INTERSPECIFIC COMPARISONS OF BEHAVIORAL RESPONSES OF SOUTHEASTERN SNAKES TO ROADS

by

KIMBERLY MARIE ANDREWS

(Under the Direction of J. Whitfield Gibbons)

ABSTRACT

Unsustainable levels of road avoidance or mortality result in the barrier effect, and therefore habitat fragmentation, disrupting metapopulation dynamics and potentially leading to genetic isolation. As ecological behaviors of snakes vary interspecifically, responses of snakes when encountering roads would also be expected to vary interspecifically. The probability of crossing the road significantly varied across species of southeastern U.S. snakes, with smaller species of snakes avoiding the road almost completely. In addition to crossing rates, species were significantly different in crossing speed and responses to a passing vehicle. Venomous snakes crossed the road more slowly than nonvenomous species or species that rely on flight for defense. However, all species crossed the road at a perpendicular angle, minimizing the time spent crossing. Scientific identification of particular vulnerabilities of snake species to roads is essential to mitigate wildlife impacts of existing roads and to design transportation systems effectively in the future.

INDEX WORDS: snake, road, vehicle, mortality, fragmentation, barrier effect, southeast, behavior, interspecific

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DEDICATION

This thesis is dedicated to my grandmother, Ruby Katherine Zurcher Andrews, who taught me to be intrigued and ask questions about nature before I ever had the chance to be fearful or wary of vast unknowns. In stormy weather, she showed me how to count the distance of the lightning and to appreciate its beauty instead of running for cover. This magnificent woman never got to see me catch a snake or give a talk to children, but is smiling at the thought of it.

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To my supporters, thanks for your encouragement and to my critics, thanks for keeping me on my toes.

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The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' (I found it!) but 'That's funny ...'

Isaac Asimov (1920 - 1992)

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CHAPTER 1

INTRODUCTION

In the United States, the road network extends approximately 3.87 million miles, comprising 1% of the nation's land (Forman & Alexander 1998). Even penetrating the nation's protected lands, 10% of these roads occur in national forests (Youth 1999). Development, traditionally defined in terms of structural buildings, has now expanded legally to include roads (i.e., Transportation Equity Act for the 21st Century [TEA-21], 1998), due to their potential to have enormous overall impacts. Roads, although only several meters wide, are increasingly being recognized by biologists as having the potential to alter numerous ecosystem balances. Although roads comprise only 1% of the land surface area in the United States, the ecological impact has been estimated to extend to 15-20% of the country's land (Forman & Alexander 1998). Streams are polluted, altering water quality and faunal communities (Welsh and Ollivier 1998); animals attempt to cross the road and are hit by vehicles (e.g., Lodé 2000); and some species behaviorally avoid the road (e.g., Forman and Deblinger 2000), which potentially restricts their range, fragments their habitat, stunts gene flow, and threatens population viability.

These impacts affect many wildlife groups of terrestrial and aquatic animals, both large and small. The federally threatened grizzly bear has experienced 80% declines in habitat use within 1 km of open roads (Schwartz 1998). Federally endangered red-legged frog populations are now found only in 1% of their original habitat in California's Central Valley, a decrease that is correlated with increasing road development in the area (FHWA 2000).

To understand ecological impacts, we must understand not only resource-limiting aspects of habitat loss but also behavioral reactions of wildlife to such loss that determine how readily wildlife continues to acquire necessary resources amidst landscape alteration. The degree to which the road poses a barrier to movement defines whether the bisected habitat is functionally contiguous (animals cross successfully in significant enough numbers that resources on both side of the road are still available and gene flow is sustainable) or fragmented (mortality rates or behavioral avoidance is high enough that populations are isolated). If the barrier effect of the road continually prohibits immigration and emigration, this isolation will eventually affect fundamental population and community dynamics.

Road impacts can vary among animal groups (frogs and traffic mortality, Ashley and Robinson 1996; snakes and the threats of avian predators, Vandermast 1999; wolves and road avoidance, Thurber et. al 1994), as well as among species within a group that displays an array of ecological tendencies. To adequately mitigate anthropogenic disturbance of wildlife patterns resulting from road development, we must understand the basics of how different groups are affected in regard to daily activities, life cycles, and migratory patterns. Furthermore, for prudent conservation measures to be realized, a balance must be achieved between the construction of roads for domestic and commercial purposes and the persistence of intact habitats and wildlife populations. This balance can be formulated effectively only with science-based designs that are conducive to both human and wildlife movements.

DIRECT EFFECTS

Direct effects are defined here as those that can be attributed to the road itself. The most obvious direct effects are immediate habitat loss (physical land area that the road covers) and on-road mortality. Habitat loss is not only a concern in terms of literal loss from road construction, but also as a precursor to future development in that area (Ritters and Wickham 2003). The threat of being killed on a road can be of even greater consequence if populations recover more readily from a one-time reduction in spatial resources than to the continual removal of individuals from a population.

Approximately 1 million vertebrates die per day on US roads (Lalo 1998) from the 190 million vehicles that travel the roads daily (FHWA 2001). Animals attempt to cross roads in an effort to access resources on the other side or to disperse permanently (i.e., emigrate) to escape unfavorable circumstances. The level of crossing success is dependent on the extent of human use of the road. A standard US highway experiences traffic volumes of approximately 20,000 cars each day at a given location, averaging a car or truck every 4 seconds (Higgins 2000). In areas of lower traffic density, larger time spans between vehicles may allow greater permeability of the road to crossing animals. A developing problem is that an increasing number of roads are experiencing increasing traffic densities, decreasing these crucial windows of time (e.g., Smith and Dodd 2003).

Florida, a state with booming population growth, observes the highest rates of mortality documented anywhere for snakes (U.S. 441, Smith and Dodd 2003) and turtles (U.S. 27, Aresco 2004). A 3.2-km section along U.S. 441 stretches across Paynes Prairie State Preserve along which excessively high levels of snake mortality were documented for over half a century (Van Hyning 1931, Southall 1991). An estimated 100,000 animals representing over 80 vertebrate species were killed annually on this highway (FHWA 2001) before the construction of "ecopassages," which reduced mortality of all vertebrates by 41% (continued mortality was primarily of hylid frogs and birds, whose natural movements were not deterred by the wall) and 93.5% with hylids and birds excluded (Barichivich and Dodd 2002).

Another example is U.S. Highway 27, which bisects Lake Jackson in Leon County, Florida, is traveled by an average of 21,500 vehicles per day (Aresco 2004). The 1.2 km of highway traversing Lake Jackson has become an impenetrable barrier to turtles, preventing virtually all movements of individuals between the two sides of the lake. Over 43 consecutive months, 10,180 reptiles and amphibians (8,833 turtles) of 44 different species were recorded either dead on the highway or attempting to cross the road at the fence. A model adapted to calculate the probability of being killed on the road (Hels and Buchwald 2001) demonstrated a 98% chance of mortality for crossing turtles. Through extensive political communication and a raised awareness of the local public (e.g., www.lakejacksonturtles.org), “ecopassages” will be constructed to provide a permanent and safe route for Lake Jackson’s wildlife.

In addition to incidental mortality, roads can also serve as a lethal attractant. In some situations, road mortality rates are confounding when carrion from road kills becomes a food source for scavengers that subsequently are killed while foraging on the original road-killed specimens (Moore and Mangel 1996). Amphibians attracted to roads by small pools of water that form in roadside ditches use these inappropriate sources of water to lay their eggs (pers. obs.). These pools of water may have high evaporation rates that desiccate eggs and leave them inviable. Roadsides can also serve as a sink for nesting habitat, affecting population demographics via increased mortality of females (Aresco, in review) and their offspring (Mumme et. al 2000).

Road mortality in the United States is a common occurrence that demands ecological investigation and regulation. Annually, 100 million lab animals are killed by experimenters and

200 million game animals are killed by hunters (Braunstein 1997). Both experimental and game take are regulated in recognition that these sources of mortality could exceed sustainable levels. Yet, nearly 400 million are killed by motorists (Braunstein 1997). Thus, mortality resulting as a consequence of roads is worthy of concern also.

