

ROADS AS CATALYSTS OF URBANIZATION: SNAKES ON ROADS FACE DIFFERENTIAL IMPACTS DUE TO INTER- AND INTRASPECIFIC ECOLOGICAL ATTRIBUTES

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

Key Words — Alive on Road, Body Size, Dead on Road, Ecology, Highway, Mortality, Sex Ratio, Snakes, Suburban, Urban

Urbanization occurs at multiple spatial scales from the opening of a store, construction of a residential neighborhood, or development of a city. All of these developments are enabled through establishment of roads. Even the construction of roads through forested land is often a harbinger of encroaching urbanization. The area affected by roads due to strong edge effects can be 2.5–3.5 times greater than that of clearcuts; therefore, road fragmentation can also be apparent in remote “protected” locations (Reed et al. 1996), urbanizing even parks and refuges. Roads are clearly an essential component of urban areas, and the documentation of declines of amphibian and reptile population species surrounding roads

are numerous (e.g., Andrews et al. 2008). Nonetheless, some amphibian and reptile species readily reside in areas experiencing anthropogenic disturbance (e.g., Neill 1950; Zappalorti and Burger 1985). Some species that appear to occur in healthy numbers in suburban areas may decline in numbers with increased urbanization (Minton 1968). The level to which roads contribute to such declines warrants investigation for all groups of herpetofauna.

Assessing the susceptibility of wildlife to urbanization is tedious, as the appropriate scale for investigation varies among taxa (Mazerolle and Villard 1999). Sampling is further complicated within a species as adult behavior cannot always be

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

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

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

MATERIALS AND METHODS

Study Site — We examined 15,697 records of 35 species of native snakes collected 1951–2005 from the 750 km² U.S. Department of Energy Savannah River Site (SRS) located in the Upper Coastal Plain in South Carolina, USA. The purpose of the large set-aside area was for building five nuclear production reactors, associated industrial facilities and office buildings, cooling canals and reservoirs, and highway systems (Gibbons 1994). The extensive SRS road system includes more than 160 km of primary two- and four-lane concrete and blacktop highways in addition to secondary dirt and gravel roads, most of which have experienced low traffic levels (< 2,000 cars/day) throughout most days since the 1950s.

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

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

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

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

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

RESULTS

We examined 15,697 records of 35 species of snakes collected over a 54-yr period (Table 1), including 2,577 (29 species) from roads. Six species have never been collected on roads in the study site area (n = 1,759; Table 1). Among 15

species of road-collected snakes, significantly more were males (64%; n = 1,002) than were females (n = 572; $\chi^2 = 127.8$, $P < 0.001$). In analyses of individual species, 7 were significantly biased in favor of males (Fig. 1). Collectively, male snakes were found on roads more frequently than were females; this trend was observed in intraspecific comparisons for 7 species, with *Lampropeltis getula* (n = 89) having the highest proportion of males (73%) among SRS species found on roads. Significantly more males (54%; n = 3,704) than females (n = 3,185; $\chi^2 = 39.1$, $P < 0.001$) were also collected in off-road habitats, but the proportion of males observed in on-road specimens was still significantly greater than that observed in off-road captures ($\chi^2 = 3,368.7$, $P < 0.001$).

Of 2,233 individuals of 17 species found on roads, significantly more were DOR (61%) than were AOR ($\chi^2 = 120.2$, $P < 0.001$). Species type was a significant factor ($df = 16$, $F = 2.13$, $P < 0.001$) influencing the propensity to be found DOR. DOR snakes were significantly more prevalent than AOR in 7 species; in contrast, *Agkistrodon contortrix* was represented by significantly more AOR specimens (Fig. 2). Total length ($df = 938$, $F = 14.69$, $P < 0.001$), mass ($df = 823$, $F = 9.47$, $P = 0.002$), and the interaction of total length and mass ($df = 806$, $F = 9.81$, $P = 0.002$) were found to be positively significant components influencing whether individual snakes of 7 species were DOR or AOR.

