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Source: Copeia, 2005(4) : 772-782

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/0045-8511(2005)005[0772:HDHISM]2.0.CO;2

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How Do Highways Influence Snake Movement? Behavioral Responses to Roads and Vehicles

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Roads affect animal survivorship and behavior and thereby can act as a barrier to movement, which exacerbates habitat fragmentation and disrupts landscape permeability. Field experiments demonstrated that interspecific differences in ecology and behavior of snakes affected responses of species when they encountered and crossed roads. The probability of crossing a road varied significantly among southeastern U.S. snakes, with smaller species exhibiting higher levels of road avoidance. Species also differed significantly in crossing speeds, with venomous snakes crossing more slowly than nonvenomous ones. All species crossed at a perpendicular angle, minimizing crossing time. A model incorporating interspecific crossing speeds and angles revealed that some species cannot successfully cross highways with high traffic densities. Individuals of three species immobilized in response to a passing vehicle, a behavior that would further prolong crossing time and magnify susceptibility to road mortality. Identifying direct and indirect effects of roads on snakes is essential for mitigating road impacts and for designing effective transportation systems in the future.

As human development continues to encroach on the environment, snakes are increasingly exposed to roads. Roads can fragment the landscape (Andrews, 1990), isolating habitat and its resident animals (Mader, 1984) that need to cross roads in an effort to assess and access resources on the other side or to disperse permanently (i.e., emigrate) to escape unfavorable circumstances. The degree to which a road poses a barrier to movement defines whether the bisected habitat is functionally contiguous (snakes cross successfully in sufficient numbers to preserve connectivity) or fragmented (rates of mortality or behavioral avoidance are substantial enough to isolate populations on opposite sides of the road). If the barrier effect of the road continually prohibits immigration and emigration, this isolation will eventually affect fundamental population and community dynamics.

Snakes are an ideal group for investigating the generality and interspecific differences of both direct and indirect road impacts (Andrews, 2004), not only because road mortality has been documented for over half a century (e.g., Van Hyning, 1931; Pough, 1966; Smith and Dodd, 2003), but also because of the breadth of ecological niches represented among species (Ernst and Ernst, 2003). Snake species exhibit a wide range of life-history strategies and vary in size, seasonal and daily activity patterns, and habitat preferences. Snakes are at risk to predation when dispersing or migrating to acquire resources and have evolved adaptations to minimize the chances of being preyed upon when traveling overland (e.g., Shine and Lambeck, 1985; Bonnet et al., 1999; Vandermast, 1999), adaptations that also vary among species. Predation avoidance strategies (Gibbons and Dorcas, 2005) include crypsis (e.g., Green Snakes, *Opheodrys*), venom (e.g., Rattlesnakes, *Crotalus*; which primarily employ crypsis and use venom secondarily), and speed (e.g., Racers, *Coluber*). Additionally, small species that are vulnerable to a greater array of predators might reduce the threat by avoiding open spaces (e.g., Ringneck Snakes, *Diadophis*; Fitch, 1999).

Snakes hesitant to traverse open spaces would presumably react similarly when encountering a road. Road avoidance in snakes has been documented in studies focusing on single species (Timber Rattlesnake, *Crotalus horridus*, Fitch, 1999 and Sealy, 2002; Common Garter Snake, *Thamnophis sirtalis*, Shine et al., 2004), but the generality of this behavior across species has not been determined. Habitat fragmentation by roads can occur with snake species that avoid roads or suffer high road mortality due to frequent crossing or slow crossing speeds. An array of snake behaviors and physiological traits may influence a snake's propensity to cross a road and its chances of crossing successfully. Consistencies would be expected for snakes that are closely related taxonomically or share similar life-history strategies. Additionally, extrinsic variables (road and environmental conditions) could also play a role in determining avoidance and crossing patterns of snakes (Table 1). These factors potentially influencing road-crossing behavior should result in detectable interspecific patterns among snakes.

We designed a two-part study to investigate interspecific variation in snake behaviors in

TABLE 1. INTRINSIC AND EXTRINSIC FACTORS OF POTENTIAL INFLUENCE ON WHETHER A SNAKE WILL ATTEMPT TO CROSS THE ROAD AND DO SO SUCCESSFULLY. 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. Factors are not mutually exclusive.

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	• Presence/Type of Median
• Speed of movement	• Vehicular travel density
• Developmental stage	• Traffic patterns/Time of day
• Reproductive condition	• Driver behavior

response to encountering 1) a road and 2) a passing vehicle. The overall purpose of the study was not to simulate the conditions of a snake naturally approaching a road, but to gauge the immediate response of the animal to two stimuli: a road and a vehicle. The research objective for the road study was to investigate snake behavior to road encounters by quantifying crossing probabilities, speeds, and angles for nine species of southeastern snakes. The research objective for the vehicle study was to compare differences among three species of snakes in immobilization rates or flight responses to an oncoming or passing vehicle and persistence of a response after the vehicle passed.

