Title

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Abstract: This study documents the magnitude of road mortality on snake species that occur in sagebrush steppe habitat, provides insight into how susceptibility to this mortality differs among species as well as by sex and age class of individuals, and examines how different landscape variables influence road-kill aggregations using a logistic regression model. I collected data by road cruising a 183-km road loop on the upper Snake River Plain in southeastern Idaho from May through October of 2003. I conducted 56 total routes, traveling 10,248 km and encountering a total of 253 snakes (0.025 snakes/km) over the six-month survey period; 93 percent of these animals were found dead on the road surface (DOR). The majority of observations belonged to two species, with gophersnakes (*Pituophis catenifer*) comprising 75 percent of all road records, and western rattlesnakes (*Crotalus oreganus*) comprising 18 percent of all road records. Monitoring data from three of the largest snake hibernacula on the site indicate that rattlesnakes are the most abundant snake species, comprising 50 percent of all captures at trapping arrays since 1994. This suggests that gophersnakes may be more susceptible to road mortality due to higher vagility, or that our monitoring efforts do not effectively estimate their populations; this question remains to be explored. Overall, I documented more traffic casualties of adults than any other age class, the majority of which were males (64%). Road mortality varied seasonally by age and sex classes for both gophersnakes and rattlesnakes. More adult male gophersnakes were discovered DOR in May and June, while the death of adult females did not exhibit a trend. I documented a significant pulse of subadult mortality during the month of September. The seasonal trends in mortality of rattlesnakes differed from gophersnakes, but were not significant. This indicates that individuals may be more susceptible to road mortality during specific movements, such as mating or migration. The logistic regression indicated that increased cover of grass along roadsides, basalt piles, and mean distance to den were positively associated with gophersnake occurrence on roads. As most grasses on the site are invasive, this result implies that habitat change due to invasive species may be increasing susceptibility of gophersnakes to mortality.

Introduction

An expansive network of roads stretches across our landscape affecting ecosystem processes in myriad ways (Forman et al. 2003). Roads transform existing vegetation into a compacted earthen surface with altered thermal and moisture characteristics and create a replacement zone of intense human activity. Therefore, roads facilitate future development of an area, increasing use of surrounding habitats by humans and the hunting, collection, and observation of wildlife (Andrews 1990; White and Ernst 2003). Road characteristics are variables that potentially affect wildlife both directly and indirectly. Several road aspects of apparent influence include age, access, substrate, and size. Finally, road placement within the context of the surrounding landscape can also influence road-kill locations, rates, and species presence.

Wildlife behavior and ecology influences the probability of wildlife being affected by roads. Animal movement across the landscape includes home range activities (e.g., foraging, thermoregulation, and territorial behavior), dispersal, mating, escape behavior, and migration. Habitat use may vary seasonally, and the frequency and type of movement differs by life stage, sex and species. Vagile species are more likely to encounter roads as a result of greater movement distance and frequency (Bonnet et al. 1999; Carr and Fahrig 2001). Sometime during the last three decades, roads with vehicles overtook hunting as the leading direct human cause of vertebrate mortality on land (Forman and Alexander 1998). Vehicles on roads kill over one million vertebrates each day in the United States (Lalo 1987). Roads can affect demography and gene flow by disrupting dispersal through mortality of breeding adults. The immediate threat to animals (i.e., being killed by traffic) can result in the effective isolation of populations (Lodé 2000). Ultimately, isolation can strongly influence long-term persistence of populations through inbreeding depression, which increases susceptibility to extinctions (Sjögren 1994, Vos and Chardon 1998). The survival of populations in fragmented habitats depends on the interaction between the spatial pattern of roads and the movement characteristics of the organisms (Carr and Fahrig 2001).

Many snake species possess life history characteristics that increase their vulnerability to roads (reviewed in Jochimsen et al. 2004). Briefly, characteristics include: the tendency to thermoregulate on road surfaces (Klauber 1939), activity patterns that coincide with traffic flow (Seigel 1986), relatively slow locomotion, long life spans, low reproductive rates and low adult mortality (Rosen and Lowe 1994; Rudolph et al. 1999), and habitat requirements that vary seasonally. For example, northern temperate snakes migrate seasonally to locate specific resources (Gregory et al. 1987; King and Duvall 1990), such as refuge, mates, prey, and egg-laying habitat (for oviparous species). These resources tend to be located in distinct habitats that are patchily distributed across the landscape. Many large-bodied snake species make a loop-like migration from a communal hibernaculum (overwintering den site) to summer foraging habitats (King and Duvall 1990). Seasonal movements are defined by three distinct phases: (1) egress, or rapid movement away from the hibernacula, (2) stationary, or periods of short-distance movements associated with foraging, gestation, or ecdysis, and (3) ingress, or long-distance movements toward the hibernacula, as described by Cobb (1994). Their populations, therefore, depend on the maintenance of "landscape linkages" between these habitats. When roads fragment patches of summer and winter habitat, traffic and associated highway mortality affect snake populations.

Understanding how mortality differentially affects individuals could provide further insight into the effects that roads have on snake populations. For example, the loss of a gravid (pregnant) adult female can have greater implications than the loss of a juvenile male. This study quantifies the relative susceptibility of different age/sex classes and species across seasons to road mortality to provide a basis for recommendations to mitigate the adverse effects of roads. For example, closing specific road sections during selected seasons could allow for migratory movements that are predictable (Seigel 1986, Podloucky 1989). In addition to protecting the snakes themselves, the importance of snakes as trophic components of terrestrial ecosystems (Rosen and Lowe 1994, Siegel et al. 2002) emphasizes the need for mitigation efforts to maintain ecosystem health. It is uncertain how roads are linked to the widespread decline of amphibian and reptile populations (Gibbons et al. 2000, Stuart et al. 2004), but unlike many potential factors, the prospect of mitigating and, even more ideally, preventing the adverse effects that can be attributed to roads seems more attainable. However, the correct placement of mitigation efforts is critical for their success (Jackson 1999).