INDIRECT EFFECTS

Indirect effects are defined here as effects that occur off-road. The list of ways that wildlife can be negatively influenced in the immediate and the general vicinity of the road aside from habitat loss (Forman 2000) and direct mortality (Hellman and Telford 1956) is lengthy: hydrological alterations (Jones and Grant 1996), noise (Tabor 1974) and light disturbance (Buchanan 1993), vehicle emissions (Hautala et. al 1995), erosion and sediment loading (McCashion and Rice 1983), heavy metal concentrations in the soil and water (Goldsmith et. al 1976), petroleum runoff (Mahaney 1994), changes in vegetation composition (Angold 1997), invasive species (Tyser and Worley 1992), changes in predator and prey concentrations (Dijak and Thompson 2000), parasitism (Robinson et. al 1995), alteration of dispersal corridors (Getz et. al 1978), edge effects (Becky Smith, unpub. data), fragmentation and/or barrier effects (Andrews 1990), behavioral modifications (Mader 1984), and possibly numerous other ways that biologists may not yet be aware of or have thus far been unable to quantify.

The indirect effects of roads are more numerous and more detrimental to wildlife than direct effects (Forman and Alexander 1998), though have received less attention because most are difficult to observe and quantify. The situation is further complicated because impacts may vary by species and locality. For example, impacts may vary with road age, substrate, and width, in addition to vehicular speeds, densities, and daily or seasonal traffic patterns. Thus, road impacts are complex; as the purpose of my research is to investigate the barrier effect of the road, factors influencing road fragmentation will be the focus.

Roads can act as barriers not only when rates of mortality exceed sustainable levels such that inadequate numbers of individuals are exchanged, but also when selective (i.e., genetic or behavioral) avoidance occurs. Road avoidance by wildlife has been documented for several organismal groups (invertebrates, Baur and Baur 1990; amphibians, Gibbs 1998; reptiles, Seigel and Pilgrim 2002; mammals, Oxley et. al 1974). The barrier effect of roads has tremendous implications as the pressure of isolation can reduce genetic diversity via the creation of subpopulations and also result in increased mating competition among fewer individuals. The ultimate threat of local extirpation becomes a concern if inbreeding depression results in more individuals of reduced fitness, lowering viability for the population as a whole. This indirect effect of isolation spurred by road avoidance, can ultimately have bottom-up effects by altering the structure of an entire food chain. The intensity of fragmentation effects varies with each organismal group as shown by Hargis et. al (1999), wherein American marten abundance decreased in edge habitats but small mammal densities increased. Therefore, road impacts on population dynamics should be examined at the level of a particular animal group before generalizing across phylogenetic boundaries.

SNAKES, IN PARTICULAR

Snakes, the focus of this research, are an ideal group to investigate the degree of generality of road impacts, both direct and indirect, not only due to road mortality that has been documented for over half a century, but to their uniqueness as an animal group in the large breadth of ecological niches represented among species.

An array of snake behavior and physiological traits may influence a snake's use or avoidance of the road and its probability of crossing successfully (Table 1). Consistencies would be expected among organisms having similar instinctive behaviors or comparable physical constraints, therefore implying interspecific patterns. Some species may be more susceptible to road impacts due to ecological demands, such as home range size, hence, the degree of dispersal necessary to satisfy critical needs such as mating, foraging, and securing hibernacula (Bonnet et al. 1999). Additional to these factors intrinsic to snakes, extrinsic variables (road and environmental conditions) could also play a role in determining cross and avoidance patterns (Table 1).

Snakes are frequent victims of road mortality (e.g., Klauber 1939, Fitch 1949, Campbell 1953, Pough 1966, Whitecar 1973, Dodd et. al 1989, Bernardino and Dalrymple 1996, Smith and Dodd 2003). In a study in Organ Pipe Cactus National Monument, the effect of individuals lost to road mortality was projected to result in local extirpations over a 5 km^2 area within 4 years, threatening the long-term persistence of the surrounding ophidian community (Rosen and Lowe 94). While the numbers of snakes killed on roads can be appallingly high, mortality measures alone do not reveal how snake populations in surrounding habitats are truly affected.

Crossing speeds and angles are pertinent in that a snake that takes a longer time to cross the road is more likely to be killed by a vehicle. Although road fragmentation as a consequence of the barrier effect is generally thought of in terms of road avoidance, the idea also naturally extends to snakes that do attempt to cross roads but have a high probability of mortality. For instance, snakes that cross the road at a wide angle or at a slower pace prolong the amount of time spent on the open road and in the direct path of traffic. The barrier effect becomes an issue here also as road mortality reaches rates such that genetic interchange is reduced or halted, dividing the local population into isolated subpopulations. The threshold at which the number of snakes being killed on the road is so significant that virtually no, or insufficient amounts of, individuals successfully cross is unknown and would vary with species and location.

Snake species demonstrate drastically different ecological strategies, ranging from fossorial and clandestine to wide-ranging habitat uses. Snakes are more vulnerable to predation when dispersing or migrating to acquire the necessary resources and have evolved adaptations to minimize the chances of being preyed upon when traveling overland (e.g., Vandermast 1999, Shine and Lambeck 1985). Such strategies include crypsis (e.g., green snakes), venom (e.g., rattlesnakes), or speed (e.g., racers and coachwhips). However, species unequipped to avoid predation are less likely to cross open spaces (e.g., ringneck snakes, Fitch 1999).

When considering the chance of a snake encountering and then crossing a road, the resulting scenario is two-fold: wide-ranging species are more likely to 1) encounter a road by simple spatial probability and 2) cross the road due to greater natural defenses against and therefore a reduced threat of predation. Consequently, snakes as a group are expected to exhibit varying levels of mortality and crossing rates among species, yielding interspecific differences in road impacts reflective of natural behavioral and ecological regimes characteristic of the species. In addition, snakes crossing the road are predicted to experience differential probabilities of mortality due to the instinctive behavior and physical ability of some species to move faster across an open space than others. The amount of time spent on the road affects the likelihood of being killed by a vehicle.

This thesis defines the “road-zone area” as the road, the right-of-way (i.e., roadside or shoulder), and vehicles. Exploring road impacts from a behavioral perspective allows determination of degrees of inhibition and readiness of movement to this environment, permitting species' sensitivities to particular impacts to be better understood. For instance, species that do cross the road are more susceptible to direct mortality. However, interspecific variation exists within that response so that species differ in the amount of time necessary to cross the road, due to speed, angle, and/or reactions to passing vehicles. Snake species that do not readily cross the road could be more directly vulnerable to barrier effects and habitat fragmentation.

Table 1. Intrinsic and extrinsic factors of potential influence on whether a snake will attempt and/or successfully cross the road. Intrinsic influences are factors innate to snakes such as physiological and ecological traits. Extrinsic factors are external to snakes and include road characteristics and surrounding environmental conditions.

Intrinsic	*Extrinsic*
• Species	• Geographic location
• Body size	• Habitat bordering the road
• Age	• Temperature
• Sex	• Shade or sun gradients
• Activity periods	• Precipitation
• Dispersal tendencies	• Substrate
• Hibernation behavior	• Width
• Foraging strategy	• Age
• Defense mechanism	• Median (also type)
• Speed of movement	• Vehicular travel density
• Developmental stage	• Traffic patterns/Time of day
• Reproductive condition	• Driver behavior

CHAPTER 2

OPEN ROAD TESTS

The research objective for the open road study was to investigate interspecific variation in how snakes behaviorally respond to the road. For instance, do some species of snakes have a greater tendency to avoid crossing the road than others? My hypotheses were:

1) Some snake species will have a higher rate of road avoidance than other species due to innate ecological inhibitions to cross open spaces.
2) Those species that cross the road will exhibit interspecific variation in crossing speed.
3) Snakes will cross the road at a perpendicular angle minimizing the length of the crossing trajectory; hence, time spent crossing the road.

MATERIALS AND METHODS

Study site

The Savannah River Site (SRS) is a 750-km^2 tract of federal land located in Aiken and Barnwell County, South Carolina, USA. The Department of Energy (DOE) site was originally used for nuclear production facilities during the latter half of the 1900s. Although nuclear material is no longer produced, the land tract is not open to the general public and is still protected as a National Environmental Research Park ([NERP], Shearer and Frazer 1997). The land is managed by the U.S. Department of Energy and secured by a contracted security firm, Wackenhut Corporation. The site contains a diversity of habitat types (wetland, forest, sandhills, etc.) that are inhabited by a high level of herpetofaunal diversity, including 35 species of snakes.

The research opportunities on site are unprecedented due to the permanent protection of federal land that has retained intact, relatively undisturbed environments for conducting herpetofaunal studies.

The behavioral trials in this study were conducted on a closed road for which Wackenhut granted site-use permission. Performing the trials on a closed road allowed controlled investigation of the snakes' responses without endangering the safety of the animals or researchers, or distracting drivers that would typically be using public roads. The closed portion of SRS Road B (northern end) was selected as the study site; the road was 1.9 km long and bordered by secondary successional forest. The road was 6.0 m (~18 ft) wide and was chosen as being one characteristic of medium traffic density.