We tested the following four hypotheses based on the assumptions indicated: 1) some snake species have a higher frequency of road avoidance than others as species vary in their innate inhibitions to cross open spaces; 2) snakes vary interspecifically in road crossing speeds, probably reflecting variations in travel speeds that occur naturally in response to potential exposure to predators; 3) snake species consistently cross the road at a perpendicular angle, minimizing the length of the crossing trajectory and time spent crossing, as the road presumably represents a threatening environment to all snakes; and 4) snakes react to a passing vehicle as they would an approaching predator, with those that rely on crypsis or venom becoming immobile and those having the ability to flee rapidly exhibiting an immediate flight response.

MATERIALS AND METHODS

Study site.—The Savannah River Site (SRS) is a 750-km^2 tract of federal land located in Aiken, Barnwell, and Allendale counties, South Carolina. The area is closed to the general public and is protected as a National Environmental Research Park (NERP, Shearer and Frazer, 1997). The site is managed by the U.S. Department of Energy and secured by a contracted security firm (Wackenhut Corporation) and contains a diversity of habitat types (e.g., wetlands, forests, sandhills) inhabited by 35 species of snakes (Gibbons and Semlitsch, 1991).

The behavioral tests in this study were conducted on a 1.9 km-long section of two-lane (6.0 m wide) asphalt road bordered by secondary successional forest. The road was closed to traffic but is characteristic of one with medium traffic density (defined here as 5000–10000 vehicles per day). Performing the tests on a closed road permitted controlled investigation of the snakes' behavioral responses without endangering the safety of the animals or researchers, or distracting drivers using public roads.

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. Capture methods included drift fences and pitfall traps, aquatic and terrestrial funnel traps, coverboards, road collecting, and opportunistic searches. Snakes were placed in individual snake bags, housed in the SREL Animal Care Facility and were not handled, processed, or otherwise disturbed between capture and testing. Sex, snout–vent length (SVL), and mass were recorded for each snake after testing was completed. Snakes were then marked by cauterization (Clarke, 1971) to avoid retesting recaptured snakes, and released at the original capture location.

Testing protocol.—Specimens were excluded from testing if they 1) were originally captured at the testing site, due to an assumed familiarity with the area, or 2) were not in optimal health (e.g., emaciated or gravid). Each individual was tested twice, once on each side of the closed road, to

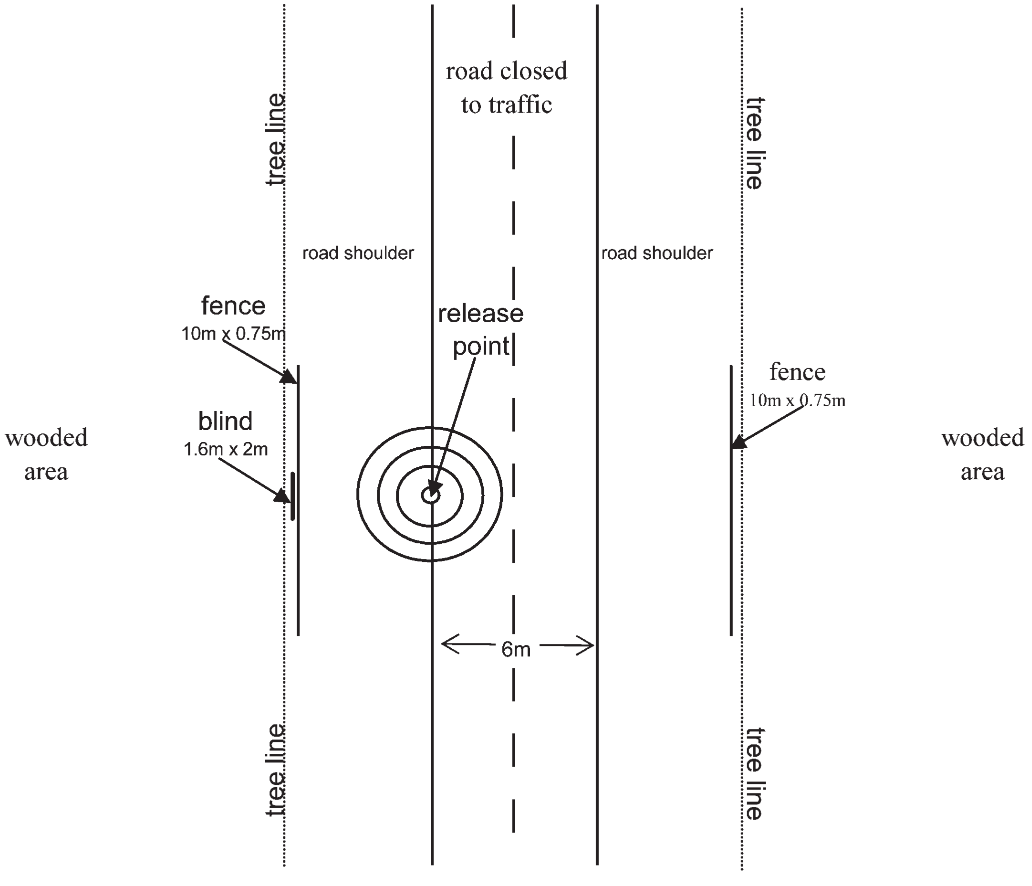

Fig. 1. Overhead view of single release site showing placement of the blind and the fence in relation to the release point at the road edge.