Research objectives

This study was designed to address three objectives: (1) quantify the road mortality of snakes on the upper Snake River Plain; (2) measure any variation of mortality with respect to species, season, sex, and age; (3) use logistic regression to evaluate the importance of habitat and landscape factors associated with road-kill locations. These correlations could then be used to identify areas that may represent high risks for snake road mortality and candidates for mitigation.

Methods

Study area

I conducted surveys along a 183-kilometer route that lies on the western edge of the upper Snake River Plain located in southeastern Idaho, USA (figure 1). This route is loop shaped and composed of six road sections with differing levels of traffic volume: US Highway 26 (45-km), US Highway 20/26 Junction (25-km), State Highway 22/33 (running N/S, 26-km), State Highway 22/33 (running E/W, 21-km), Franklin/Lincoln Boulevard (restricted access, 39-km), and US Highway 20 (27-km). Annual average daily traffic (AADT) estimates obtained from Idaho Transportation Department are reported as 1200, 2200, 610, 730, 300, and 1700 vehicles per day, respectively. In addition, I observed pulses of high traffic volumes during early morning and evening commuting hours on weekdays. All roadways are two lanes (approximately 10 m in width) and paved.

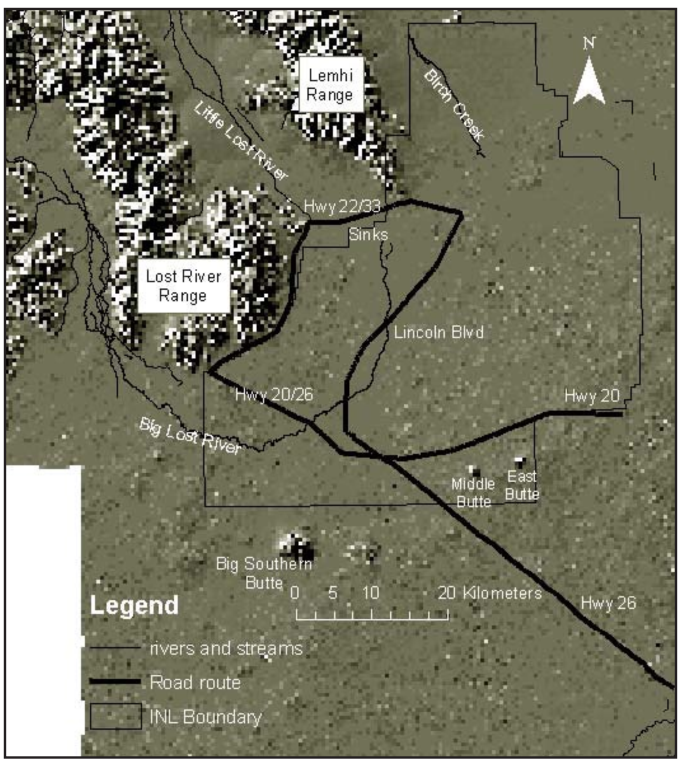

Figure 1. Shaded relief map of the Idaho National Laboratory (INL), showing the 183-km survey route (thick black line) with landscape features labeled. The inset shows the location of the INL in Idaho, USA.

The majority of the route lies within the Idaho National Laboratory (INL) (the boundary of which is designated by a thin border in fig.1), a Department of Energy facility established in 1949. Its establishment created one of the largest contiguous reserves (2,315 km) of sagebrush steppe ecosystem in the world. Sagebrush steppe describes the extensive vegetation type of the Intermountain West in the United States, which is dry habitat characterized by sagebrush, shrubs, and grasses (Anderson et al. 1996). Over the past 130 years, human disturbance, grazing, and increased fire frequency have radically altered this ecosystem. Fortunately, public access onto the INL is restricted, and approximately 40 percent of the total area has been closed to grazing since the 1950s. The value of this site for ecological research has been recognized since 1975, with on-going studies monitoring both plant and animal communities. However, grazing, agriculture, and low levels of urbanization occur along the periphery of the INL, which is managed by the Bureau of Land Management (BLM) and private owners.

Natural vegetation of the INL is predominantly a sagebrush-grass community consisting of shrub overstory with a perennial grass and forb understory. Anderson and Inouye (2001) estimated the total plant cover at 38 percent in 1995, with shrubs contributing 52 percent, perennial grasses 15 percent, and forbs 7.5 percent of that total. Habitat adjacent to roadsides comprises grasses, the degree of which varies across the study area. Many disturbed areas on the site (including roadsides) were intentionally seeded with crested wheat grass (*Agropyron* spp.), a non-native species that is resistant to native plant colonization. In addition, cheatgrass (*Bromus tectorum*), a common invasive in this ecosystem, is present.

The landscape of the study area reflects a history of volcanic activity. Mean elevation across the INL is about 1,500 m with the lowest values in the north-central portion of the site, and highest atop East Butte. Adjacent to the western and northwestern boundaries of the site are the Lost River and Lemhi Mountain ranges. The landscape is interspersed with buttes and craters with lava outcrops and tubes concentrated across the southern portion of the site. These features possess certain structural and thermal attributes characteristic of snake hibernacula (overwintering sites) (Doering 2005).

The Environmental Surveillance, Education and Research Program (ESER) manages and coordinates research concerning wildlife and habitat on and near the INL. Since 1975, students and faculty from Idaho State University have conducted research on the herpetofauna communities that occur on the INL. Visual searches have documented species occurrence (Linder and Sehman 1977, Cooper and Peterson 1996); the thermal ecology and activity patterns of reptiles have been investigated (Guyer and Linder 1985a, b; Cobb 1994); and research examining predator prey interactions and the response of snakes to habitat change is currently underway (Jenkins unpublished data). Furthermore, the ISU Herpetology Laboratory continues to monitor the three largest known hibernacula on a yearly basis since 1994; several thousand snakes have been marked, and population estimates are available (ESER Annual Environmental Reports 1994 – 2004: www.stoller-eser.com/Publications.htm).