Pilot study

A pilot study was conducted in 2002 in which all species (n=27) captured on the SRS that year were tested (individuals; n=226). The purpose of the pilot study was to identify target species that included representatives that were aquatic and terrestrial, venomous and non-venomous, and varying in average adult body size in order to include species with different predators, movement styles, speeds, and defense reactions. In addition to the selection of target species, the pilot study was instrumental in analyzing methodological aspects of testing such as release location and design. With the exception of crossing speeds and angles, data from the pilot study are not used in the core analysis.

Nine target species were identified for the core season (Table 2), for which data were collected in spring, summer, and fall of 2003. Some species of concern that are frequently found dead on the road (Andrews and Gibbons, in prep.) had to be eliminated due to testing difficulties.

For example, the copperhead (*Agkistrodon contortrix*), a primarily nocturnal species, was tested in the pilot study after dark using a red-filter light to observe movement. However, the difficulty of observing the trial in the dark with minimal lighting and the risk of being unable to recapture the snake required excluding the species from the study. Some rare species of concern (e.g., coachwhips [*Masticophis flagellum*] and pine snakes [*Pituophis melanoleucus*]) had to be omitted due to too few individuals being captured alive in the wild, resulting in insufficient sample sizes.

Study specimens

Specimens were acquired via the widespread collection of snakes on the SRS by the Savannah River Ecology Lab (SREL) Herpetology Lab and other site employees who regularly capture or report snakes. Many snakes used in the core study were captured in and around a Carolina bay wetland, Ellenton Bay, as part of the SREL Herpetology Lab's on-going research projects in which a drift fence (Gibbons and Semlitsch 1981) completely encloses the wetland. Trapping methods include pitfall buckets, coffee cans, funnel snake traps, coverboards, and opportunistic searches. Additional specimens were acquired from other study sites and road captures on the SRS.

Site-wide snake captures are recorded in the SREL long-term snake database (1951-present; Andrews and Gibbons, in prep.) before release at their original points of capture. Snakes were housed in the SREL Animal Care Facility between trials (see below) and followed by standard processing (i.e., length, mass, sex) and marking by cauterization (Clarke 1971) for recapture identification purposes. All measurements and marking were performed after the individual was used in the behavioral trials. Snakes were contained in individual snake bags or pillowcases and were not handled or disturbed between capture and testing. Specimens were omitted from testing if they 1) were originally captured on Road B (study site), due to an assumed familiarity with the area, or 2) were not in optimal health (e.g., emaciation). Each individual was tested twice, once on each side of the closed road to determine any directional component or habitat cues. An individual was only tested once per day to minimize stress.

All snakes were tested during natural periods of peak movement according to their documented seasonal activity patterns on the SRS. Additionally, daily testing times were assigned to each species according to these natural movement patterns and historical documentation of likely road capture times (Gibbons and Semlitsch 1991, Conant and Collins 1998, Ernst and Ernst 2003, Tony Mills pers. comm.). For instance, nocturnal or crepuscular animals were tested in early morning (first light) or at dusk. Diurnal animals were tested early to mid-morning during summer and in the early afternoon of moderate seasons (i.e., spring and fall).

Release methods

Six “release sites” were constructed at the study site, three on each side of the road (sample shown in Figure 1). This design of using multiple sites on each roadside permitted each individual to be tested on opposite sides of the road. Also, continuous testing at the same release site of the same species or of species in predator-prey relationships could be avoided, thus eliminating the potential for snakes to detect the pheromone trail of a previously tested individual. The actual release sites were separated by ~12 m and placed at an area in which the roadsides were relatively flat and evenly vegetated with equivalent habitat types on both sides of the road. Ten-meter-long hardware-cloth fences were constructed at each release site along the tree line to function as catchment devices to minimize escape before the researcher could recapture snakes at the end of the trial. In order for the researcher(s) to remain concealed throughout the trial, a camouflage blind was constructed using PVC piping (1.6 m x 2.0 m) as a support for the fabric. The blind was placed immediately behind the catchment fence on the side of release.

The release bucket beneath which the snake was placed was a black plastic planting pot with holes drilled in the bottom. The bucket was tied upside-down with string to a 5.1-m bamboo pole. The bamboo pole allowed the researcher to stand behind the blind and lift the bucket to release the snake while remaining concealed during release and throughout the trial (Figure 2). The release bucket was placed at the road edge halfway on the asphalt and halfway on the vegetated roadside to allow the snake to sample both substrates before trial initiation. Snakes were transported to the study site in the bag from their original capture. The bag was untied and placed under the bucket to prevent exposure of the snake to the surrounding area prior to the trial. The bag was removed by holding a corner and sliding it from beneath the bucket, leaving the snake underneath. This same technique was used with venomous species by using a snake hook and tongs and with the aid of a field assistant. Upon securing the snake under the bucket, the researcher(s) stood behind the blind and allowed the snake one minute to settle before lifting the bucket and initiating the trial.

Three sizes of buckets were used to provide comparable amounts of space for small, medium, and large snakes. Buckets were used only once during a daily test and were washed in a Basil 3500 cage-washing machine between trials to further minimize pheromone impact from snakes previously tested. Trials were videotaped when time permitted and field assistance was available.

Environmental variables

As these trials were functionally an outdoor lab experiment, attempts were made to standardize environmental testing conditions as much as possible. Tests were not conducted while raining, and road temperature margins (15ºC - 55ºC) were set to avoid testing in temperatures outside of those of natural movement tendencies (Gibbons and Semlitsch 1991, SREL, unpub. data). To allow for maximum consistency of temperatures across the road-zone area, tests were performed at times when sun orientation resulted in no light/shade gradient on the site. The environmental conditions recorded at each trial were road, ground, and air temperatures (taken at release point), humidity, barometric pressure, 24-hour rainfall, and ranked measurements of cloud cover and wind strength. While effects of the environmental variables were analyzed, the purpose of collecting these data was to investigate the robustness and consistency of trial standardization as opposed to a targeted attempt to look at environmental factors affecting levels of road crossing.

Response measures

While analysis consisted of a binary response, cross or avoidance, data collection involved three response variables: cross, avoid, and deter. Deterrence was classified as an avoidance response in which the snake entered the road, but turned back toward the woodland on the release side before crossing the entire road. This testing strategy allowed inquiry into which snake species might attempt to cross the road but would ultimately avoid it, in contrast to those that did not enter the road beyond the release point.

At trial initiation (bucket lift from behind the blind), a stopwatch was started to record total time of the trial. Search behaviors and their time of occurrence within the trial were also recorded to better enable the identification of an overly disturbed snake (e.g., tail vibration) and to determine whether snakes used naturally observed behaviors for exploring the road-zone environment. These behaviors consisted of tongue flicking, head raising, and lateral head bobbing typical of rat snakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*).

Trials were concluded and the snake was recaptured after the individual reached the fence either at the tree line of the release side (avoid) or on the opposite side of the road (cross). The end time of the test was noted and the snake rebagged. In the event that a snake crossed the road, the entry and exit times and the length of crossing trajectory were recorded for later calculation of crossing speed. Additionally, the angle of the crossing trajectory relative to the road (90º=perpendicular to traffic direction) was recorded to determine if snakes took the shortest route possible to get to the other side, minimizing time spent in the road, or whether they searched and moved sporadically while crossing. Any additional notable behavioral observations or factors of potential influence were recorded as comments for future reference. If the testing series was complete for the individual, the snake was returned to the lab for measurements before being released at its original point of capture. Trials were excluded from final analysis if the snake 1) never moved, or 2) demonstrated defensive behavior during the test (i.e., rattlesnake rattle).

Statistical analyses

Variable influences were modeled in two manners: 1) incorporating all parameters and 2) via a category analyses in which the variables were classified as control (release site number, side of the road of release [left or right], time in captivity, and whether the snake was initially caught on the road), physical (sex, snout-vent length [SVL], and mass), and environmental (date, time, temperatures: road, ground, and air, humidity, barometric pressure, 24-hour rainfall, wind, and cloud cover). Model fitness was analyzed using stepwise regression (PROC LOGISTIC, SAS Institute, Inc., Cary, NC, 1999). Additionally, as individuals were tested twice and the dataset violated assumptions of repeated measures designs, models were run including all tests and only the first test of an individual. Odds ratios were calculated to investigate potential biases of carryover effects from the first test on the outcome of the second (Agresti 1996). Response probabilities were analyzed per species using Chi-square tests (PROC FREQ, SAS Institute, Inc., Cary, NC, 1999). Variable influences on crossing speeds and angles were also analyzed using stepwise regression (PROC REG, SAS Institute, Inc., Cary, NC, 1999). Interspecific differences in crossing speeds and angles were investigated using the Kruskal-Wallis test (StatSoft, Inc. Tulsa, OK, USA. 1998) after the removal of outliers (PROC UNIVARIATE, SAS Institute, Inc., Cary, NC, 1999).

