immediate vicinity of roads (e.g., Jones et al. 2000). The impervious nature of roads elevates precipitation runoff, fluctuations in flow velocities, and flooding in adjacent wetlands, diminishing suitable habitat for amphibian breeding, foraging, and development (Richter 1997). Increased water-level fluctuations and flow velocities can result in lower amphibian richness in affected wetlands

(Richter and Azous 1995). An additional consequence of abnormal flooding for most pond-breeding amphibians is the increased likelihood of recolonization by predatory fish in formerly fish-free isolated wetlands. Alternatively, changes in microhabitat surrounding the road can result in reduced cover and leaf litter and therefore drier soils, which could influence the abundances of some amphibian species, particularly woodland salamanders (e.g., Marsh and Beckman 2004). Reduced moisture levels are possibly compounded by problems of chemical run-off and siltation (Semlitsch et al. 2007) in influencing species abundances.

Increased sedimentation, initially resulting from road construction and erosion, is also problematic for amphibians. Salamander population densities declined due to runoff from amplified soil erosion of stream banks, increased amounts of particulate material, and the scouring of stream channels in urban streams (Orser and Shure 1972). Additional studies have documented reductions in amphibian densities or their invertebrate prey populations in streams experiencing sediment loading from roads (e.g., Welsh and Ollivier 1998; Semlitsch 2000). Erosion stemming from road development and urbanization also destroys beach habitat, an effect that can critically impair nesting and hatching success rates for sea turtles (e.g., Kamel and Mrosovsky 2004).

Vehicular by-products and compounds associated with road degradation contribute to deposition of pollutants on and around roads. Exposure to toxic compounds may alter reproduction and have long-term lethal effects on wildlife (Lodé 2000). Mahaney (1994) found that water treatments with high petroleum contamination inhibited tadpole growth and prevented metamorphosis. Physiological (i.e., respiratory) and behavioral alterations were observed in lizards and frogs exposed to ozone (Mautz and Dohm 2004). Acid precipitation resulting from automobiles acts as an immune disruptor in adult frogs (Northern Leopard Frog, *Rana pipiens*;

Vatnick et al. 2006). Lead levels in soil and vegetation are negatively correlated with distance from roads (e.g., Scanlon 1979), and concentrations were positively correlated with traffic density (e.g., Goldsmith et al. 1976). Lastly, compounds from cars such as inorganic anions (e.g., chlorides and sulphates) and mechanical deterioration of car parts may be present in areas extending up to 30 m from the road (Hautala et al. 1995; Croteau et al. 2008).

Chemical compounds associated with road maintenance are also emerging as road effects of concern. Chloride from de-icing salt runoff contaminates fresh waters peripheral to road systems (Environment Canada 2001; Kaushal et al. 2005), implicating the agent as a factor in reduced embryonic *A. maculatum* (Turtle 2000) and larval Wood Frog (*Rana sylvatica*, Sanzo and Hecnar 2006) survival in roadside pools. Karraker (2008) found reduced reproductive effort and survival in *A. maculatum*, *R. sylvatica*, and Green Frogs (*Rana clamitans*) exposed to de-icing salts. Forman and Deblinger (2000) suggested that road salts altered aquatic habitats up to 200 - 1500 m from a busy suburban highway corridor. Wood (2001) demonstrated compromised water quality due to roadside herbicide applications. Kohl and colleagues (1994) found that 2-33% of herbicides applied to road shoulders leach out into runoff during the first storm following application. Mass salamander deaths along forest roads in Minnesota have been attributed to desiccation from exposure to calcium chloride that is used as a dust-control agent, and pilot studies suggested that salamanders avoid treated areas as 50% fewer cross in comparison to untreated areas (deMaynadier and Hunter 1995).

Less is known about physiological effects of road-associated pollutants on reptiles (but see Campbell and Campbell [2001] for a general review of contaminant effects on snakes and Gardner and Oberdörster [2006] for an overview of reptile toxicology). However, it is reasonable that similar issues exist with the uptake of pollutants directly from the environment or from prey items (e.g., Storelli and Marcotrigiano 2003; Krysko and Smith 2005), where transferred concentrations vary between sexes and among body sizes (e.g., Rainwater et al. 2005). Scanlon (1979) found higher levels of heavy metals in invertebrate-eating shrews than plant-eating rodents, suggesting that bioaccumulation of heavy-metal contamination that is road-related should be explored in herpetofauna.

Noise and Light Pollution.— Vehicular traffic alters environmental conditions of habitats adjacent to roads via vibration and noise, which can modify animal behavioral and movement patterns (Bennett 1991). Effects of traffic noise and vibrations on vertebrates include hearing loss, increase in stress hormones, altered behaviors, and interference of breeding communications (Dufour 1980; Brattstrom and Bondello 1983; Forman and Alexander 1998). Road noise and ground vibration may disrupt cues necessary for orientation and navigation during migratory movements of some amphibians (e.g., breeding frogs and salamanders). Low-frequency vibrations on the ground surface stimulate the emergence of Spadefoot Toads (*Scaphiopus*) as they are thought to mimic rainfall (Dimmitt and Ruibal 1980). Background noise from off-road vehicles often results in modification of calling behavior in male anurans and may impair the ability of females to discriminate among call types and to discern locations of calling males during breeding migrations (Hourglass Treefrog, *Hyla ebraccata*, and Yellow Treefrog, *Hyla microcephala*, Schwartz and Wells 1983; Gray Treefrog, *Hyla versicolor*, Schwartz et al. 2001). Sun and Narins (2004) found that airplane and motorcycle noise reduced the calling frequency of some anuran species which in turn increased the frequency of another. Impacts observed in off-road environments would be exaggerated in urban environments, which present even greater noise and lighting interference.

Artificial lighting along roads and urban areas alters foraging, reproductive, and defensive behaviors of herpetofauna (e.g., anurans, Buchanan 2006; salamanders, Wise and Buchanan 2006). Exposure to artificial light can cause nocturnal frogs to suspend normal behaviors and remain motionless long after light has been removed (Buchanan 1993). More research needs to be done to assess the overall impacts of lighting in urban areas before informed recommendations can be made (Perry et al. 2008). An exception occurs on developed beaches where disorientation due to artificial lighting from urban areas has proven to be a significant problem for the ocean-finding ability of hatchling sea turtles (e.g., McFarlane 1963) and nesting females (e.g., Witherington 1992).

Movement Behaviors.— The study of road effects on herpetofaunal movement and behavior promises to be a fruitful area of investigation. As landscape features that alter and fragment natural habitats, roads may impede movements of amphibians and reptiles via alteration of size, shape, or spatial arrangement of habitat patches (e.g., Fahrig and Merriam 1994). Barrier effects are defined as occurrences when 1) animals are killed on roads in numbers that functionally prevent genetic exchange between populations; 2) surrounding habitat quality is reduced such that animals cannot persist; or 3) animals behaviorally avoid roads, contributing to isolation and habitat fragmentation. Vehicles can force wildlife to adapt their behavior either by posing an impenetrable barrier, in which animals selectively avoid the road due to awareness of traffic as suggested by Klauber (1931) or through other little-understood influences on crossing behavior (Andrews and Gibbons 2005).

Behavioral avoidance of roads by herpetofauna is poorly documented, and species differences are less understood than is species-specific mortality on roads. Road avoidance may occur as a result of several road characteristics, such as traffic, noise, road substrate, openness, and others not yet determined. Models show that differing catalysts for avoidance can influence differing levels of vulnerability at the population level (Jaeger et al. 2005), therefore indicating a need for species-level considerations. Roads can hinder amphibian movement (e.g., Gibbs 1998b), and reduced permeability can even occur on low-use forest roads (e.g., Marsh et al. 2005). Barrier effects from roads may vary depending upon the specific type of movement being made. For example, a greater proportion of natal dispersal movements occurred across roads in Maine (22.1%) than either migratory (17.0%) or home-range movements (9.2%; deMaynadier and Hunter 2000). *Ambystoma tigrinum* tracked during emigrations from breeding ponds moved all directions within surrounding habitat, but avoided open habitats, including fields, paved roads, and urban areas (Madison and Farrand 1998). Roads have also been shown to alter movement patterns of Desert Tortoise populations (*Gopherus agassizii*, Boarman and Sazaki 1996). Blue-tongued Lizards (*Tiliqua scincoides*) were able to persist in suburban settings in Australia via their ability to use artificial cover and feed on garden species, but were found to actively avoid roads (Koenig et al. 2001). Although data revealed that Land Mullets (*Egernia major*) in Australia selectively used edge-habitat adjacent to roads for thermoregulatory purposes, radio-tracked individuals actively avoided crossing roads (Klingenböck et al. 2000).

A variety of researchers have noted road avoidance by snakes (e.g., Timber Rattlesnake [*Crotalus horridus*], Fitch 1999, Sealy 2002, Laidig and Golden 2004; Red-sided Garter Snake [*Thamnophis sirtalis parietalis*], Shine et al. 2004; Eastern Hognose Snake [*Heterodon platirhinos*], Plummer and Mills 2006). Radiotelemetry data clearly revealed road avoidance tendencies of Massasaugas (*Sistrurus catenatus,* Weatherhead and Prior 1992; B. Kingsbury, pers. comm.) and Tiger Rattlesnakes (*Crotalus tigris*, Goode and Wall 2002). Radiotelemetry data on *D. couperi* indicated that snakes did not cross paved roads, although they readily crossed dirt roads and trails (Hyslop et al. 2006). *Drymarchon couperi* activity (*n*=32) occurred within boundaries of paved roads, although 6 individuals were within 100 m of paved roads. Seigel and Pilgrim (2002) observed shifts in composition of *S. catenatus* crossing a road after a flood; neonates crossed in numbers higher in proportion to their abundance in habitats surrounding the road. Andrews and Gibbons (2005) performed experiments that revealed significant levels of variation among species in road avoidance rates where a positive correlation was found between crossing frequency and body length, likely due to natural behaviors of smaller snakes to avoid open spaces (e.g., Klauber 1931; Dodd et al. 1989; Fitch 1999; Enge and Wood 2002). Some snakes attempt to cross, but deter and retreat (Andrews and Gibbons 2005), ultimately not crossing, a behavior that has been sporadically observed in the field (Holman and Hill 1961; Franz and Scudder 1977). Individuals that enter a road but do not cross are still exposed to direct mortality and road fragmentation. Increasing awareness of the prevalence of behavioral avoidance of roads within and among snake species suggests a topic of interest from both ecological and evolutionary perspectives. Beyond considerations of road avoidance as a learned behavior, genetically-inherited avoidance of roads has not been directly documented, but if a genetic component for response to roads and traffic exists within species, behaviors that increase survival would be under selection. For instance, in areas of greater habitat connectivity, individuals that tend to avoid roads would survive and breed successfully. Alternatively, in landscapes that are fragmented to the extent that mate accessibility is reduced within a patch, individuals that risk crossing roads might be the successful breeders.

In summary, indirect impacts from roads on herpetofauna vary considerably within and among taxonomic groups. Many indirect effects of roads are poorly understood and some have yet to be considered, posing unknown challenges for investigators to determine their ultimate impacts on herpetofauna. Potential discoveries of the indirect effects of roads on amphibian and reptile biology promise a wealth of opportunities to conduct meaningful behavioral and ecological research applicable to herpetofaunal conservation on a global scale.

EFFECTS ON THE HIGHER LEVELS OF ECOLOGICAL ORGANIZATION

Population Level Impacts.— The difficulty in monitoring road impacts at the population and community levels is reflected in the lack of available data, although larger scale repercussions of road impacts on herpetofauna are probably underestimated (Vos and Chardon 1998). Roads may affect population size and demography of amphibians and reptiles in a variety of ways, but as Findlay and Bourdages (2000) suggest, understanding the full effect of roads on herpetofaunal populations may be delayed and could take decades to elucidate. For example, breeding in a population of Columbia Spotted Frogs (*Rana luteiventris*) in Yellowstone National Park did not cease at a roadside pond until almost two decades following the relocation of a highway that separated breeding, foraging, and hibernation sites (Patla and Peterson 1999).

Despite early evidence by Klauber (1939) that a California highway resulted in the local decline of snakes, documentation of amphibian and reptile population declines as a result of roads, directly or indirectly, has been limited and often speculative. In many instances, effects on population density and structure from traffic-related mortality and continued loss of individuals can only be inferred (e.g., Mitchell 1994). However, declines associated with increased road densities and traffic levels have been documented in frogs (e.g., Fahrig et al. 1995) and snakes (e.g., Rudolph et al. 1999; but see Mazerolle [2004] for amphibians and Sullivan [2000] for snakes]). Rudolph et al. (1999) suggested that populations of large snake species are reduced by

50% or more at a distance of 450 m from a road of moderate use, with effects still apparent up to 850 m. Population densities of *G. agassizii* (Boarman and Sazaki 1996; von Seckendorff Hoff and Marlow 2002) and *C. picta* (Fowle 1996) were lower in habitats closer to highways. Gibbs and Shriver (2002) simulated movement patterns for pond and terrestrial turtles against road density and traffic volumes. Results indicated that roads would result in the mortality of >5% of the populations of land and large-bodied pond turtles, a percentage that they suggest is likely unsustainable for long-lived species.

Many amphibians and reptiles exhibit intraspecific variation in ecological requirements and strategies between sexes (e.g., Johnson 2003; Koenig et al. 2001; Morreale et al. 1984; Reinert and Zappalorti 1988), across life history stages (e.g., deMaynadier and Hunter 1999; Jochimsen 2006), and seasons (e.g., Carpenter and Delzell 1951; Gibbons and Semlitsch 1987). Variation in movement patterns and abundances may consequently result in differential road mortality rates (e.g., snakes, Rudolph and Burgdorf 1997; Bonnet et al. 1999; Jochimsen 2006; Andrews and Gibbons 2008). For example, mortality rates are highest in species and individuals that exhibit the greatest vagility. Bonnet et al. (1999) reported a propensity of dispersing neonate snakes (i.e., *Coluber, Natrix*) to be killed on roads in France while Brito and Álvares (2004) noted a greater abundance of DOR adult vipers (*Vipera latastei* and *Vipera seoanei*) in Portugal. Jochimsen (2006) observed that adult male *P. catenifer* were more susceptible to road mortality during spring egress from hibernacula, while dispersing subadults accounted for 74% of autumn mortality. Titus (2006) noted variation in *A. contortrix* movement frequencies exhibited by road capture rates when comparing both adult males and females, and adults and juveniles.

Different responses to impacts from urbanization and road development lead to skewed population structure in amphibians and reptiles via altered sex ratios and composition of age classes. Fukumoto and Herrero (1998) concluded that road mortality caused the loss of 1.4 – 2.0% of breeding Long-toed Salamander (*Ambystoma macrodactylum*) adults which they suggest contributed to a female biased (3:1) sex ratio. Female turtles are more likely to be killed on roads (Wood and Herlands 1997; Marchand and Litvaitis 2004; Steen and Gibbs 2004; Aresco 2005b), due in part to nesting activities (e.g., Gibbs and Steen 2005; Steen et al. 2006). Conversely, a higher proportion of male lizards (e.g., Rodda 1990) and snakes (Bonnet et al. 1999; Sealy 2002; Jochimsen 2006; Andrews and Gibbons 2008) die on roads because males disperse further than females in some species. Further, sex bias in road captures can be seasonally variable as seen in the Texas Horned Lizard (*Phrynosoma cornutum*), although Sherbrooke (2002) found male bias while Moeller et al. (2005) detected more females on roads overall. Intraspecific variation in road impacts can often be linked to spatial and temporal attributes of dispersion, which can most often be correlated with mating systems. For instance, males of polygynous species are often the more risk-prone sex as they are responsible for courting and defending multiple females within a territory, as seen with West Indian Rock Iguanas (*Cyclura lewisi*) on Grand Cayman Island (Goodman et al. 2005). Further studies designed to explore the variation of sex bias in road captures driven by ecological behaviors are needed to investigate influences on population sustainability.

Genetic Effects on Populations.— Amphibian and reptile species often have restricted or patchy distributions and small effective population sizes. Roads may serve as barriers that restrict gene flow and decrease genetic diversity through a combination of direct mortality and inbreeding. In functionally-small populations, these effects may significantly increase the probability of local extinction (Rodriguez et al. 1996). Few studies have empirically documented genetic effects on herpetofauna due to roads, but those that have support the hypothesis that roads reduce gene flow and decrease genetic diversity in amphibians (e.g., Reh and Seitz 1990; Hitchings and Beebee 1998; Lesbarrès et al. 2003), especially when populations are constrained within urban areas (Hitchings and Beebee 1997; Rowe et al. 2000; Scribner et al. 2001; Vos et al. 2001).

Virtually all genetic studies of road impacts on herpetofauna heretofore have focused on amphibians, although reptiles could sustain comparable genetic impacts from roads. Further, the same life history traits such as long-life spans, low reproductive rates, and delayed maturity of many reptile species that could result in more severe genetic effects from roads than that observed with amphibians also increase the difficulty in discerning the role that road and urban fragmentation has on genetic isolation. Nonetheless, modern genetic approaches offer great potential for providing insight into how roads affect populations of both amphibians and reptiles and future research should be informative. For instance, the emergence of landscape genetics has merged the arenas of population genetics and landscape ecology (Manel et al. 2003). The discipline aims to assess population substructure at fine taxonomic levels across varying geographic scales, which is achieved by detecting genetic discontinuities (i.e., distinct genetic change within a geographic zone) as they are correlated with environmental features, including barriers such as mountains, temperature gradients, or as applicable in this discussion, roads. This increase in technological ability will allow for more accurate genetic investigations of populations surrounding roads, thereby permitting impact assessments within populations as applicable to an evolutionary time scale.

Community Level Impacts.— Data on community-level impacts on herpetofauna are lacking in general, although in some instances lower species richness is correlated with road density (herpetofauna, Dickman 1987; amphibians, Findlay and Houlahan 1997; Halley et al. 1996; Knutson et al. 1999; Lehtinen et al. 1999; Vos and Stumpel 1996; snakes: Kjoss and Litvaitis 2001). As with populations, cumulative effects on biodiversity may take decades to become apparent (Findlay and Bourdages 2000).

Analyses of road impacts on herpetofauna at ecological scales higher than the individual or species are inherently difficult, because larger, more significant impacts on populations and communities are not instantaneous. Due to natural fluctuations across spatial and temporal scales, effective analyses require long-term research. Unfortunately, long-term initiatives are typically limited by logistics (e.g., time and funding), and trade-offs between ideal experimental designs and resource availability prohibit the larger-scale or longer-term projects. Ecological modeling offers one alternative using numbers collected from short-term surveys to predict long-term effects. However, only through data collection at population and community levels will the full extent of road impacts be realized. This challenge must be met in order for our understanding of road impacts to progress, and issues of scale (both spatial and temporal) should be addressed to enable biologically valid data extrapolations.

SOLUTIONS

The formation of road ecology as a field has fostered action by scientists, conservation advocates, and agencies to design various measures to prevent, mitigate, or compensate for road impacts on surrounding habitats and wildlife (Forman et al. 2003). Many methods may be implemented once a conflict between wildlife and infrastructure is recognized, but the most common solution is the construction of crossing structures. The general function of a crossing structure is to provide safe passage for an animal across the road and to provide connectivity between habitats adjacent to the road (Forman et al. 2003). The synthesis by Jochimsen et al. (2004) provides a composite summary of the various mitigation structures based on descriptions provided by Jackson (1996), Forman et al. (2003), and the USFS website - Wildlife Crossings Toolkit (www.wildlifecrossings.info). Further, Andrews et al. (2006) present pre-construction solution assessments and a tabular presentation of post-construction mitigation projects.

Most projects have focused on larger mammalian fauna, but over the past two decades the drive to develop methods to mitigate road effects on amphibians and reptiles has increased. Although road closure is often pondered as an option to reduce impacts, it is usually only feasible in remote areas with limited public access, such as protected forests and refuges (e.g., Arroyo toad, *Bufo californicus*, Eastwood and Winter 2006). The more common solution involves the installation of culverts (i.e., underpasses, ecopassages) coupled with barrier fences to increase permeability of the road and reduce mortality for population persistence; however, fences may have limited utility with animals that exhibit high road avoidance (Jaeger and Fahrig 2004). This mitigation design was initiated in Europe at the Toad Tunnel Conference in Germany in 1989 (Langton 1989) that addressed topics regarding mortality of amphibians, tunnel design, and structure characteristics that influenced animal passage. Innovative approaches are evolving in determining mitigation designs. For instance, while many projects monitor road mortality alone to determine culvert placement, a project in Poland supplemented field data by conducting interviews with local park officials to identify precise locations of amphibian choruses and breeding ponds (Brodziewska 2006). Further, several European countries have successfully used pipes and directive rails (Germany), fine-meshed fencing (France and Netherlands), and concrete trenches (Switzerland) to direct amphibians to culverts rather than using expensive concrete barrier walls (Bank et al. 2002; see Schmidt and Zumbach 2008 for more details).

Several specific projects emphasize the importance of mitigation efforts in herpetofaunal conservation. Installation of a barrier fence, three bridges, and 24 culverts along State Highway 58 in California reduced road mortality of *G. agassizii* and several species of snakes (Boarman et al. 1998). This project has proven effective at facilitating tortoise movement across the highway, aiding in the recovery of populations within the road-effect zone. The exceptional mortality levels observed on U.S. Highway 441 at Paynes Prairie in Florida catalyzed biologists and local commuters to seek alternatives. In 2001, Florida DOT constructed an Ecopassage across Highway 441 at Paynes Prairie (Dodd et al. 2004) and the number of road-killed ranid frogs, alligators, snakes, and turtles declined considerably. Road mortality of vertebrates decreased by 93.5% (if hylid treefrog mortality is excluded). Treefrogs are able to trespass the concrete barrier, demonstrating that mitigation devices may not always be effective at reducing mortality of all species. U.S. Highway 27 created a virtually impassable barrier to turtle movement across Lake Jackson in Florida motivating Aresco (2005a) to install barrier fences along the highway to guide animals to a single culvert to ensure safe passage. The mortality rate was significantly lowered from 11.9 to 0.09 individuals/km/day (Aresco 2005a). Mark-recapture efforts and visual monitoring indicated successful turtle movement across the road, and tunnel installation is in the planning stage, with collaboration between scientists, engineers, and community planners (see www.lakejacksonturtles.org, accessed 26 August 2008).

Overall, studies designed to evaluate factors affecting passage use and effectiveness for amphibians and reptiles have lagged behind those of mammals. Many studies are inadequately designed to appraise the value of wildlife passages, because they simply compare pre- versus post-construction count data or concentrate on one species. Few develop and test hypotheses or list predetermined criteria that provide a basis from which to assess passage performance (Forman et al. 2003; Schmidt and Zumbach 2008). Additionally, long-term monitoring is needed for several reasons: (1) to put passage use needs into a population context (abundances and distributions in the vicinity) across broad time scales (frequency of crossing); (2) to determine the behavior of wildlife approaching roads and structures; (3) to determine the level of wildlife avoidance of roads or structures due to inherent behaviors or predator concentrations; (4) to establish the time lag between structure placement and species use; (5) to assess the long-term connectivity within the surrounding landscape. This last point is central to achieving the most critical objectives of mitigation: (a) reduction of mortality and (b) safe passage of wildlife. Some of these issues have been addressed for amphibians and reptiles, revealing that multiple variables can affect structure efficacy (Puky 2003; Jochimsen et al. 2004; Lesbarrères et al. 2004; Jackson and Griffin 2000; Mata et al. 2005). However, a general survey summarizing the status of North American mitigation regimes found a broadening in the number of species considered in projects, an increase in monitoring time of structures, and an increase in the number and diversity of participants solicited in the process (Cramer and Bissonette 2006). Post-construction mitigation measures serve only as a second option as they do little to minimize, remove, or avoid the majority of indirect effects of roads, and because retrofitting is more costly, both fiscally and environmentally.

Proactive planning is a necessary tool. Geographic Information Systems (GIS) can expedite site-specific considerations to identify potential problem areas prior to the blueprint stage of road planning (Clevenger et al. 2002; White and Ernst 2003) thereby avoiding construction in ecologically sensitive places. Selection of datasets is an important consideration in addressing ecological impact due to scale issues and variation in the level of inclusion of minor roads across datasets (e.g., Hawbaker and Radeloff 2004). Animals that exhibit spatial patterns of road mortality enable the identification of crossing hotspots and predictive modeling options that can direct mitigation designs (e.g., Ramp et al. 2005). Consideration of wildlife ecology and movement corridors during the process of road planning ultimately reduces construction costs by avoiding later costs associated with mitigative structures, which may total millions of dollars. Many European countries have established national policies that require ecological evaluations of potential projects (Seiler and Eriksson 1997). Transportation and environmental agencies in Switzerland have initiated a defragmentation program that involves identification and restoration of areas where road infrastructure bisects critical wildlife habitat (Trocmé 2006). In the U.S., Florida has been a leader in proactive planning through the development of an interagency "Efficient Transportation Decision Making Process" (ETDM; White and Ernst 2003). Ultimately, the success of mitigating the effects of roads on wildlife and habitats will depend on effective communication and cooperation between government agencies, engineers, local citizen communities, non-profit organizations, and scientists.

Dialogues and activities between professional and citizen sectors are arising with increasing frequency. Training sessions on biological and engineering techniques have been organized (e.g., Jacobson and Brennan 2006), some of which are focused specifically on amphibians and reptiles (e.g., M. N. Marchand, pers. comm.). Transportation designs should be based on the needs of the local human populace and wildlife for a plan that targets the desirable and ecologically-sustainable level of urbanization; therefore, much of the decision process should be designed and enforced at the local level (e.g., FHWA [Federal Highway Administration] 2004). A steering committee of eight federal agencies, including FHWA, U.S.