Study species

Herpetofauna surveys document the occurrence of six snake species on the INL. The majority of these species belong to the Colubridae family including: racer (*Coluber constrictor*), nightsnake (*Hypsiglena torquata*), striped whipsnake (*Maticophis taeniatus*), gophersnake (*Pituophis catenifer*), and terrestrial gartersnake (*Thamnophis elegans*). *Crotalus oreganus* (western rattlesnake) is the lone representative of the Viperidae family. All species are known to overwinter communally at hibernacula distributed across the site. Racers and striped whipsnakes are diurnally active species that possess excellent vision, long tails, and are known for their speed (Nussbaum et al. 1983). Night snakes are small in body size, rear-fanged, and generally nocturnal or crepuscular; they tend to be associated with rocky outcrops (Nussbaum et al. 1983). Gophersnakes are large, active foragers that kill prey via constriction (Nussbaum et al. 1983) and are very adept burrowers (Ernst and Ernst 2003). Gartersnakes tend to be found in the vicinity of water, are associated with vegetation, and are viviparous (females give birth to live young) (Ernst and Ernst 2003). Finally, western rattlesnakes are sit-and-wait predators, medium-sized, and viviparous (Ernst and Ernst 2003). Many of these species migrate seasonally between hibernacula and summer foraging ranges that may be separated by greater than 2 km (Ernst and Ernst 2003).

Data collection: systematic routes

I quantified the road mortality of snakes along a 183-kilometer route by driving slowly in a vehicle (48 kmph), and recording all snakes observed on the road surface. In 2003, I drove a minimum of five days/week during the egress of snakes from hibernacula (May-June 2003) and up to three days/week from July through early October to monitor over the ingress period. I rotated the start time of each survey to account for the variation of snake activity across the seasons, as well as the direction I traveled around the route (clockwise or counterclockwise). Morning surveys were initiated prior to 1000, evening surveys after 1700 – 2000, afternoon surveys between 1200 and 1400. I conducted the initial survey (Survey #1) in the morning, the following survey (Survey #2) during the evening, and finally drove the next survey (Survey #3) in the afternoon, and continued this cycle through the end of this study. I did this to ensure that survey times were not biased to coincide with peak hours of snake activity. I attempted to conduct an equal number of surveys for each time period across all months. The duration of each survey ranged from four to eight hours dependent on traffic volume and number of snakes observed. In 2004, I reduced sampling efforts and conducted an additional 12 surveys between June 5 and October 3.

Data collection: description of snake characteristics

During each survey, I recorded variables for each snake that I encountered. I recorded whether the snake was alive on road (AOR) or dead on road (DOR), reported the observation time, and GPS coordinates (UTM, Zone 12, NAD 27 Datum) for the location using a hand-held GPS receiver (GeoExplorer II, Trimble Navigation Ltd. Sunnyvale, CA, USA). I also recorded the distance (m) to the next mile marker and the road segment on which the animal was observed. I measured both total length and snout-vent-length (SVL) of each snake. In some cases, only a portion of the carcass remained and I recorded the length of that portion. I used SVL measurements to estimate the age class for each individual based on published data of sexual maturation and SVL relationship for each species (Parker and Brown 1980, Diller and Wallace

1996, C. Jenkins unpublished data). Finally, I recorded the sex of each individual. I then marked carcasses with two spots, one close to the snout and the other to the vent, using a biodegradable spray paint and left all carcasses on the road, which allowed for easy visual identification during subsequent surveys.

Data analysis

I compared the mean number of snakes observed per survey to detect differences across the months among adult males, adult females, and juveniles for both gophersnakes and western rattlesnakes. Statistical analyses are restricted to the survey year of 2003 due to the intensity of effort. Analyses based on day number or survey week could not be conducted because the data were highly non-normal in this form. The distribution for snake mortality observed per survey across months departed significantly from a normal distribution, and attempts to log transform the data did not improve normality, so I used the non-parametric Friedman tests to detect differences. When significant, I then conducted a Wilcoxon Signed Ranks Test for *post hoc* comparisons. I used sequential Bonferroni corrections when making multiple comparisons so as not to inflate the alpha level.

Data collection: generation of "non-crossing points"

I created a shapefile of the survey route using ArcMap (version 9; Environmental Science Research Institute, Redlands, CA) GIS (Geographic Information System) by selecting and exporting specific road sections from the Area of Concern (AOC) roads data maintained at Idaho State University's GIS Training and Research Center website (http://giscenter.isu.edu). The AOC refers to land areas that surround Yellowstone and Grand Teton National Parks in Idaho, northwestern Wyoming, and southwestern Montana. I used Tool 5 of SANET: A Toolbox for Spatial Analysis on a Network (Version 1.2; Okabe et al. 2003) to generate a shapefile of random points along the entire route. This tool places points randomly on a road network based on a Poisson point distribution. I then generated a shapefile of x, y coordinate data for all snake crossings (snakes discovered both AOR and DOR) that I added to the ArcMAP project. This allowed me to visually compare the two shapefiles. I identified a random point as "non-crossing" if its position on the route was at least 30 meters from the snake crossing localities (to account for GPS error) and exported the coordinates.

Data collection: description of habitat and landscape characteristics

I measured site-specific attributes of the surrounding habitat for each snake observation and for the equal number of non-crossing points generated by SANET. First, I classified the road shoulder slope into one of six categories in a similar manner to Clevenger et al. (2003): (1) road surface raised compared to surrounding landscape; (2) no slope; (3) road surface sunken relative to surrounding landscape; (4) one side flat, one sunken; (5) one side flat, one side raised; and (6) one side sunken, one raised. I then measured the distance from the pavement edge to the closest vegetative cover, and to the nearest shrub for both sides of the road. I then walked 10 m straight out from the pavement edge into the adjacent habitat to estimate percent cover and major type (classified as shrub, grass, or forb) and percent shrub cover within a 157 m^2 area of the roadside. I measured these values for both road sides for each location. Based on these field measurements, I calculated additional categories for use in the logistic regression analysis, such as mean and minimum distance from the road edge to vegetation and shrub, and mean and minimum percent vegetation cover and shrub cover. I also created six different categories to describe the major cover type spanning both sides of the road: (1) shrub, shrub; (2) grass, grass; (3) forbs, forbs; (4) shrub, grass; (5) shrub, forbs; and (6) grass, forbs. Finally, I searched for mammal burrows and recorded this variable binomially based on burrow density on both roadsides within the 157 m^2 area (0 for < 5 burrows; 1 ≥ 5 burrows), and noted the presence of basalt outcrops within 100 m of each location by recording a "1" if present and a "0" if absent.