RESULTS

Thirteen species were tested over the 2003 season (tests, n=458; individuals, n=222), although analyses were focused on the nine identified target species. Multiple analyses were run to determine the consistencies in models using all tests after applying exclusion criteria (n= 383) and only the first test of an individual (n=186). Although the results were similar, only the first test was used in the final analysis, as within-subject effects could not be ideally incorporated into the model itself. The odds ratio demonstrated a greater tendency of an individual to repeat the response of the first test in the second, but was marginally random (θ=1.09). Additionally, an effect of side of the road on response was observed ($p<0.02$) when all tests were included but was no longer significant when only the first tests were used.

The species effect was highly significant in all models ($p<0.0001$). In the category analyses, no control or environmental variables exhibited significance. For the physical measures, SVL was found to be significant ($p<0.05$), with shorter snakes having a greater tendency to avoid the road. Per-species analyses did not yield significance for any of the variables with the exception of SVL ($p<0.05$) for the canebrake rattlesnake, for which larger specimens had a greater tendency to avoid the road. Racers marginally demonstrated a greater avoidance tendency when tested on the left side of the road ($p=0.05$). When racers were removed from the analysis, the side of the road effect was not observed in any of the models (i.e., generalized or category). Chi-square analyses conducted on a per-species basis yielded significance in response probabilities for six of the nine target species (Figure 3).

The effect of species was highly significant for crossing speed (Kruskal-Wallis test, $p<0.0001$, Figure 4). Species were not significantly different in crossing angles ($p=0.06$) as no species significantly deviated from a perpendicular (90º) crossing trajectory (Table 3). For interspecific comparisons with crossing speed, five outliers were removed (*C. constrictor*, n=4; *C. horridus*, n=1). For angle analysis, six outliers were removed from the dataset (*C. constrictor*, n=1; corn snake [*Elaphe guttata*], n=1; *H. platirhinos*, n=4).

Model results did not vary for crossing speed and angle analysis whether all tests were included or only the first tests were used. SVL, mass, and road temperature were significant for effect on speed (SVL and mass, $p<0.01$; road temperature, $p<0.0001$). SVL and mass parameter estimates showed that longer and lighter snakes move faster than did short and stout snakes. Per-species regression analyses exhibited an effect of mass ($p<0.05$) for the eastern hognose (*Heterodon platirhinos*), the cottonmouth (*Agkistrodon piscivorus*) and the banded watersnake (*Nerodia fasciata*). Road temperature had a specific effect on cottonmouths ($p<0.01$).

DISCUSSION

Road-crossing behaviors

Interspecific body length comparisons showed that smaller species of snakes had a greater tendency to avoid rather than cross the road. This finding is consistent with the observation that smaller snakes are more likely to have avian predators and are at greater risk of predation when in more exposed terrains (Fitch 1999, Gibbons and Dorcas 2005). Additionally, smaller snakes, which move shorter distances (e.g., *Diadophis punctatus* averages 1-3 m/day, Fitch 1999), are less likely to encounter a road, decreasing the likelihood that these species have had previous exposure to the road if some level of learned behavior exists. However, since little is known about learned behavior for snakes in regards to roads, we do not know how or if exposure would alter behavior. Regardless, it remains that smaller snake species in this study (i.e., *D. punctatus, T. coronata*), exhibited high avoidance rates. This avoidance generalization was also observed in the pilot study; data from the pilot study that were not used in analysis showed 100% avoidance levels of both *D. punctatus* (n=6) and *T. coronata* (n=10).

The only meaningful grouping of species is ringneck snakes and southeastern crowned snakes, the two smallest species, which are heavily fossorial, spending predominantly more time under litter and other debris than other species targeted in this study. These snakes minimize time spent in the open (e.g., *D. punctatus*, Fitch 1999), and therefore are less likely to encounter or cross roads. Despite the avoidance rates observed in this study, both the ringneck snake (Fitch 1999) and the southeastern crowned snake (Messenger 2003) have been observed to cross roads. In both cases, the surveyed roads bisected areas with high densities of these species. In areas with these densities, encountering the road is unavoidable for some individuals and crossing is likely to occur in some instances. However, crossing observations of 10-20 snakes in an area where 1000's are present in the immediate vicinity of the road does not represent a substantial amount of the population. The small number of road crossings relative to abundance support significant degrees of road avoidance for these species of snakes. Therefore, individuals of these species found crossing the road are likely the exception and not the norm for the species.

Clear patterns did not emerge for avoidance rates across species in terms of other ecological groupings (i.e., aquatic/terrestrial, venomous/non-venomous; Table 2). However, the ecological groups were not evenly represented (e.g., 2 aquatics, 6 terrestrials), so a thorough comparison could not be made. Even with comparable group sizes, trends possibly would not have been detectable on the group level, as ecological needs and patterns vary greatly within each group across species. Also, as road placement within a habitat is likely the key factor determining what does or does not cross the road, crossing cannot be generalized at this level. Aquatic snakes cross where roads immediately bisect a water body (e.g., *Nerodia fasciata*, Smith and Dodd 2003) and terrestrial species cross where roads bisect their primary habitat (e.g., pigmy rattlesnakes, *Sistrurus miliarius*, SREL unpub. data).

Three non-fossorial species of snakes that showed >70% road avoidance, *C. horridus, E. obsoleta, and H. platirhinos*, are all species frequently found on the road, such that road cruising is one of the more productive techniques used to find them. However, the observed level of avoidance during testing suggests that not all individuals that encounter roads actually cross them. Road crossings could be a consequence of home range dynamics, such that if snakes often encounter the road via dispersal mechanisms, frequent road observations could be made even if only 20-30% crosses. Thus, even the species that are more equipped to deal with the predatory threats of open spaces via body size or venom, still respond to the road as a potentially dangerous environment.

An effect on response probability was observed based on the side of the road on which the test was initiated. The displacement factor is not of concern in interpretation of the results of this study as snakes were collected from many different locations on the SRS and still exhibited species-specific tendencies. Therefore, this effect suggests the potential importance of habitat cues in movement patterns in regards to directional decisions by snakes. In addition to directional cues, trace scents from prey, predators, including other snakes could have influenced crossing patterns. As the study was conducted outdoors, it is unknown what snakes or other animals may have crossed the road, or even the testing area itself, outside of actual testing times. This factor cannot be conclusively addressed from this particular study but warrants future investigation into the degree of sensitivity of snakes to detect prior use of an area by other animals, even when the snake is placed in unfamiliar territory.

Coluber constrictor showed a significant tendency to cross the road even though the maximum expected cross rate in this study was 1:1 (no preference). These data do not necessarily suggest that racers prefer to cross the road, or are choosing the road over the nearby forest habitat. Racers were possibly more perceptive of researcher presence or the site set-up and were attempting to move away from the area. However, search behaviors were exhibited by racers in these tests prior to crossing, demonstrating that the snake acclimated before going in one direction or the other. As mentioned before, one reason a snake might cross a road is to emigrate from unfavorable circumstances (e.g., resource depletion or presence of a predator). Although it cannot be ascertained why racers showed an above-expected crossing rate, it can be concluded that the species will readily cross the road. This conclusion is also supported by existing road capture data on the SRS (Andrews and Gibbons, in prep.).

Although there was not a significant effect on response probabilities from whether a snake was initially caught on the road, this factor was not specifically tested in this study. The potential for learned behavior to formulate an altered reaction to the road after an initial encounter could influence crossing, or avoidance, patterns at the inter- or intraspecific level. As was seen with these results, older (i.e., larger) canebrake rattlesnakes (*Crotalus horridus*) had a greater tendency to avoid the road than did younger (<1000 mm SVL) ones. *Crotalus horridus*, an example of a wide-ranging snake species, are inhabitants of an increasing number of areas penetrated by roads, thereby increasing the chance that an individual snake has encountered a road. Additionally, most of the rattlesnakes used in this study were initially captured on the road before testing. The data set was not diverse enough in initial capture technique with this species to do a detailed analysis on preexposure to a road but is a topic in need of investigation. Eastern diamondback rattlesnakes (*Crotalus adamanteus*) have been observed to truncate their home ranges along roads (Bruce Means, pers. comm.), and timber rattlesnakes (*Crotalus horridus*) have also been observed to travel parallel to country roads (Fitch 1999).