Army Corp of Engineers, U.S. Fish and Wildlife Service, NOAA National Marine Fisheries, Bureau of Land Management, National Park Service, and U.S. Forest Service, produced a report to assist in transportation designs at the ecosystem level (Eco-Logical: An Ecosystem Approach to Developing Infrastructure Projects; http://www.environment.fhwa.dot.gov/ecological/eco_index.asp, accessed 26 August 2008). Citizen initiation in dealing with road issues has increased (e.g., Nelson et al. 2006), likely due to an increased awareness regarding ecological problems associated with roads and the availability of alternatives.

THE ROAD AHEAD

Ecologists, engineers, government officials, and the general public are increasingly aware that roads create ecological disturbances and destruction at multiple levels. The approach in the U.S. has been to alleviate traffic problems by building new roads, an action that is rarely effective, often generating new traffic instead of reducing existing volumes (e.g., Pfleiderer and Dieterich 1995). Until 2005, when the Bush administration overturned the Roadless Areas Ruling (enacted in 2001 by President Clinton), national forests were protected from further road development. Consequently, no areas outside of established wilderness in the U.S. are protected from this expanding infrastructure. As in North America, herpetofauna throughout the world have the potential to be negatively influenced by roads as a consequence of urbanization, either directly from on-road mortality or indirectly as a result of a variety of ecological impacts, particularly increased human accessibility to the landscape.

Knowledge of road impacts on herpetofauna no longer consists only of on-road mortality. The range, quantity and, potentially, the severity of indirect impacts of roads and urban development on amphibians and reptiles far exceed those incurred from direct mortality of wildlife. Huge gaps exist in our knowledge of secondary environmental effects on wildlife. Designing controlled and replicated experiments in urban and suburban settings is challenging due to the complex spatial mosaic and political divisions of ownership and occupancy (Felson and Pickett 2005). Scientists must accept the challenge and proceed with the understanding of the complexity of road impacts and the seemingly immeasurable amount of variation inherent in diagnosing the problem and developing the solution.

Post-construction mitigation measures are being developed globally. Since the construction of the first amphibian tunnels in 1969 near Zurich, Switzerland (Puky 2003), many structures have become viable alternatives for reducing direct effects of roads for some amphibian and reptile species (Jochimsen et al. 2004). However, the minimization of indirect effects, such as pollution, cannot be accomplished with mitigation structures. Additionally, few studies adequately monitor the efficacy of road-crossing structures in reestablishing connectivity (but see Clevenger and McGuire 2001; Dodd et al. 2004), which is most often the purpose of construction. In light of the many indirect effects that have been identified, and many more that remain to be documented, proactive transportation planning to maintain habitat connectivity, public education, and communication among professional sectors of society are the most effective way to minimize and mitigate road impacts and the *only* effective mechanism for avoidance of road impacts.

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Table 2.1. Factors and corresponding citations that provide supporting documentation of how a particular variable can potentially influence the frequency and abundance of road-killed amphibians and reptiles. Table taken from Andrews et al. (2006).

Factor	Reference
Road placement (roadkill aggregation)	Mitchell 2000 Jochimsen 2006 Titus 2006 Langen et al. 2007
Speed limit	Cristoffer 1991
Obliteration of carcasses	Clevenger et al. 2001 Hels and Buchwald 2001 Smith and Dodd 2003
Traffic Density	Fahrig et al. 1995 Mazerolle 2004
Abiotic conditions	K.M. Andrews unpubl. data
Scavengers	Kline and Swann 1998 Smith and Dodd 2003 Antworth et al. 2005
Observer error	Klauber 1931 Boarman and Sazaki 1996 Mazerolle 2004
Sampling technique	Enge and Wood 2002 Langen et al. 2007
Injured individuals leave road	Dodd et al. 1989 Jochimsen 2006
Survey timing	Duever 1967 K. Messenger unpubl. data
Passing vehicles displace carcasses	Jochimsen 2006
Environmental variation	Ashley and Robinson 1996

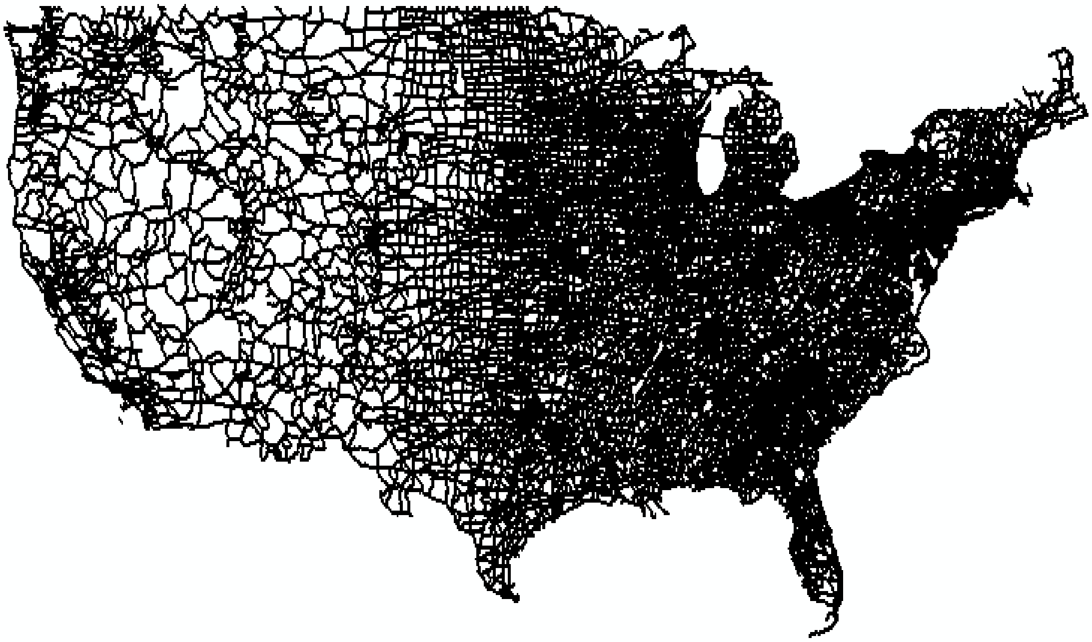
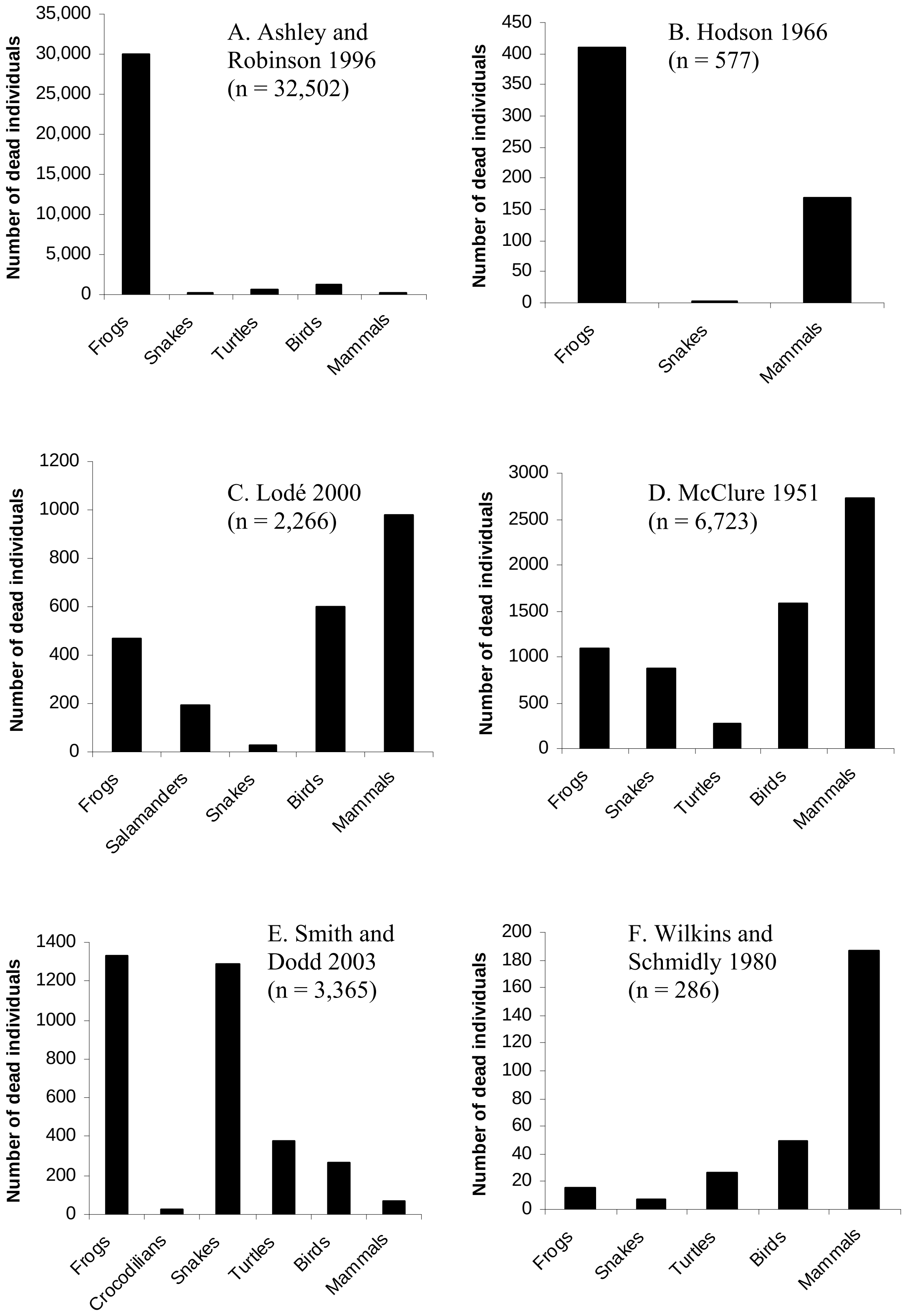


Figure 2.1. Major roads and trails in the United States. Data available as a Geological Information Systems (GIS) shapefile at www.geocomm.com created with ESRI ARC/INFO (version 7.0.4) published by the U.S. Geological Survey, Reston, Virginia, 1997. This shapefile was originally digitized by the National Mapping Division based on the sectional maps contained in "The National Atlas of the United States of America" published by the USGS in 1970, with updates based on the National Highway Planning Network database published by Federal Highway Administration. Contact person: Bruce Wright, U.S. Geological Survey, 521 National Center, Reston, VA, 20192.


A. Ashley and Robinson 1996 (n = 32,502)

B. Hodson 1966 (n = 577)

C. Lodé 2000 (n = 2,266)

D. McClure 1951 (n = 6,723)

E. Smith and Dodd 2003 (n = 3,365)

F. Wilkins and Schmidly 1980 (n = 286)

Figure 2.2. Comparison of road mortality among different vertebrate groups. Each graph represents a separate study (n= total number of individuals across all groups). (A) 3.6 km survey

route in Long Point, Ontario (2,549 total km traveled). (B) 3.2 km survey route in Corby, England (2,336 total km traveled). (C) 68.2 km survey route in western France (2,250.6 total km traveled). (D) incidental driving in Nebraska (123,200 total km traveled). (E) 3.2 km survey route in Paynes Prairie, Florida (336 total km traveled). (F) 47.2 km survey route in southeastern Texas (1,768 total km traveled). Figure adapted from Andrews et al. (2006).

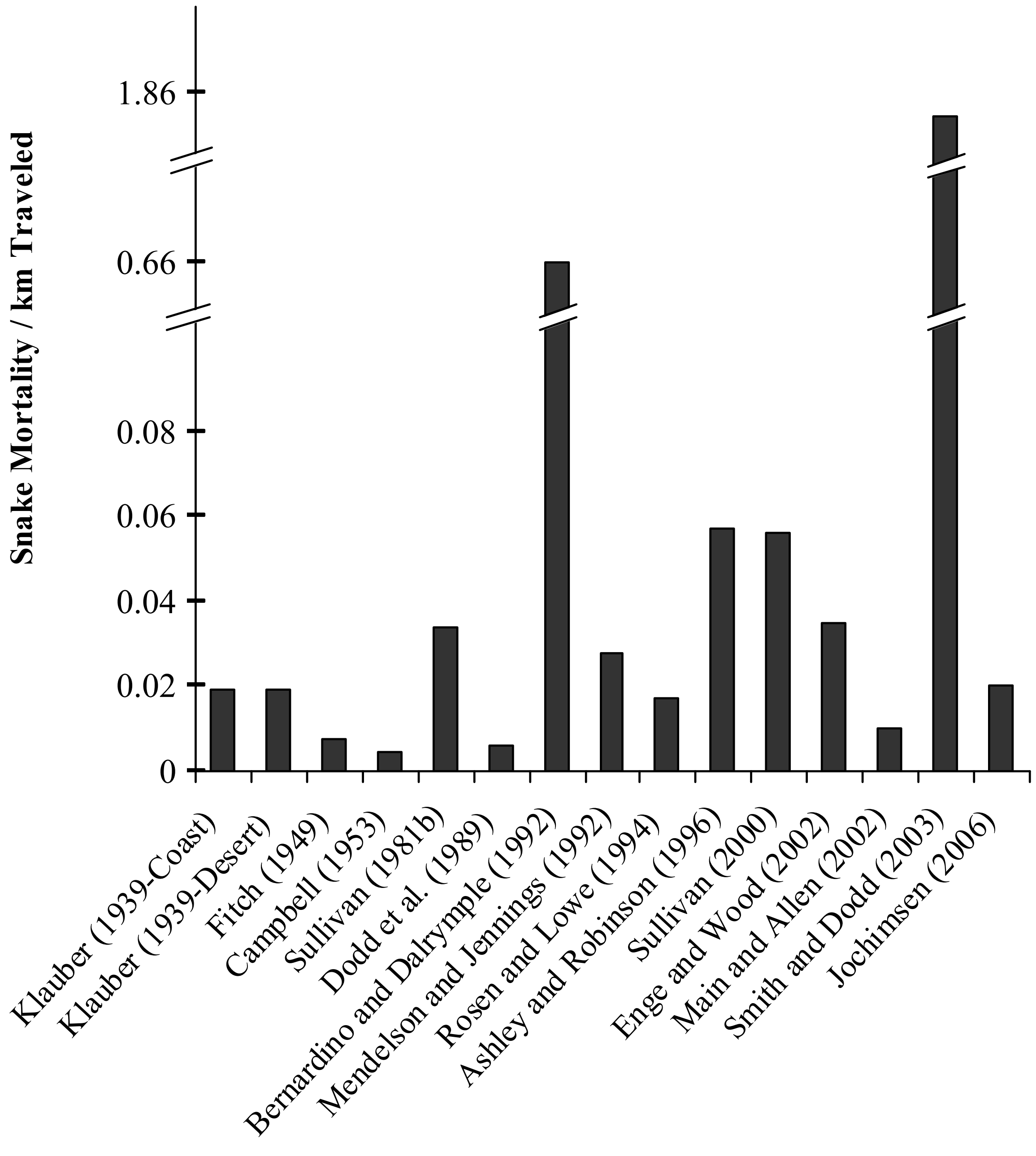


Figure 2.3. Relationship between numbers of snakes found dead on the road (DOR) and distance traveled. Data collected from 14 separate surveys taken at different times and locations in the United States. References for each survey are given on x-axis. Figure taken from Jochimsen (2006).

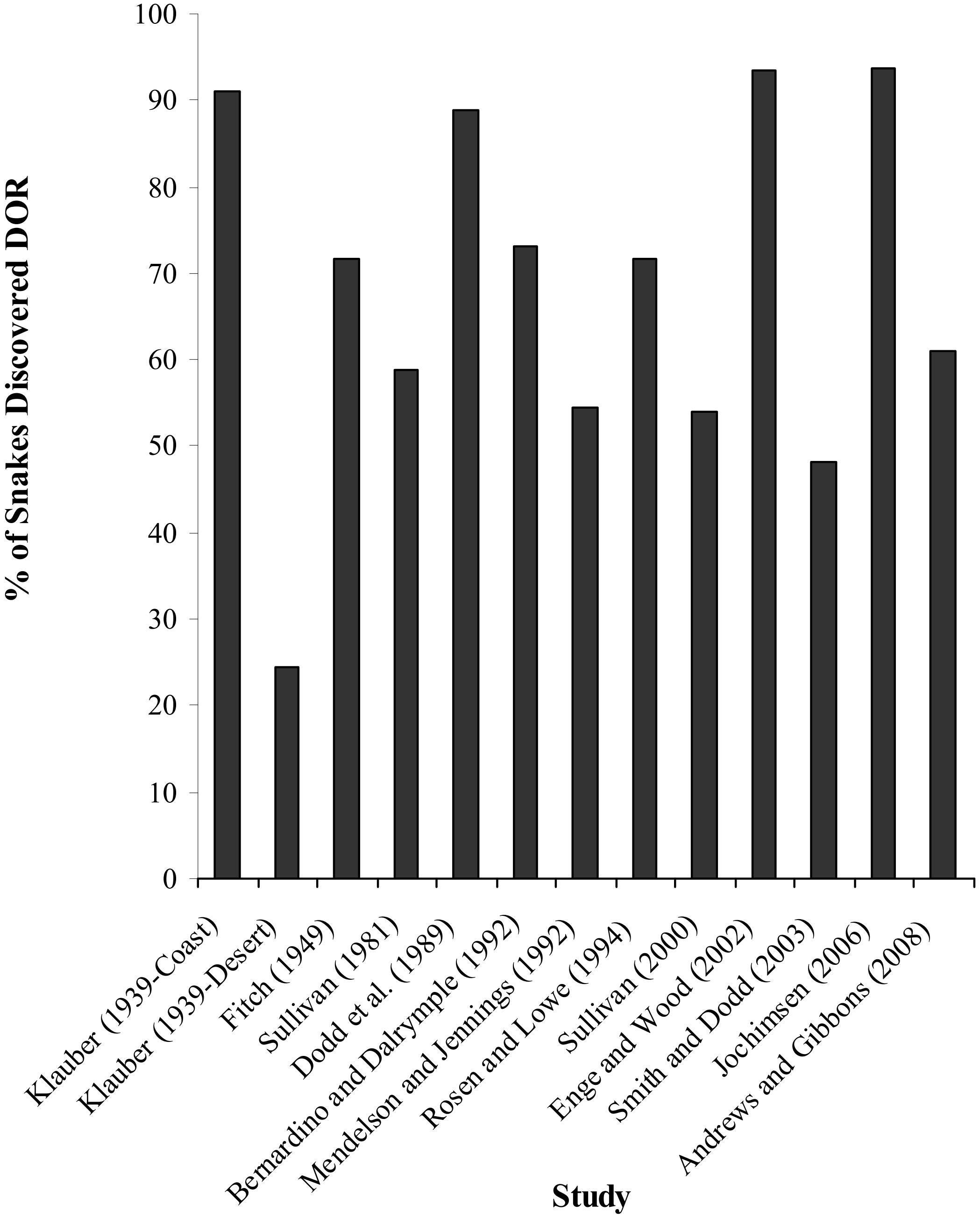


Figure 2.4. Proportion of snakes that were dead on the road (DOR) of total (alive and dead). Data collected from 14 separate surveys at different times and locations. References for each survey are given on x-axis. Figure adapted from Jochimsen (2006).

CHAPTER 3

ROADS AS CATALYSTS OF URBANIZATION:

SNAKES ON ROADS FACE DIFFERENTIAL IMPACTS DUE TO INTER- AND INTRASPECIFIC ECOLOGICAL ATTRIBUTES[2]

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[2] Andrews, K. M., and J. W. Gibbons. 2008. *In* J. C. Mitchell, R. E. Jung Brown and B. Bartholomew (eds.), Urban Herpetology, pp. 145-153. Herpetological Conservation vol. 3, Society for the Study of Amphibians and Reptiles, Salt Lake City, UT. Reprinted here with permission from the publisher.

ABSTRACT

Roads enable human access to previously undeveloped land and thereby are catalysts for urbanization. Assessments of the differential impacts of roads among and within wildlife species in pre-urbanized areas can offer insights into how species will be affected by roads in urban and suburban areas. We used a long-term (1951-2005) snake database from the Savannah River Site in South Carolina, USA to evaluate inter- and intraspecific differences among snakes captured on roads vs. off-road habitats. Data were collected on 15,697 snakes (35 species) of which 2,577 (29 species) were road captures. In evaluating differences in road-use between sexes of 15 species (n = 1,574), we found that significantly more were males. In the analyses of individual species, 7 of the 15 were significantly male-biased and none were female-biased. Significantly more males than females were also collected in off-road habitats. However, the proportion of males (64 %) observed in on-road specimens was significantly greater than that observed in off-road captures (54 %). Of 2,233 captures of 17 snake species for which condition on road was known, significantly more were dead-on-road (DOR; 61%) relative to the number of alive-on-road (AOR). Eight species had significantly higher DOR frequencies, compared to one with a significantly higher AOR frequency. For seven species, longer and heavier individuals were more likely to be DOR. Snakes captured on the road were significantly longer and heavier than those observed in off-road captures. On-road captures within species were significantly larger than off-road captures in five species and significantly smaller in one. Our findings indicate that when assessing the impact of roads and subsequent urbanization on snakes, attention must be given to the differential impacts roads have among species and in relation to individual sex and body size within species.

Key words: Alive on Road, Body Size, Dead on Road, Ecology, Highway, Mortality, Sex Ratio, Suburban, Urban

INTRODUCTION

Urbanization occurs at multiple spatial scales from the opening of a store, construction of a residential neighborhood, or development of a city. All of these developments are enabled through establishment of roads. Even the construction of roads through forested land is often a harbinger of encroaching urbanization. The area affected by roads due to strong edge effects can be 2.5-3.5 times greater than that of clearcuts; therefore, road fragmentation can also be apparent in remote “protected” locations (Reed et al. 1996), urbanizing even parks and refuges. Roads are clearly an essential component of urban areas, and the documentation of declines of amphibian and reptile population species surrounding roads are numerous (e.g., Andrews et al. this volume). Nonetheless, some amphibian and reptile species readily reside in areas experiencing anthropogenic disturbance (e.g., Neill 1950; Zappalorti and Burger 1985). Some species that appear to occur in healthy numbers in suburban areas may decline in numbers with increased urbanization (Minton 1968). The level to which roads contribute to such declines warrants investigation for all groups of herpetofauna.

Assessing the susceptibility of wildlife to urbanization is tedious, as the appropriate scale for investigation varies among taxa (Mazerolle and Villard 1999). Sampling is further complicated within a species as adult behavior cannot always be used to accurately interpret juvenile behavior, especially where ontogenetic shifts occur in physiological vulnerabilities (e.g., desiccation) and predators (Rothermel and Semlitsch 2002). Reptiles, as part of the world's hidden biodiversity (Gibbons et al. 2000), are often challenging to study because of difficulties in obtaining adequate sample sizes, in particular, due to their secretive nature and low abundance. Road cruising, the common technique of searching for animals on roads from vehicles, has been used effectively with many snake species for decades (e.g., Klauber 1939; Fitch 1949; Campbell

1953; Pough 1966; Dodd et al. 1989; Krivda 1993; Seigel and Pilgrim 2002). Ironically, one value of road cruising is to collect dead-on-road (DOR) snakes, which serve as indicators of the extent to which particular roads can be lethal transects.

As the number of roads that fragment the landscape increase (Andrews 1990), higher mortality is assured for many vertebrate groups, including snakes. Ascertaining why certain species or individuals exhibit differential patterns of road use or crossings is critical for development of effective management strategies. Also, many intrinsic (e.g., reproductive state, home-range size, daily activity patterns) and extrinsic (e.g., season, weather, and proximity of a road to particular habitats) variables influence whether a snake will cross a road successfully (e.g., Dodd et al. 1989; Andrews and Gibbons 2005), some of which have been considered quantitatively (e.g., Rosen and Lowe 1994; Bonnet et al. 1999; Enge and Wood 2002). Nonetheless, few studies have had adequate sample sizes to evaluate the interspecific and intraspecific relationships of sex ratios, mortality levels, and body sizes of snakes on roads in areas with high species diversity.

In this paper we examine differential capture rates of snake species in a prescribed region of the southeastern United States based on records collected over a 54-year period. Our primary goal was to evaluate inter- and intraspecific differences in sex and status [DOR or alive-on-road (AOR)] of on-road captures. A secondary goal was to assess differences in species richness, sex, and body size between on-road and off-road captures. Lastly, we discuss how these trends apply to snakes on roads in urban and suburban areas.

MATERIALS AND METHODS

Study site.— We examined 15,697 records of 35 species of native snakes collected during 1951-2005 from the 750 km^2 U.S. Department of Energy Savannah River Site (SRS) located in the Upper Coastal Plain in SC, USA. The purpose of the large set-aside area was for siting five nuclear production reactors, associated industrial facilities and office buildings, cooling canals and reservoirs, and highway systems (Gibbons 1994). The extensive SRS road system includes more than 160 km of primary two- and four-lane concrete and blacktop highways, in addition to secondary dirt and gravel roads, most of which have experienced low traffic levels (< 2000 cars/day) throughout most days since the 1950s.

Aside from these man-made features, the remainder of the site (approximately 90%) consists of a variety of natural and semi-natural habitats that originally included agricultural fields (approximately 50% of the site) and abandoned farm ponds. These old-field habitats (now mostly replaced by planted pine), in addition to second-growth upland and bottomland hardwood forests, more than 200 Carolina bay wetlands, a continuous (~5,000 ha) cypress-gum swamp bordered by the Savannah River, and other terrestrial and aquatic habitats typical of the Upper Coastal Plain (Gibbons 1990) comprise the remainder of the SRS. A distinctive feature of the study site is that for more than a half-century, the majority of the large tract of controlled-access land encompassed by the SRS has received minimal environmental impacts from urbanization, agriculture, or industry (Gibbons 1994).