Data collection: GIS variables associated with locations

I used a GIS database to measure supplementary landscape variables that I would be unable to estimate accurately in the field. I used the AOC vegetation coverage assembled by Idaho GAP Analysis Project in 2001 available on the ISU GIS Training and Research website to measure vegetative composition at three spatial scales. I first generated coverages of the snake crossing and non-crossing point shapefiles and created a buffer centered on each location to calculate the percentage of each vegetation type within three different circular areas based on 50, 100, and 500 meter radii. I accomplished this with use of an AML (Arc Macro Language) written by Bob Klaver (USGS EROS Data Center). The AOC coverage classifies vegetation into 72 different cover types. However, the majority of my areas encompassed only seven different categories, four of which (silversage, blacksage, low sage, and big sage) I consolidated into sagebrush; the remaining three classes included grassland, agricultural, and urban areas.

In addition, I measured variables related to hibernacula and thermoregulation, both of which are physiological needs for snakes. I calculated the distance from each crossing and non-crossing location to all known snake hibernacula (Doering 2005) within 10 km using ArcInfo. Using the output files, I calculated the minimum distance of each point to den habitat and the mean distance to all hibernacula within 10 km. I also calculated an index of solar radiation for each crossing and non-crossing point. I used an AML (Jeff Evans, USDA Forest Service, Rocky Mountain Research Station, Moscow, Idaho) that computes a radiation index (continuous variable between 0-1) based on aspect (Roberts and Cooper 1989). A landscape oriented in a north-northeast direction (typically the coolest and wettest orientation) receives an index of 0, while south-southwesterly slopes receive a 1, with other aspects intermediate to these extremes.

Data analysis: modeling the factors associated with snake crossings

I used logistic regression to model the probability of a snake crossing point as a function of habitat and landscape variables. Specifically, for this study, locations were assigned a 0 for non-crossing points and a 1 for snake crossing points. I used the SAS statistical package version 9.1 for all analyses (SAS Institute Inc., Cary, NC). I used all records of snake occurrence along the survey route, both DOR and AOR, and refer to these points as snake crossing points (n = 251). I ran separate regression models for gophersnakes (n = 187) and western rattlesnakes (n = 46) due to the different ecology of these species. However, I did not include two of the gophersnake records due to GPS error, and did not analyze crossing data for terrestrial gartersnakes or striped whipsnakes due to their low sample sizes (n = 16 and 2, respectively). The western rattlesnake data would not converge during logistic regression analysis, likely a byproduct of low sample size, so the results will focus on gophersnakes.

The original model included 72 explanatory variables, which I reduced to a final set of 12 variables based on biological meaning and multi-collinearity diagnostics (table 1). I tested all the potential explanatory variables for collinearity prior to the analysis, calculating variance inflation factor (VIF) (Belsley et al. 1980) and then calculated Pearson correlation coefficients. When two variables were correlated (r > 0.7) I excluded one from the analysis (Menard 2002). Pearson correlation coefficients for mean distance to den and minimum distance to den were 0.626, so close to 0.7 that I included only mean distance to den in the final set of explanatory variables. I classified major cover and slope as indicator variables using category 1 (major cover = shrub, shrub; and slope = raised road surface) of both as a reference class to compare against all other categories. I compared Akaike Information Criterion (AIC) (Akaike 1973) values and classification accuracies to select the "best approximating model" (Burnham and Anderson 1998). To adjust for small sample size, I calculated AICc, which adds a correction factor of to AIC values (Hurvich and Tsai 1989). The significance of explanatory variables and associated coefficients was based on Wald statistics (Hosmer and Lemeshow 1995; Menard 2002). This statistic has a chi-square distribution that tests the null hypothesis that a parameter is 0, in other words, that the corresponding variable has no effect given that the other variables are in the model (Menard 2002).

Table 1. Description of variables collected in the field and generated with a GIS included in the logistic regression analysis

Potential explanatory variables	Measure	Description
Continuous variables		
DSHRUBAVG	cm	Mean distance to sagebrush accounting for both roadsides
MEANDIST	m	Mean distance to all known and predicted snake hibernacula within 10 km
PCOV10AVG	%	Estimated percent habitat cover within a 10 m radius of road edge
PCAG	%	Percent of agricultural cover within a 50, 100, and 500 m buffer radius using GIS
PCGRASS	%	Percent of grass cover within a 50, 100, and 500 m buffer radius using GIS
PCURBAN	%	Percent of urban developed areas within a 50, 100, and 500 m buffer radius using GIS
SOLARRAD	index (0 -1)	Index that measures solar radiation based on aspect of surrounding landscape using GIS
VEGRDAVG	cm	Mean distance to vegetation from the road edge accounting for both roadsides
Categorical variables		
BASALT	P/A	Presence of basalt pile within 100m of location
BURROW	P/A	Presence of 5 or more mammal burrows within 10 m radius of location
MCOV	1 - 6	Dominant roadside vegetation within 10 m accounting for both edges (1 = shrub, shrub;2 = grass, grass; 3 = forbs, forbs, 4 = shrub, grass; 5 = shrub, forbs; 6 = grass, forbs)
SLOPE	1 - 6	Road side topography in respect to roadbed (1 = both sides raised; 2 = no slope; 3 = both sides sunken; 4 = one side flat, one sunken; 5 = one side flat, one side raised; 6 = one side sunken, one raised)

Results and Discussion

Inter-specific variation and demography

I conducted 56 surveys between 15 May and 12 October, 2003, traveled a total of 10,248 km, and observed 253 snakes (0-16 per survey; mean = 4.5) of four species belonging to families Colubridae and Viperidae; however, two species accounted for the majority of records. I observed gophersnakes most often on roads (comprised 74.7% of the records) and western rattlesnakes more frequently than the remaining two species (comprised 18.2% of the records) (figure 2). The relative percentage of observations by species was comparable between 2003 and 2004. Ninety-three percent of the individuals were discovered DOR, yielding a mortality rate of 0.023 snakes/km. I documented more traffic casualties of adults than any other age class, the majority of which were males (64%) (table 2). Daily variability of snake mortality was high with the number of DOR snakes per route ranging from 0-14 (mean = 4.2). The mean number of road-kills per survey was highest during the month of September, despite the survey effort being half that of May and June. I did not observe any individuals during 11 of the 56 surveys, and the number of sampling days without snake observations was highest in late July and early August.