Despite the exclusion of secondary testing of individuals, the dataset was substantial enough to model and detect trends. Individuals showed a greater propensity to repeat the response of the initial test in the second test although this was likely confounded by the species effect, as many of the species do, in fact, respond with relatively consistent behavioral tendencies when confronted with a road.

Crossing speeds and angles

A strong species component was found with crossing speeds, which is explainable by natural differences in body size and movement styles across species (Gibbons and Dorcas 2005).

The lowest average crossing speeds were observed with *A. piscivorus* and *C. horridus*. In addition to the physical implications of these species being slower due to higher length to mass ratios, venomous snakes are equipped to use venom, not flight, as their defense mechanism (Gibbons and Dorcas 2005). Therefore, these snakes are at less risk than nonvenomous species in terms of a bird or other predator attacking them while crossing open spaces. This reduced threat is demonstrated in this study in slower crossing speed.

Long, slender snakes cross the road more quickly as observed for *C. constrictor* and their average crossing speeds in this study. *M. flagellum*, another long, slender representative, was not tested in the core season but showed comparable cross speeds in the pilot study (n=2). The three species (*A. piscivorus, H. platirhinos, N. fasciata*) for which a mass effect was shown are all snake species that are stout-bodied in adult stages when in physically optimal conditions (Gibbons and Dorcas 2005).

Collectively, snakes moved faster at warmer road temperatures, with a specific effect being seen with the cottonmouth. This general response of increased speed at warmer temperatures has been documented (e.g., Blouin-Demers et. al 2003, Heckrotte 1967). The true role of temperature in road-crossing behaviors cannot be concluded from this study as snakes were tested within constrained temperature conditions. However, as road temperature showed significance despite controlled efforts, it is likely that this factor is of considerable influence in road crossing patterns. Particular crossing frequencies have been documented to be correlated not only with season, but also during certain times of day (e.g., Klauber 1939), likely due to natural temperature fluctuations within a day.

Crossing angle did not vary significantly across species, as no species substantially deviated from a perpendicular (90º) crossing angle. This observation suggests that snakes, regardless of whether they view the road as a threat, spend no more time crossing than necessary. Although search behaviors (e.g., tongue flicking, head raising) were commonly observed in individuals at the beginning of the test, snakes were not observed to actually search to the same degree once on the road. After initial searching and upon making a directional decision of crossing the road or avoiding it, snakes typically proceeded with consistent movement. The shortest route possible was taken, a behavior that was independent of interspecific rates of crossing speed.

In summary, highly significant levels of species-specific variation are apparent in 1) how readily a species will cross the road, and 2) crossing speeds when a crossing attempt occurs. Although this study was not designed to test for importance of variables both intrinsic and extrinsic to the snake, physical features of the individual snake or species itself, certain habitat cues, and road temperatures (as a consequence of time of day or season) can potentially influence both avoidance rates and crossing speeds.

Table 2. Target species selected for the road tests in the 2003 core season. Categories designate whether a species is (A) aquatic or (T) terrestrial, (V) venomous or (N) non-venomous, or (L) large or (S) small in average body form.

Species	***Common***	***Habitat***	***Venom***	***Size***
Agkistrodon piscivorus	Cottonmouth	A	V	L
Coluber constrictor	Black racer	T	N	L
Crotalus horridus	Canebrake rattlesnake	T	V	L
Diadophis punctatus	Ringneck snake	T	N	S
Elaphe guttata	Corn snake	T	N	L
Elaphe obsoleta	Rat snake	T	N	L
Heterodon platirhinos	Eastern hognose	T	N	S
Nerodia fasciata	Banded watersnake	A	N	L
Tantilla coronata	Southeastern crowned snake	T	N	S

Table 3. Means and sample sizes of crossing angles for target species of snakes. Species had no effect on crossing angle (p=0.06) as demonstrated by minimal deviation from a perpendicular (90º) for all species.

Species	n	Mean angle (º)
E. obsoleta	17	84.4
C. constrictor	82	85.5
C. horridus	21	89.4
E. guttata	13	91.4
H. platirhinos	15	92.1
N. fasciata	20	94.0
A. piscivorus	29	94.1

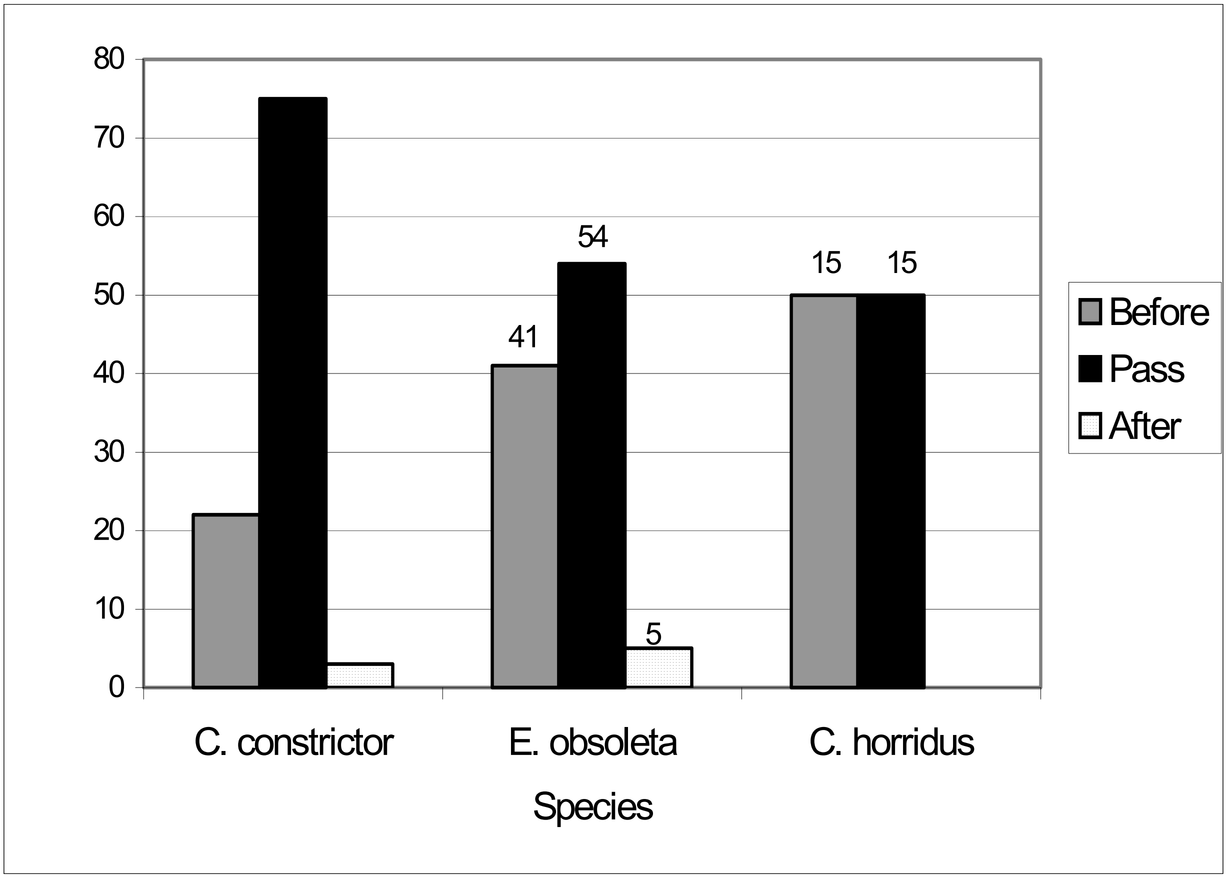

Figure 1. Overhead view of single release site showing placement of the blind and the fence in relation to the release point of the snake at the road edge. Release sites were arranged in 3 pairs for a total of six.

Figure 2. Side shot of release set-up showing fence, release pole and bucket, blind and researcher position. Two additional pairs of release sites are not shown.