Long-term Snake Database.— Ecological research began on the SRS in 1951 when the area was designated as a national defense facility and closed to the public. The first records of local snakes were gathered in 1951 (Freeman 1955; R. Humphries unpub. data). For this paper we use a database that represents the majority of snake records from the SRS from 1951-2005. This snake database is part of an on-going project by the Savannah River Ecology Laboratory (SREL) to consolidate unpublished archived records, raw data from theses and dissertations, and other herpetofaunal data records taken on the SRS. Records in which the snake was conclusively captured on a road (paved, gravel, or dirt substrates) were used to investigate ecological attributes of snakes crossing roads, including sex ratios, status (i.e., dead or alive), and body size. Data acquired from a diversity of other methods (e.g., drift fences/pitfall traps, coverboards, aquatic traps, opportunistic captures) used in off-road habitats served as a comparison for sex ratios and body sizes characteristic of species on the SRS.

The complete database was compiled from both opportunistic and targeted captures. Some on-road snake observations were acquired during prescribed road cruising routes, whereas most were made incidentally, the latter often resulting in underestimates of common species that were not recorded, smaller species that were not detected, faster snakes that were missed, and venomous snakes that were not captured or recorded. However, large sample sizes and extensive collecting and recording efforts over many years by many different methods were prevalent for most snake species.

Data Analyses.— To incorporate species that were periodically caught on roads, inter- and intraspecific comparisons were based on analyses of 21 species having more than 20 on-road observations for which information regarding the demographic factors of interest had been recorded. Our initial objective was to examine links between species composition of snakes on roads and their sex, individual status (i.e., dead or alive), body size variables (i.e., length and mass). Secondarily, we conducted intraspecific analyses for variables that had a statistically significant influence on road use.

The availability of more than 2,500 road-collected snakes provided an opportunity to make meaningful comparisons of certain traits among and within species and their relationship to roads that would not emerge with small sample sizes over short durations. As we were not limited by sample size, we selected the chi-square test for goodness of fit to examine whether male:female sex ratios and frequencies of AOR or DOR road observations were significantly different (StatSoft, Inc. 1998). Our dataset supported the assumptions of normality and equal variances using a variety of tests (i.e., Tukey's and Duncan's tests; Bartlett's and Levene's Homogeneity of Variance tests; PROC GLM, SAS Institute, Inc. 1999). Hence, we performed a one-way ANOVA test (PROC GLM, SAS Institute, Inc. 1999) to assess the influence of species type on the likelihood that a snake was captured alive or dead. Secondly, we used a two-way ANOVA to determine the influence of body length and mass on the propensity to be found dead on the road. Lastly, a two-way ANOVA was used to compare differences in the mean and variation of body length and mass for snakes captured on roads (n = 2,577) with measurements of snakes captured in off-road habitats (n = 13,120), which were considered to be the best available comparison for snake species at SRS.

RESULTS

We examined 15,697 records of 35 species of snakes collected over a 54-year period (Table 3.1), including 2,577 (29 species) from roads. Six species have never been collected on roads in the study site area (n = 1,759; Table 3.1). Among 15 species of road-collected snakes, significantly more were males (64%; n = 1,002) than were females (n = 572; $\chi^2 = 127.8$, P <

0.001). In analyses of individual species, seven were significantly biased in favor of males (Fig. 3.1). Collectively, male snakes were found on roads more frequently than were females; this trend was observed in intraspecific comparisons for seven species, with *Lampropeltis getula* (n = 89) having the highest proportion of males (73.2%) among SRS species found on roads. Significantly more males (54%; n = 3,704) than females (n = 3,185; $\chi^2 = 39.1$, $P < 0.001$) were also collected in off-road habitats, but the proportion of males observed in on-road specimens was still significantly greater than that observed in off-road captures ($\chi^2 = 3{,}368.7$, $P < 0.001$).

Of 2,233 individuals of 17 species found on roads, significantly more were DOR (61%) than were AOR ($\chi^2 = 120.2$, $P < 0.001$). Species type was a significant factor (*df* = 16, F = 2.13, P < 0.001) influencing the propensity to be found DOR. DOR snakes were significantly more prevalent than AOR in seven species; in contrast, *Agkistrodon contortrix* was represented by significantly more AOR specimens (Fig. 3.2). Total length (*df* = 938, F = 14.69, P < 0.001), mass (*df* = 823, F = 9.47, P = 0.002), and the interaction of total length and mass (*df* = 806, F = 9.81, P = 0.002) were found to be positively significant components influencing whether individual snakes of seven species were DOR or AOR.

Total length (*df* = 10,365, F = 836.31, P < 0.0001) and mass (*df* = 9,095, F = 178.32, P < 0.0001) of snakes captured on roads were significantly greater than those of individuals from off-road habitats. In comparing on-road with off-road captures of 15 species, we found road-collected snakes to be significantly larger (i.e., total length, mass, or both) in five species and significantly smaller in one (*Elaphe alleghaniensis*); Table 3.2).

DISCUSSION

More than 2,500 records of 29 species of snakes on roads yielded a unique opportunity to explore selected characteristics of species and individuals related to their propensity to be observed on roads. More than 13,000 captures of these 29 species in off-road situations provided the data necessary to compare sex ratios and average body sizes of on-road vs. off-road captures. Six local species not observed on SRS roads (Table 3.1) were excluded from further analyses; however, the more than 1,700 captures of these six species bring caution to the bias inherent in relying on a single collecting technique (in this case, road cruising) for conducting broad scale (e.g., community-level) inventories. These data and previous studies clearly demonstrate that road cruising should not be used as the sole method to determine diversity or abundance estimates for local snake populations due to the many variables that influence the effectiveness of road cruising as a survey technique (Case 1978; Bonnet et al. 1999; Enge and Wood 2002; Seigel and Pilgrim 2002; this study). While road cruising will continue to be a uniquely useful tool for assessing the presence of some species amidst increasing urbanization, it should be used circumspectly as a supplementary technique.

Observed differences between on-road and off-road species richness could presumably be attributed to species occurring in low abundance in localized populations (*Rhadinaea flavilata, Virginia striatula*; Gibbons and Semlitsch 1991), those occupying specific sites not immediately adjacent to frequently traveled roads (*Regina rigida, Seminatrix pygaea*), or a combination of both (*Carphophis amoenus, Regina septemvittata*). Differential measures of species richness are also likely influenced by road placement in relationship to densities and dispersion characteristics of snake populations. The habitats and microhabitats through which a road passes can greatly affect the probabilities of which species and individuals are most likely to be encountered (e.g., Mendelson and Jennings 1992; Smith and Dodd 2003). Additionally, behavioral tendencies to cross roads should be investigated interspecifically, as propensities to avoid roads have been documented among several species of snakes (Andrews and Gibbons 2005). The issue of behavioral impacts from roads and urbanization has not been addressed in depth and in regard to certain details but appears to be a substantial factor in snake response to a changing landscape.

Male-biased road captures (as well as mortality) have been documented previously in several snake species (e.g., Aldridge and Brown 1995; Bonnet et al. 1999; Whitaker and Shine 2000; Sealy 2002), but the prevalence of sex-ratio biases among species, as observed here, has not been noted. Males would be expected to encounter roads more often than females due to larger home ranges (e.g., Sealy 2002), greater activity and wider ranges than females during breeding seasons (e.g., Bonnet et al. 1999), and because of trailing behavior by males (e.g., Shine 2003), such that one female crossing a road may lure several males to take the same path. Likewise, because of these same traits, males would be expected to be encountered more frequently than females by researchers in off-road habitats when using drift fences with pitfall or box traps, minnow traps, time-constrained searches, or through random encounters (Leiden et al. 2000; Ryan et al. 2002). We also found a higher proportion of males in off-road habitats, yet males were observed in even higher frequencies on roads than in off-road habitats, leading to the unequivocal conclusion that males of most species of snakes are more likely to cross roads than are females.

The findings reported here that male snakes rather than females are consistently more prevalent on roads challenges an interpretation that snakes are widely and commonly attracted to roads for thermoregulatory purposes (e.g., Klauber 1939; Bernardino and Dalrymple 1992). The logic against thermoregulatory behavior being a determinant of road use is compounded further because gravid females seek warmer microhabitats (e.g., Gibson and Falls 1979; Brown and Weatherhead 2000). Therefore, females of a species presumably would be represented on the road in greater proportion than observed in off-road situations. Yet the proportion of all female snakes on roads was only 36%, compared with 46% in off-road situations. The male prevalence of snakes on roads contrasts sharply with reports for turtles, in which females are killed more frequently, due in part to the attraction of gravid turtles to road shoulders as nesting habitats or because of crossing roads en route to nesting areas (Wood and Herlands 1997; Marchand and Litvaitis 2004; Steen and Gibbs 2004; Gibbs and Steen 2005; Aresco 2005). Because gravid female turtles are frequently killed, turtle populations may be particularly at risk from roads.

We recorded significantly more DOR than AOR specimens, as would be expected, because a dead snake’s persistence on the road allows a wider window of time for observation. Nonetheless, the proportion of DOR snakes (61%) on SRS roads was appreciably lower than what would be expected in surveys conducted on public roads, even those with low traffic levels (e.g., 93% DOR, Enge and Wood 2002). As most SRS roads experience minimal traffic levels, road surveys produced high AOR capture rates, therefore resulting in a lower DOR/AOR ratio. One species, *A. contortrix*, had a significantly lower prevalence of DOR individuals than did other species, presumably a consequence of a species having a predominately nocturnal activity pattern when already low traffic density levels were at their lowest. In contrast, *Crotalus horridus* are also active nocturnally on the SRS but are often found diurnally, when traffic levels are higher. Additional reasons for the higher probabilities for road mortality of *C. horridus* are that they are larger in body size, have the slowest road-crossing speeds reported for any snake (Andrews and Gibbons 2005), and are one of the most maligned species in the region, leading to much intentional killing by drivers. Additionally, snakes more likely to be found DOR were larger (longer and heavier), variables that inherently increase a snake's chances of being killed simply by being a larger target for a driver, both unknowingly and intentionally. Subsequently, we suggest that in areas of increasing urbanization, large snake species that readily cross roads are at a disadvantage for individual survival and population persistence.

Our results indicated that snakes on roads were generally larger than individuals captured in off-road habitats. A simple explanation for the bias towards larger individuals on roads is due to the observer bias for detecting larger, heavier snakes (e.g., Fitch 1949) because they are easier to observe. Also, larger snakes may be more likely to venture across open spaces, such as roads, because of a reduced threat of avian predation (Fitch 1949; Enge and Wood 2002; Andrews and Gibbons 2005). In contrast, an observer would not necessarily detect larger snakes in greater proportion than small ones of a species because camouflage and escape behaviors would be more effective in off-road habitats. Additionally, smaller road-killed snakes undergo vehicular degradation or may be more difficult to detect or identify than large ones after being scavenged, reducing the likelihood of observing the snake (Enge and Wood 2002; Antworth et al. 2005; Andrews unpub. data). Aside from *ad hoc* interpretations, the smaller size of *E.* [*obsoleta*] *alleghaniensis*) and the significant interaction between length and mass of *Heterodon platirhinos* (Table 3.2) have no ready explanations that are apparent to us. Regardless, the small body size of some of these species is not a sole reason for their lack of observation, as a variety of other small species (e.g., *Storeria dekayi, Cemophora coccinea*; Table 3.1) were found commonly on SRS roads.

Our data do not delineate specific factors affecting differential road use by particular groups of snakes. However, they do support the assumption that ecological attributes of the individual or species can influence whether or not a snake will cross a road. Traits that could affect road use and behavior include predator avoidance/defense strategies (some species rely on crypsis, venom, or large size when traveling overland whereas others rely on speed; Andrews and Gibbons 2005), mating strategies (males of some species trail females or travel extensively in search of mates during the mating season; Shine et al. 2004), habitat preference (some species are fossorial or partial to heavy ground litter for concealment; Fitch 1949), home range size (individuals of wide-ranging species are more likely to encounter roads; Bonnet et al. 1999), and activity patterns (nocturnal species may be less likely to suffer road mortality than diurnal species due to patterns asynchronous to traffic peaks; Klauber 1939). Whether the persistent loss of individuals observed in this paper is one that is sustainable at the population level of organization is yet to be determined. However, most models thus far suggest inevitable population declines as a result of prolonged mortality levels (e.g., Rosen and Lowe 1994; Kline and Swann 1998).

Ecological patterns such as those identified in this study elucidate species sensitivities to differential road impacts (turtles, Gibbs and Shriver 2002; Steen et al. 2006) that can gear future studies to measure correlations between changes in abundance over time and abiotic and biotic factors. For instance, *Pituophis melanoleucus*, *A. contortrix*, and *C. horridus* had exceptionally high numbers of individuals found on roads. While these data demonstrate a high interaction between these species and roads, they do not directly reveal how populations will fare in urban settings with high road densities. Two of these species (*P. melanoleucus* and *C. horridus*) were found DOR significantly more frequently than AOR, which would indicate a serious threat, a concern also voiced by Rudolph et al. (1999) with *Pituophis ruthveni* and *C. horridus*. These species should be investigated using standardized sampling efforts to determine if this trend is actually attributed to a low level of crossing success. In contrast, species occurring in high densities such as *Coluber constrictor* may be more resilient to low levels of human development despite a high propensity to be DOR. These questions are the sort that researchers seeking to understand impacts of roads on snakes need to be asking.

Data documenting negative impacts of roads on herpetofauna are becoming increasingly numerous and diverse, and solutions have been identified to address some of the problems that are being confronted in urban environments (Andrews et al. 2006). However, with regard to snakes, species-specific predictions continue to be difficult to make on the basis of the current status of research examining impacts of roads on direct mortality (including this study). Nonetheless, the data demonstrate that roads will clearly take an increasing toll on snake populations as urban and suburban road density and traffic levels increase. Studies on how roads affect species richness and populations thus will become increasingly important. Some will be urgent, requiring quick impact assessments; others will best be addressed with a search for long-term solutions that are more effective than existing options (see also Jaeger and Fahrig 2000). Herpetologists need to be involved in such studies from the outset. Due to the inability of impervious surfaces to provide complete support of habitat requirements for any herpetofaunal species, there would presumably be a threshold for quantity of impervious surface coverage over which species persistence is not achievable regardless of the level of species resilience to general road impacts. Although species and topics must be prioritized, urbanization must be defined in a manner that incorporates all aspects of landscape development and human expansion, with roads being recognized as a dominant feature of the landscape that will directly and indirectly affect the persistence of most species of snakes and other herpetofauna.

Roads are undeniably a facilitator of urban sprawl, and roads must be factored in as a priority source of environmental impact in urban settings. The next critical step is to quantify how differential patterns of road use impact wildlife population structure and stability through time. Until we are able to extrapolate the loss of individuals to population and ecosystem levels in an ecologically useful manner, our understanding of the impacts of roads and urbanization on wildlife populations will be insufficient.

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10024, "Reptile and amphibian research--general field studies") and the South Carolina Department of Natural Resources (Collection Permits: 56-2003, 07-2004).

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Table 3.1. Snakes captured on the Savannah River Site, South Carolina, USA, between 1951 and 2005. Column title “On” = number of individuals captured on roads. Column title “Off” = number of individuals captured in off-road habitats. **Elaphe obsoleta = Elaphe alleghaniensis*

Species	**Common name**	**On**	**Off**	**Total**	**% On**
Pituophis melanoleucus	Pine Snake	152	18	170	89
Agkistrodon contortrix	Copperhead	214	30	244	88
Crotalus horridus	Timber (Canebrake) Rattlesnake	335	85	420	80
*Elaphe obsoleta**	Eastern Rat Snake	220	115	335	66
Masticophis flagellum	Eastern Coachwhip	123	81	204	60
Heterodon simus	Southern Hog-nosed Snake	115	83	198	58
Elaphe guttata	Corn Snake	160	133	293	55
Sistrurus miliarius	Pygmy Rattlesnake	27	23	50	54
Heterodon platirhinos	Eastern Hog-nosed Snake	178	289	467	38
Nerodia erythrogaster	Red-bellied Watersnake	44	112	156	28
Coluber constrictor	Eastern Racer	446	1198	1644	27
Micrurus fulvius	Eastern Coral Snake	1	4	5	25
Opheodrys aestivus	Rough Green Snake	42	149	191	22
Lampropeltis getula	Common Kingsnake	89	317	406	22
Thamnophis sirtalis	Common Garter Snake	80	334	414	19
Storeria dekayi	DeKay’s Brown Snake	21	107	128	16
Cemophora coccinea	Scarlet Snake	52	305	357	15
Agkistrodon piscivorus	Cottonmouth	75	477	552	14
Thamnophis sauritus	Eastern Ribbon Snake	30	201	231	13
Lampropeltis triangulum	Scarlet Kingsnake	11	90	101	11
Farancia abacura	Red-bellied Mud Snake	36	322	358	10

Nerodia fasciata	Southern Watersnake	75	1488	1563	5
Farancia erytrogramma	Rainbow Snake	6	230	236	3
Diadophis punctatus	Ring-necked Snake	11	521	532	2
Virginia valeriae	Smooth Earth Snake	3	156	159	2
Storeria occipitomaculata	Red-bellied Snake	10	710	720	1
Nerodia floridana	Florida Green Watersnake	3	224	227	1
Tantilla coronata	Southeastern Crowned Snake	9	1384	1393	> 0
Nerodia taxispilota	Brown Watersnake	9	2179	2188	> 0
Seminatrix pygaea	Black Swamp Snake	0	1660	1660	0
Virginia striatula	Rough Earth Snake	0	37	37	0
Regina septemvittata	Queen Snake	0	13	13	0
Rhadinaea flavilata	Pine Woods Snake	0	9	9	0
Regina rigida	Glossy Crayfish Snake	0	31	31	0
Carphophis amoenus	Eastern Worm Snake	0	5	5	0
Total		**2577**	**13120**	**15697**	

Table 3.2. Total body length, body mass, and/or the interaction were significantly different between on-road and off-road captures in seven Savannah River Site snake species between 1951 and 2005 (N=sample size). Average total lengths (TL) are shown for captures on the road and in off-road habitats for each species, followed by the F- and p-values resulting from ANOVA analyses of total length, mass and the interaction of the two variables.**Elaphe obsoleta = Elaphe alleghaniensis*

Species	**TL N**	**Ave. TLon**	**Ave. TLoff**	**TL F**	**TL p**	**Mass N**	**Mass F**	**Mass p**	**TL*mass F**	**TL*mass p**
F. abacura	266	93.00	54.00	26.54	<0.0001	205	20.79	<0.0001	22.56	<0.0001
C. constrictor	1094	103.00	94.00	58.64	<0.0001	1129	---	---	---	---
M. flagellum	148	158.89	129.60	11.42	0.0011	137	---	---	---	---
A. contortrix	117	69.60	57.00	11.07	0.0012	107	6.26	0.014	---	---
*E. obsoleta**	239	128.00	138.00	4.35	0.0388	218	---	---	---	---
T. sirtalis	202	64.50	47.28	---	---	178	6.24	0.0134	4.97	0.0271
H. platyrhinos	289	53.60	54.47	---	---	260	---	---	4.49	0.0356

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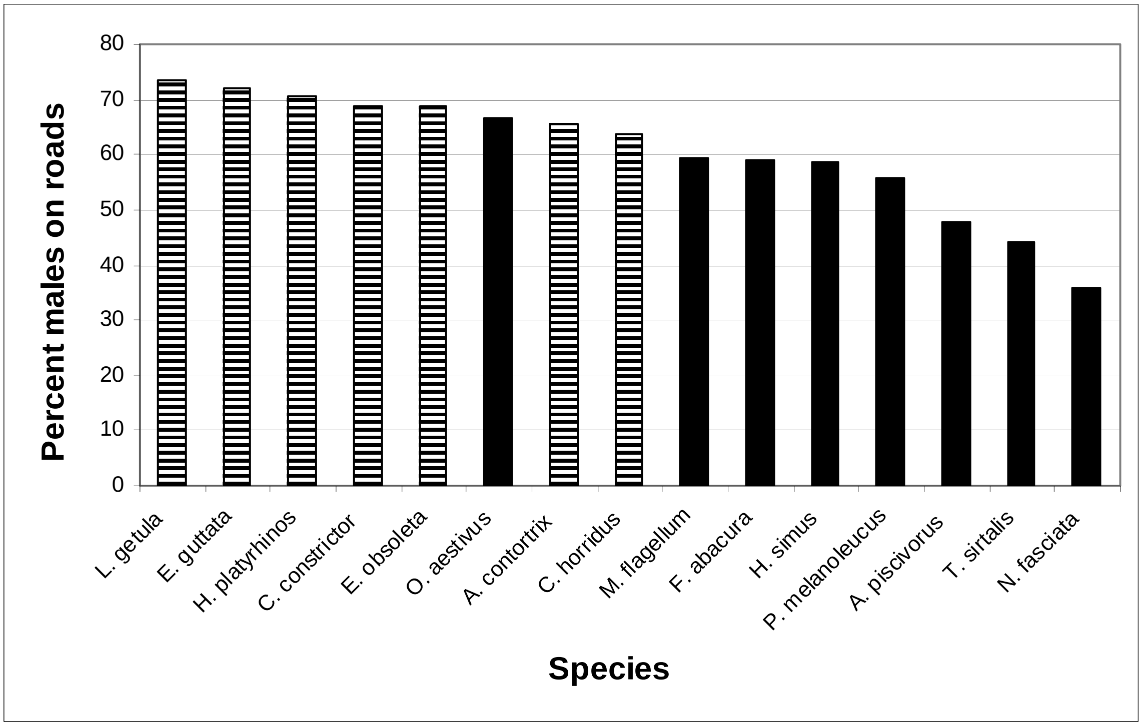

Figure 3.1. Sex ratios of snakes found on Savannah River Site roads in South Carolina between 1951 and 2005. Bars with horizontal lines represent species with significantly more males than females (Chi-square test for goodness of fit; $P < 0.01$) **Elaphe obsoleta* = *Elaphe alleghaniensis*

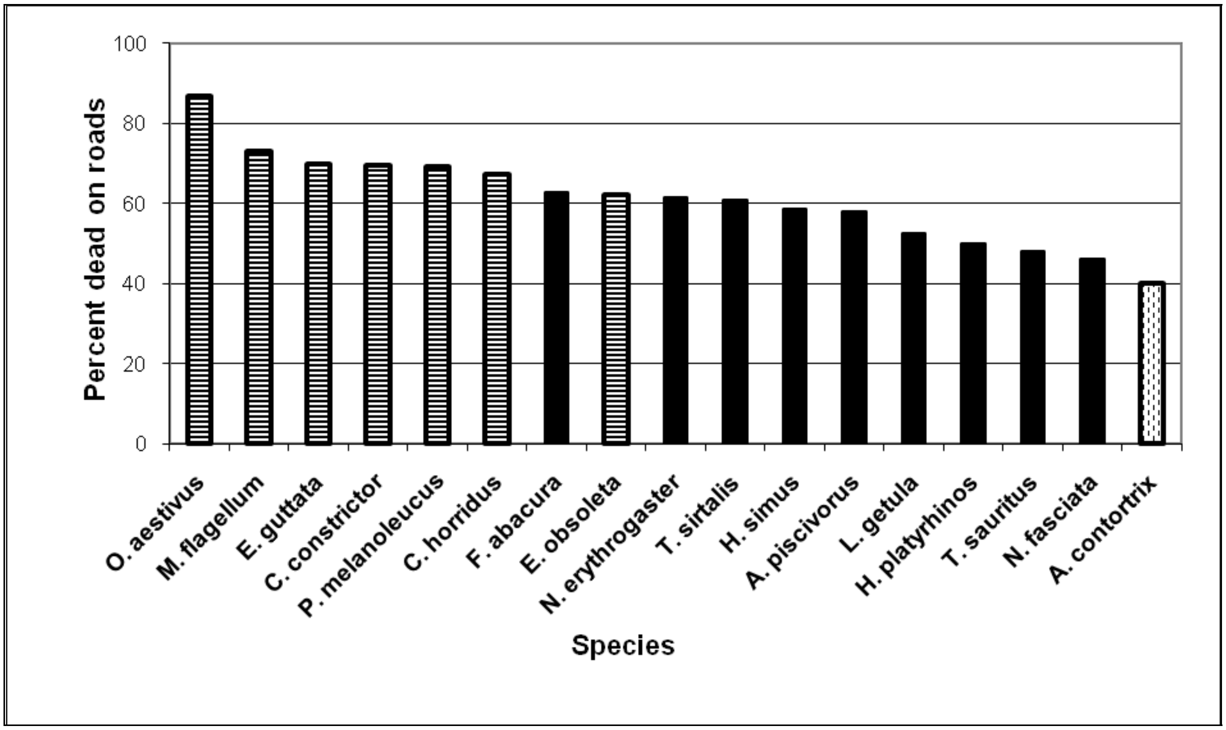

Figure 3.2. Percent of dead-on-road (DOR) snakes found on Savannah River Site roads in South Carolina between 1951 and 2005. Bars with horizontal lines represent species that exhibited a significant tendency to be found either DOR or alive-on-road (AOR; Chi-square test for goodness of fit; $P < 0.01$) *Elaphe obsoleta* = *Elaphe alleghaniensis*

CHAPTER 4

HOME-RANGE SIZES OF TIMBER RATTLESNAKES (*CROTALUS HORRIDUS*) ARE AFFECTED BY INITIAL LANDSCAPE DEVELOPMENT[3]

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[3] Andrews, K. M. To be submitted to Biological Conservation.