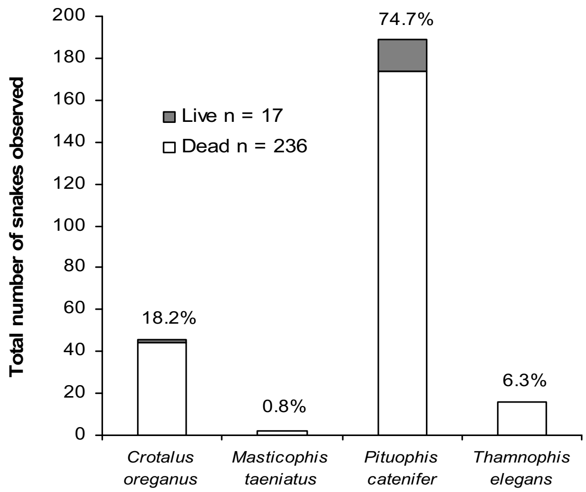

Figure 2. Summary of individuals observed by species during systematic road surveys (n=56) conducted between 15 May and 12 October, 2003 across the Idaho National Laboratory (INL). Values listed above each bar indicate the % of the observations represented by each species.

Table 2. Summary of snake road-kills by species and age class observed during systematic road surveys (n=56) conducted between 15 May and 12 October, 2003 across the Idaho National Laboratory (INL).

Species	Common Name	Age Class		
		Adult	Juvenile	Neonate
Crotalus oreganus	western rattlesnake	32	12	1
Masticophis taeniatus	striped whipsnake	2	0	0
Pituophis catenifer	gophersnake	112	39	36
Thamnophis elegans	terrestrial gartersnake	15	0	1
Totals		161	51	38

When compared to published studies that have measured snake mortality on roads, my results suggest that the magnitude of road mortality along the upper Snake River Plain is intermediate. The mortality rates documented per kilometer of road traveled ranged between 0.005 - 1.854 with an overall mean of 0.188 for 15 rigorous datasets (figure 3). My study has the eighth highest casualty rate (0.023 DOR/km), and is similar to several studies conducted in desert habitats located in regions known for their herpetofauna richness (Mendelson and Jennings 1992, Rosen and Lowe 1994). Three of the four studies with extreme values (Bernardino and Dalrymple 1992, Ashley and Robinson 1996, Smith and Dodd 2003) were conducted along short stretches of highways that bisect wetland habitats and associated movement corridors of snake species. In terms of the percent of individuals discovered DOR during road-cruising surveys, values ranged from 24-93 percent (mean = 69%) with this study ranked as one of the highest (figure 4).

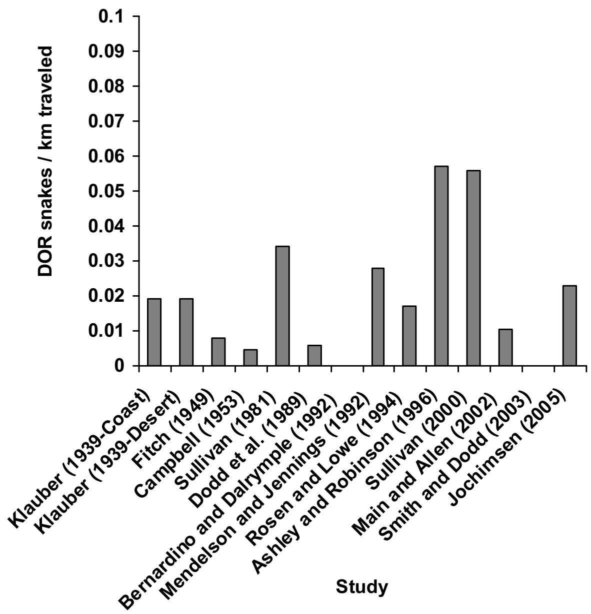

Figure 3. Summary of snake mortality on roads by published studies, including results from this survey conducted between 15 May and 12 October 2003 across the Idaho National Laboratory (INL) located in Idaho, USA. Bernardino and Dalrymple (1992) reported a mortality rate of 0.66, and Smith and Dodd (2003) reported a mortality rate of 1.854.

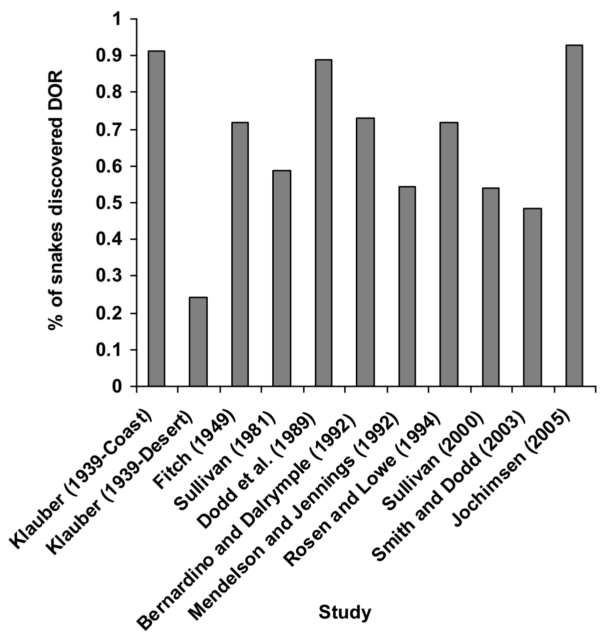

Figure 4. Summary of percent of total snakes observed dead on roads from published studies, including results from this survey conducted between 15 May and 12 October, 2003 across the Idaho National Laboratory (INL) located in Idaho, USA.