determine if a directional component influenced crossing behavior. An individual was only tested once per day to minimize stress. Tests were excluded from final analyses if the snake 1) never moved or 2) demonstrated defensive behavior during the test (e.g., tail vibration). Lastly, daily testing times were assigned to each species according to its natural movement patterns and historical documentation of likely road capture times (Gibbons and Semlitsch, 1991; Ernst and Ernst, 2003). Nocturnal or crepuscular species were tested in early morning (first light) or at dusk. Diurnal species were tested early to mid-morning during summer and in early afternoon in spring and fall.

Release methods.—Six release sites (three on each side of the road, 12 m apart; Fig. 1) were constructed at the study site, in places where the roadsides were relatively flat and evenly vegetated with equivalent habitat types on both sides of the road. The use of multiple release sites reduced the potential for snakes to detect the pheromone trail of a previously tested individual. Hardware-cloth fences (10 m long) were erected at each release site along the tree line to minimize escape of snakes following the test. To conceal observers during the test, a blind was built from PVC piping (1.6 m × 2.0 m) and camouflage fabric and was placed immediately behind the fence on the side of release.

The release bucket was a black plastic planting pot with holes drilled in the bottom for string attachment. Three bucket sizes were used to provide comparable amounts of space for small-, medium-, and large-sized snakes. Buckets were washed in a Basil 3500 cage-washing machine between tests. The bucket was tied upside-down to a 5.1-m bamboo pole, allowing the observer to stand behind the blind and lift the bucket to release the snake while remaining concealed for the entirety of the test. 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 initiation of the test.

At the release site, the bag containing the snake was untied and placed under the bucket. The bag was removed by holding a corner and sliding it out from under the bucket, leaving the snake underneath and preventing exposure to the surrounding area prior to the test. The snake was allowed one minute to acclimate before we initiated the test by lifting the bucket. Search behaviors and their time of occurrence during the test were recorded to assess if a snake was disturbed (e.g., tail vibration) and whether snakes used typical search behaviors (e.g., tongue flicking, head raising, and lateral head bobbing) for exploring the road environment.

Environmental variables.—While effects of the environmental variables were analyzed, the purpose of collecting these data was to maximize standardization rather than a targeted attempt to examine environmental factors affecting road-crossing behaviors.

A suite of conditions were recorded for each test: temperatures at the release point (road, ground, and air), humidity, barometric pressure, previous 24-hour rainfall, and ranked measurements of cloud cover and wind strength. A road temperature range (15 C–55 C, across seasons) was set to avoid testing in temperatures outside of those of documented movement tendencies (Gibbons and Semlitsch, 1991; Andrews and Gibbons, unpubl. data). Note that the full range of temperatures was not applied to all species across all seasons during which data were collected. 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 paired release sites across the road from each other. Tests were not conducted during or immediately after rainfall.

Road tests.—Data collection included three categories: cross, avoid, and deter. Deterrence was classified as an avoidance response in which the snake entered the road but retreated toward the release side before crossing the entire road. A test was terminated when the snake reached the fence on the opposite side of the road (cross) or the tree line of the release side (avoid), at which point the snake was recaptured. When a snake crossed the road, the entry and exit times and the length of crossing trajectory were recorded for calculation of road crossing speed. Additionally, the angle of the crossing trajectory relative to the road (90° = perpendicular to the direction of the lanes) was recorded after the test was completed using a protractor and measuring tape.

TABLE 2. TARGET SPECIES SELECTED FOR THE ROAD TESTS. Categories designate whether a species is (A) aquatic or (T) terrestrial, (V) venomous or (N) nonvenomous, or (S) small, (M) medium, or (L) large in average body size.

Species	Habitat	Venom	Size
Agkistrodon piscivorus	A	V	L
Coluber constrictor	T	N	L
Crotalus horridus	T	V	L
Diadophis punctatus	T	N	S
Elaphe guttata	T	N	L
Elaphe obsoleta	T	N	L
Heterodon platirhinos	T	N	M
Nerodia fasciata	A	N	L
Tantilla coronata	T	N	S

In 2002, a pilot study was conducted with 27 species (n = 225 individuals; Andrews, 2003) to identify target species exhibiting a range of life-history strategies and behavioral responses to roads. Nine species were selected for testing during the core season (March–November 2003) including species that were aquatic or terrestrial, venomous or non-venomous, and that varied in average adult body size (Table 2). Data from the pilot study were not used in the core analysis, with the exception of crossing speeds and angles.