ABSTRACT

Conversion of undeveloped and rural areas is rapidly occurring through the process of expanding urbanization. Consequently, habitat loss and degradation have had pervasive effects on wildlife through both direct forms of mortality and habitat fragmentation. One observed effect has been the alteration of movement patterns and space use. This study focuses on home ranges of timber rattlesnakes (*Crotalus horridus*) in coastal South Carolina, at a field site in the early stages of residential and recreational development. To compensate for biases in home range estimations, and to compare techniques, home ranges were calculated using minimum convex polygons (MCP), fixed kernel distributions, and LoCoH nearest neighbor convex hulls (NNCH). Home range sizes determined from radio locations were tested for effects of sex, body condition, development, road density and distance to nearest open space. Using a crossed variable of sex and development, sex affected all home range area estimations and development affected full (95%) range sizes. Overall, home ranges in developing areas were significantly larger than in undeveloped areas. This effect was observed for MCP and fixed kernel calculations, but not for NNCH. These latter NNCH analyses revealed that snakes are not necessarily using more space in developed areas, but have larger and more fragmented ranges. When analyzing breeding, foraging, and wintering kernels separately, sex influenced breeding and foraging areas, and development affected foraging ranges. There was a high degree of site fidelity to overwintering sites for almost all individual snakes. Home range fidelity (interannual range overlap) was reduced in developing habitats where range shifts observed among years and within individuals was greater, although neither sex nor development influenced the overall degree of overlap between years. This initial assessment of fragmentation is important to develop an understanding of the process of urbanization and wildlife population declines. These data exemplify the type of information that is readily translatable to the multiple stakeholders (biologists, managers, developers, local land planners, and general public) that need to be involved in the process of conserving wildlife in developing landscapes.

Key words: Fragmentation, Habitat Management, Kernel, LoCoH, MCP, Urbanization

INTRODUCTION

Development and habitat loss pose the most serious threats to reptile persistence (e.g., Gibbons et al. 2000), particularly for large, venomous snakes that are susceptible to both incidental and intentional mortality as human densities and encounter probabilities increase. The process of urbanization has demonstrated deleterious and irreversible effects on biodiversity and ecosystem-level trophic dynamics (e.g., McKinney 2002, Faeth et al. 2005). Aside from direct mortality and habitat loss, wildlife ecology could be altered due to responses to landscape change, such as habitat fragmentation. The propensity for avoidance of roads, open spaces, and human-dominated areas and reduced home ranges in the presence of urbanization has been documented for snakes, turtles, and mammals among others (e.g., Sealy 2002, Riley et al. 2003, Andrews and Gibbons 2005, Grgurovic and Sievert 2005, Andrews et al. 2008). Here, I used radio telemetry to investigate influences of initial stages of residential and recreational development on home range sizes in a large predatory snake.

The timber rattlesnake (*Crotalus horridus*) is the only wide-ranging woodland rattlesnake species in the world (e.g., Brown 1993). This species is still thought of as broadly ubiquitous, including in southern regions (Gibbons 1972, Tennant and Bartlett 2000) where it is often referred to as the canebrake rattlesnake. However, there are apparent declines noted for populations throughout its range due to a suite of pressures attributable to habitat loss, habitat degradation, road mortality, and both intentional and incidental mortality (e.g., Brown 1993). Although *C. horridus* receives no legal protection in South Carolina where this study was conducted, it is listed as vulnerable, critically imperiled, or imperiled in 20 of the 31 U.S. states in which it occurs, and has been extirpated from Maine, Rhode Island, and Ontario, CA (CITES 2000). This species is an ideal candidate for this investigation as it is still considered more common than the eastern diamondback rattlesnake (*Crotalus adamanteus*, Waldron et al. 2008) but is susceptible to conservation pressures that warrant both immediate and long-term concerns. Further, it serves as an excellent model to examine fragmentation effects and human-wildlife coexistence because it: 1) exhibits large home ranges (e.g., Reinert and Zappalorti 1988) and therefore, is more likely to respond to fragmentation and road effects (Clark et al. 2010); 2) has high adult survivorship (e.g., Brown et al. 2007) and therefore, is a good model for urban effects on key species in ecosystems; 3) exhibits high interannual site fidelity (e.g., Brown et al. 1982, this study (Chapter 5)) and therefore, is likely to implicate levels of spatial adaptability in response to habitat loss; and 4) is a large venomous snake and therefore, is a good model for outreach and education efforts with developers and property owners.

The objectives of this study were to assess the potential effects on home range sizes (overall, within-season activity ranges, and interannual ranges) of *C. horridus* in South Carolina of sex, body condition, development phase, road density, and distance to nearest manmade open space. I hypothesized that 1) body condition would be positively correlated with home range size; 2) males would have larger home ranges than females; 3) home range size would be affected by development phase through increased overlap in activity ranges and decreased overlap in interannual ranges; 4) road density would be inversely related to home range size; and 5) distance to nearest open space would be positively related to home range size.

MATERIALS AND METHODS

Study sites.— This investigation was conducted using radiotelemetry data collected in Beaufort Co., South Carolina. The field site was approximately 8,094 ha in size and was largely bounded by both brackish and freshwater rivers. During the Pleistocene Epoch (approximately 10,000 ybp), the site was a barrier island. The property included a diversity of upland pine stands (previously managed for northern bobwhite (quail, *Colinus virginianus*), maritime forests, mixed pine-hardwood, and salt marsh hammocks. A natural diversity of wetlands, bogs, and other ephemeral freshwater bodies was present, but much of the hydrological landscape was altered due to ditching for agriculture (e.g., cotton, indigo, rice) that occurred in the initial settlement of the property in the early 1700s (Kennedy 2005).

This site was privately-owned and undergoing residential and recreational development during my study. Prior to acquisition by the developer, the property had been owned and managed by Union Camp Corporation primarily as a private hunting preserve, and for periodic timber harvesting. These activities warranted regular prescribed burning and management of wildlife openings that maintained habitat quality. These traditional wildlife and habitat management techniques were employed to the best of the ability of the on-site natural resource entity, but were limited due to expanding development in Beaufort Co. (U.S. Census Bureau 2010, http://quickfacts.census.gov/qfd/states/45/45013.html, accessed 9 October 2010) and in-house resource limitation.

The coastal property was acquired by developers in 2001 and construction was initiated in 2002. The developers prioritized land protection via areas limited to human access and conservation easements. Further, current land-use plans target smaller, more concentrated housing communities interspersed with ecological conservation areas within the larger landscape. Due to the early stage of development planning and construction and the reduced rate of land conversion as influenced by recent economic recession, much of the property was still in its pre-development state. Research on *C. horridus* was initiated in 2006 to determine movement patterns and habitat use relative to the developing landscape. Research was coordinated with the managing resource agency and the developer, and through staff and property owner outreach and education.

Radio Telemetry.— Radio telemetry was used to collect data on free-ranging *C. horridus* from 2006-2010. Specifically, I collected data to quantify home range size and habitat use, and monitored responses of snakes to development for the purposes of making recommendations on rattlesnake and habitat management, and risk reduction for human residents of the development. Snakes were hand-collected both opportunistically and through targeted field searches. All snakes were reproductively-mature adults based on reproduction and growth data from Savannah River Site in Aiken Co., SC (Gibbons 1972; Table 4.1). Telemetered snakes were distributed across the field site to allow for characterization of movement patterns and home ranges in developing and undeveloped areas (Figure 4.1). Radio transmitters (SI-2, 13 g., 36 mos.; Holohil Systems, Carp, ON) were surgically implanted, and snakes were anesthetized with isoflurane using an isoflurane vaporizer. Physical parameters (snout-vent length [SVL], mass, sex) were collected during surgical procedures. Snakes were monitored in captivity for 24-48 hours following surgery prior to their release at the site of capture. Handling and surgery protocols were approved under the University of Georgia Animal Use Protocol #A2006-10175; protocols were revised and approved annually (current – #A2009-6119).

Snakes were monitored for up to three years; individuals presented here were tracked for two years on average (*n* = 18) and locations were conducted weekly during all months of the year using radio receivers (Communications Specialist, Inc., R-1000, Orange, CA) and a Yagi (3-way) directional antenna. Snake locations were recorded using a Global Positioning System (GPS; Trimble GeoXT, Sunnyvale, CA) and post-processed using GPS Pathfinder Office v.4.10

(Trimble Navigation Limited, Sunnyvale, CA). Points generally achieved an estimated spatial accuracy of <2 m.

Home Range Estimations.— Burt (1943) first defined the home range as, "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." However, this definition has been charged as inadequate as it incorporates excursive movements and does not take a statistical (i.e., relative frequency distribution) approach to home ranges. Brown and Orians (1970) provided a definition as, "the area in which an animal normally lives, exclusive of migrations, emigrations, or unusual erratic wanderings." There are various methodologies available to calculate home range size from radiotelemetry data (e.g., White and Garrott 1990). All have advantages, biases, and limitations which should be carefully weighed before selecting one or multiple methodologies to apply (Kernohan et al. 2001). The minimum convex polygon (MCP) is the more traditional technique of analysis (Mohr 1947) and simply draws a polygon around the outer location points to completely enclose the use area; however, this approach tends to overestimate the amount of area used and does not include temporal aspects which disproportionately weight areas of high or low use (Jennrich and Turner 1969). This method is included here to facilitate comparison with previous home range analyses. The fixed kernel method is a nonparametric method that instead produces a utilization distribution (Van Winkle 1975) by assessing the probability of occurrence at each point in space (Worton 1987, 1989). This technique is considered to be a more accurate predictor of home range size (Seaman and Powell 1996). Kernels are advantageous in that they work well with small amounts of data (≤ 50 points), are robust to autocorrelation, and allow for multiple centers of activity (e.g., Seaman et al. 1999, Kernohan et al. 2001). While kernel methods are particularly sensitive due to the selection of a smoothing parameter (*h*), this sensitivity can be reduced with careful judgment (e.g., Row and Blouin-Demers 2006, Fieberg 2007). Due to these various biases, any single method can lead to misleading presentations of space use, and therefore, I employed multiple methods for home range calculations.

I generated home range estimates using three methods: 100% Minimum Convex Polygons (MCP; Mohr 1947), fixed kernel distributions (Silverman 1986, Worton 1989), and adaptive LoCoH (*a*-LoCoH), a nearest neighbor convex hull method (NNCH; Getz and Wilmers 2004, Getz et al. 2007). ArcMap 9.2 (Hawth's Analysis Tools, v. 3.27) was used for calculation of MCPs and kernels, and NNCHs were generated using R script through a web interface (http://locoh.cnr.berkeley.edu). Fifty and 95% isopleths were used for home range size comparison with fixed kernels and NNCHs. Differences in average home range size among methods were explored using T-tests (Proc Ttest).

Börger et al. (2006) suggest using 90% isopleths to calculate home range to avoid overestimation of home ranges due to atypical dispersions. However, for the objectives here, these excursions often involve increased distance movements in an anthropogenically heterogeneous landscape matrix which correlates with increased mortality probabilities. Therefore, 95% isopleths are relevant to the effects that are targeted with these objectives. Further, 95% isopleths allow for a more direct comparison with 100% MCPs. Lastly, I used 50% isopleths to represent "core" use areas due to increased bias of inner isopleths (< 50%) relative to outer isopleths (Börger et al. 2006).

Smoothing parameters (*h*) for utilization distributions were calculated using ArcView 3.3 Animal Movement Extension (Hooge and Eichenlaub 1997) by the ad hoc reference method (Silverman 1986). The reference method was selected due to its sensitivity to linear barriers

(Blundell et al. 2001), which is applicable to this study due to rattlesnakes' propensity to edge use (Waldron et al. 2006a, 2006b) and their response to roads as barriers (e.g., Andrews et al. 2008). Additionally, the reference method is thought to be more sensitive to philopatry to a single site, such as rattlesnakes repeated use of hibernacula (e.g., Brown et al. 1982, this study (Chapter 5)), in comparison to the frequent default Least Squares Cross Validation method (e.g., Gitzen et al. 2006).

The adaptive method for LoCoH is a revised method to the original *k*-LoCoH, which is similar to the fixed kernel method in that it involves generating distributions for a fixed number of locations, but within *k-1* nearest neighbors (Getz et al. 2007). The adaptive method creates hulls from the maximum number of nearest neighbors such that the sum of their distances from the root point is less than or equal to *a* (Getz et al. 2007). This approach was selected as it is particularly sensitive to hard boundaries in a landscape that structures the animal's home range, such as a river, mountain, or road (Getz et al. 2007). Recommended values of both *a* and *k* are specific to each data set and analyses and must be generated based on data performance for a range of options. Getz and colleagues (2007) use $k = \sqrt{n}$, where n = sample size of dataset, to determine optimal values for analysis. The rule of thumb for a starting point for testing *a* is the maximum distance between any two points in the data set. Here, half of the distance between the two farthest points was tested as the minimum *a* and the total distance as the maximum *a*. Variable combinations of *a* and *k* were tested and selected based on visual inspection of a graph of *a* and home range size. When achieving the appropriate *a* and *k*, home range size plateaus; this plateau is indicative that all spurious holes have been filled in the estimate (Figure 4.2). When home range size again changes after the plateau, it indicates that real (i.e., topographically legitimate, such as a lake) gaps in the home range are filling and home range size is becoming biased.

Telemetry data tend to be nonindependent, and much discussion has been given on how to deal with autocorrelation (e.g., Swihart and Slade 1985). Importantly, eliminating autocorrelation removes biologically relevant information on an animal's true movement patterns (e.g., De Solla et al. 1999, Blundell et al. 2001, Cushman et al. 2005). De Solla and authors (1999) further found that subsampling does not reduce autocorrelation, and maintaining a constant sampling frequency is the best mitigation for increasing accuracy and precision of estimates.

Home Range Analysis.— I used repeated measures ANOVA with a split-plot design to examine whether home range size differed by method and to look for potential effects of sex and development (a binary variable based on whether the snake was in a developing or undeveloped area). To further understand how sex and development may interact to influence home range, a "treatment" variable was created that crossed sex and development to examine variation among males and females in developing and undeveloped areas. The individual snake ID was included in the model as a nested variable. Lastly, body condition was calculated as the residuals of SVL (mm) versus mass (g). Based on these residuals, body condition did not significantly affect home range size and was therefore not included in the models. Two models were developed to test variation in size of 1) "full" ranges [MCPs, 95% fixed kernels, and 95% NNCHs] and 2) "core" ranges [50% fixed kernels and 50% NNCHs]. Lastly, I employed t-tests (Proc Ttest) to ascertain if differences within development levels (i.e., developing vs. undeveloped) varied among and within home range calculation methods.

To analyze how space use was partitioned within an activity season, radio locations were categorized as breeding (September-October), wintering (November-February), or foraging (March-August) locations. Activity was temporally divided based on observed behavioral pulses in the field. Breeding season was assigned based on observations of male and female pairing, courtship, and copulation. Wintering season followed breeding season and was based on the return to hibernacula and cessation of movement and overall surface activity for the majority of days. Lastly, foraging season extended for the remainder of months when snakes were actively observed in ambush postures and coiled digestion of boluses. These activity seasons represented the time periods inclusive to the majority of these activities; however, there was occasional overlap among seasons, such as foraging observations in December.

Activity kernels (50 and 95%) were calculated for each individual ($n = 14$) using ArcMap 9.2 (Hawth's Analysis Tools), and ArcView 3.3 (Animal Movement extension; Hooge and Eichenlaub 1997) was again used to calculate h. An ANOVA was conducted to examine for effects on home range size from activity season and individual snakes. Each activity type was tested for effects of sex, development, road density, and distance to nearest open space. Further, spatial overlap in activity kernels was calculated with the Overlap feature in ArcMap 9.2 and converted to a percentage overlap variable. I examined whether the degree of overlap varied with different activity types, sex, and development.

Lastly, 95% kernels were created for each year to examine the degree to which rattlesnakes used the same areas among years (i.e., home range fidelity). Spatial overlap in annual kernels was calculated with the Overlap feature in ArcMap 9.2 and converted to a percentage overlap variable. I again examined whether the degree of overlap varied with sex, development, road density, and distance to nearest open space. Finally, to examine the change in area used among years (i.e., home range shifts), I calculated percent change (+/-) among years and examined whether sex, development, road density, and distance to nearest open space influenced the amount of space used. Normality was tested in all analyses using Shapiro-Wilk tests ($\alpha = 0.05$), and log transformations were conducted to achieve normality (Proc Univariate). All statistical analyses were performed using SAS version 9.2 and JMP version 8.0 (SAS Institute 2008, Cary, NC).

Landscape Change.— Land cover maps were created using Geographic Information Services (GIS; ArcMap 9.3.1) to assess the effects of open space and roads associated with the development on snake home ranges. Maps were created for the initial conditions (2006) and current conditions (2010). For both years, roads were classified as paved or unpaved, and were categorized as main (e.g., regularly trafficked and usually paved), forest (unpaved one-lane roads), or construction (previously forest roads that were unpaved and had been widened to accommodate two-way dump truck and heavy machinery traffic). Additionally, old forest roads that were no longer trafficked were included as former roads since road footprints would still contribute to edge and open space effects. Finally, to weight the relative width of different road types, polylines (linear features in GIS) for main roads were buffered by 10 m, construction roads by 20 m, and forest and former roads by 3 m. Buffer distances were determined by actual road widths in the field.

Additionally, equestrian, biking, and walking trails were delineated. Open spaces also included wildlife food plots, equestrian fields, home lots, clearcuts, a golf course, and other commercial and administrative development. These various features were merged into a single layer (Figure 4.3) to generate raster layers of Euclidean distances to nearest open space and road densities (ArcMap 9.3.1, Spatial Analyst extension). Distances and densities were associated with each radio location using ArcMap 9.2, Hawth's Analysis Tools (v. 3.27; Intersect Point Tool). Initial (2006) and current (2010) values were compared (Proc Ttest) for both distances to open space and road densities to assess whether the mean values of these landscape features within snake home ranges significantly changed over the course of this study. ANOVAs (Proc GLM) were used to test for additional effects from distance to nearest open space and road density on home range size (MCPs, 95% and 50% fixed kernels, and 95% and 50% NNCHs).

RESULTS

Home Range Size.— Average home range sizes calculated using MCPs, fixed kernel distributions, and NNCHs varied considerably ($n = 1217$ locations; 18 snakes: 9 males, 9 females; Table 4.2). MCPs and 95% fixed kernels differed significantly ($F = 2.81$, $P = 0.04$). However, both MCP and 95% kernel estimates were significantly larger than those generated using LoCoH (MCP-NNCH, $F = 15.65$; Kernel-NNCH, $F = 43.99$; $P < 0.0001$).

Since home range size data were not normally distributed, a Box Cox transformation was used to stabilize variance prior to conducting the split-plot analyses for both methodological comparisons of full (MCP, 95% fixed kernels, and 95% NNCH) and core (50% fixed kernels and 50% NNCH) home range areas. The method of home range calculation significantly influenced the estimated area used by snakes for their full use areas ($F = 19.03$, $P < 0.0001$), which was largely driven by the LoCoH estimations as also exhibited by t-test comparisons. Treatment exhibited a strong effect on home range area ($F = 20.51$, $P < 0.0001$). In this analysis, both sex and development were highly significant, but the interaction term was not. The effect of individual snake when nested within the treatment variable did not explain a significant amount of the variation in the model.

For the analysis of core area sizes, I applied the same transformation and split-plot design. Again, estimates generated from the 50% fixed kernels and 50% NNCHs were significantly different ($F = 65.42$, $P < 0.0001$). The treatment variable was again highly significant ($F = 7.68$, $P = 0.002$), although not as strongly as observed with the full home range analysis. This significance was driven by sex, where males had larger home ranges than females in both developed and undeveloped areas. Range size did not vary within sex between development levels. Lastly, the effect of individual snakes when nested in the treatment variable did not significantly influence home range size for the core analysis.

Significant differences were detected in home range sizes within development levels, where developing areas actually resulted in larger home range than undeveloped areas ($F = 14.31$; $P < 0.0001$). To more specifically test whether this pattern varied with methodology, each calculation for the three methods and isopleths percentile was examined separately. Significant differences in developing and undeveloped habitats were identified for MCPs ($F = 7.79$, $P = 0.009$) and fixed kernel distributions (50%, $F = 47.70$; 95%, $F = 40.49$; $P < 0.0001$), but not for either the 50% or 95% NNCHs (Figure 4.4).

Activity Season Kernels.— Activity kernels were calculated for each snake for breeding, foraging, and wintering seasons ($n = 14$; Table 4.3). Since the year did not significantly influence home range size ($P > 0.05$), data were pooled across years for an individual snake. There was a significant effect of individual snake on activity range size ($F = 4.42$, $P = 0.0006$), with a high level of variability in range size occurring among individuals (Table 4.2). The type of activity significantly influenced overall home range size. Breeding range size was consistently larger than foraging ranges with the exception of four snakes that exhibited larger foraging ranges. Wintering ranges were consistently the smallest. When activity kernels were analyzed separately for effects of sex, development, road density, and distance to nearest open space, breeding season was affected by sex ($F = 16.54$, $P = 0.003$), and foraging season was affected by development ($F = 6.64$, $P = 0.030$), but influences from sex were marginal ($F = 4.48$, $P = 0.063$). The size of wintering season kernels was not driven by any of the variables tested in this model. Overall, activity season kernels were larger in developing areas relative to those in undeveloped areas for all three activity types (Figure 4.5).

Overlap in activity season kernels was calculated to investigate space partitioning among these broader activity types. The type of activity influenced the degree of overlap among kernels, where winter kernels had the greatest degree of overlap with both breeding and foraging kernels. Percent overlap in activity kernels did not vary significantly between sexes or development levels.

Home Range Fidelity.— On average, *C. horridus* home ranges overlapped 56.8% among years (SD = 21.8; Min = 10.5%; Max = 98.5%). The degree of interannual overlap in space use was not significantly influenced by sex, development, road density, or distance to nearest open space. Further, the percent change in the amount of space used among years was highly variable, but averaged a 20.3% shift in area annually. The degree of spatial shift was also not influenced by sex, development, road density, or distance to nearest open space, although reduced overlap in ranges among years was regularly observed in developed habitats.

Landscape Change.— The development footprint increased by 67% during the course of this study as 6% of the site was developed in 2006, and 10% in 2010 (Figure 4.3). Distances to nearest open space values measured at each snake location did not significantly differ between 2006 and 2010 ($n = 1217$; $P > 0.05$). However, road densities did significantly change over time ($n = 1217$; $P < 0.0001$). Road density increased significantly from the initiation of the study in 2006, increasing by 17% over the course of the study and being responsible for 18% of the overall development footprint increase (274 ha). Further, neither road density nor distance to nearest open space exhibited an effect on any of the log-transformed home range estimates (MCP, 50% and 95% fixed kernels, 50% and 95% NNCH).

DISCUSSION

Home Range Size.— *Crotalus horridus* has been the focus of more radiotelemetry studies than any other North American pit viper species, but the majority of work has been conducted in mountainous (i.e., northerly) regions of its range (but see Waldron et al. 2006a). Both MCP and fixed kernel distributions have been used to calculate home ranges, but this study is the first to employ NNCHs with this species, or pit vipers, to the best of my knowledge. Range sizes can be difficult to compare among studies due to differences in selected methodologies and in the variability of parameter calculation (e.g., smoothing parameters for kernels). Literature-based estimates are included here (Table 4.4) to demonstrate both the inherent variability in home range size for individual snakes, to allow for a comparison of home range size estimates across the range of the species, and to expose the challenge of comparing space requirements among methods. The average home range sizes for males observed in this study (77.01 ha) exceeded the 95% kernel calculations of male *C. horridus* from Hampton Co., South Carolina (48.38 ha;

Waldron et al. (2006a)), but female *C. horridus* ranges were smaller in Beaufort Co. (12.13 ha) than those observed by Waldron et al. (2006a) in Hampton (30.82 ha). Anderson (2010) reports the largest published home range size observed for *C. horridus* – a male in Missouri who's MCP spanned 465 ha. While the difficulty in comparing home range estimations across studies challenges our ability to address generalized management needs for this species, the true management challenge remains that *C. horridus* has extensive space use requirements throughout its range.

Males exhibited larger home range sizes for both the full range model (MCP, 95% fixed kernels, 95% NNCH) and the core range model (50% Kernel, 50% NNCH; Table 4.5). These results support all other *C. horridus* radiotelemetry studies in observing larger home range sizes for males (Table 4.4). This clear and consistent difference in home range sizes between males and non-gravid females was driven by the increased movement patterns of males during breeding season, and is discussed below in the *Activity Season Kernels* section. None of the telemetered females gave birth, or demonstrated the increased basking and decreased movement behaviors typical of gravid females, so I was unable to include gravid females for comparison. The binary development variable also had an effect on the full range model, as discussed below in the *Landscape Changes* section.

Home range size differed significantly among methods for the binary development variable. Interestingly, when analyzing the data independently by method, this significance only held for MCPs, and 50% and 95% fixed kernels, and not for either NNCH calculations (50% and 95%). LoCoH is a more conservative home range estimator because it responds readily to real gaps in the animal's home range, such as linear barriers or equestrian fields. Therefore, NNCH calculations were much smaller than either MCPs or fixed kernels. These findings revealed that development activity and fragmentation did not reduce the area used by *C. horridus*, but to the contrary, expanded their range size. While the literal amount of space used may actually be comparable, their activity ranges are larger and more fragmented.

This assessment reinforces the usefulness of employing multiple methodologies for home range calculation in heterogeneous and human-dominated landscapes. While LoCoH yields more accurate, precise range estimations of actual use, it is limited in portraying the broader expanse of space use. While MCPs and fixed kernels overestimate the amount of habitat used and are limited in articulating barriers finer-scale habitat use, their value remains. The biases and discrepancies should not preclude the use of these methodologies. Rather, they simply provide more tools in our toolboxes for answering the variety of questions that are being posed in the expanding field of urban ecology. For instance, as biologists, we need to understand literally, and probabilistically which areas the animals are most likely to spend their time in – to what they are attracted and that from which they are repelled, and NNCHs are more appropriate in that instance. However, with regard to venomous snakes, developers are more broadly interested in knowing everywhere the animal might visit, even if it is on an excursive movement, for the purposes of assessing encounter probabilities and risk reduction strategies. In answering these latter questions, MCPs and fixed kernels will be more representative. Based on these results, I encourage the employment of multiple home range methodologies to allow for increased flexibility in responding to biological, political, and sociological conservation questions.