The relative abundance of snake species across the INL differed between road surveys and den surveys conducted annually by the ISU Herpetology Laboratory from 1989 to 2003. Over 4,000 individuals have been captured by hand, trap, or along drift fence arrays across the 15-year survey period. These data suggest that western rattlesnakes are the most abundant snake on the site (76% of all captures) with gophersnakes (11% of all captures) and gartersnakes (9% of all captures) comprising the next greatest percentage (C. R. Peterson, unpublished data). These results contrast greatly with my survey data, where gophersnakes comprised the overwhelming majority of road observations gathered over 2003 and 2004 (76%) (figure 5). This could be a consequence of biases associated with the survey methods. We collect snakes at the hibernacula during egress and ingress when rattlesnakes are most obvious and tend to make their presence known by rattling. Gophersnakes may not be as readily encountered due to their subterranean behavior (Grothe 1992, Ernst and Ernst 2003). A radiotelemetry study conducted in southwestern Idaho revealed that individuals surfaced on only 63 percent of the days they were tracked (Grothe 1992). Furthermore, an assessment of hand versus drift fence survey methods reported a higher susceptibility of *Pituophis* to drift fence capture (Diller and Wallace 1996). Road surveys also estimate snake presence along a transect, with road mortality analogous to trap captures along the drift fences. When the proportion of new captures is compared for only drift fence and trap data since 1994 on the INL, western rattlesnakes comprise 53 percent while gophersnakes and terrestrial gartersnakes increase to 22 percent (figure 5). The disproportionate representation of gartersnakes along roads may be tied to their association with water (Koch and Peterson 1995) because this resource is limited across the desert. The majority of individuals that I observed were clustered adjacent to agricultural fields with irrigation. Finally, the small number of striped whipsnake captures (3% of capture data) and road observations (0.5%) suggest small population size on the site, and reflect the difficulty in capturing this species due to its speed and vigilance (Hirth et al. 1969, Enge and Wood 2002).

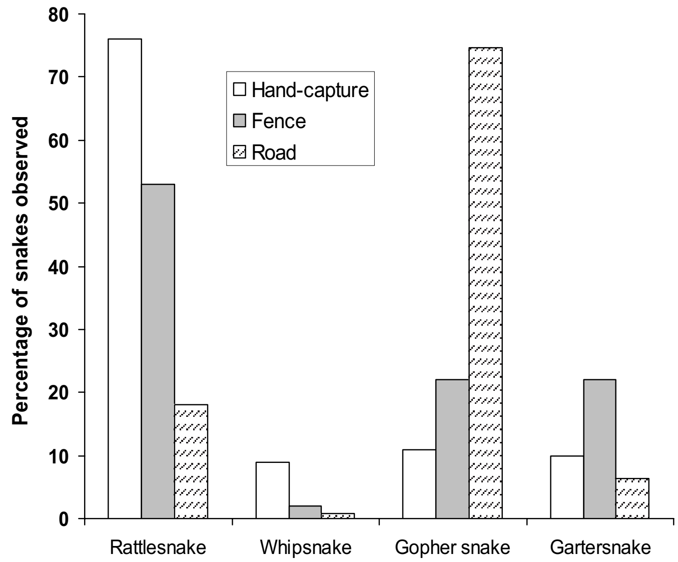

Figure 5. Comparison of snakes captured based on three sample techniques across the Idaho National Laboratory (INL) Idaho, USA

These results raise an interesting question, are gophersnakes more susceptible to road mortality on the eastern Snake River Plain? Diller and Wallace (1996) compared the ecology of *Pituophis* with *Crotalus* in southwestern Idaho, and described them as habitat generalists with a greater propensity for movement. This suggests that individuals would encounter roads more often as a consequence of their vagility, exposing them to an increased risk of road mortality. In further support of this argument, a study designed to compare the overall susceptibility of different snake families to road mortality found that relative to population density, species that use frequent movements experience a higher mortality risk than do sedentary foragers (Bonnet et al. 1999). Finally, when exploring the published road studies, it is evident that these two genera are observed more often than others on roads, with *Pituophis* comprising the majority of observations.

However, there are only a few studies that have investigated habitat use and movement of gophersnakes (Parker and Brown 1980, Diller and Wallace 1996, Rodriguez – Robles 2003), so this question remains to be explored. Specifically, my results suggest that gophersnakes may be overwintering in hibernacula that are not yet documented across the study area, or possibly in small mammal burrows as observed in Indiana (Schroder 1950). Their population densities may be higher than previously calculated based on hibernation site data, especially in the vicinity of roadsides. This species is a relatively large snake, creating a conspicuous target when stretched across the road. I observed motorists purposely swerving to kill snakes on multiple occasions as have others (Enge and Wood 2002). Furthermore, during the repeated surveys, I noted a difference in behavioral response to a passing vehicle between the two species. Gophersnakes tended to remain stretched and freeze for a short time when a vehicle passed, in contrast to western rattlesnakes, which tended to coil if not hit by the first vehicle.

Intraspecific variation of seasonal trends

Seasonal patterns of mortality varied by sex and age class for the two major species observed. Classifying gophersnakes first by age, then by sex for adults only, revealed significant differences, after sequential Bonferonni correction, of observations among the three groups during May (Friedman Test, $X^2 = 10.585$, $P = 0.005$), June (Friedman Test, $X^2 = 14.0$, $P = 0.001$), and September (Friedman Test, $X^2 = 13.04$, $P = 0.001$). These results were attributed to a greater number of adult male casualties than adult females in May (Wilcoxon Signed Ranks Test, P = 0.005, significant after sequential Bonferonni correction) and June (Wilcoxon Signed Ranks Test, $P = 0.002$, significant after sequential Bonferonni correction), and a greater number of adult male casualties than subadults in June (Wilcoxon Signed Ranks Test, $P = 0.005$, significant after sequential Bonferonni correction) (figure 6). The comparison of dead subadult observations to adults in September was significant for males, but only marginally so for comparison with females, after sequential Bonferonni correction (Wilcoxon Signed Ranks Test, P = 0.018 for males (Bonferonni corrected P = 0.025) and P = 0.017 for females (Bonferonni corrected P = 0.0167). Seasonal trends of mortality differed numerically for western rattlesnakes compared to gophersnakes, although patterns were not significant. Following the breakdown of individuals by age, the trend for adult males is bimodal across months with peaks in June, July, and September (figure 7). The mean number of subadult road casualties was unimodal peaking in June. The only difference in the monthly mean numbers of road-kills among rattlesnake groups that approached significance occurred in June as compared to the other months (Friedman test, X^2 = 8.64, P = 0.013, with a sequential Bonferroni correction P = 0.01).