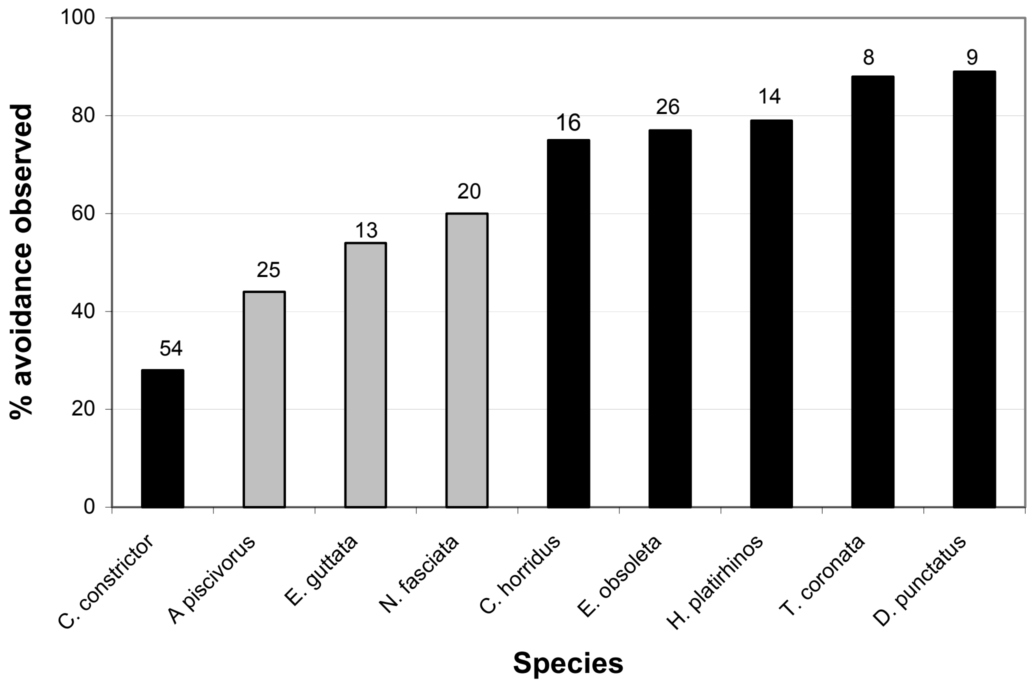

Figure 3. Avoidance rates observed for nine southeastern snake species. Note that black bars represent species having a significant tendency ($p<0.05$) to cross the road (*C. constrictor*) or avoid the road (*C. horridus*, *E. obsoleta*, etc.). Gray bars indicate species for which cross:avoid probabilities did not vary significantly from unity. There was a highly significant effect on crossing probability by species ($p<0.0001$). Sample sizes are listed above the bars (n = first test individuals).

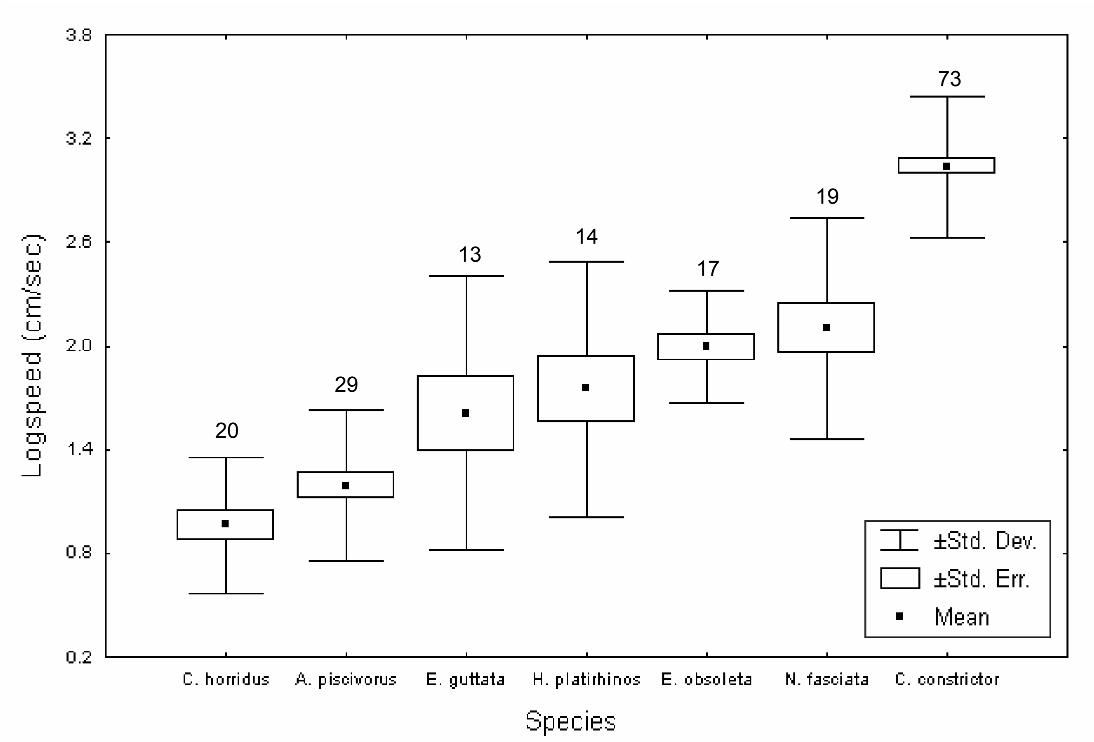

Figure 4. Crossing speeds for all target species with n>10 crossing occurrences. There was a highly significant effect on crossing speed by species (p<0.0001). Sample sizes are listed above the whiskers.

CHAPTER 3

VEHICLE TESTS

The research objective for the vehicle study was to determine if 1) snakes respond to a passing vehicle, and 2) this response varies across species. My hypothesis was that snakes would react to the vehicle as they would an approaching predator. Species that rely on crypsis were predicted to freeze and species that have the ability to flee were predicted to exhibit flight responses to the passing vehicle.

MATERIALS AND METHODS

Vehicle tests were conducted on the closed portion of Road B with the same materials, source of specimens, and release method as the road tests. Therefore, some information on procedures will not be reiterated in this chapter (see Chapter 2). Individuals were tested twice, using the same criteria as those used in the road tests with the exception of not testing each snake on opposite sides of the road, as direction of movement was not of primary interest in the vehicle tests. Additionally, pheromone impacts were of less concern than in the road tests 1) because the research focus was not dependent on direction and 2) due to space constraints at the study site (i.e., the vehicle needed to have room to stop after passing the release site and before the chain-linked fence closing the road at its northern end). The collection of environmental variables was identical to the road tests except that humidity, barometric pressure, and 24-hour rainfall were not measured.

Since the same release method and site design were used, no pilot study was necessary for the vehicle tests. Additionally, the breadth of interspecific investigation for the vehicle tests was not as extensive and included only three species: rat snakes (*Elaphe obsoleta*), black racers (*Coluber constrictor*) and canebrake rattlesnakes (*Crotalus horridus*). Species selected for the vehicle tests were ones that represented different defense strategies and could be acquired in sufficient sample sizes. All data were collected in spring, summer, and fall of 2003.

Additional materials

A 2002 Chevrolet Silverado 1500 pick-up truck was used for all vehicle tests. A vehicle of moderate weight was used as it is not currently known whether a response to a passing vehicle would be catalyzed by vibration and/or sight of the oncoming car. The snake was released under the bucket using the same technique developed in the road tests. After containment of the individual, the researcher went behind the blind and lifted the bucket while the driver in the vehicle was positioned at the start point 0.3 km down the road from the release point.

Response measures

As with the road tests, trial initiation began when the researcher lifted the bucket. To avoid disturbance or further interaction with the snake, thereby not forcing the snake into the road, the snake had the same directional options as in the road tests (i.e., cross, avoid, deter). These response variables were recorded but were considered responses secondary in research focus. The primary response variables of interest were a flight or freeze reaction (the snake completely stopped movement in response to the passing vehicle). It was also recorded if the snake showed no reaction and continued moving, not altering speed or direction with the passing vehicle. However, this behavior was rarely observed (n=7) and therefore was not categorized as a response variable in the final analyses.

The timing of the response as related to the passing vehicle (categorized as "before pass," "at pass," or "after pass") was recorded. In the event of a flight response, a direction was categorized as 1) “forward” if the snake continued along its trajectory but with increased speed, 2) “reverse” if the snake turned back in the opposite direction of its original trajectory, or 3) “opposite vehicle” if the snake deviated from a perpendicular crossing to moving parallel in the road away from the approaching vehicle. After the vehicle drove past the snake, an “after pass” response was recorded of whether the snake 1) continued to flee, 2) restarted movement from a freeze reaction, or 3) continued to freeze. Snakes were recaptured within 1 min. of a vehicle pass to prevent escape. Therefore, the "after pass" response is a short-term observation and does not represent the maximum amount of time a snake could remain immobilized.