Variable influences were examined with 1) a general model that incorporated all potential covariates and 2) category models in which variables were either classified as experimentally controlled (release site number, side of the road of release, time held in captivity, and whether the snake was initially caught on a road), physical (sex, SVL, and mass), or environmental (date, time, temperatures of road, ground, and air, humidity, barometric pressure, 24-hour rainfall, wind, and cloud cover). Model fit was analyzed using stepwise regression (PROC LOGISTIC, SAS Institute, Inc., Cary, NC, 1999). Full models were developed for all snakes with ''species'' included as a variable, and species-specific models were developed separately for each species. The use of multiple models allowed us to describe effects of covariates in greater detail for each species. Though individuals were tested twice, repeated measures designs could not be applied to the data set; therefore, models were run including all tests and only the first test of an individual, and 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, 1998) after the removal of outliers (PROC UNIVARIATE, SAS Institute, Inc., Cary, NC, 1999).

Vehicle tests.—Vehicle tests were conducted between March and November 2003. Due to the possibility that snakes might respond differently to different vehicles, a single vehicle (a 2002 Chevrolet Silverado 1500 pick-up truck) was used for all tests. The same release method and site design were used as in the road tests but only three snake species (Eastern Ratsnake: *Elaphe obsoleta*; Eastern Racer: *Coluber constrictor*; and *Crotalus horridus*), representing three distinct defense strategies (crypsis, speed, and venom, respectively), were tested. The collection of environmental variables was identical to the road tests except that humidity, barometric pressure, and 24-hour rainfall were not measured.

After containment of the snake under the bucket, the observer stood behind the blind and lifted the bucket while the driver was positioned in the vehicle at the start point 0.3 km down the road from the release point. Once the snake demonstrated consistent movement into the road the observer behind the blind cued the driver by radio to drive (35 mph) past the snake. Upon approach, the observer informed the driver of the snake's location to minimize the distance between the passing vehicle and the snake without threatening the safety of the animal. No incidental injury or mortality of study specimens occurred while conducting this study.

The snake was not forced into the road and therefore had the same directional options as in the road tests (i.e., cross, avoid, deter). The primary variable of interest was whether the snake fled, became completely immobile, or showed no reaction (continued moving without altering speed or direction) in response to the passing vehicle. Additionally, the timing of the response in relation to the vehicle (before, at the instant of, or after the vehicle passed) was recorded. As the snake was not always in the same physical location relative to the road in every test, distance between the snake and the vehicle could not be strictly standardized, but only minimized and was estimated to the nearest 0.25 m.

After the vehicle passed the snake, a secondary response was recorded of whether the snake 1) continued to move, 2) resumed movement after immobilizing, or 3) continued to remain immobile. Snakes were recaptured within one minute of the vehicle passing to prevent escape. Therefore, the secondary response is a short-term observation and does not represent the maximum amount of time a snake may remain immobilized.

Stepwise regression (PROC LOGISTIC, SAS Institute, Inc., Cary, NC, 1999) was used to determine any covariate effects on responses to the passing vehicle by investigating both general and category models and on a grouped and individual species basis as described above. Odds ratios were again calculated to determine the degree of consistency between the responses of an individual's first and second test (Agresti, 1996). Chi-square analysis was used to investigate response probabilities of each species (PROC FREQ, SAS Institute, Inc., Cary, NC, 1999).

Results

Road tests.—Over the 2003 season, 193 individuals of the nine target species were tested. Multiple analyses were run after applying exclusion criteria (n = 38) to determine the consistencies in models using all tests (excluded tests, n = 355) and using only the first test of an individual (n = 185). 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; if θ = 1, there is no correlation between the response exhibited in the first test and that in the second).

The effect of species on road avoidance was highly significant in stepwise models ($P <$ 0.0001). Snout–vent length was significant ($P <$ 0.05), with smaller species demonstrating a greater tendency to avoid the road (Fig. 2). Single-species regressions did not yield significance for any of the variables with the exception of SVL (P $<$ 0.05) for *C. horridus*, in which larger specimens had a greater tendency to avoid the road. *Coluber constrictor* demonstrated a marginally greater avoidance tendency when tested on the west side of the road (P = 0.05). Chi-square analyses conducted on a single-species basis yielded response probabilities for six of the nine target species that deviated significantly from expected (50:50; Fig. 2), with only *C. constrictor* avoiding the road less frequently than expected. Most snakes that exhibited avoidance did not attempt to cross the road, but two species (Cottonmouth, *Agkistrodon piscivorus*; Southern Watersnake, *Nerodia fasciata*) entered the road and then deterred almost 50% of the time; Ring-necked Snakes,