The higher numbers of certain age and sex classes with respect to seasons indicates that individuals may be more susceptible to road mortality during specific movements. For gophersnakes, mating generally occurs in the spring, while western rattlesnakes usually mate in summer and early fall (Ernst and Ernst 2003). More adult gophersnake and western rattlesnake males were killed during the spring migration presumably while searching for mates or moving towards foraging grounds, while juveniles were most susceptible during dispersal, following hatching in the fall (gophersnakes) or movements in the spring (western rattlesnakes). These peaks of road mortality follow activity patterns reported for telemetered snakes. A number of studies report that male gophersnakes tend to be active on more days and move more frequently than females (Parker and Brown 1980, Grothe 1992), although on average there is not a significant difference between the maximum distances moved from the hibernacula between the sexes (Parker and Brown 1980). Radiotelemetry studies have demonstrated that males of the closely related prairie rattlesnake move greater distances than females, although they are inactive over a greater number of days (King and Duvall 1990).

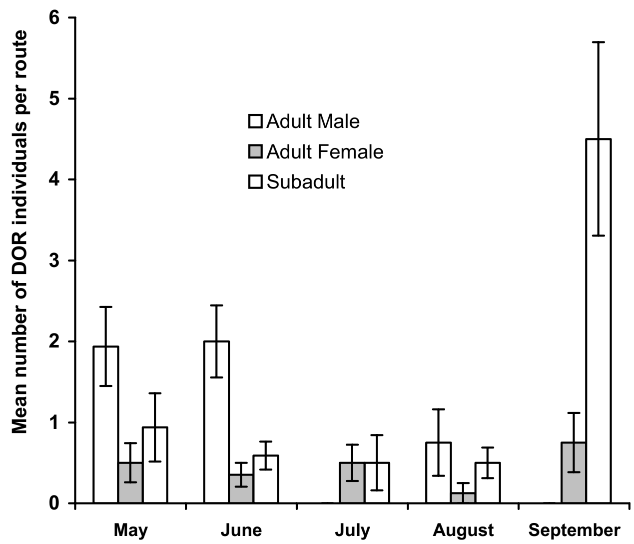

Figure 6. Monthly comparison of mean numbers of adult male, adult female, and subadult road casualties for gophersnakes (*Pituophis catenifer*) observed per survey during 2003 on the INL, with one standard error above and below the mean.

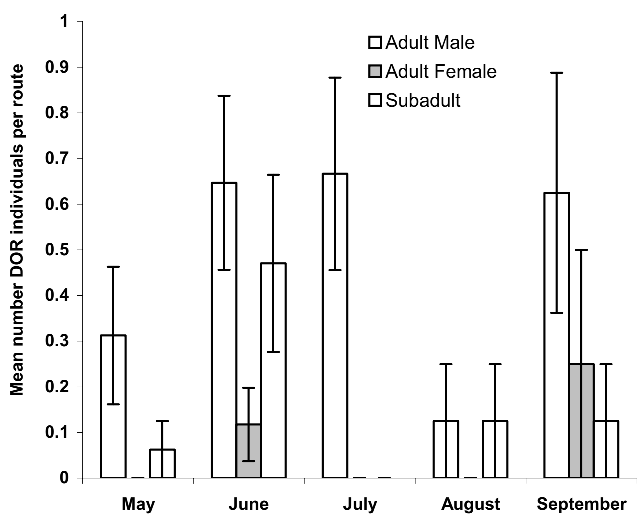

Figure 7. Monthly comparison of mean numbers of adult male, adult female, and subadult road casualties for western rattlesnakes (*Crotalus oreganus*) observed per survey during 2003 on the INL, with one standard error above and below the mean.

Movement patterns also explain why females may be susceptible to road mortality for only a portion of the entire activity period. Female western rattlesnakes were more susceptible to being road killed during both spring and fall migrations; none of these individuals were gravid. Cobb (1994) observed that gravid individuals generally remained within a 1-km distance from the hibernacula, possibly a result of thermoregulatory behavior. Female gophersnakes are reported to undergo egg-laying migrations in late spring or early summer (Parker and Brown 1980) although I did not observe a significant increase in numbers of observed DOR. Both western rattlesnakes and gophersnakes have slightly male-biased sex ratios, based on all captures over the 10-year survey period. These biases could be representative, or simply a byproduct of males being more active than females (Grothe 1992).

Modeling the factors associated with gophersnake crossings

Logistic regression analysis produced eight models that were all supported using an AIC criterion, all of which had a Nagelkerte R^2 greater than 0.9 and classification accuracies between 94-95 percent. These models contained eleven different types of variables. Four variables reflecting roadside habitat and landscape features were included in every supported model (table 3). These included the mean percent cover within a 314-m^2 area around the road, the vegetation type that comprises the majority of this cover, the presence of basalt outcrops or piles within 100 meters from the roadside, and the mean distance between the snake location and hibernacula within 10 km. Specifically, grass as the major cover on both sides of the road (MCOV 2) was positively associated with crossing points and was the most important variable in every model (table 3; figure 8). The second and third most important variables in every model were the mean percent cover within a 314-m^2 area and the presence of basalt, respectively, which were both positively correlated with crossing points (table 3). Finally, while the order of importance varied, mean distance to den, MCOV 4, and MCOV 6 were all positively correlated with crossing points, while MCOV 5 was negatively correlated with crossing points (table 3).