Activity Season Kernels.— Breeding season movements of males were the predominant influence on the area of activity season ranges. These results support the findings of every other radiotelemetry study that also documented larger home ranges in male *C. horridus* than in females (Reinert and Zappalorti 1988, Sealy 2002, Laidig and Golden 2004, Savitzky and Petersen 2004, Adams 2005, Waldron 2006a, Waldron 2006b, Anderson 2010). Male *C. horridus* attain a larger body size than females, which frequently leads to intraspecific variation in range size among sexes (e.g., Harestad and Bunnell 1979). This differentiation in body size serves multiple purposes. First, males experience aggressive interactions through non-fatal combat (e.g., Klauber 1956, Sutherland 1958) and therefore, larger body size is advantageous. Secondly, and importantly, larger body sizes permit wider-ranging movements of males, which facilitate mate acquisition with females who are more sedentary for purposes of fat storage conservation. Rattlesnakes are capital breeders, meaning that they “rely upon energy gathered at some previous time, and store until later use” (Bonnet et al. 1999a). Both sexes forage throughout most of the year in the southern part of their range and experience low energy expenditure, so that they will have the necessary capital during breeding season, during which they expend these reserves fully, particularly in the case of gravid females. It is essential that they be strategic about accruing body reserves for mating season movements (males) and reproduction and embryo development (females).

Most snakes included in this analysis (n = 14) had larger breeding ranges than foraging or wintering ranges (Table 4.3). The four snakes with larger foraging ranges included both males and females and snakes in both development treatments so there was not a clear pattern as to any influence from sex or development on these patterns. It is further worth noting that two of the four individuals were observed in courtship and mating activities during the course of this study.

While foraging ranges tended to be smaller than breeding ranges, this space use was still substantial and varied considerably in area, between and within sexes (Table 4.3). This variance likely explains in part why sex was not a significant driver of foraging range size. Further, females have as great a need, if not greater, as males to forage as extensively as possible to prepare for reproduction. To maintain the large body size of this species for both sexes, they need to forage widely, which tends to be correlated with larger home ranges (e.g., McNab 1963). However, much of foraging season is spent in ambush posture since sit-and-wait predators often invest significant amounts of time (sometimes multiple weeks) for a single meal (e.g., Reinert et al. 1984). *Crotalus horridus* specializes on small endotherms range-wide, but is fairly opportunistic in terms of prey species and tends to consume relative to the availability and diversity of local small mammal populations (Reinert et al. 1984, Clark 2002).

Whether a snake was in a developed area (*n* = 7) or not (*n* = 7) influenced foraging range size independently of sex. Many of the largest foraging ranges observed in this study occurred in developing areas (Table 4.3). In fact, the largest range observed (snake 317) was in a developing area. This snake among others was observed to conduct extensive, foraging forays to nearby forest remnants. Intermediate locations were confirmed so it is known that the snake was not captured and moved by humans.

No effects of sex, development, road density or distance to nearest open space were apparent for wintering kernel size. Due to high levels of site fidelity to hibernacula, and therefore, the small concentrated area required for this activity, neither the variation between sexes or development levels emerged as having an influence on winter range size. *Crotalus horridus* has been observed to experience high interannual site fidelity to wintering locations in mountainous regions (Brown et al. 1982, Reinert and Zappalorti 1988, Sealy 2002, Anderson 2010), but this study is the first to document site fidelity in southern *C. horridus*. Most snakes included in these analyses (*n* = 14) returned to the same wintering spot in multiple years (see Chapter 5). The two that used different overwintering sites were males in developed areas that are still currently being tracked to determine whether they continue to scout for new hibernacula, or eventually settle for a new wintering location.

Activity kernels varied in the degree of overlap, and these results further support the findings of studies by Waldron and colleagues (2006b) and Anderson (2010). Winter ranges overlapped the most extensively with breeding and foraging seasons for both males and females (Figure 4.6). Further, substantial overlap of breeding and foraging ranges occurred for both males and females (Figure 4.6), but was not as extensively as that observed by Waldron et al. (2006b) where foraging ranges largely overlapped with breeding ranges. The intention of this analysis was to determine if sex or development influenced the degree to which snakes were partitioning their space use among activities, and, therefore, whether there were demographic or anthropogenic pressures on this space use. However, while this study did not support this occurrence at this initial stage of fragmentation, the question remains an open one that will ultimately be answered with longer-term data taken in a more developed landscape than what was available here.

Home Range Fidelity.— Due to philopatric tendencies of *C. horridus* in all seasons, which is particularly apparent with site selection in the winter, overlapping ranges among years are common with this species in other multi-year tracking in northern part of their range (e.g., Reinert and Zappalorti 1988). However, high levels of spatial and temporal fidelity are not typical for all snake species, some of which demonstrate shifting activity centers (e.g., natricines; Madsen 1984, Tiebout and Cary 1987). No statistical correlation was found in this study to attribute the degree of shifting, or conversely fidelity, with sex, development, road density, or distance to nearest open space, although gradual and variable shifts in space use were observed in the field with both males and females in developing areas. Additionally, the degree of range expansion or attrition (percent change in area used between years) did not vary with these modeled parameters.

Longer-term data will be useful to differentiate between home range shifts and lifetime range sizes. Savitzky and Petersen (2004) tracked two female *C. horridus* for 5-6 years; based on those area projections, only 60-75% of their cumulative ranges would have been apparent after four years of tracking. Unfortunately, resource limitations in most studies do not permit tracking individuals for ≥ 5 years. Further, lifetime home ranges could never truly be quantified as space use is determined by the spatial dynamics of prey availability and mate distribution and thereby, ranges would continue to adjust spatially even for the most philopatric species. It is our responsibility when making recommendations to understand that the projections of space use are often underestimates relative to the lifetime potential of the animal. To the best of our data's ability, researchers should quantify space requirements and the drivers of home range size and configurations as it pertains to population-level management and conservation strategies.

While direct habitat loss is a critical issue for global biodiversity, the effects of habitat degradation should not be underestimated, particularly for ectothermic animals that can be so readily affected by microhabitat alteration and destruction (e.g., Goode et al. 1995). This case is particularly important for these large-bodied, low maintenance ectotherms. *Crotalus horridus* is a habitat generalist but relies on a forest structure that allows sufficient light penetration and thermal gradients to bask around foraging and overwintering sites (e.g., Brown 1993). Continued practices of prescribed burning prevent vegetation overgrowth that could reduce these opportunities. In this study, some of the noted range shifts were not away from areas that had experienced habitat removal, but from unburned areas that may have become too densely vegetated. Lastly, hunting for purposes of deer culling and invasive feral hog management will facilitate not only habitat maintenance. Unfortunately, in many locations, snakes, and venomous species in particular, are killed when found by hunters (e.g., Galligan and Dunson 1979). However, this activity was not a source of mortality in this study as hunters were always accompanied by local resource managers who supported the project and discouraged killing of snakes.

It is noteworthy that snakes have already been observed in this study to gradually shift their home ranges into remaining forest patches in concomitant with and presumably in response to construction activity and habitat degradation. While we are in our infancy in understanding the mechanics and ultimate population-level viability of these shifts, it is important and encouraging that snakes are responding to the changing landscape and assessing new opportunities. These animals are hard-wired to learn their environment in an efficient and accessible manner. In coastal habitats, microhabitat features change readily due to periodic flooding and storms, and it is likely they would have adapted the flexibility to adjust their activities and learn new locations to accomplish foraging needs in these naturally dynamic environments (e.g., Kamil 1983). That being said, there are clear management implications that rattlesnakes could shift away from development activity, but only if adequate forest remnants and conservation areas exist for them to adjust their activity to that are free of the pressures that make them shift.

Landscape Change.— While development had an effect on home ranges, the continuous variables of distance to nearest open space and road density did not exhibit effects on any of the home range size analyses. Distance to nearest opening served as a proxy for this initial stage of habitat fragmentation to test for an influence on *C. horridus* activity configuration relative to habitat edges. While rattlesnakes have been shown to be deterred from highly trafficked edges and open spaces (e.g., Sealy 2002, Laidig and Golden 2004, Andrews et al. 2008), they are also frequently attracted to edges for the thermoregulatory benefits of post-foraging and gravid states (e.g., Reinert and Zappalorti 1988, Savitzky and Petersen 2004, Waldron et al. 2006a).

Road development accounted for the third largest type of infrastructure increase behind the construction of stormwater lagoons (30%) and clearcuts (36%), the latter of which were created to store earth and dirt displaced to build the lagoons (Figure 4.7). Road mortality, which will be addressed in a separate manuscript, resulted in the premature death of three snakes to date. All mortalities were during breeding season in fall 2007; road mortality did not occur in subsequent fall seasons due to reduced level of construction traffic from reduced construction activity in the economic recession. This reprieve is temporary; as human activity increases both in terms of traffic and construction, mortality inevitably will as well.

Road density has demonstrated negative effects on herpetofaunal populations, although little is known about snakes (see Andrews et al. 2008 for review). Road mortality in many snake species is male-biased from increased breeding season movements, which inherently increase the frequency and likelihood of their crossing roads (Andrews and Gibbons 2008), and encountering humans (e.g., Aldridge and Brown 1995), both of which subsequently reduce survival probabilities (e.g., Bonnet et al. 1999b). Sealy (2002) noted skewed sex ratios that were attributed to male-biased removal from the population due to increased mortality during breeding season, in particular on roads. More investigations into the ultimate consequences of these spatial adjustments among the sexes and increased mortality on population and community levels would be timely and contribute to conservation efforts associated with landscape development.

Monitoring wildlife responses to landscape change to acquire continual data on behaviors during pre- and initial-development phases at this field site is a unique research opportunity. The effect of housing and road densities, traffic, and subsequent effects of mortality and development will be further explored. While this study provided insight into *C. horridus* movement patterns during the initial phases of construction of residential and recreational development, the study can continue to determine whether the *C. horridus* population can persist in a more urbanized area, and how this may vary with fragmentation stage.

To understand the ecological mechanisms behind the noted declines in rattlesnakes and other wildlife in response to development and to strategize as to whether there are viable alternatives for mitigating mortality, displacement and removal, we must observe the process and patterns of decline. Many anthropogenic variables confound our ability to do long-term research in these environments. The nature of being solely a scientific observer, with no manipulative and little controlled design potential, challenges our ability to design experiments and produce robust results (e.g., Felson and Pickett 2005). However, in attempts to conserve some of these "ubiquitous," but now declining species along the southern coast, it is imperative to understand that the natural history of wildlife includes not only their baseline biology in undeveloped habitats, but their behaviors in urban environments as well.

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Table 4.1. Snout-vent length [SVL], mass, and sex) of adult telemetered *Crotalus horridus* in Beaufort Co., South Carolina.

Snake ID	Sex	SVL (mm)	Mass (g)
31	F	1078	1043
44	F	1085	840
58	F	1134	998
121	F	1255	963
211	F	1160	720
351	F	1025	960
356	F	1195	1380
368	F	1220	1640
769	F	1100	998
109	M	1338	1089
168	M	1120	1100
171	M	1345	2360
317	M	845	405
378	M	1300	1452
395	M	1135	1060
403	M	1270	1452
759	M	1310	2460
943	M	1020	943

Table 4.2. Summary statistics of home range sizes (ha) for adult *Crotalus horridus* at a field site in Beaufort Co., South Carolina, using three different methods: minimum convex polygons (MCP), fixed kernel distributions (50% and 95%), and LoCoH nearest neighbor convex hulls (50% and 95%).

Method	**N**	**Average (ha)**	**Std. Dev.**	**Minimum (ha)**	**Maximum (ha)**
MCP	18	41.14	45.85	6.66	200.70
Kernel (50%)	18	7.55	14.08	0.98	62.94
Kernel (95%)	18	44.57	76.85	7.57	344.63
LoCoH (50%)	11	1.04	0.94	0.12	2.85
LoCoH (95%)	18	13.27	11.59	1.03	36.12

Table 4.3. Activity range size for adult *Crotalus horridus* (n = 14) at a field site in Beaufort Co., South Carolina, using 95% fixed kernel estimates for their overall, breeding, foraging, and wintering seasons. Sex of the snakes (male = 1, female = 2) and development (whether they resided in a developed area (Develop = 1) or undeveloped area (Develop = 0)) are included.

Snake ID	Overall	Breed	Forage	Winter	Sex	Develop
168	48.93	34.77	85.68	0.80	M	1
317	344.64	523.29	413.70	234.74	M	1
395	42.73	67.25	53.68	0.13	M	1
759	58.38	66.57	44.26	1.17	M	1
943	32.34	20.82	44.11	0.03	M	1
109	38.03	47.33	26.42	0.53	M	0
378	32.66	41.19	31.00	0.46	M	0
403	55.71	129.63	6.37	1.52	M	0
31	7.57	15.53	5.51	0.14	F	1
351	23.71	8.44	27.84	0.35	F	1
58	11.32	11.48	9.83	0.90	F	0
211	10.53	17.88	9.92	0.21	F	0
356	10.83	7.47	12.21	0.76	F	0
769	16.37	27.37	15.40	1.06	F	0

Table 4.4. Home range size data from other radio-tracking studies of *Crotalus horridus* across their range. Average estimates are in bold; ranges are included in parentheses under the averages. All values are in hectares. (*not reported; O = Overall average, M = Male, F = Female). Values from this study are included for comparative purposes.

MCP 100%			**95% Kernels**			**50% Kernels**				
O	*M*	*F*	*O*	*M*	*F*	*O*	*M*	*F*	**State**	**Reference**
*	**94.3**	**31.2**	*	*	*	*	*	*	WV	Adams 2005
*	* (6-465)	* (2-17)	*	*	*	*	*	*	MO	Anderson 2010
266.7 (1.5-722.2)	*	*	*	*	*	*	*	*	NJ	Laidig and Golden 2004
27.4 (1.8-123.5)	**48.6** (3.5-123.5)	**13.3** (1.8-46.4)	**45** (1.3-219.2)	**83.7** (8.0-219.2)	**24.4** (1.3-89.7)	**4.5** (0.3-25.2)	**6.3** (0.5-21.6)	**3.3** (0.3-25.2)	NJ	Reinert and Zappalorti 1988
*	**90.7**	**35.4**	*	**74.7**	**31.3**	*	**10.7**	**4.9**	VA	Savitzky and Petersen 2004
24.5 (10.9-64.8)	**40.2** (15.5-64.8)	**14.1** (10.9-20.3)	*	*	*	*	*	*	NC	Sealy (2002)
*	*	*	*	**48.4** (8.6-107.5)	**30.8** (10.7-134.1)	*	*	*	SC	Waldron et al. 2006a
41.14 (6.66-200.70)	**70.65** (38.49-200.70)	**11.63** (6.66-19.33)	**44.57** (7.57-344.63)	**77.01** (32.34-344.63)	**12.13** (7.57-23.71)	**7.55** (0.98-62.94)	**13.04** (4.32-62.94)	**2.05** (0.98-3.88)	SC	Andrews 2010 (this study)

Table 4.5. Summary of home range metrics for adult male and female *Crotalus horridus* in Beaufort Co., South Carolina, using the various estimation approaches: minimum convex polygons (MCP), 50% and 95% fixed kernels, and 50% and 95% LoCoH nearest neighbor convex hulls.

Method	Sex	N	Average (ha)	Std. Dev.	Minimum (ha)	Maximum (ha)
MCP	M	9	70.65	49.92	38.49	200.70
	F	9	11.63	3.88	6.66	19.33
Kernel (50%)	M	9	13.04	18.78	4.32	62.94
	F	9	2.05	0.94	0.98	3.88
Kernel (95%)	M	9	77.01	100.79	32.34	344.63
	F	9	12.13	4.99	7.57	23.71
LoCoH (50%)	M	5	1.81	0.87	0.70	2.85
	F	6	0.40	0.26	0.12	0.79
LoCoH (95%)	M	9	21. 80	10.79	7.28	36.12
	F	9	4.74	2.30	1.03	7.75

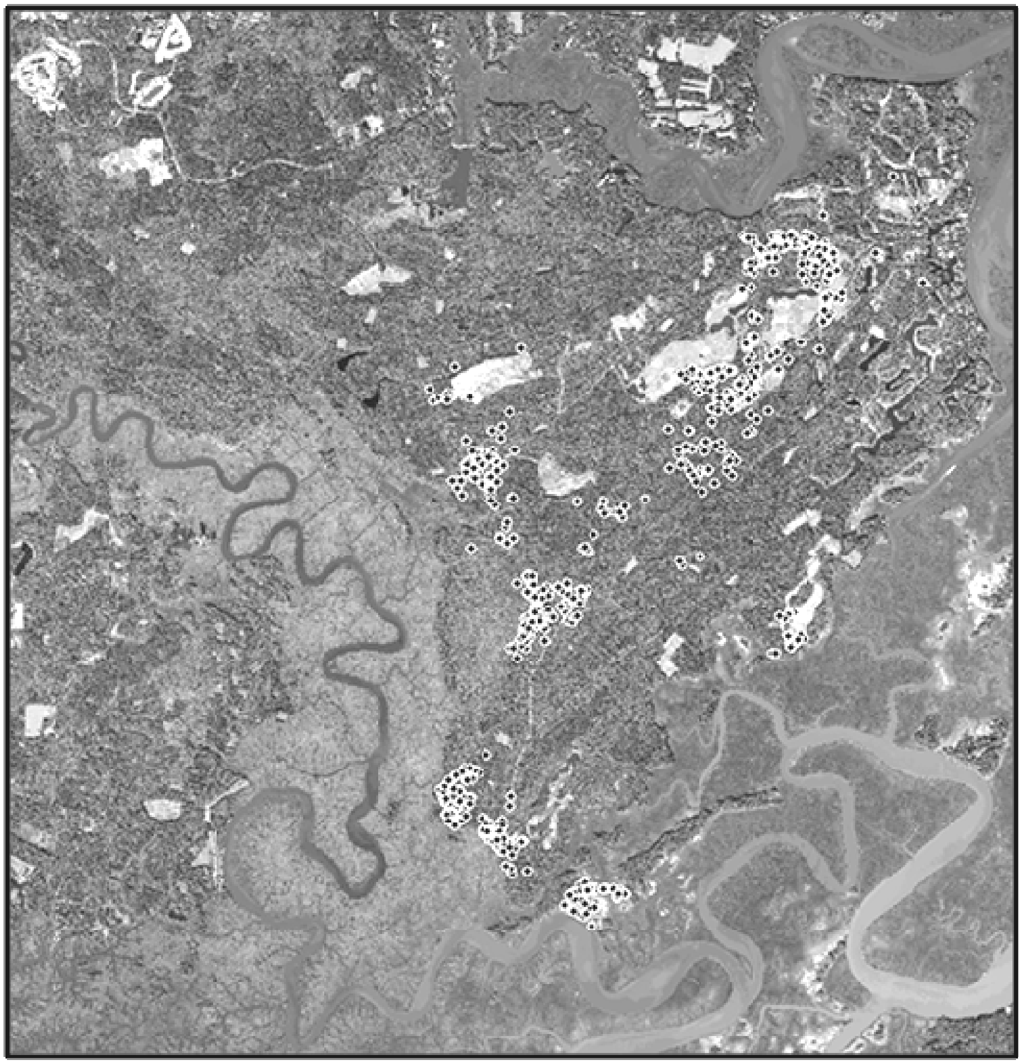

Figure 4.1. All snake locations for adult telemetered *Crotalus horridus* at an 8,094 ha field site in Beaufort Co., South Carolina. Locations are represented by black dots with white outlines (*n* = 1483). Telemetered individuals were located in developing and undeveloped areas (see Figure 4.3 below).

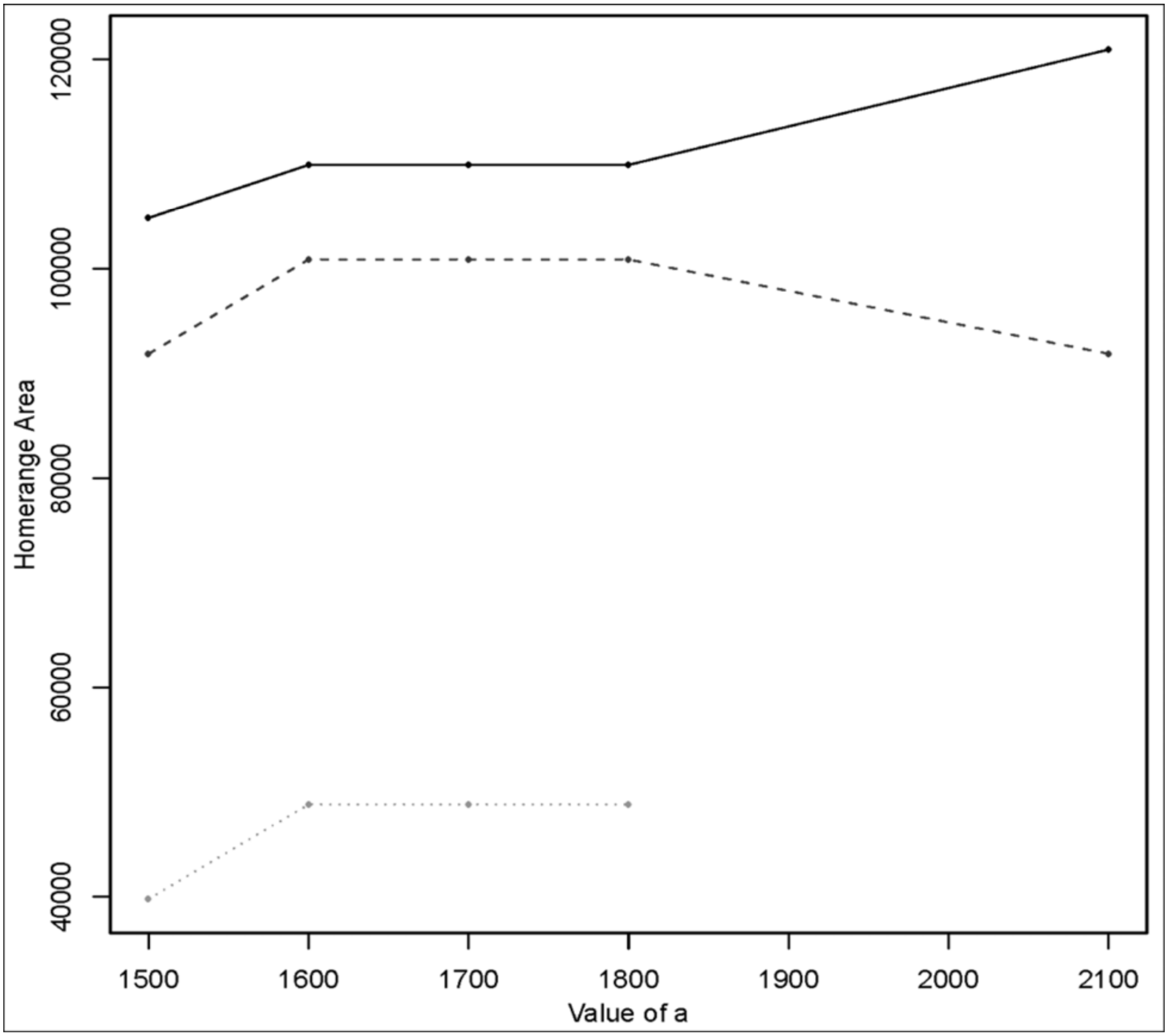

Figure 4.2. Graphical output used to determine value of *a* (radius used to calculate nearest neighbor convex hulls based on *k*-1 nearest neighbors). Selected *a* is determined by identifying the point of first plateau; in this instance, *a* = 1600. The lines represent different isopleths (75, 90, and 95%, bottom to top). This graph represents an adult male *Crotalus horridus* in an undeveloped area in Beaufort Co., South Carolina.