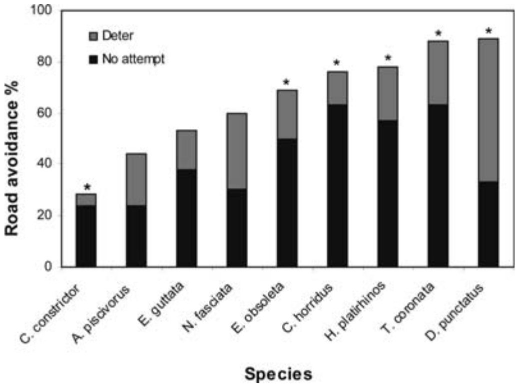

Fig. 2. Road avoidance rates for nine southeastern snake species. Asterisks above bars represent species that significantly deviated from expected ($P < 0.05$). Black = individuals that retreated to the woods without entering the road (i.e., no attempt). Gray = individuals that attempted but did not cross the entire road (i.e., deter). Species had a highly significant effect on crossing probability ($P < 0.0001$). Sample sizes, in order by species, are *C.c.* 54, *A.p.* 25, *E.g.* 13, *N.f.* 20, *E.o.* 26, *C.h.* 16, *H.p.* 14, *T.c.* 8, *D.p.* 9.

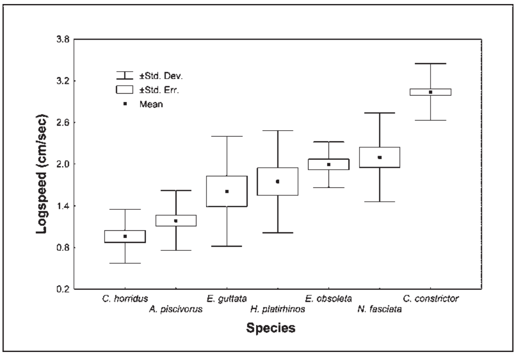

Fig. 3. Crossing speeds for all target species with $n > 10$ crossing occurrences. The effect of species on crossing speed was highly significant ($P < 0.0001$). Sample sizes, in order by species, are *C.h.* 20, *A.p.* 29, *E.g.* 13, *H.p.* 14, *E.o.* 17, *N.f.* 19, *C.c.* 73.

Diadophis punctatus, deterred in 63% of all avoidance occurrences.

The species effect on crossing speed was also highly significant (Kruskal-Wallis test, $P < 0.0001$, Fig. 3); five outliers were removed (*C. constrictor*, $n = 4$; *C. horridus*, $n = 1$). Snout–vent length and mass ($P < 0.01$), and road temperature ($P < 0.0001$) had significant effects on crossing speeds. Long, slender-bodied species crossed faster than short, stout species, and speed was positively correlated with road temperature across species. Species were not significantly different in crossing angles ($P = 0.06$), and no species significantly deviated from a perpendicular (90°) crossing trajectory ($P > 0.05$); six outliers were removed from the dataset (*C. constrictor*, $n = 1$; Cornsnake [*E. guttata*], $n = 1$; Eastern Hog-nosed snake [*Heterodon platirhinos*], $n = 4$).

Vehicle tests.—A total of 218 tests ($n = 113$ individuals) were conducted and no differences were found between results for the model after applying exclusion criteria (excluded tests, $n = 42$), using all tests ($n = 175$), and only using first tests ($n = 84$). Additionally, responses of an individual did not vary between tests (odds ratio, $\theta = 4.37$). All models and analyses demonstrated a high significance both at the species level (stepwise regression, $P < 0.0001$) and on a per-species basis for all three species (Chi-square; *C. constrictor*, $P < 0.0001$, *C. horridus*, $P = 0.00$, *E. obsoleta*, $P < 0.0001$; Table 3). All *C. horridus* ($n = 30$; first test, $n = 13$) exhibited an immobilization response and thus this species was excluded from covariate analyses. Tests in which individuals displayed no response to the vehicle (*C. constrictor*, $n = 6$; *E. obsoleta*, $n = 1$) had no overall effect on the likelihood of a particular response and are not included in presentation of the data. Finally, no measured variable (environmental, physical, or controlled) had a statistically significant effect on response to the vehicle in any of the regression models ($P > 0.05$).

The position of the snake on the road relative to the vehicle exhibited no effect on response. However, both the timing and type of reaction by the snake after the vehicle had passed differed among species ($P < 0.05$). *Coluber constrictor* and *E. obsoleta* were more likely to immobilize as the vehicle passed whereas *C. horridus* froze 50% of the time even before the vehicle passed (Table 3). Few snakes (3%) commenced an immobilization reaction after the vehicle had passed. Most (62%) froze as the vehicle passed, and the remainder (35%) froze before the vehicle passed. After the vehicle passed, more than half the snakes resumed movement within a few seconds (55%), but a large proportion (36%) remained immobile on the road until the test was complete (Table 3). Both *E. obsoleta* and *C. horridus* resumed movement 65–70% of the time after the vehicle passed, but 53% of the *C. constrictor* remained immobile.