Total length ($df = 10,365$, $F = 836.3$, $P < 0.0001$) and mass ($df = 9,095$, $F = 178.3$, $P < 0.0001$) of snakes captured on roads were significantly greater than those of individuals from off-road habitats. In comparing on-road with off-road captures of 15 species, we found road-collected snakes to be significantly

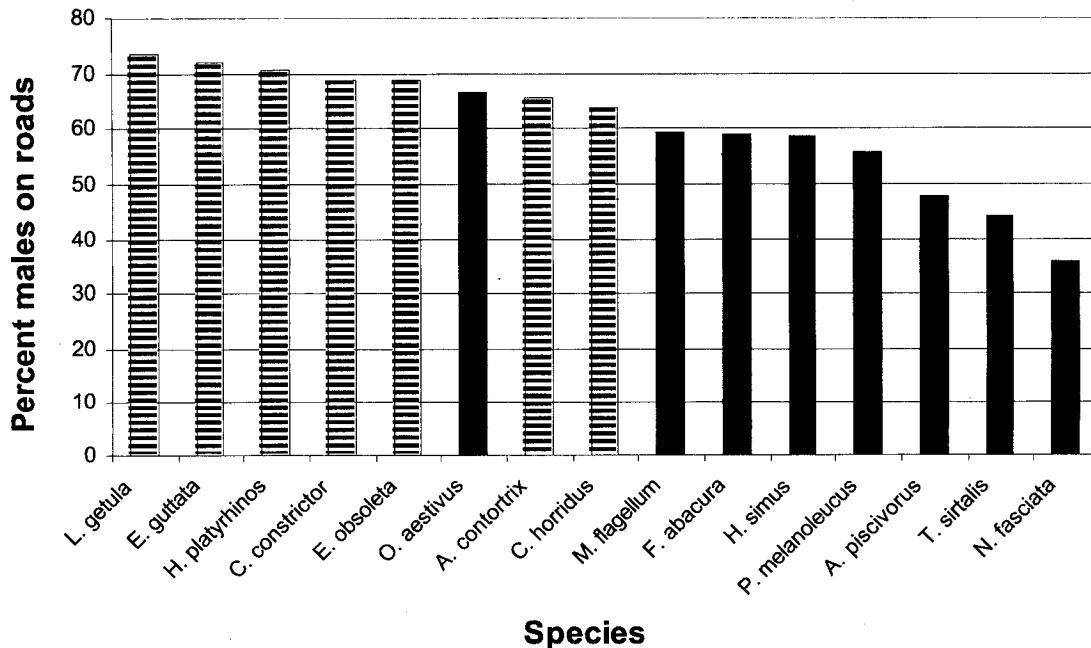


Fig. 1. Sex ratios of snakes found on Savannah River Site roads in South Carolina between 1951 and 2005. Bars with horizontal lines represent species with significantly more males than females (Chi-square test for goodness of fit, $P < 0.01$). *E. obsoleta* = *E. alleghaniensis*.

Table 1. Snakes captured on the Savannah River Site, South Carolina, USA, between 1951 and 2005. "On" = number of individuals captured on roads, "Off" = number of individuals captured in off-road habitats. **Elaphe obsoleta* = *Elaphe al-leghaniensis*.

Species	Common name	On	Off	Total	% On
<i>Pituophis melanoleucus</i>	Pine Snake	152	18	170	89
<i>Agkistrodon contortrix</i>	Copperhead	214	30	244	88
<i>Crotalus horridus</i>	Timber (Canebrake) Rattlesnake	335	85	420	80
<i>Elaphe obsoleta</i> *	Eastern Rat Snake	220	115	335	66
<i>Masticophis flagellum</i>	Eastern Coachwhip	123	81	204	60
<i>Heterodon simus</i>	Southern Hog-nosed Snake	115	83	198	58
<i>Elaphe guttata</i>	Corn Snake	160	133	293	55
<i>Sistrurus miliarius</i>	Pygmy Rattlesnake	27	23	50	54
<i>Heterodon platirhinos</i>	Eastern Hog-nosed Snake	178	289	467	38
<i>Nerodia erythrogaster</i>	Red-bellied Watersnake	44	112	156	28
<i>Coluber constrictor</i>	Eastern Racer	446	1198	1644	27
<i>Micrurus fulvius</i>	Eastern Coral Snake	1	4	5	25
<i>Opheodrys aestivus</i>	Rough Green Snake	42	149	191	22
<i>Lampropeltis getula</i>	Common Kingsnake	89	317	406	22
<i>Thamnophis sirtalis</i>	Common Garter Snake	80	334	414	19
<i>Storeria dekayi</i>	DeKay's Brown Snake	21	107	128	16
<i>Cemophora coccinea</i>	Scarlet Snake	52	305	357	15
<i>Agkistrodon piscivorus</i>	Cottonmouth	75	477	552	14
<i>Thamnophis sauritus</i>	Eastern Ribbon Snake	30	201	231	13
<i>Lampropeltis triangulum</i>	Scarlet Kingsnake	11	90	101	11
<i>Farancia abacura</i>	Red-bellied Mud Snake	36	322	358	10
<i>Nerodia fasciata</i>	Southern Watersnake	75	1488	1563	5
<i>Farancia erythrogramma</i>	Rainbow Snake	6	230	236	3
<i>Diadophis punctatus</i>	Ring-necked Snake	11	521	532	2
<i>Virginia valeriae</i>	Smooth Earth Snake	3	156	159	2
<i>Storeria occipitomaculata</i>	Red-bellied Snake	10	710	720	1
<i>Nerodia floridana</i>	Florida Green Watersnake	3	224	227	1
<i>Tantilla coronata</i>	Southeastern Crowned Snake	9	1384	1393	> 0
<i>Nerodia taxispilota</i>	Brown Watersnake	9	2179	2188	> 0
<i>Seminatrix pygaea</i>	Black Swamp Snake	0	1660	1660	0
<i>Virginia striatula</i>	Rough Earth Snake	0	37	37	0
<i>Regina septemvittata</i>	Queen Snake	0	13	13	0
<i>Rhadinaea flavilata</i>	Pine Woods Snake	0	9	9	0
<i>Regina rigida</i>	Glossy Crayfish Snake	0	31	31	0
<i>Carphophis amoenus</i>	Eastern Worm Snake	0	5	5	0
Total		2577	13120	15697	