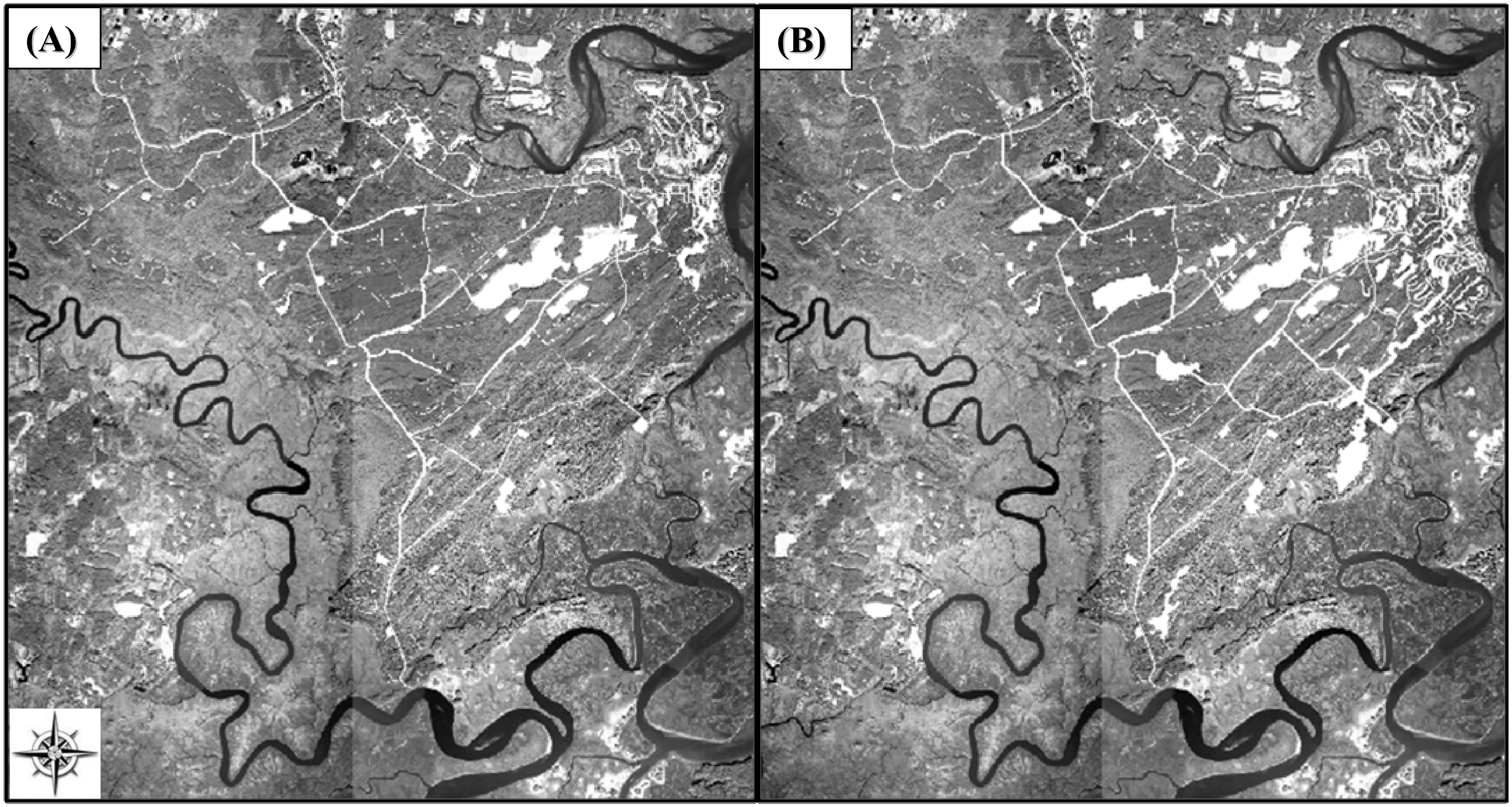

Figure 4.3. Aerial photography of an 8,094 ha field site in Beaufort Co., South Carolina in (A) 2006 and (B) 2010. The site is bound by the three rivers shown here, with the exception of the northwestern portion of the site. White areas represent features (e.g., buildings, clearcuts, fields, roads and trails, stormwater lagoons) that were incorporated into open space calculations.

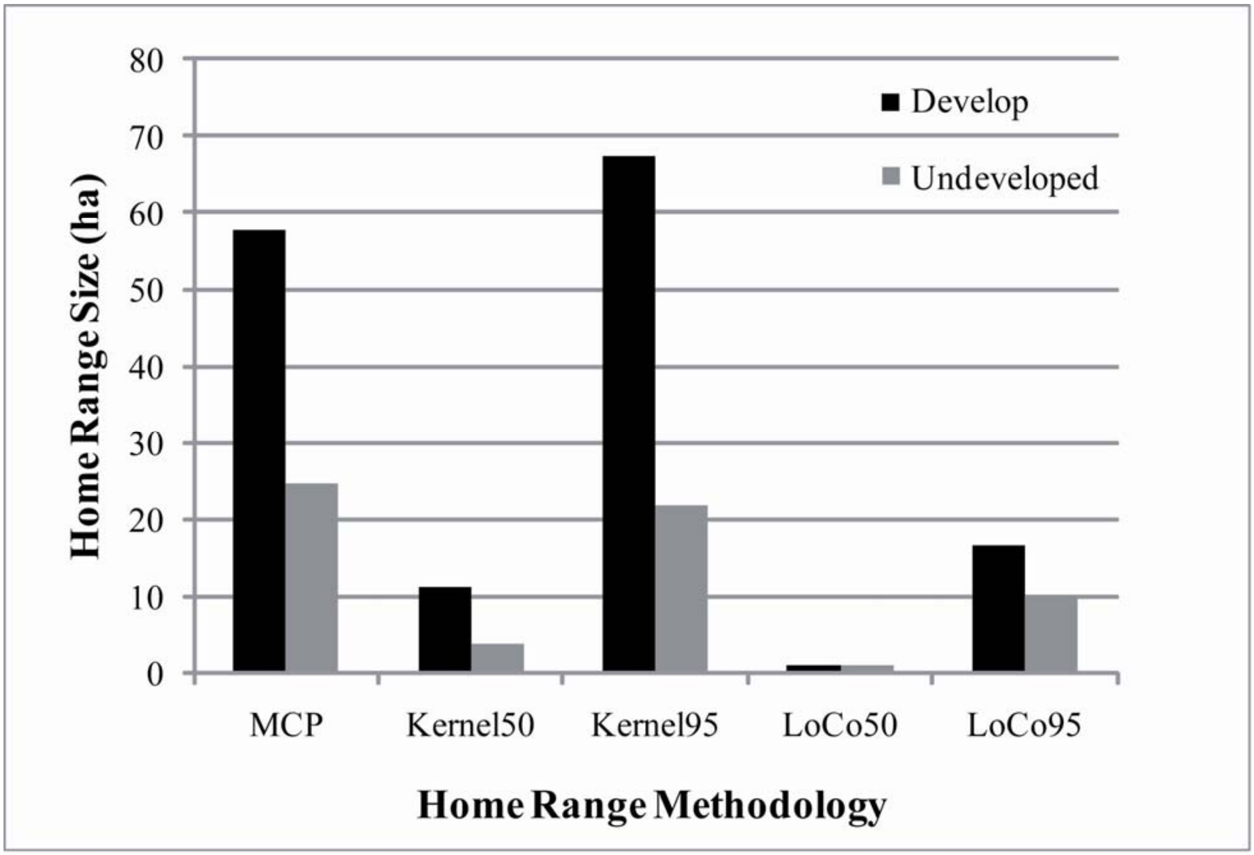

Figure 4.4. Average home range sizes of *Crotalus horridus* in Beaufort Co., South Carolina in developing and undeveloped areas for each home range calculation methodology. Differences among development treatments were significant for all analyses (MCP, fixed kernels [50% and 95%]) other than LoCoH nearest neighbor convex hulls (50% and 95%).

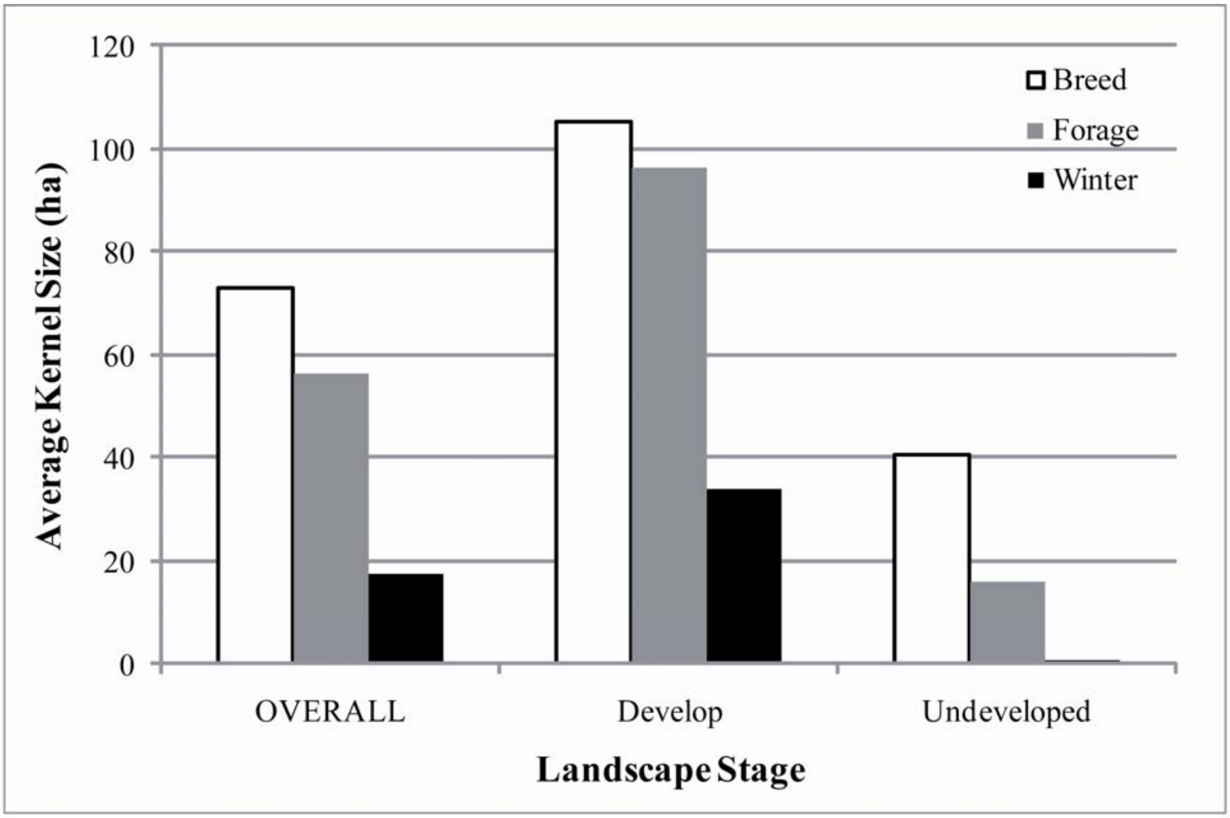

Figure 4.5. Average size of fixed kernels for adult *Crotalus horridus* for each activity type (breeding, foraging, and wintering) overall, and relative to development phase at a residential development site in Beaufort Co., South Carolina.

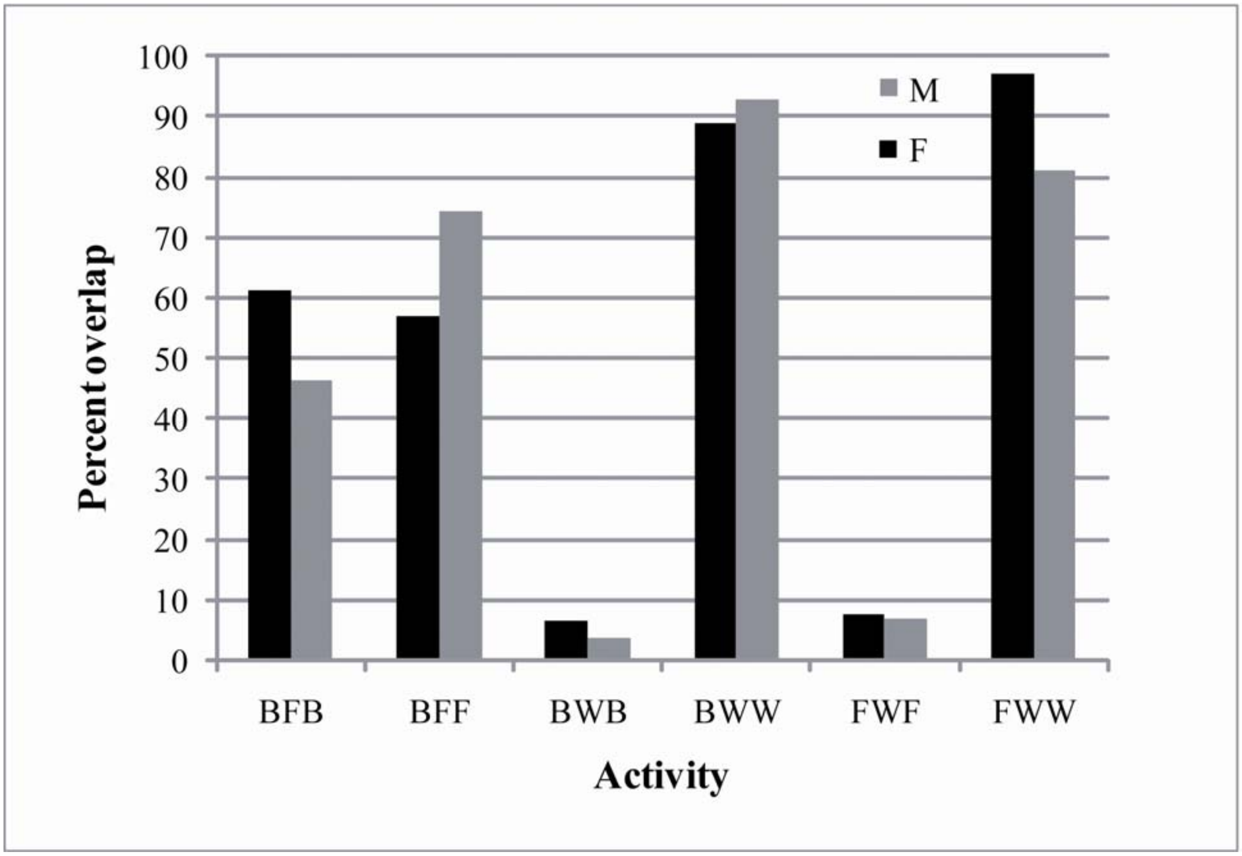

Figure 4.6. Percent overlap in activity ranges for adult male and female *Crotalus horridus* in Beaufort Co., South Carolina. As an example of how these values were calculated, the percent overlap for BFB is the area of overlap (ha) of breeding and foraging season kernels divided by the area of the breeding season kernel. X-axis labels are further defined as: BFF (Breeding-Foraging season overlap/Foraging range), BWB (Breeding-Winter season overlap/Breeding range), BWW (Breeding-Winter season overlap/Winter range), FWF (Foraging-Winter season overlap/Foraging range), and FWW (Foraging-Winter season overlap/Winter range).

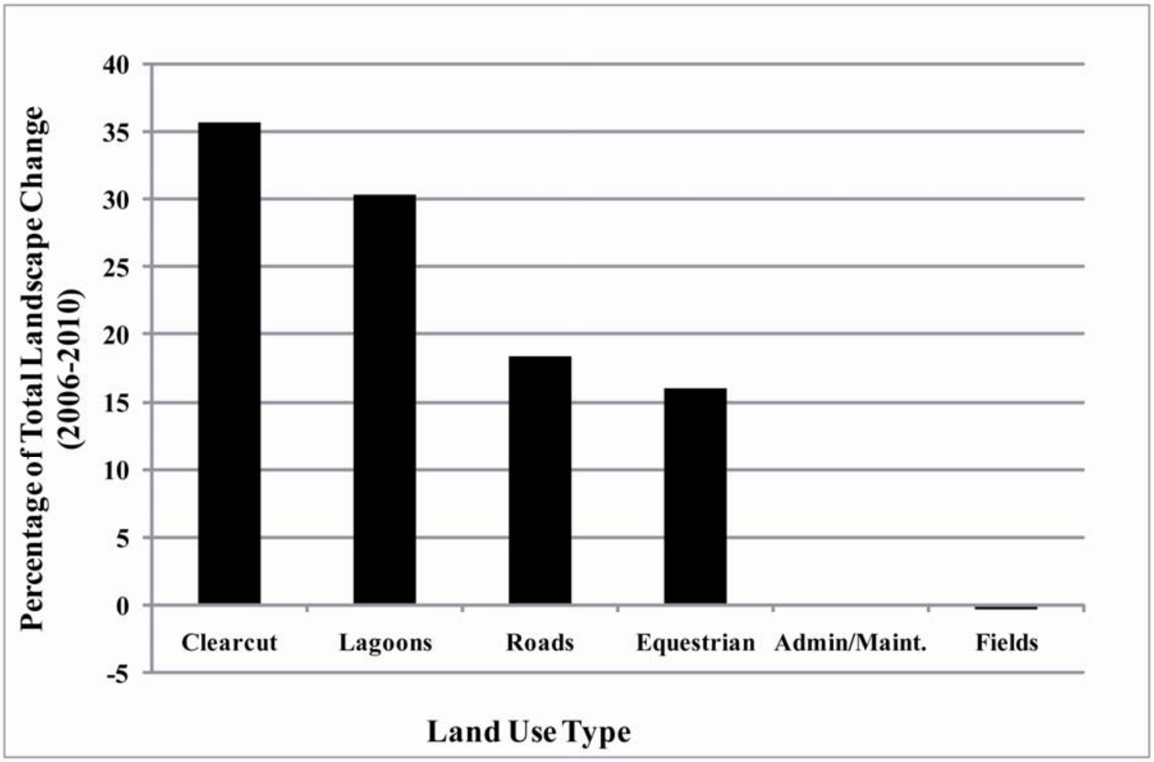

Figure 4.7. Percentage of total change in development footprint (2006-2010) for six landscape features at a residential development in Beaufort Co., South Carolina. Equestrian includes equestrian fields, trails, and home lots. Administration/Maintenance includes all commercial and office buildings; there was 0% increase in these features. Fields represents wildlife food plots, and the only land use type that decreased (0.27%).

CHAPTER 5

COMPARATIVE OVERWINTERING ECOLOGY OF A COASTAL AND AN INLAND POPULATION OF TIMBER RATTLESNAKES (*CROTALUS HORRIDUS*) IN THE SOUTHERN UNITED STATES[4]

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[4] Andrews, K. M., and J. L. Waldron. To be submitted to Journal of Animal Ecology.

ABSTRACT

The timber rattlesnake (*Crotalus horridus*), the rattlesnake species with the broadest geographical range, exhibits a high level of phenological variability among populations in breeding season, reproductive frequency, and hibernation patterns. Here, we investigated timber (= canebrake) rattlesnakes in the southern part of their range. Data on 35 telemetered individuals were examined using coastal (Beaufort Co.) and inland (Hampton Co.) field sites in South Carolina. Surface activity and the number of hibernacula (i.e., structure) used by snakes between October and April were analyzed for potential effects of body condition, sex, temperature, rainfall, and photoperiod on seasonal, monthly, and daily time scales. At seasonal and monthly scales, average temperature and snake body condition were consistently included in the best supported models. Average temperatures (daily and 3 days prior), precipitation, and photoperiod were in top-ranking individual daily models. The two sites were significantly different in the dominant hibernacula and structure types (e.g., stump, root mass, armadillo burrow) used during the wintering season and the months immediately preceding and following core hibernation periods. Lastly, we found no effects at the coastal site of initial development activity or the distance from snake locations to the nearest manmade open space, although road density did have an effect. These data not only allow us to further understand variability of this species within a region, but provide insight into the flexibility of this ectothermic, low-maintenance predator to slight differences in its environment.

Key words: Body Condition, Climate, Development, Habitat, Hibernation, South Carolina, Structure, Thermal

INTRODUCTION

Temperature and other abiotic conditions are strong drivers in emergent behaviors of ectotherms (e.g., Huey et al. 1989). Bound by behavioral thermoregulation (e.g., Pough 1983), environmental conditions limit these animals in some aspects, but can make them productive in others. Thermoregulation is a key feature of their behaviors in both active and inactive periods and in particular through microhabitat selection of a retreat, and positioning within a retreat (e.g., Huey et al. 1989). Therefore, an assessment of these retreating behaviors during the coldest part of the year can be quite revealing of their overall strategies for surviving the winter. Further, snakes are ideal models for these investigations due to their elongate bodies and high surface-to-body area and a resulting ability to maximize spatial and temporal thermal variability through microhabitat selection and body posturing (e.g., Lillywhite 1987; Peterson et al. 1993).

The geographic range of the timber rattlesnake (*Crotalus horridus*) spans the broadest diversity of ecological habitats of any North American rattlesnake. Hence, activity and habitat-use patterns vary extensively within the species (e.g., Allsteadt et al. 2006; Sexton et al. 1992). Despite a relatively abundant amount of literature on this particular species, we still know little about how to translate this variability into management recommendations for species-level conservation plans. Specifically, *C. horridus* populations in the southern part of their range, where they are often referred to as canebrake rattlesnakes, remain under-studied relative to northern populations. Baseline data on habitat-use patterns and phenology in *C. horridus* in these warmer climates are needed, a need that is becoming increasingly urgent due to rapid and large-scale residential and commercial development pressure in warm, coastal environments. Further, southern conspecifics are larger (SC, Cale and Gibbons 1972; Gibbons 1972) relative to those in cooler regions (e.g., NY, Brown 1993), which implicates larger body sizes to maintain in terms of foraging, reproduction, and overwintering physiology.

Hibernacula of *C. horridus* have been fairly well-characterized in the northern part of their range where, for the most part, they exhibit site fidelity to communal dens (e.g., Anderson 2010; Clark et al. 2010; Cobb et al. 2005). Their reliance on these denning locations strongly influences home range configuration through habitat-use patterns prior to and following inactive seasons (Galligan and Dunson 1979; Brown et al. 1982; Reinert and Zappalorti 1988; Brown 1993; Laidig and Golden 2004; Adams 2005; Browning et al. 2005). However, overwintering habitat and activity characterization for southern populations of *C. horridus* have not been published. In general, less research has been conducted on these populations than at northern sites, at least in part because the detectability of *C. horridus* is lower as they are more spatially dispersed and cannot be as easily surveyed and captured *en masse* as at denning-site aggregations upon spring emergence.

Climate change may also have consequences for ectotherms. Current models for the southeastern U.S. predict increases in temperature ranging from 2.5ºC to 5ºC, as well as changes in patterns and quantities of precipitation and increased flooding from sea-level rise (e.g., Karl et al. 2009). Wildlife biologists are in a state of rapid assessment of climate change effects that can have global consequences on ectotherms, which could influence predator-prey dynamics (e.g., Bickford et al. 2010, Sperry et al. 2010) or disproportionately affect species richness of ectotherms (Moreno-Rueda and Pizarro 2007). Temperature is the most frequently studied variable used in investigating potential shifts over time or animals' adaptability to rapid and slight environmental changes (Visser 2008). Hence, field assessment of the influence of abiotic conditions on surface activity and hibernacula use in *C. horridus* is a timely exercise.

For comparative purposes, we selected a coastal and an inland population in South Carolina for study. We used radiotelemetry data collected between 2002 and 2010. We quantified winter activity at three temporal scales: seasonal/annual, monthly, and daily (i.e., individual snake locations). We predicted that 1) snakes from coastal and inland field sites would differ significantly in surface and hibernacula activity; 2) temperature would have a positive relationship with surface activity; 3) snakes with lower body condition would bask more (greater surface activity); and 4) snakes with higher body condition would have the physical reserves to move more frequently during winter (use greater numbers of hibernacula).

MATERIALS AND METHODS

Study sites.— This investigation was conducted using radiotelemetry data from two study sites in South Carolina. The coastal field site was located in Beaufort Co., was approximately 8,094 ha in size, and largely bounded by both brackish and freshwater rivers. During the Pleistocene Epoch (i.e., approximately 10,000 ybp), the site was a barrier island. The property included upland pine stands (previously managed for northern bobwhite (quail, *Colinus virginianus*), maritime forests, mixed pine-hardwood, and salt marsh hammocks. A natural diversity of wetlands, bogs, and other ephemeral freshwater bodies was present, but much of the hydrological landscape was altered due to ditching for agriculture (e.g., indigo, cotton, rice) that occurred in the initial settlement of the property in the early 1700s (Kennedy 2005).

This site was privately-owned and undergoing residential and recreational development during this study. Prior to acquisition by the developer, the property had been owned and managed by Union Camp Corporation primarily as a private hunting preserve, and for periodic timber harvesting. These activities warranted regular prescribed burning and maintenance of wildlife openings. These management techniques were still employed to the best of the ability of the on-site natural resource entity, but were limited due to expanding development in Beaufort Co. (U.S. Census Bureau 2010, http://quickfacts.census.gov/qfd/states/45/45013.html, accessed 9 October 2010) and in-house resource limitation.

The coastal property was acquired by developers in 2001 and construction was initiated in 2002. The developers prioritized land protection via areas limited to human access and conservation easements. Further, current land-use plans targeted smaller, more concentrated housing communities interspersed with ecological conservation areas within the larger landscape. Due to the early stage of development planning and construction and the reduced rate of land conversion as influenced by recent economic recession, much of the property was still in its pre-development state.

The inland field site was state-owned property in Hampton Co., South Carolina that was managed (e.g., prescribed fire, wildlife openings) for wildlife and pine savanna preservation by the South Carolina Department of Natural Resources. This location was approximately 4,900 ha in size; study snakes were located across approximately 2,800 ha of this property and were collected over three field seasons (2002-2004). For further site description, see Waldron et al. (2006a). The two field sites were 65 km apart and differed in average temperature for October-April by approximately 1ºC (*coastal*: 14.78ºC; *inland*: 13.46ºC). The coastal site in Beaufort Co. has an average elevation of approximately 7 m above mean sea level, and an average of 23 m at the inland site in Hampton Co.

Radio Telemetry.— Radio telemetry was used at both field sites to collect data on free-ranging *C. horridus* to monitor home-range size and habitat use. Additionally at the coastal field site, we incorporated responses to development features. Snakes were hand-collected both opportunistically and through targeted field searches. All snakes were reproductively-mature adults based on reproduction and growth data from Savannah River Site in Aiken Co., SC (Gibbons 1972). Radio transmitters (SI-2, *coastal*: 13 g., 36 mos.; *inland*: 11-13 g., 24 mos.; Holohil Systems, Carp, ON) were surgically implanted. Snakes included in these analyses were restricted to individuals monitored for entire wintering seasons (October-April; *coastal*: non-gravid females, $n = 9$, males, $n = 9$; *inland*: non-gravid females, $n = 9$, gravid females, $n = 1$, males, $n = 8$). For transmitter placement techniques, see Waldron et al. (2006a); techniques used for coastal snakes were comparable to those used at the inland site where snakes were anesthetized with isoflurane using an isoflurane vaporizer. Post-operative coastal snakes were instead monitored in captivity for 24-48 hours following surgery prior to their release at the site of capture. Handling and surgery protocols for coastal snakes were covered under the University of Georgia Animal Use Protocol #A2006-10175; protocols were revised and approved annually (current – #A2009-6119). Procedures for inland snakes were conducted under Clemson University Animal Use Protocol #20032 and #50062.