Discussion

Road tests.—Our three hypotheses concerning snake responses to roads were supported by the findings. Species differed in road avoidance rates and road crossing speed but did not differ in crossing angles.

TABLE 3. (A) IMMOBILIZATION RESPONSES TO A PASSING VEHICLE FOR THREE SPECIES OF SOUTHEASTERN SNAKES. All species deviated significantly from expected (50 : 50). Interspecific differences were highly significant ($P < 0.0001$). Sample sizes, in order by species, are *C.c.* 90, *E.o.* 55, *C.h.* 30. (B) Timing of immobilization of snakes in response to a passing vehicle. ''Before'' represents the proportion that became motionless as the vehicle approached, in contrast to ''after,'' which is the proportion that immobilized after the vehicle passed. The ''pass'' category is the proportion that stopped moving at the instant the vehicle was alongside the snake. Time of the reaction in relation to the vehicle passing differed among species ($P < 0.05$). Sample sizes, in order by species, are *C.c.* 60, *E.o.* 54, *C.h.* 30. (C) Secondary responses of snakes after the vehicle passed. ''Move'' represents where the snake fled and continued to flee after the vehicle passed. ''Restart'' represents where the snake immobilized but resumed movement after the pass. ''Freeze'' represents where the snake immobilized and remained motionless for up to a minute after the vehicle passed. Species had a significant effect on the probability of a particular response after the vehicle passed ($P < 0.05$). Sample sizes, in order by species, are *C.c.* 20, *E.o.* 33, *C.h.* 23.

	A	B			C		
		Timing of response (%)			After vehicle pass (%)		
Species	Immobilization to vehicle (%)	Before	Pass	After	Move	Restart	Freeze
Coluber constrictor	64	22	75	3	30	15	55
Elaphe obsoleta	98	41	54	5	0	70	30
Crotalus horridus	100	50	50	0	0	70	30

The two smallest species (*D. punctatus* and *T. coronata*) almost never crossed the road. Smaller snakes that are more likely to have avian predators and suffer greater predation risk when in exposed terrain (Fitch, 1999) often adopt secretive or fossorial life styles. Small snakes also typically move shorter distances (e.g., *D. punctatus* averages 1–3 m/day; Fitch, 1999) than larger species, reducing their chances of encountering a road. We are not suggesting that small snakes never cross roads, but that roads do not offer environmental conditions conducive to overland movement by these species, resulting in behavioral road avoidance. High population densities in some areas may result in an underestimate of deterrence rates of these species (e.g., *D. punctatus*, Fitch, 1999; *T. coronata*, K. Messenger, unpubl. data).

The side of the road on which the road-crossing test was initiated had a species-level effect on avoidance levels in *C. constrictor*. This response suggests the potential importance of directional cues in snake movement patterns. Olfactory cues may also influence crossing patterns; however, these were minimized by our experimental design. Shine et al. (2004) observed that scent trails were obscured on gravel roads, but whether this applies to other road substrates (e.g., asphalt) remains unknown. No study has addressed the sensitivity of snakes in detecting habitat cues that influence directional movement, but road placement within a habitat is likely a key factor determining whether snakes cross the road and may be more influential than previously documented.

Larger *C. horridus* (i.e., >1000 mm SVL) had a greater tendency to avoid the road than did smaller individuals. Regardless of any significance of this observation, road avoidance in adult rattlesnakes has been sporadically documented. Eastern Diamondback Rattlesnakes (*C. adamanteus*) have truncated their home ranges along roads (B. Means, pers. comm.), and Timber Rattlesnakes (*C. horridus*) have traveled parallel to roads (Fitch, 1999; Sealy, 2002). Seigel and Pilgrim (2002) observed a decrease in the number of adult Massasaugas (*Sistrurus catenatus*) crossing roads proportional to neonates. Our data for initial capture technique of *C. horridus* were not diverse enough to do a detailed analysis on prior exposure to a road, but this topic deserves further investigation.

Coluber constrictor tended to cross the road more frequently than expected. Although it cannot be ascertained why racers exhibited an above-expected crossing rate, existing road capture data of more than 2500 racers from the SRS (Andrews and Gibbons, unpubl. data) provide ample support that this species will readily cross roads. Although it seems likely that *C. constrictor* would be in some way negatively impacted by the amount of road mortality that we have observed, it is possible that this species could still be experiencing proportionately less severe fragmentation effects (i.e., mortality and isolation) than species that cross roads less frequently and more slowly.