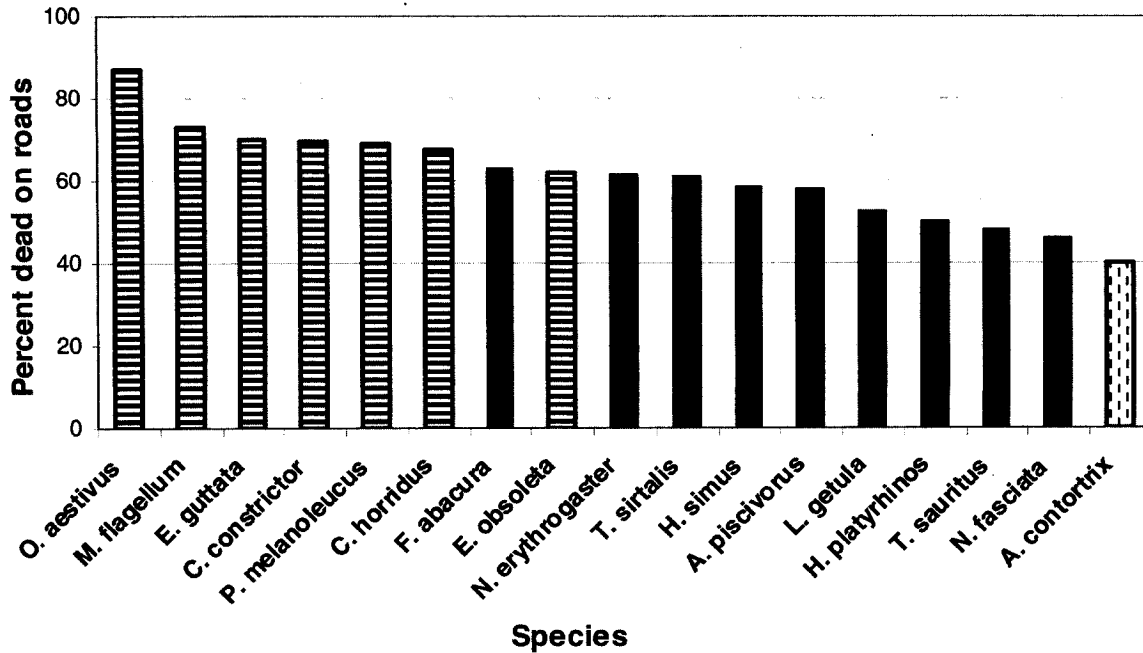


Fig. 2. Percent of dead on road (DOR) snakes found on Savannah River Site roads in South Carolina between 1951 and 2005. Bars with horizontal lines represent species that exhibited a significant tendency to be found either DOR or AOR (Chi-square test for goodness of fit, $P < 0.01$). *E. obsoleta* = *E. alleghaniensis*.

larger (i.e., total length, mass, or both) in 5 species and significantly smaller in one (*Elaphe alleghaniensis*); Table 2).