Coastal snakes were monitored for up to three years; the individuals presented here were tracked for two years, on average. Snakes were located weekly during all months of the year using radio receivers (Communications Specialist, Inc., R-1000, Orange, CA) and a Yagi (3-way) directional antenna. Locations were recorded using a Global Positioning System (GPS; Trimble GeoXT, Sunnyvale, CA) and post-processed using GPS Pathfinder Office v.4.10 (Trimble Navigation Limited, Sunnyvale, CA). Points generally achieved an estimated spatial accuracy of <2 m.

Inland snakes were monitored for up to one year and located five days each week during spring, summer, and fall using a radio receiver (Telonics, TR-2, Mesa, AZ) and a 2-element directional antenna. From December-March (inactive season), snakes were tracked every 2-4 weeks. Snake locations were recorded using a Global Positioning System (GPS; Trimble Pro XR, Sunnyvale, CA) with real-time differential correction and an estimated spatial accuracy of <5 m.

Habitat and Snake Data Collection.— Various microhabitat data were collected at each snake location at both field sites. For this study, we restricted our methodological presentation to data analyzed for this *post hoc* analysis. When snakes were directly observed, we recorded body postures, and data were analyzed categorically (i.e., ambush, coil, extended). We recorded snakes as either underground or 'no visual' when surface status could not be confirmed. Additionally, body condition was calculated as the residuals of snout-vent length (SVL; mm) versus mass (g), based on measurements obtained upon initial capture of the snakes. Further, habitat parameters were collected on activity surrounding hibernacula and other microhabitat structures used in the months immediately preceding and following hibernation (submerged, or not exposed to the surface the majority of the time) in order to include the preparatory and recovery periods of wintering seasons. Further, because we observed high levels of variability in the timing of ingress and egress; we included weather and telemetry data from months that encompassed all submergence activity across all years, between both sites. We quantified how many hibernacula were used, and categorized hibernacula as follows: armadillo burrows, logs & debris, root masses & trees, and stumps.

Weather Data.— Environmental data for both study sites were obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center (http://www.ncdc.noaa.gov/oa/climate/climatedata.html, accessed 18 September 2010). Daily or hourly surface data were collected from weather stations that were an average of 30 km of the two study sites. For our candidate models, we included the average daily temperature, daily minimum and maximum temperatures, and daily precipitation. Photoperiod was calculated using sunrise and sunset data from the NOAA Earth System Research Lab's Solar Calculator (http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html, accessed 18 September 2010). Photoperiod did not differ significantly between years or field sites (years, $t = 1.35$; sites, $t = 1.74$; $P > 0.05$); therefore, daily measurements were used across seasons and weather station locations.

Season Models.— Season models represented the largest temporal scale considered in this study. For season models, we included weather and radiotelemetry data collected from individuals (*coastal*, $n = 18$; *inland*, $n = 18$) that were tracked during an entire winter season (i.e., 1 October – 30 April). Surface activity was defined in all models as the number of times an individual was observed on the surface relative to the total number of times the snake was tracked in that season. All radio locations were achieved during daylight hours but were varied within and among individuals so that no individual was always tracked at the same time of day.

We used events-trials logistic regression (Proc Logistic; *event* = number of surface-active observations per season, *trial* = number of radio locations per season) to assess the effects of site, sex, body condition, and daily temperatures (average, minimum, and maximum), on surface activity. Secondly, we modeled the influence of site, sex, body condition, and weather (temperature and precipitation parameters) on the number of hibernacula that were used by individuals within each season of observation using Poisson regression (Proc Genmod). A single hibernaculum was defined as a single structure that provided subterranean refuge from cold temperatures. For example, if a snake did not have to surface to move to another location, but could move within a root network, we counted the structure as a single hibernaculum. We calculated the numbers of hibernacula used within a season for each individual.

For seasonal analyses, we developed a series of candidate models (Tables 5.1, 5.2) using Akaike Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). We used the same candidate models in both surface activity and hibernacula use analyses, which allowed us to differentiate between surface activity that reflected basking behavior, and that which reflected an individual's movement between hibernacula. Parameters with correlation coefficients greater than $r = 0.50$ were removed from analyses. We used models with $\Delta AIC_c \leq 2.00$ for inference. Daily precipitation, maximum, and minimum temperatures were correlated with daily average temperature and therefore, removed from the models. Because weather parameters did not vary by site (i.e., 95% confidence intervals for *coastal* [$\bar{x} = 15.07$; upper 95% confidence interval = 15.60, lower 95% confidence interval = 14.54] and *inland* [$\bar{x} = 14.14$; upper 95% confidence interval = 14.44, lower 95% confidence interval = 13.84]), we included study site as a possible predictor of surface activity and hibernacula use.

We conducted an *a priori* ANOVA and determined there were no differences among seasons in surface activity and hibernacula use ($n = 7$; $P > 0.01$). We used one season per snake in our analysis in order to retain body condition as a variable in our models, and selected the season for each individual in which body condition was measured ($n = 27$; *coastal* = 17, *inland* = 10). This selection corresponded with the first year the snake was tracked. We used the Williams method to adjust for overdispersion (Williams 1982) in the events-trials logistic regression models; we incorporated the constant (0.0817), which was derived from the global model, into reduced candidate models. We standardized continuous predictor variables (i.e., body condition and weather parameters) using z-transformations.

Month Models.— We examined the influence of sex, body condition, weather parameters, and photoperiod on surface activity and the number of hibernacula by month (October-April) to obtain a finer temporal scale. Minimum and maximum temperatures and photoperiod (i.e., average monthly photoperiod standardized against seasonal average photoperiod) were removed due to correlation with average temperature, and thus we retained precipitation and average daily temperature in this analysis. We retained one season per snake (monthly data for an individual), and again selected the season for each individual in which the body condition was measured. Candidate models (Tables 5.1, 5.3) were selected using AIC ≤ 2.00 and it was not necessary to correct for small sample size in these analyses. For surface activity, we again used events-trials logistic regression (*events* = number of surface observations per month; *trials* = number of radio locations per month), incorporating the Williams method to adjust for overdispersion; we used a constant as the scale parameter (0.2522) in all reduced models, which was derived from our global model. For the number of hibernacula, we used Poisson regression for count data (Proc Genmod). Again, we z-transformed continuous predictor variables before analysis.

Individual Models.— At the finest scale of our analysis, we assessed the influence of weather and photoperiod on surface activity and behavior (i.e., posture) of snakes. All radio locations for each individual recorded between 1 October and 30 April were included in the individual-scale analysis. Posture was treated as a categorical response variable (i.e., ambush, coil, extended, underground). Specifically, rattlesnakes in ambush (resting head on log or tree, or coiled with snout extending beyond its outer coil) were assumed to be foraging, coiled snakes were assumed basking, and extended was considered an indication of movement. Underground indicated that the snake was subsurface or under (i.e., unexposed to air temperature) a hibernacula structure. Observations where we did not see the snake, or could not confirm its position above or belowground were removed from the analysis.

Surface activity was treated as a binary response variable (i.e., underground = 0, observed on surface = 1). For our weather parameters, we also included temperatures from three days prior to the track location (average, minimum, and maximum). With the exception of daily precipitation, all continuous predictor variables were standardized using a z-transformation. Photoperiod was again transformed by standardizing daily photoperiod values against the average daylight length of the four weeks prior to the radio location. In these models, it was unnecessary to transform precipitation as values were zero-inflated. All of these parameters were correlated with average daily temperature and removed with the exception of the precipitation, photoperiod, and the daily minimum three days prior to the track location. Candidate models (Tables 5.1, 5.4) were analyzed by using a binary logistic regression model to assess surface activity and multinomial logistic regression to assess influences on posture (ambush, coil, extended; Proc Logistic).

Hibernacula.— We compared the types of hibernacula used at both locations to investigate microhabitat structural differences among field sites using the Fisher’s exact test (Proc Freq).

Development.— As the coastal site differed from the inland site in experiencing development activity, we wanted to examine the influence of this changing landscape by conducting site-specific analyses, and to offer further explanation for any differences between sites. Snakes in developed areas were compared with snakes in undeveloped areas to determine if they differed in the percentage of time they spent on the surface, and the number of hibernacula each season and each month (Proc Anova).

Land cover maps were created using Geographic Information Services (GIS; ArcMap 9.3.1) to assess the effects of open space and roads from development or initial landscape fragmentation on our models since these activities were not present at our inland site. Maps were created for the initial conditions (2006) and current conditions (2010). For both years, roads were classified as paved or unpaved, and were categorized as main (e.g., regularly trafficked and usually paved), forest (unpaved one-lane roads), or construction (previously forest roads that were unpaved and had been widened to accommodate two-way dump truck and heavy machinery traffic). Additionally, old forest roads that were no longer trafficked were included as former roads since road footprints would still contribute to edge and open space effects. Finally, to weight the relative width of different road types, polylines (linear features in GIS) for main roads were buffered by 10 m, construction roads by 20 m, and forest and former roads by 3 m. Buffer distances were determined by actual road widths in the field.

Additionally, equestrian, biking, and walking trails were delineated as “open spaces.” Open spaces additionally included wildlife food plots, equestrian fields, home lots, clearcuts, a golf course, and other commercial and administrative development. These various features were merged into a single layer to generate raster layers of Euclidean distances to nearest open space and road densities (ArcMap 9.3.1, Spatial Analyst extension). Distances and densities were associated with each radio location using ArcMap 9.2, Hawth’s Analysis Tools (v. 3.27; Intersect Point Tool). Initial and current values were compared (Proc Ttest) for both distances to open space and road densities to assess whether the mean values of these landscape features had significantly changed over the course of this study. Additionally, we ran multi-scale analyses to determine if road density influenced surface activity (*season*: Proc GLM; *individual*: Proc Logistic). All statistical analyses were performed using SAS versions 9.1.3 and 9.2 (SAS Institute 2008, Cary, NC).

RESULTS

Season Models.— For the analyses of surface activity, three models were used for inference: site, body condition, and the interaction between body condition and the seasonal average of daily average temperatures, respectively (n = 27; Table 5.5). At this coarse temporal scale, site and body condition more strongly influenced surface activity than temperature, but parameter estimates from top-ranking models were not significant ($P > 0.05$). When investigating the effects on the number of hibernacula within a season, the same three models received the highest support: site, body condition, and the interaction between body condition and the seasonal average of daily average temperatures (n = 27; Table 5.5). Body condition and site were the most important parameters. Parameter estimates from the top-ranking models indicated that body condition was positively associated with the number of hibernacula, but no other parameter estimates were significant (Table 5.6). The parameter weights in the AIC_c models demonstrated that body condition was the most important driver of the number of hibernacula used, followed by the interaction between body condition and the seasonal average of daily average temperatures, followed by the seasonal average of daily average temperatures.

Month Models.— Month had a significant effect on both surface activity and the number of hibernacula used per month (n = 272; $P < 0.0001$). For the analyses of surface activity, three models were used for inference: body condition and the monthly average of daily average temperatures, the monthly average of daily average temperatures, and our weather model (the monthly average of daily average temperatures and monthly precipitation), respectively (n = 168; Table 5.5). Surface activity was positively associated with the monthly average of daily average temperatures, but there was no significant relationship with body condition (n = 168; Table 5.6). Similarly, we saw this relationship in our second-ranked model with the monthly average of daily average temperatures (Table 5.6). The weather model, although supported, did not yield significance for the monthly average of daily average temperatures or monthly precipitation. Parameter weights indicated that the monthly average of daily average temperatures was the most important driver of surface activity at the month scale, followed by body condition.

The analysis of the number of hibernacula at the month scale inferred the top models, respectively: the monthly average of daily average temperatures, body condition and the monthly average of daily average temperatures, and weather (the monthly average of daily average temperatures and monthly precipitation; Table 5.5). In our top-ranking model, the monthly average of daily average temperatures was negatively associated with number of hibernacula (Table 5.6). We again saw this relationship in our second-ranked model with average temperature (Table 5.6) but body condition was not significant. Lastly, in our third-ranking weather model, the monthly average of daily average temperatures had a negative association with number of hibernacula (Table 5.6) and monthly precipitation was not significant. Therefore, at the month scale, the monthly average of daily average temperatures positively influenced surface activity, but negatively influenced the number of hibernacula used.

Individual Models.— At the scale of the individual, we did not detect a difference in surface activity among sites ($P > 0.05$), but detected an effect of season ($P < 0.0001$) and individual snake ($n = 965$; $P < 0.0001$). Only the global surface model ($n = 965$; Table 5.5) received support in our assessment of surface activity at this scale. Maximum likelihood estimates indicated that surface activity was positively associated with daily average temperatures, positively associated with minimum temperatures three days prior to tracking, and negatively associated with photoperiod (Table 5.6). Daily precipitation was marginally significant ($\beta = -0.178 \pm 0.088$; $\chi^2 = 3.535$; $P = 0.060$).

Again, only the global model for posture was supported ($n = 965$; Table 5.5); model weights were 0.00 for all other candidate models. The maximum likelihood estimates revealed significant values for all three aboveground postures (ambush, coil, extended) for daily average temperatures, which indicated snakes were more likely to be on the surface in warmer temperatures ($n = 965$; Table 5.6). Additionally, minimum temperatures three days prior to tracking were significant for all three aboveground postures as well (Table 5.6). Snakes were more frequently in ambush posture on days with shorter photoperiods (Table 5.6), although this relationship was not as strong as with daily average temperatures. The analysis of maximum likelihood estimates also produced a marginally significant effect that daily precipitation reduced the likelihood for snakes to be coiled on the surface (Table 5.6). The distribution and frequency of various postures among field sites was comparable (Figure 5.1).

Hibernacula.— The types of hibernacula used among the coastal and inland sites differed significantly ($n = 83$; $\chi^2 = 17.72$; $P = 0.0005$); elevated root masses, logs, and debris piles were used more frequently by snakes at the coastal site, whereas stumps were used most frequently at the inland site (Figure 5.2). Logs and debris piles (includes slashpiles) were the structure type used most frequently at both sites (n = 32; 38.55%).

Development.— We did not detect an effect of development on surface activity, or number of hibernacula used seasonally or monthly (n = 29; $P > 0.10$). Mean distances from snake locations to nearest open space did not significantly differ between 2006 and 2010 (n = 700; $P > 0.05$), nor did they significantly affect surface activity. However, road densities did significantly change over time (n = 700; $P < 0.0001$). The effect of road density on surface activity varied with scale: at the season level, no significant effect was evident (n = 39; F = 3.15; P = 0.084). However, at the individual scale, road density was associated with surface activity (n = 497; $\chi^2 = 13.44$; P = 0.0002).

DISCUSSION

Our study demonstrates the variability of behavioral responses at varying temporal scales, a pattern not uncommon in ecology, and one observed specifically with vertebrates, both within and between years (e.g., Burhans et al. 2002; Weatherhead 1989). The interpretation of biological field data can be complicated by issues of scale, and therefore, by the ability of researchers to interpret results relative to the spatial or temporal variability (e.g., Schneider 2001). We assessed the effects of weather, snake, and habitat parameters on *C. horridus* surface activity during winter, and the preceding and following months of hibernation. We conducted analyses based on seasonal and monthly summaries, and on daily data from radiotelemetry locations (October-April), including when an individual entered or left a hibernaculum.

Season Models.— At the seasonal scale (i.e., annual), we observed a strong effect of site as our top-ranking model for both surface activity and the number of hibernacula used within a wintering season; body condition emerged as the second-ranking model for both parameters; lastly, the model containing body condition and average daily temperatures was the third-ranking model used for inference (interaction term for surface but not for hibernacula; Table 5.5). The maximum likelihood estimates were only significant for body condition in the third-ranking model and were positively correlated with hibernacula use (Table 5.6). This positive association in which snakes with higher body condition selected more hibernacula supported our hypothesis. However, since the parameter estimates for body condition were not significant, our results did not support the hypothesis that snakes with lower body condition would bask more.

Even slight differences in temperature and other characteristics of the thermal environment can translate to interpopulation variation in activity and bioenergetics of snakes (e.g., mottled rock rattlesnakes, *Crotalus lepidus*, Beaupre 1995). On the other hand, it would be unexpected to find differences between sites from the perspective of the physiological requirements behind surface activity as *C. horridus* populations have not exhibited intrinsic metabolic differences based on geographic distance alone in investigations comparing *C. horridus* populations in Arkansas and Virginia (Beaupre and Zaidan 2001). These authors also did not detect differences between sexes. However, the coastal snakes in our study were larger (in both SVL and mass) in comparison to the inland snakes, but represented a broader size range (Table 5.7). It is possible that the differences in body size and condition among the snakes sampled could explain some of the differences between sites but more data are needed in general to understand how physical parameters influence overwintering behaviors in rattlesnakes.

Rattlesnakes, and large snakes in general, can be sensitive to slight shifts in temperature, and body size in ectotherms is tied to heating and cooling rates and therefore, surface activity (e.g., Ayers and Shine 1997). Further, a sympatric species, *C. adamanteus*, demonstrated a lack of physiological thermoregulation as their basking temperatures did not significantly differ from biophysical models (Rice et al. 2006). While further research is needed to understand thermoregulatory patterns of these large southeastern pit vipers, it is reasonable to hypothesize that a similar phenomenon could apply to *C. horridus*. Lastly, *C. horridus* adults have high survivorship and few predators (e.g., Brown 1993); therefore, the risk of predation while basking or being exposed is not a substantial limiter on basking behaviors. As all snakes included in this assessment were adults, we feel confident that behavioral responses to predation risk that are seen in smaller snakes in thermoregulatory (e.g., Webb and Whiting 2005) or exposed situations (e.g., Andrews and Gibbons 2005) did not confound our assessment of surface activity.

Month Models.— Our monthly models for both surface activity and the number of hibernacula used within a month revealed influences of body condition and average temperatures as also seen at the seasonal scale (Table 5.5). These models were the top-ranking model for surface activity and the second model for the monthly hibernacula assessment. Average temperature alone was the top-ranking model for hibernacula response and the second for surface activity (Table 5.5). Weather (precipitation and average temperature) was the third-ranking model for both responses (Table 5.5).

Data analyses at the monthly scale were important for demonstrating the influence of month-to-month variability that could not be captured at the scale of seasonal averages. Our results again demonstrated that abiotic factors can influence activity within and between populations, particularly as it relates to body condition (Table 5.6). Average temperature had the greatest relative influence on surface activity. Rattlesnakes were more likely to be on the surface when conditions were warmer than average. Body condition had the second highest parameter weight, and positively influenced surface activity, but this relationship was not significant.

Lastly, weather played a role in the model, but neither of the maximum likelihood estimates for average temperature or precipitation was significant. This pattern was similarly observed with monthly hibernacula use, although the parameter weights for body condition and precipitation were equal. These findings highlight the need to analyze data sets such as these at multiple scales, as we were unable to investigate the influence of precipitation at the seasonal scale where it was correlated with average temperature. The influence of precipitation on reptile activity can vary greatly among taxa (e.g., Brown and Shine 2002), although positive effects of precipitation on snake activity and movement have been noted, particularly in the western United States (e.g., Campbell 1953).

In the monthly hibernacula model, average temperature exhibited a significant negative relationship with the number of hibernacula used. Therefore, cooler temperatures resulted in the use of a greater number of hibernacula. This negative trend was again expressed with average temperatures in our second model, although body condition estimates were not significant. In our third weather model, average temperature again had a negative relationship with number of monthly hibernacula and precipitation was not significant. Therefore, overall, we observed a positive relationship between average temperatures and surface activity, and a negative association between average temperatures and the number of hibernacula used in a month.

Since rattlesnakes have to be conservative in energy expenditure due to low-foraging frequency, these patterns may be indicative of a trade-off during the wintering season when energy can either be allotted to increased basking (and in some instances, foraging and digestion), or in moving to select a new overwintering location. Presumably, *C. horridus* in South Carolina would not need to hibernate at as great a depth as in northern populations since the ground does not freeze in most years. The negative association between number of monthly hibernacula and average temperatures could be indicative of a need to find deeper and warmer refugia when temperatures drop below average. However, this pattern could have been influenced by our inclusion of October and April when rattlesnakes were rarely inactive and therefore, our numbers of hibernacula are lower in these warmer months.

While these differences in elevation could differentially influence the number of hibernacula used due to regular flooding from even small amounts of precipitation at the coastal site, we did not detect a site effect at the monthly level. However, these differences in elevation are minute in comparison to *C. horridus* habitat in mountainous regions of their range. This pattern warrants further assessment of *C. horridus* patterns in the southern part of its range where northern-range dynamics do not seem to be directly applicable. The significance of month as a variable is intuitive and it is ubiquitously understood that organismal activity varies with month. The implications are relevant as we assess the effects of climate change, and the potential that wildlife will temporally adjust their activities to accommodate warmer or cooler temperatures, which could also result in shortened or extended active/inactive seasons (e.g., Sperry et al. 2010).

Individual Models.— Individual behavior varied seasonally and within and between populations, a pattern that was possibly correlated with body condition based on the results presented here. While only the global model was inferred, the maximum likelihood estimates yielded significance for effects of average daily temperatures, the minimum daily temperature three days prior to the track day, and photoperiod (Table 5.6). Temperature and photoperiod have played determining roles for activity cycles for *C. horridus* (Martin 1992). In a study on diamondback watersnakes (*Nerodia rhombifera*), Tu and Hutchison (1995) found higher levels of variability in snake responses to temperature and photoperiod in seasonal and individual capacities. Some studies have found little association between photoperiod and dormancy (e.g., red-sided garter snake, *Thamnophis sirtalis parietalis*, Whittier et al. 1987).

Our posture response models only inferred the global model as well, although the maximum likelihood estimates for average temperatures and minimum temperature three days prior to the track day were significant (Table 5.6). Precipitation appeared to be negatively associated with surface postures, although this relationship was only marginally significant for coiled posture (Table 5.6). Average temperature was positively correlated with all three surface postures (Table 5.6), an association that is correspondent with the overall pattern that snakes are more likely to be on the surface during warmer temperatures. We saw this pattern again for all three aboveground postures with the minimum temperature three days prior to the track day (Table 5.6). Although this observation makes biological sense with this conservative, large reptile that is constrained by minimum temperatures, we anticipate that the association of average temperature and general surface activity would have yielded significant relationships for any of the temperature parameters that could have been modeled if they were not removed due to lack of independence.

Hibernacula.— The vegetative structure used for overwintering hibernacula and in the months preceding and following hibernation were significantly different between coastal and inland field sites. Our results showed that woody debris (logs and stick piles) and root masses (above and belowground) were the primary structures used at the coastal site while stumps are the most important feature for overwintering at the inland site. Further, coastal snakes seemed to use a higher diversity of structure than at the inland site where 61% of snakes used stumps (Figure 5.2).

We were limited in the interpretation of the results on hibernacula use as we did not collect data on availability (but see Waldron 2005 for inland site characterization for *C. horridus*). However, the maritime forest at the coastal site provided an abundance of root masses and woody debris. Conversely, we can state that the increased level of habitat management at the inland site, subsequently resulting in an abundance of regularly burned stump holes, is a habitat feature that is not as prevalent at the coastal site. Due to the convoluted internal layout of some of these stump and root systems, and the articulation of both vertical and horizontal depths of snakes within their hibernaculum, structural differences could possibly explain some of the variation observed among sites in our season models. Further investigation is needed to assess how these microhabitat drivers are influencing overwintering activity in southern populations of *C. horridus*, and in particular how it contrasts with the more permanent rock outcrops and communal denning strategies of northern *C. horridus* (e.g., Brown 1993).

Development.— We did not see an effect of development activities at the coastal site on surface activity or hibernacula use in the snakes. Road density increased by 17% over the course of the study, and was responsible for 18% of the overall development footprint increase (274 ha). Road development accounted for the third largest type of infrastructure increase behind the construction of stormwater lagoons (30%) and clearcuts (36%), which were created to store earth and dirt removed to build the lagoons.

We did not see an effect on surface activity from distance from snake locations to the nearest manmade habitat opening, yet we did see the potential for road density to influence surface activity during the wintering season, although the data and objectives presented here did not provide further explanation. Most edge use observed at the coastal site occurs in warmer times of the year while snakes are foraging or digesting and may have been detectable by distance analyses that includes year-round activity. Similarly, even when exposed in open areas, or along edges, snakes tended to be coiled next to some vegetation or other potential retreat. This behavior was also observed in a study comparing edge use by northern watersnakes (*Nerodia sipedon*) and eastern garter snakes (*Thamnophis sirtalis*) where *T. sirtalis* was often adjacent to open edges, but remained next to retreats (Burger et al. 2004). Edge use was recorded for black ratsnakes (*Elaphe o. obsoleta*) as well where authors noted that edge habitats are high in thermal quality and open spaces are low (Blouin-Demers and Weatherhead 2002).

Development and habitat loss pose potentially the most serious threats to reptile persistence (e.g., Gibbons et al. 2000), particularly for large, venomous snakes that are susceptible to both incidental and intentional mortality as human densities and encounter probabilities increase. The monitoring of wildlife responses to landscape change will continue at this field site, and it is critical to acquire data on behaviors during pre- and initial-development phases. The effect of road density, traffic, and subsequent effects of mortality and fragmentation will be further explored.

Conclusions.— Throughout much of their range, *C. horridus* communal denning sites reflect localized genetic relatedness (e.g., Anderson 2010) due to site fidelity (e.g., Clark et al. 2010) and scent-trailing offspring (e.g., Brown and MacLean 1983; Cobb et al. 2005). In South Carolina, *C. horridus* does not communally hibernate to this same degree (e.g., Waldron et al.

2006b; this study), although multiple individuals at a single location have been observed at both field sites (KMA and JLW, pers. obs.). Although we have observed this spatial association with both adults and juveniles, we are not clear on how space is partitioned within the hibernaculum and whether the adults are in separate chambers, as observed with pine snakes (*Pituophis melanoleucus*) in the Pine Barrens of New Jersey (Burger et al. 1988).