As the snake was not always in the same physical location across tests, distance between the snake and the vehicle could not be strictly standardized, but only minimized. To measure any effect that distance from the vehicle might have on response, the position of the snake and car relative to each other was recorded by dividing the testing area into sections (with corresponding left or right side: road shoulder, edge, and middle of the lane, or middle of the road if the position was along the dividing lane line). Metric distances between the snake and the vehicle at pass were estimated within 0.25 m.

Search behaviors were recorded as in the road tests along with predator responses characteristic of the target species; *E. obsoleta* often kink as a crypsis mechanism and *C. constrictor* have been noted to “bow,” raising the upper half of their body. Once the snake began full movement, defined here as the stage beyond searching when a direction has been selected and movement is consistent, the observer (researcher behind the blind) used walky talkies to cue the driver to drive (35 mph) past the snake. Before approach, the observer informed the driver of the snake's location to minimize the distance between the vehicle and the snake without threatening the safety of the animal. No incidental mortality of study specimens occurred while conducting this study. Trials were excluded from final analysis if the snake 1) never moved, 2) demonstrated defensive behavior during the test (i.e., rattlesnake rattle), or 3) stopped moving before possible detection of the vehicle (when the vehicle was still out of sight).

Statistical analyses

Stepwise regression (PROC LOGISTIC, SAS Institute, Inc., Cary, NC, 1999) was used to determine any effects of covariates on responses to the passing vehicle in both generalized and category models (see description in Chapter 2). Odds ratios were calculated to determine the degree of consistency between the responses of the first test and the second (Agresti 1996). Chi-square analysis was used to investigate response probabilities of each species (PROC FREQ, SAS Institute, Inc., Cary, NC, 1999).

RESULTS

A total of 218 trials (individuals, n=216) were conducted. There were no differences between results for the model using all tests after exclusion (n=177) and only using first tests (n=84). Additionally, responses of an individual did not vary between tests (θ=4.37), justifying the inclusion of both tests. All models and analyses demonstrated a high significance both at the species level ($p<0.0001$) and on a per-species basis (*C. constrictor*, $p<0.0001$. *C. horridus*, $p=0.00$, *E. obsoleta*, $p<0.0001$). *C. horridus* were removed from covariate analyses, as there was a 100% freeze response rate (all tests, n=32; first test, n=13). Tests where no response to the vehicle was observed (*C. constrictor*, n=6; *E. obsoleta*, n=1) are included in the presentation of the data (Figure 5) but had no overall significance in the likelihood of a particular response. Finally, no measured variable (environmental, physical, or control) had a statistically significant effect on response.

Distance between the snake and the vehicle and the position of the snake in relation to the road exhibited no effect on response. Both timing of the reaction in relation to the vehicle passing, and the secondary reaction of the snake after the vehicle pass, were significant at the species level ($p<0.05$). In the analysis of timing of reaction for each species, *C. constrictor* and *E. obsoleta* were more likely to freeze as the vehicle passed whereas *C. horridus* froze 50% of the time (n=15 of 30; Figure 6) before the vehicle passed. Few snakes demonstrating a freeze reaction responded only after the vehicle pass (n=5 of 144, 3%). Sixty-two percent (n=89 of 144) froze when the vehicle passed and the other 35% was comprised of snakes that froze before the vehicle passed (n=50 of 144). After the vehicle passed, over half the snakes began moving again (n=42 of 76, 55%; Figure 7), but a large proportion remained immobilized (n=28 of 76, 36%) on the road afterwards. Both *E. obsoleta* and *C. horridus* restarted movement 65-70% of the time after the vehicle pass, with the largest percentage of a continued freeze reaction occurring with *C. constrictor* (n=11 of 28, 52%).

DISCUSSION

The degree of "freeze" responses was observed more frequently than initially hypothesized. The hypothesis was correct in that *C. horridus*, which relies on crypsis as a defense, did freeze in response to the vehicle. Racers had a higher freeze response than expected, but this tendency has also been observed in the field in close encounters (pers. obs.). As with the road tests, trials were performed within a bounded temperature range and environmental conditions were controlled as much as possible. Therefore, it is not surprising that no variables showed significance. Additionally, response to a vehicle would likely not be as affected by extrinsic or intrinsic factors as the stimulus of a passing vehicle is more abrupt and pronounced than other extrinsic stimuli.

Conditions in which no response was observed could not be pursued due to the infrequency of no exhibition of response. However, in five of the seven tests (6 *C. constrictor* , 1 *E. obsoleta*) in which no response was observed, the snake was either on the road shoulder or the distance between the snake and the vehicle was 4 m or greater, suggesting that possibly if the snakes are a "safe" distance from the vehicle or closer to the woods or habitat, they are not visibly affected compared to those in the road or closer to the vehicle.

Distance between the snake and the vehicle and position of the snake in relation to the vehicle would likely have an effect on a flight-or-freeze response, but too little variation in the data was available to demonstrate an effect. Again, this constraint is likely due to an attempt to continually minimize distance between the vehicle and the snake in the tests without injury to the snake. Studies inquiring into responses of snakes to specific distances from the vehicle are needed to determine if this factor is of significant influence. The majority of snakes froze as the vehicle passed as opposed to before or after the actual pass. Additionally, the majority of snakes restarted movement after the vehicle passed, suggesting that although a passing vehicle temporarily interrupts road crossing, it is a momentary reaction. *C. horridus* that remained immobilized often did so for up to a minute. However, the maximum length of time was not quantified in order to be time-efficient, assuring that daily testing was completed within established temperature margins and before the sun moved such that shadows were cast on the road and testing area.

In conclusion, vehicle responses mimic how snakes respond to a predator or unrecognized stimuli in natural habitat. The freeze response appears to be more momentary, with the possible exception of canebrakes, which did exhibit prolonged immobilization. However, in reality where snakes are encountering more than a single vehicle, this response could significantly prolong the amount of time it takes to cross the road provided that the response observed with a single vehicle would be consist with each additional passing vehicle. In other words, these data suggest that the time it takes to cross the road is positively correlated with traffic density for species that freeze in response to passing vehicles. This in-road behavior needs to be considered as a factor increasing the threat of mortality with a group that already is not adept at crossing roads due to secretive natures or presumed vulnerability to natural predators in open spaces.

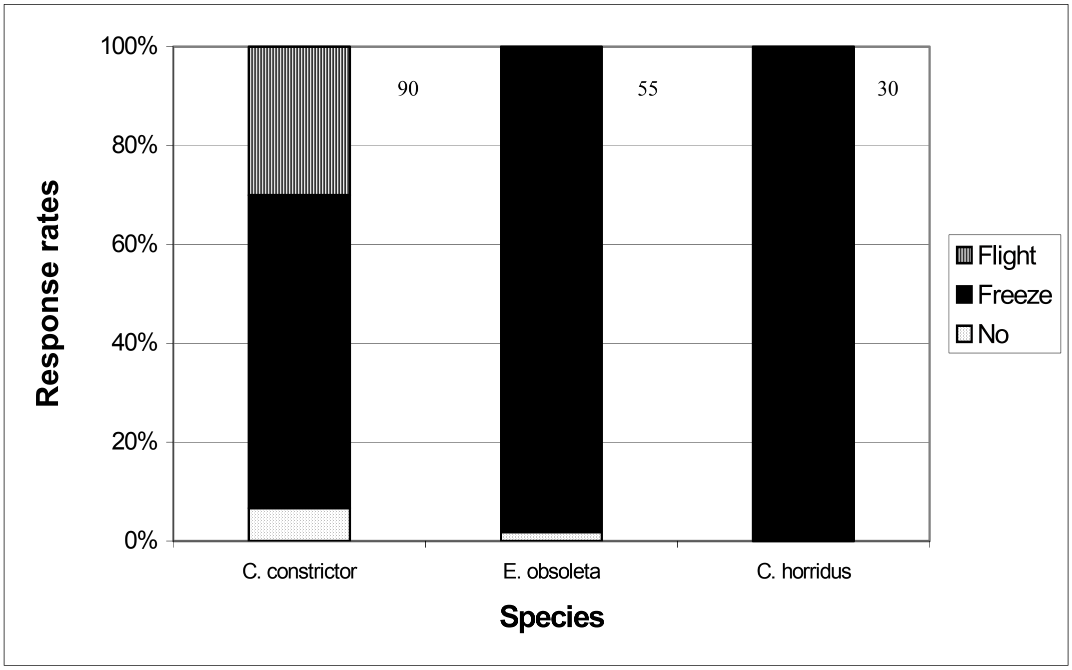

Figure 5. Vehicle response rates for three species of southeastern snakes. All species were significant in deviating from unity. Interspecific differences were found to be highly significant (p<0.0001). Sample sizes are listed to the right of each species' bar.