DISCUSSION

More than 2,500 records of 29 species of snakes on roads yielded a unique opportunity to explore selected characteristics of species and individuals related to their propensity to be observed on roads. More than 13,000 captures of these 29 species in off-road situations provided the data necessary to compare sex ratios and average body sizes of on-road vs. off-road captures. Six local species not observed on SRS roads (Table 1) were excluded from further analyses; however, the more than 1,700 captures of these 6 species bring caution to the bias inherent in relying on a single collecting technique

(in this case, road cruising) for conducting broad scale (e.g., community-level) inventories. These data and previous studies clearly demonstrate that road cruising should not be used as the sole method to determine diversity or abundance estimates for local snake populations due to the many variables that influence the effectiveness of road cruising as a survey technique (Case 1978; Bonner et al. 1999; Enge and Wood 2002; Seigel and Pilgrim 2002; this study). Although road cruising will continue to be a uniquely useful tool for assessing the presence of some species amidst increasing urbanization, it should be used circumspectly as a supplementary technique.

Observed differences between on-road and off-road species richness could presumably be attributed to species occurring in low abundance in localized populations (*Rhadinaea flavilata*, *Virginia striatula*; Gibbons and Semlitsch 1991),

Table 2. Total body length, body mass, and/or the interaction were significantly different between on-road and off-road captures in 7 Savannah River Site snake species between 1951 and 2005 (n = sample size). Average total lengths (TL) are shown for captures on the road (TLon) and in off-road (TLoFF) habitats for each species, followed by the F- and P-values resulting from ANOVA analyses of total length, mass and the interaction of the two variables. **Elaphe obsoleta* = *Elaphe alleghaniensis*.

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

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

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

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

gravid female turtles are frequently killed, turtle populations may be particularly at risk from roads.

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

Our results indicated that snakes on roads were generally larger than individuals captured in off-road habitats. A simple explanation for the bias towards larger individuals on roads is due to the observer bias for detecting larger, heavier snakes (e.g., Fitch 1949) because they are easier to observe. Also, larger snakes may be more likely to venture across open spaces, such as roads, because of a reduced threat of avian predation (Fitch 1949; Enge and Wood 2002; Andrews and Gibbons 2005). In contrast, an observer would not necessarily detect larger snakes in greater proportion than small ones of a species because camouflage and escape behaviors would be more effective in off-road habitats. Additionally, smaller road-killed snakes are physically degraded by vehicles and may be more difficult to detect or identify than large ones after being scavenged, reducing the likelihood of observing the snake (Enge and Wood 2002; Antworth et al. 2005; K. Andrews unpubl. data). Aside from *ad hoc* interpretations, the smaller size of *E. [obsoleta] alleghaniensis* and the significant interaction between length and mass of *Heterodon platirhinos* (Table 2) have no ready explanations that are apparent to us. Regardless, the small body size of some of these species is not a sole reason for their lack of observation, as a variety of other small species (e.g., *Storeria dekayi*, *Cemophora coccinea*; Table 1) were found commonly on SRS roads.

Our data do not delineate specific factors affecting differen-

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

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

Data documenting negative impacts of roads on herpetofauna are becoming increasingly numerous and diverse, and solutions have been identified to address some of the problems that are being confronted in urban environments (Andrews et al. 2008). However, with regard to snakes, species-specific predictions are difficult to make on the basis of the current status of research examining impacts of roads on direct mortality (including this study). Nonetheless, the data demonstrate that roads will clearly take an increasing toll on snake populations as urban and suburban road density and traffic levels increase. Studies on how roads affect species richness and populations thus will become increasingly important. Some will be urgent, requiring quick impact assessments; others will best be addressed with a

search for long-term solutions that are more effective than existing options (see also Jaeger and Fahrig 2000). Herpetologists need to be involved in such studies from the outset. Due to the inability of impervious surfaces to provide complete support of habitat requirements for any herpetofaunal species, there would presumably be a threshold for quantity of impervious surface coverage over which species persistence is not achievable, regardless of the level of species resilience to general road impacts. Although species and topics must be prioritized, urbanization must be defined in a manner that incorporates all aspects of landscape development and human expansion, with roads being recognized as a dominant feature of the landscape that will directly and indirectly affect the persistence of most species of snakes and other herpetofauna.

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

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