Geographic variation in aggregating behaviors is not surprising considering the differences within the species regarding habitats, abiotic pressures, and behavioral adaptations to environmental stressors. In addition to communal denning behaviors, Sexton et al. (1992) further categorized wintering behaviors in Nearctic pitvipers for individuals who: 1) hibernate individually within the warm season activity areas; 2) seek temporary refuge beneath surface objects; or 3) are active. These behaviors are not unheard of in near-tropical regions of the temperate zones, and year-round activity is observed with dusky pigmy rattlesnakes (*Sistrurus miliarius barbouri*) in Florida (May et al. 1996). In contrast, *C. horridus* hibernate for up to 7 months in the northern portions of their range (Brown 1992; Martin 1992), where they do not surface between ingress and egress; however, we observed regular surface activity during warmer spells of the winter for both adult males and females. Interestingly, these abiotic extremes result in different spatial ecologies and habitat selection patterns (Brown et al. 1982; Waldron et al. 2006a) in terms of site fidelity and the numbers of hibernacula used within a season. Coastal snakes typically not only do not have to avoid freezing, some of their hibernacula are simply under ground cover (e.g., beneath a log) and not necessarily subsurface.

Snakes can afford to be more opportunistic in milder winters because the risk of mortality from surface activity is reduced, and foraging opportunities may present themselves. Our objective of this paper was not to quantify how these various influences could affect survivorship, although the question is of essential importance from a conservation perspective. We observed only two mortalities at the coastal site and no overwintering mortality at the inland site. While it was beyond the objective of this particular study to assess survivorship, it is interesting to note that both mortalities at the coastal site were females that died in February after frequent surface activity and unsuccessful foraging attempts throughout the winter.

Presumably, adults could experience greater fluctuation in body condition within a season (in particular, post-partum females or individuals during drought or resource-limited years) which could express itself as more dramatic influences in wintering behavior. It would be interesting to incorporate post-partum females who have compromised body condition, although we did not include them in this particular manuscript. Further, the question should be posed in future studies of how juvenile rattlesnakes could be affected by these abiotic and habitat variations relative to adults. Juvenile snakes can experience greater sensitivity to winter weather and therefore, could be the more vulnerable demographic to changes in the environment (e.g., Altwegg et al. 2005). Further, although young snakes can demonstrate behavioral plasticity in thermoregulation in response to thermal shifts in the initial stages of their life, they essentially imprint these initial conditions which then results in reduced flexibility to deal with annual variation that they experience later in life, a pattern that could have consequential effects in the face of climate change (Aubret and Shine 2010). These various relationships warrant further exploration.

Flexibility in site selection is likely more than opportunistic in this region as coastal environments are lower in elevation and therefore, have greater propensities to flood. This hydrological consideration is certainly a factor on the coast; despite site fidelity observations at hibernacula for most individuals, the environment of a root mass or decomposing log is more transitory than large rock outcrops, and natural environmental changes to temporary refuges both among and within years may necessitate a snake having to locate a new hibernaculum. This necessity to relocate would not be as high risk in the southern United States as in the Northeast because more habitats would be available in the South that would be suitable for overwintering. In addition, the sufficient habitat options are more diverse and more broadly spatially distributed, which is likely why we do not see the aggregation tendencies observed in northern snake populations (e.g., *C. horridus*, Brown 1993; *P. melanoleucus*, Burger et al. 1988; *T. s. parietalis*, Aleksiuk 1976).

Hopefully, this habitat use flexibility (spatially and temporally) in warm-climate populations would prove useful as their habitat changes from anthropogenic alterations to microhabitat availability. We have not pursued how this spatial distribution of overwintering habitat may influence genetic diversity within a population in the southern parts of the species' range. However, intraspecific variation may pose differential responses to climate change where populations have reduced or concentrated heterozygosity, particularly in combination with landscape fragmentation and habitat loss (Douglas et al. 2009).

A foundational understanding of thermal responses of ectotherms to their abiotic environment and their ability to adapt to given habitat availability will be imperative for assessing potential effects of climate change. Rattlesnakes and other large-bodied ectotherms provide a prime example of species that may not deal well with rapid environmental adjustments due to their sensitive thermoregulatory requirements and low feeding frequency. In addition to the difficulty of predicting how climate change may influence spatial distribution and habitat use of individuals within a population or population genetics, we can only guess at how temperature shifts may trigger shifts in activity seasons, although we have observed shifts already in several taxonomic groups (snakes, Moreno-Rueda et al. 2009; plants, insects, birds, Bauer et al. 2010; marmots, Ozgul et al. 2010). Further, range shifts have been observed with both insect (e.g., Battisti et al. 2005) and migratory bird communities (e.g., Robinson et al. 2009). This spatial adjustment would not only be detrimental for large-bodied rattlesnakes due to the energy expenditure from dispersing and high risk of mortality in human-dominated landscapes, it may be logistically infeasible due to the reduced amount of habitat remaining for coastal populations. Lastly, aside from direct responses, organisms could be forced to make temporal and spatial adaptations due to shifts in both plant and animal prey bases.

Theoretically, rattlesnakes and other ectotherms could benefit from longer activity seasons and milder winters in terms of increased foraging opportunities (and therefore, resource acquisition for reproduction). Additionally, there could be reduced stress from winter temperatures that can result in increased mortality, which arguably are among the greatest constraints for temperate reptiles (e.g., Gregory 2009). However, this increased activity period could also result in prolonged physical stress of a longer active season, or increased exposure that results in increased detectability, and therefore in increased intentional mortality in anthropogenically driven landscapes.

The variability observed among these field sites elucidates that we cannot generalize among populations even within the state, or subregions within the southern part of *C. horridus* range. It is likely this variation is simply indicative of phenotypic plasticity and local adaptation that can be common among snakes (Shine 2005) and often reflective of biotic, abiotic, and habitat differences. Coordination of existing data sets such as these will prove fruitful for understanding some of this variability at differing temporal, spatial, and ecological scales and therefore, generating predictive power with existing data sets as we proactively and reactively attempt to assess and predict climate change influences on ectothermic communities.

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Table 5.1 – Parameter definitions for variables included in the season-, month-, and individual-scale candidate models (see Tables 5.2-5.4). "X" denotes in which models they were included.

Parameter	**Definition**	**Season**	**Month**	**Individual**
Site	Field sites – inland or coastal	X	X	
BC	Snake body condition (residuals)	X	X	
SEX	Snake sex – male or female	X	X	
BC*SEX	Interaction term for snakes' body condition and sex	X	X	
AVE	Average daily temperatures	X	X	X
BC*AVE	Interaction term for snakes' body condition and average daily temperature	X	X	
3DAYLOW	Daily minimum temperature three days prior to the radio location			X
PRECIP	Total precipitation (sum of season, month, or day, respective to each model scale)	X	X	X
PRECIP*AVE	Interaction term for total precipitation and average daily temperature			X
PHOTO	Daily photoperiod standardized against average seasonal photoperiod			X
PHOTO*AVE	Interaction term for photoperiod and average daily temperature			X

Table 5.2. Candidate models for season models for surface activity and hibernacula use analyses. The same candidate models were used for both surface and hibernacula analyses. Models shown here are revised from our *a priori* models after removing correlated variables ($r > 0.5$). Parameters are defined in Table 5.1.

SEASON	SITE	BC	SEX	AVE	BC*AVE	BC*SEX
Global	X	X	X	X	X	X
SITE	X					
SITE SEX	X		X			
BC		X				
SEX			X			
BC SEX		X	X			
BC AVE		X		X		
AVE				X		
BC*AVE					X	
BC*SEX						X

Table 5.3. Candidate models for monthly models for surface activity and hibernacula use analyses. The same candidate models were used for both surface and hibernacula analyses. Models shown here are revised from our *a priori* models after removing correlated variables ($r > 0.5$). Parameters are defined in Table 5.1.

MONTH	SITE	BC	SEX	AVE	PRECIP	BC*AVE	BC*SEX
Global	X	X	X	X	X	X	X
SITE	X						
SITE SEX	X		X				
BC		X					
SEX			X				
BC SEX		X	X				
BC AVE		X		X			
AVE				X			
Weather				X	X		
PRECIP					X		
BC*AVE						X	
BC*SEX							X

Table 5.4. Candidate models for individual models for surface activity and hibernacula use analyses. The same candidate models were used for both surface and hibernacula analyses. Models shown here are revised from our *a priori* models after removing correlated variables ($r > 0.5$). Parameters are defined in Table 5.1.

INDIVIDUAL	AVE	3DAYLOW	PRECIP	PRECIP*AVE	PHOTO	PHOTO*AVE
GLOBAL	X	X	X	X	X	
AVE	X					
LOW		X				
PRECIP			X			
Weather	X	X	X			
PRECIP AVE	X		X			
PRECIP*AVE				X		
PHOTOPERIOD					X	
PHOTO AVE	X				X	
PHOTO*AVE						X

Table 5.5. Top-ranking AIC models for season (A; *n* = 27), month (B; *n* = 168), and individual (C; *n* = 965) analyses of surface activity and hibernacula use.

A SEASON	**Model**	**K**	**AIC_c**	**ΔAIC_c**	**ω_i**
SURFACE	SITE	2	316.39	0.00	0.31
	BC	2	317.52	1.13	0.18
	BC*AVE	2	318.34	1.95	0.12
HIBERNACULA	SITE	2	98.23	0.00	0.29
	BC	2	98.76	0.53	0.22
	BC AVE	3	99.59	1.36	0.15
B MONTH	**Model**	**K**	**AIC**	**ΔAIC**	**ω_i**
SURFACE	BC AVE	3	384.37	0.00	0.54
	Ave	2	384.73	0.36	0.45
	Weather	3	386.11	1.74	0.23
HIBERNACULA	AVE	2	351.99	0.00	0.57
	BC AVE	3	353.98	1.99	0.21
	Weather	3	353.99	2.00	0.21
C INDIVIDUAL	**Model**	**K**	**AIC**	**ΔAIC**	**ω_i**
SURFACE	Global	7	913.754	0.00	1.00
POSTURE	Global	7	2039.798	0.00	1.00

Table 5.6. Maximum likelihood estimates from logistic regression models of surface activity and hibernacula use from coastal and inland canebrake rattlesnakes (*Crotalus horridus*). Selected models for each analysis are listed in order of increasing ΔAIC values. Only models with significant parameter estimates are shown here.

Analyses	**Model**[a]	**Parameters**[b]	**Estimate ± SE**	χ^2	***P***
Season Hibernacula	BC AVE	BC	0.029 ± 0.014	4.34	0.037
Month Surface	BC AVE	AVE	1.274 ± 0.159	64.350	<0.0001
	AVE	AVE	1.271 ± 0.1583	64.484	<0.0001
Month Hibernacula	AVE	AVE	-0.388 ± 0.089	19.02	<0.0001
	BC AVE	AVE	-0.388 ± 0.089	19.02	<0.0001
	Weather	AVE	-0.388 ± 0.090	18.76	<0.0001
Individual Surface	Global	AVE	1.407 ± 0.121	135.999	<0.0001
		3DAYLOW	0.600 ± 0.093	41.378	<0.0001
		PHOTO	-0.391 ± 0.195	4.022	0.045
Individual Posture	Global	PRECIP (coil)	-0.316 ± 0.164	3.7319	0.053
		AVE (ambush)	1.390 ± 0.139	100.303	<0.0001
		AVE (coil)	1.437 ± 0.153	88.595	<0.0001
		AVE (extended)	1.412 ± 0.186	57.785	<0.0001
		3DAYLOW (ambush)	0.808 ± 0.110	54.026	<0.0001
		3DAYLOW (coil)	0.288 ± 0.116	6.138	0.013
		3DAYLOW (extended)	0.647 ± 0.147	19.503	<0.0001
		PHOTO (ambush)	-0.701 ± 0.228	9.439	0.002

[a] Candidate models are presented in Tables 5.2-5.4.
[b] Parameters are defined in Table 5.1.

Table 5.7. Physical parameters of *Crotalus horridus* from a coastal and an inland field site.

				SVL (mm)			**Mass (g)**		
Site	***n***	**Male**	**Female**	***Ave***	***Min***	***Max***	***Ave***	***Min***	***Max***
Coastal	17	8	9	**1145**	845	1345	**1149**	405	2460
Inland	10	6	4	**1066**	980	1160	**987**	735	1380

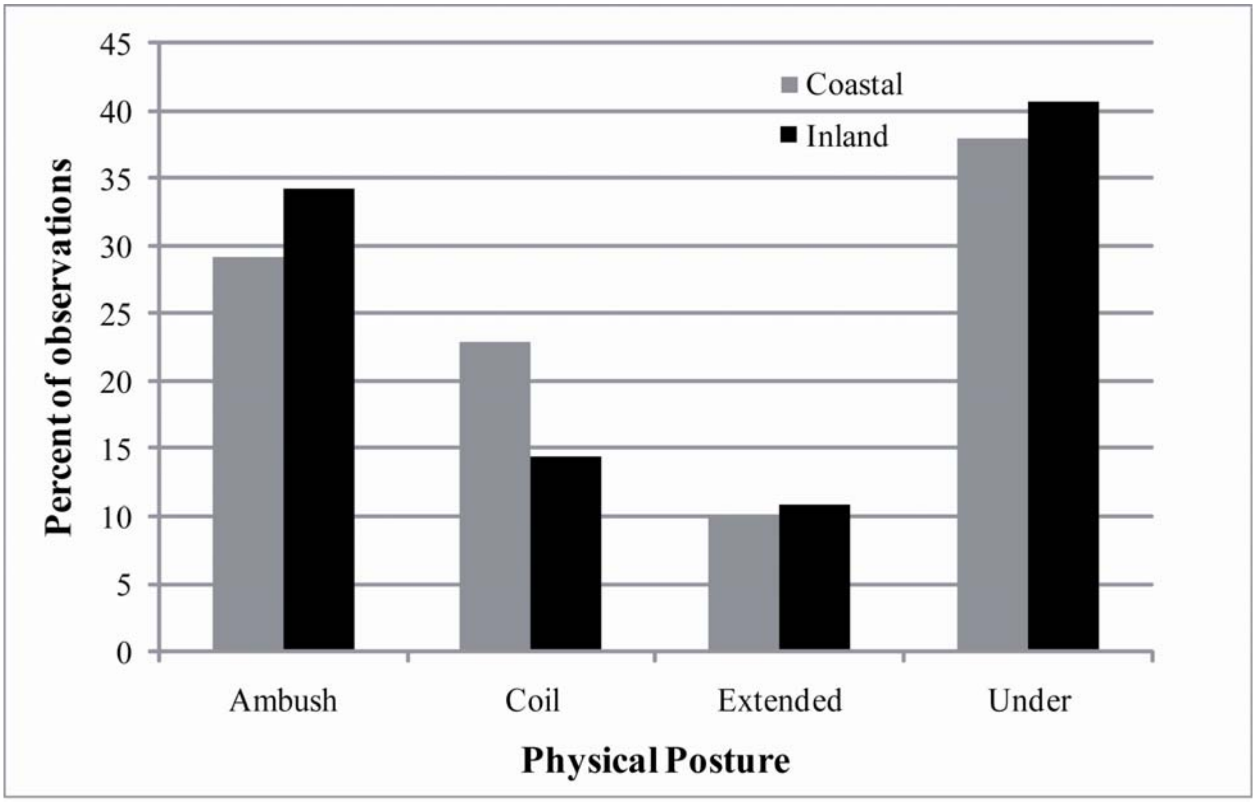

Figure 5.1. Percentage of adult *Crotalus horridus* observed in each of four posture categories at a coastal and an inland field site in South Carolina.

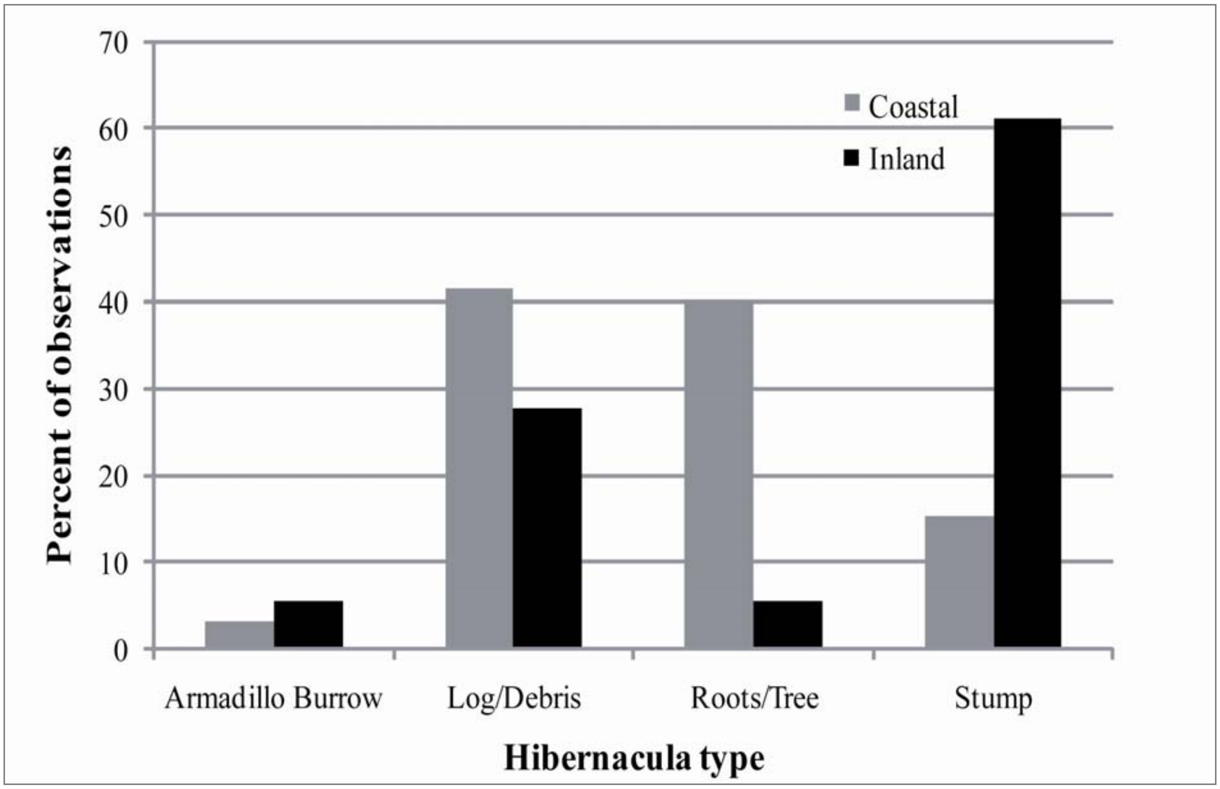

Figure 5.2. Percentage of *Crotalus horridus* observed relative to overwintering structure types at a coastal and an inland field site in South Carolina.

CHAPTER 6

CONCLUSIONS

The overall objective for this dissertation was to provide an assessment of snake behaviors around landscape fragmentation features, in particular the initial stages of construction of residential and recreational development and roads. I have characterized the existing knowledge of a variety of responses not only with snakes but other herpetofauna and the variation both within and among taxa and species in Chapter 2, and within introduction and discussion sections in other chapters. These behaviors can result in avoidance, attraction, and neutral responses, which could simply be responses that we are not yet able to detect on a shorter-term time scale or with these particular data sets. The baseline assessment of behaviors lends information to biologists, land and wildlife managers, and developers and land planners on how to manage from the perspectives of both wildlife and landscapes and habitat patch dynamics.

In these arenas of conservation biology, human dimensions must be incorporated as these aspects influence outcomes more so than biological information. This conundrum warrants that biologists incorporate sociology, psychology, and education and outreach to attempt to adjust mentalities and perceptions about non-charismatic or disliked species, such as snakes. Further, it charges wildlife conservation biologists to continue to design scientifically-robust research in urban settings where we do not have the power to manipulate or control variables as is ideal for the execution of traditional science and statistical evaluation. Lastly, my intention is that these investigations can contribute to a “call to arms” for biologists to be prepared to deal with existing problems that are exacerbated by larger-scale issues and those that involve time lags before effects are detectable, such as genetic isolation, long-term population viability, and changing climates. While we can collect all of the data that we want, we will never make progress unless this information is translated in appropriate manners and placed in the hands of developers and land planners. Further, unless we not only deliver that information, but inspire these authorities as to *why* ecology matters to them (ethically and economically), this information will never be grasped, prioritized, and implemented. Hence, changes will never occur, and we will only continue to collect data to document issues, as opposed to resolving them.

In Chapter 3, our goal was to assess variation within a snake community to determine which species were most actively found on roads, and how these patterns varied within species. These data facilitate prioritization of mortality-prone species and demographics, hence creating a foundation on which to categorize which species are more vulnerable to roadkill, and which species (avoiders) may be more susceptible to fragmentation. To characterize road effects, we must be able to distill which of these behavioral mechanisms are driving the greatest alterations in surrounding populations. As roads enable human access to previously undeveloped land and thereby are catalysts for urbanization, assessments of the differential impacts of roads within and among wildlife species in pre-urbanized areas can offer insights into how species will be affected by roads in urban and suburban areas. We used a long-term (1951-2005) snake database from the Savannah River Site in South Carolina, USA to evaluate inter- and intraspecific differences among snakes captured on roads vs. off-road habitats. Data were collected on 15,697 snakes (35 species) of which 2,577 (29 species) were road captures. In evaluating differences in road-use between sexes of 15 species (n = 1,574), we found that significantly more were males. In the analyses of individual species, 7 of the 15 were significantly male-biased and none were female-biased. Significantly more males than females were also collected in off-road habitats. However, the proportion of males (64%) observed in on-road specimens was significantly greater than that observed in off-road captures (54 %). Of 2,233 captures of 17 snake species for which on-road capture condition (alive vs. dead)was known, significantly more were dead-on-road (DOR; 61%) relative to the number of alive-on-road (AOR). Eight species had significantly higher DOR frequencies, compared to one with a significantly higher AOR frequency. For seven species, longer and heavier individuals were more likely to be DOR. Snakes captured on the road were significantly longer and heavier than those observed in off-road captures. On-road captures within species were significantly larger than off-road captures in five species and significantly smaller in one. Our findings indicate that when assessing the impact of roads and subsequent urbanization on snakes, attention must be given to the differential impacts roads have among species and in relation to individual sex and body size within species.

In Chapter 4, my goal was to assess the potential for development activity to influence spatial use and home ranges of the timber rattlesnake (*Crotalus horridus*), a large venomous snake that is an important ecosystem predator. Conversion of undeveloped and rural areas is rapidly occurring through the process of expanding urbanization. Consequently, habitat loss and degradation have had pervasive effects on wildlife through both direct forms of mortality and habitat fragmentation. This study focused on home ranges of *C. horridus* in coastal South Carolina, at a field site in the early stages of residential and recreational development. To compensate for biases in home range estimations, and to compare techniques, home ranges were calculated using minimum convex polygons (MCP), fixed kernel distributions, and LoCoH nearest neighbor convex hulls (NNCH). Home range sizes determined from radio locations were tested for effects of sex, body condition, development, road density and distance to nearest open space. Using a crossed variable of sex and development, sex affected all home range area estimations and development affected full (95%) range sizes. Overall, home ranges in developing areas were significantly larger than in undeveloped areas. This effect was observed for MCPs and fixed kernel calculations, but not for NNCHs. These latter LoCoH analyses revealed that snakes were not necessarily using more space in developed areas, but activity ranges were larger and more fragmented. When analyzing breeding, foraging, and wintering kernels separately, sex influenced breeding and foraging areas (males had larger ranges than females), but development only affected foraging ranges (ranges in developing habitats were larger than in undeveloped areas). Home range fidelity (interannual range overlap) was reduced in developing habitats where range shifts observed among years within individuals was greater, although neither sex nor development influenced the overall degree of between years. This initial assessment of fragmentation is important to understanding the process of urbanization and wildlife population declines. These data are examples of the type of information that is readily translatable to the multiple stakeholders (biologists, managers, developers, local land planners, and general public) that need to be involved in the process of conserving wildlife in developing landscapes.

In Chapter 5, we assessed overwintering behaviors with the purpose of studying how a limiting factor for survival can elucidate vulnerabilities that may interact with changing features in the landscape. In addition, we compared how behaviors vary among field sites in South Carolina in order to document the sensitivity and variation among populations and therefore, how slight changes in climate may differentially influence this large, ectothermic species. The timber rattlesnake (*Crotalus horridus*), the rattlesnake species with the broadest geographical range, exhibits a high level of phenological variability among populations in regards to breeding season, reproductive frequency, and hibernation patterns. Here, we investigated *C. horridus* in the southern part of their range. Data on 35 telemetered individuals were examined using a coastal (Beaufort Co.) and an inland (Hampton Co.) field site in South Carolina. Surface activity and the number of hibernacula (i.e., structure) used between October and April were analyzed for potential effects of body condition, sex, temperature, rainfall, and photoperiod on seasonal, monthly, and daily time scales. At seasonal and monthly scales, average temperature and body condition were consistently part of our model selection. Average temperatures (daily and minimum three days prior to tracking) were significant in individual daily models, and precipitation and photoperiod also accounted for some of the variation. The two sites were significantly different in terms of habitat influences and the dominant hibernacula and structure types (e.g., stump, root mass, armadillo burrow) used during the wintering season and the months immediately preceding and following core hibernation spells. Lastly, multi-year tracking data at the coastal site indicated no effects from initial development activity or the distance from radio-tracked locations to the nearest manmade open space, although road density did have an effect on surface activity. These data not only allow us to further understand the interpopulational variability of this predator within a region, but provide insight into the flexibility of this ectothermic, low-maintenance predator to slight differences in its environment.