Not all individuals of species commonly found on roads (e.g., *C. horridus*, *E. obsoleta*, *H. platirhinos*; Andrews and Gibbons, unpubl. data) consistently crossed during testing (>70% road avoidance; Fig. 2). However, seasonal documentation of road crossings could be influenced by home range size and dispersal tendencies relating to hibernation sites or mate-searching patterns (Krivda, 1993; Bonnet et al., 1999), situations that could compel species that normally avoid roads to attempt to cross. Whether a snake was initially caught on the road had no significant effect on response probabilities nor did the test number per individual, although the potential for learned behavior by individuals could presumably influence crossing or avoidance patterns.

Crossing speeds differed greatly by species and can be explained in part by interspecific differences in body size and movement styles. We observed the lowest average crossing speeds in the venomous species, *A. piscivorus* and *C. horridus*. Fitch (1999) described *C. horridus* as crossing roads ''so slowly, movement was likely to be unnoticed.'' Our data confirm this behavior with *C. horridus* and extend the observations to another venomous species, *A. piscivorus*. In addition to the physical implications of species with higher mass to length ratios being slower, viperid snakes have venom as an ultimate defense mechanism and would be at lower risk than nonvenomous species to birds or other predators attacking them while crossing open spaces. Although pit vipers would have less pressure to move quickly in an open environment, they may still perceive a road as a potentially dangerous environment and be reluctant to cross.

The three species (*A. piscivorus*, *H. platirhinos*, *N. fasciata*) for which a mass effect on crossing speed was found are stout-bodied as adults. In the road tests, the correlation between mass and speed was negative. Long, slender snakes typically cross roads more quickly, as observed for average crossing speeds of *C. constrictor*. Collectively, snakes moved faster at warmer road temperatures, a general response previously documented (e.g., Heckrotte, 1967; Blouin-Demers et al., 2003). Additionally, crossing frequencies by snakes can be correlated not only with season but also with time of day (e.g., Klauber, 1939), likely due in part to natural diel temperature fluctuations. The precise role of temperature in road-crossing behaviors cannot be established from this study as snakes were tested within a broad, albeit constrained, range of temperatures, but temperature is likely a factor of considerable influence in road crossing patterns.

After initial searching and upon making a decision to cross the road or avoid it, snakes typically proceeded perpendicularly with consistent movement. This behavior differs from that of amphibians, which tend to cross at a wider distribution of angles, often orienting in a specific direction; therefore, for amphibians, crossing angles would vary with site (Hels and Buchwald, 2001). Snakes, in contrast, took the shortest route possible, a behavior independent of interspecific differences in crossing speed.

Vehicle tests.—*Coluber constrictor*, a species relying on rapid flight to escape from predators, had a higher immobilization response than hypothesized. Although we predicted that *E. obsoleta*, which employs crypsis, would immobilize, the response rate was also higher than expected. The hypothesis was fully supported for *C. horridus*, which relies on both crypsis and venom as defenses, as immobilization was observed in every test. In five of the seven tests in which no response was apparent (six *C. constrictor*, one *E. obsoleta*), the snake was either on the road shoulder or the distance between snake and vehicle was 4 m or more. When snakes perceive themselves to be a ''safe'' distance from the vehicle or close to the bordering habitat they may not adopt defensive behaviors. Focused studies on responses of snakes relative to position on the road and distance from the vehicle are needed to determine precisely how these factors influence the behavior of snakes crossing roads.

The majority of snakes became immobilized at the instant the vehicle passed rather than before or after. Additionally, the majority resumed movement shortly after the vehicle passed, suggesting that immobilization is generally a momentary reaction. However, *C. horridus* often remained immobilized up to one minute or more after the vehicle had passed.

The immobilization response, exhibited by three species during the vehicle tests, may contribute to the widespread belief that snakes commonly use roads to thermoregulate. Immobilization was often coupled with the snake flattening its body against the asphalt, which could lend to an appearance of basking. Thermoregulation likely does occur in some situations (e.g., Bernardino and Dalrymple, 1992) but probably under low-traffic conditions or in desert locations where animals are accustomed to open landscapes. However, the observation that individuals of even fast-moving species such as *C. constrictor* will immobilize when a vehicle approaches invites caution about interpretations based on seeing a snake lying motionless in the road.