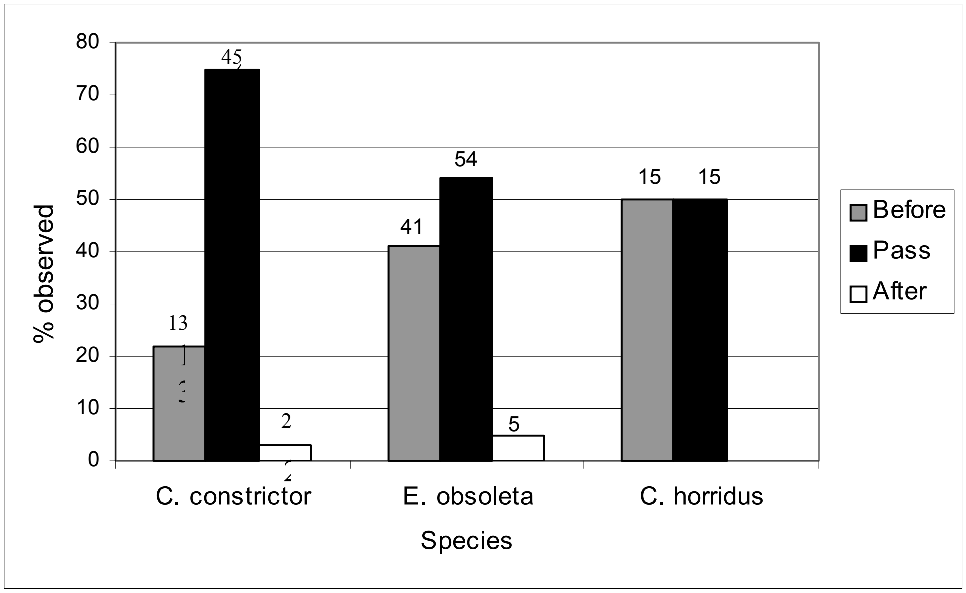

Figure 6. Timing of responses as related to a passing vehicle. "Before" represents the proportion of responses exhibited before the vehicle passed. The "pass" category represents responses exhibited at the vehicle pass. "After" represents the proportion of observed responses that occurred after the vehicle passed. Time of the reaction in relation to the vehicle passing was significant at the species level ($p<0.05$). Sample sizes are listed above the bars.

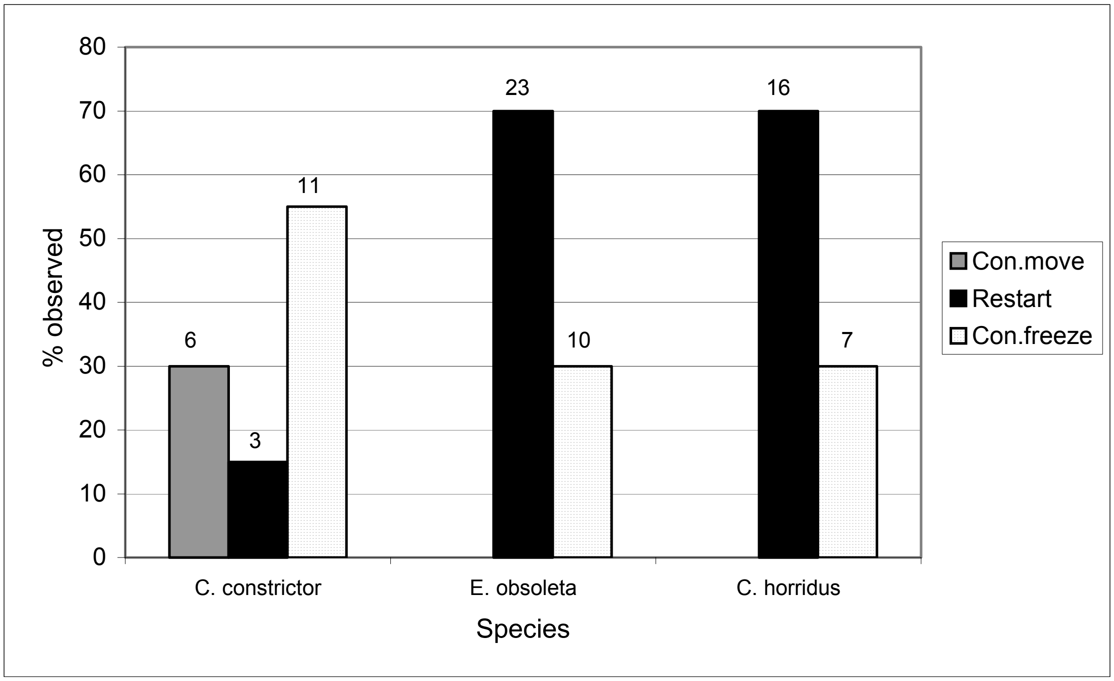

Figure 7. Secondary responses observed after the vehicle passed. "Con. move" represents responses in which the snake fled in response to the vehicle and continued to flee after the vehicle passed. "Restart" represents instances in which the snake froze in response to the passing vehicle but restarted movement after the pass. "Con. freeze" represents responses in which the snake froze in response to the passing vehicle and continued to freeze after the pass. Species had a significant effect on the probability of a particular response after the vehicle passed ($p<0.05$). Sample sizes are listed above the bars.

CHAPTER 4

GENERAL CONCLUSIONS

The study of "road ecology" is a newly forming field (Forman et. al 2003) with an increasing number of zoologists, chemists, hydrologists, and ecologists recognizing irreparable landscape alteration from the nation's transportation infrastructure. Understanding the biology behind these alterations will allow for efficient mitigation practices and the development of more environmentally sound transportation designs in the future. The research of this thesis was designed to identify sensitive species and the potential diversity in type and degree of road impacts across snake species.

While some species of snakes likely suffer primarily from on-road mortality (e.g., racer, *Coluber constrictor*), these species are more likely to experience less severe impacts than a snake that rarely crosses or that crosses slowly. This study found high levels of avoidance with smaller snake species that are likely to be sensitive to road impacts, as roads could present impenetrable barriers in some localities that are more easily avoided than taking the risk of crossing open space. The barrier effect can also arise with species that cross slowly (e.g., canebrake rattlesnake, *Crotalus horridus*), resulting in high levels of mortality, after which population stability could suffer from the pronounced loss of individuals. Fitch (1999) described the road crossing behavior of *C. horridus* as crossing "so slowly, movement was likely to be unnoticed." This behavior is again demonstrated in these data, not only for *C. horridus*, but also for the other venomous target species, the cottonmouth, *Agkistrodon piscivorus*.

The vehicle tests showed a higher than expected freeze response across the three species tested. This behavior further prolongs the amount of time crossing the road. Although snakes verifiably use the road for thermoregulation in some locations and under particular environmental conditions (e.g., Ashley and Robinson 1996), it is possible that this freeze behavior has further contributed to idea that snakes commonly use the road for thermoregulatory purposes. Thermoregulation likely occurs at times of the day in which the road is not heavily traveled by vehicles or in regions, such as the West, where the landscape is vast (i.e., animals more accustomed to open spaces) and where traffic densities are much lower in many locations in comparison to eastern regions of the country.

Although a range of species behaviors is observed across snakes as a group, these data make it apparent that snakes to do not deem the road area a favorable environment, but rather a threat as evidenced by crossing snakes using the shortest route possible. As seen from this research, impacts cannot be generalized even within an animal group. Perhaps some are maintaining viable populations amidst road development, but perhaps others will go locally extinct without implementation of measures minimizing road impact. The difference between the two categories needs to be apparent so that resources and future research can be prioritized for the sensitive species.

Future research

As this study was designed to investigate behavioral effects at an interspecific level, research into intraspecific comparisons needs to be conducted with the identified sensitive species, as was seen with *C. horridus* whose response appears to be affected in part by body size or developmental stage. The seasonality of road mortality has been documented both across and within seasons (e.g., Case 1978, Sherbrooke 2002), but a greater understanding of the conditions of road avoidance needs to be achieved in order to document a representative section of road impacts on wildlife. My study found that temperature affects crossing speed, but the study was not designed to test directly if temperature, or other environmental variables, affect crossing rates, a topic for which future research is needed.

As details are documented and multiple factors are considered, impacts can be investigated at the population level as to how roads are affecting ecological processes at these landscape levels. The degree of permeability of the road determines whether the conduits that wildlife relies on for dispersal and survival remain open.

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