Road ecology.—Our results revealed the potential diversity of road impacts across snake species and suggest a level of sensitivity of some species to roads. The study of ''road ecology'' is a newly forming field (Forman et al., 2003) with an increasing number of ecologists, chemists, and

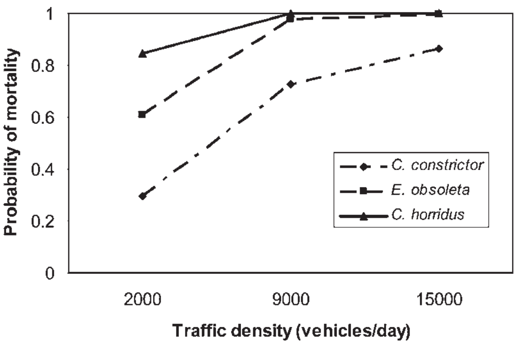

Fig. 4. Probability of mortality for three different snake species at varying traffic densities based on observed crossing speeds. Traffic densities characteristic of low, medium, and high flows are presented for hypothetical roads. Note that densities achieved in cities, or in some areas during peak patterns (>15,000 vehicles/day) are not represented. Model is adapted from Hels and Buchwald (2001) in which $p(\text{death}) = 1-e^{-}(Na/v(\cos\alpha))$ where N = traffic density (traffic/lane/day), a = kill zone width, v = average velocity of snake species (m/sec), and α = deviation from a perpendicular cross.

hydrologists recognizing irreparable landscape alteration from the nation's transportation infrastructure. Understanding the biology behind these alterations will allow for efficient mitigation practices and for future development of more environmentally sound transportation designs.

Our road tests revealed no generalized behavior in road encounters among snake species with the exception of crossing angle. Many species-specific behaviors reflect natural responses to open spaces and the potential risk of encountering predators. In assessing how different species are affected by roads, we should first consider the natural behavior and ecology of the species in question. Although our study was not designed to test the importance of all extrinsic and intrinsic variables, certain habitat cues and road temperatures clearly influence both avoidance rates and crossing speeds of snakes.

It is of conservation importance that not all snakes are equally susceptible to the same suite of road impacts. Those that avoid roads are subject to habitat fragmentation if the road forms an impermeable behavioral barrier. Snakes that enter the road but deter and ultimately avoid crossing are not only subject to direct mortality by entering the road but also to fragmentation because few individuals successfully cross. Those species that cross roads have unequal probabilities of mortality resulting from a combination of crossing speed, propensity to cross, and activity levels. Species that suffer high rates of mortality on roads are subject to fragmentation in situations where insufficient numbers of individuals successfully cross to maintain necessary population-level dynamics. Further, snakes are a maligned group of animals subject to the additional threat of intentional killing of individual snakes as they attempt to cross roads (Langley et al., 1989).

Responses by snakes to vehicles presumably mimic how they respond to predators or to unrecognized stimuli in natural habitats. The use of characteristic predator responses by all species, in combination with crossing by the shortest path possible, suggests that snakes do not deem the road to be a favorable environment. The immobilization response appears to be more momentary, with the exception of *C. horridus*, which exhibited extended immobilization. In high-traffic situations immobilization could significantly prolong the amount of time necessary to cross a road. Thus, for species that immobilize repetitively in response to passing vehicles, the time required to cross is positively correlated with traffic density. In-road immobilization behavior needs to be considered as an additional factor increasing the threat of mortality for some snake species.

Future applications.—These data can be applied to models relating crossing probabilities of species with road characteristics. We used crossing speeds and angles documented in this study to estimate the probability of mortality per individual crossing the road for three of the target species under low, medium, and high traffic densities (Fig. 4). This model was adapted from Hels and Buchwald (2001) and used by Gibbs and Shriver (2002) with turtles. Our initial application of the model shows that faster species (i.e., *C. constrictor*) are more likely to cross successfully than slower species (e.g., *C. horridus*) that could experience detrimentally high mortality levels at even medium traffic densities.

Exploring road impacts from a behavioral perspective allows determination of degrees to which the road poses a barrier to snake movements, but as seen from this research, road impacts cannot be generalized even within an animal group. In conservation applications, this study demonstrates that planning and development based on single-species management designs may not be effective for other species. However, in many situations the ability to simultaneously plan for the wildlife community, while identifying needs of species worthy of concern would be ideal. Some snakes may be able to maintain viable populations amidst road development, but others may go locally extinct without the implementation of measures to minimize road impact. The responses of different snake species to roads must be recognized so that resources and future research can be prioritized for species sensitive to road fragmentation.

Acknowledgments

Appreciation is extended to those from SREL who caught snakes used in this research and helped with the field tests, with special recognition to P. Mason, B. Lawrence, L. Wilkinson, and L. Ruyle. We thank T. Mills and S. Poppy for construction assistance at the field test sites and D. Zhao for statistical advice. We appreciate M. Underwood and Wackenhut Corporation for providing a protected road area for conducting field experiments and for permission to conduct research on SRS highways. We thank S. Harper and J. Willson for providing comments on the manuscript. Snakes were captured under scientific research permit #56-2003 from the South Carolina Department of Natural Resources, and the study was approved under University of Georgia Animal Use Proposal A2003-10135. Research was conducted with support of the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through Financial Assistance Award no. DE-FC09-96SR18546 to the University of Georgia Research Foundation. This research supports the goals of Partners in Amphibian and Reptile Conservation (PARC).

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