The other variables included in at least one model were presence of >five burrows (1 model, negatively correlated), mean distance to nearest shrub (1 model, negatively correlated), percent agriculture within 100 meters (1 model, negatively correlated), percent agriculture within 500 meters (3 models, negatively correlated), percent urban within 500 meters (2 models, positively correlated), flat slopes (6 models, positively correlated), and solar radiation (7 models, positively associated) (table 3). None of these variables received a high rank in any model. The most important variable was flat slope, which ranked 7th in three models (table 3).

The majority of parameters included in the logistic regression analysis were important predictors of snake crossings. Several characteristics of roadside habitats and features of the surrounding landscape influence snake crossings and, therefore, identify high-risk areas for road mortality. Cover adjacent to roadside areas was the most significant. Habitat composition calculated with GIS did not appear to play an important role in predicting snake presence, except at the greatest distances from road areas. However, there are two weaknesses in using the GAP cover data: (1) the classification accuracy has not been evaluated, and (2) habitat changes have occurred since its creation (e.g., fire). Coverages based on recent remote sensing may improve the accuracy of these data, potentially influencing whether they are maintained in a logistic regression model.

Table 3. Variables included in supported logistic regression models (based on AIC) identifying habitat and landscape features influencing snake crossings on roads on the INL, Idaho, USA. Variables in each model are ranked by importance based on Wald Chi-square value, with the sign in parentheses indicates direction of correlation.

Variables								
BASALT	3(+)	3(+)	3(+)	3(+)	3(+)	3(+)	3(+)	3(+)
BURROW								12 (-)
DSHRUBAVG							9(-)	
MCOV 2-grass,grass	1(+)	1(+)	1(+)	1(+)	1(+)	1(+)	1(+)	1(+)
MCOV 4-shrub,grass	8(+)	6(+)	8(+)	7(+)	7(+)	6(+)	7(+)	8(+)
MCOV 5 -shrub,forb	6(-)	4(-)	6(-)	6(-)	4(-)	4(-)	4(-)	6(-)
MCOV 6 -grass,forb	5(+)	5(+)	5(+)	5(+)	5(+)	5(+)	6(+)	5(+)
MEANDIST	4(+)	7(+)	4(+)	4(+)	6(+)	7(+)	5(+)	4(+)
PCAG100				10 (-)				
PCAG500	9(-)		9(-)					9(-)
PCURB500			11(+)					11(+)
PCOV10AVG	2(+)	2(+)	2(+)	2(+)	2(+)	2(+)	2(+)	2(+)
SLOPE-flat	7(+)		7(+)	8(+)	8(+)		8(+)	7(+)
SOLARRAD	10(+)	8(+)	10(+)	9(+)	9(+)		10(+)	10(+)
Model AIC_c	**102.44**	**103.45**	**103.49**	**104.01**	**104.04**	**104.06**	**104.10**	**104.32**
Model R^2	**0.9313**	**0.9169**	**0.9325**	**0.9297**	**0.9274**	**0.9139**	**0.9296**	**0.9338**
Cross-validation accuracy	**95.2**	**94.7**	**94.9**	**94.4**	**94.9**	**93.9**	**94.7**	**94.7**

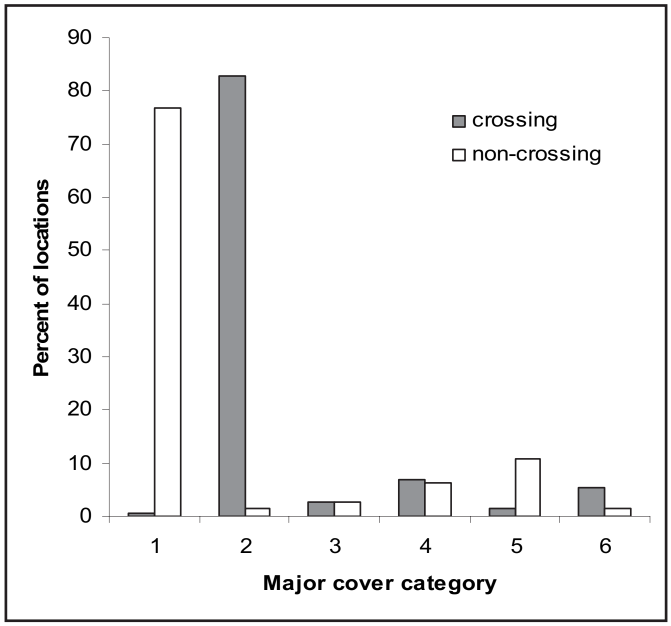

Figure 8. Histogram showing distribution of dominant cover for snake crossing and non-crossing locations across the INL, Idaho USA. Category number describes vegetation composition taking both road sided into account where 1 = shrub, shrub; 2 = grass, grass; 3 = forbs, forbs; 4 = shrub, grass; 5 = shrub, forbs; and 6 = grass, forbs.

Cover type along roadsides is the most important predictor of gophersnake presence on roads. The study area is referred to as a sagebrush steppe ecosystem (Anderson et al. 1996) characterized by sagebrush and perennial grasses. However, the majority of species I recorded along roadsides were invasive grasses that can out-compete sagebrush (cheatgrass and crested wheatgrass). These grass species spread along roadside areas, and are associated with habitat changes. One explanation for the association of gophersnakes with this cover type is that this species occurs more often in grassland habitat. Alternatively, individuals may perceive this habitat as unsuitable and, therefore, move through it quickly, thereby encountering roads at a greater frequency. There are only a few studies that have investigated habitat use and movement of gophersnakes (Fitch 1949, Parker and Brown 1980, Diller and Wallace 1996, Rodriguez – Robles 2003). They describe this species as habitat generalists, suggesting that it is unlikely that this result is due solely to the first explanation. For example, hand and drift fence capture data from southwestern Idaho show a uniform distribution of this species through all habitats (Diller and Wallace 1996, Cossel 2003).

The feeding habits of gophersnakes are varied, and many studies describe this species as an active forager. They are efficient burrowers (Carpenter 1982) that seek out and capture their prey within subterranean retreats or nests (Klauber 1947), or by seizing prey while at rest during evening hours (Rodríguez-Robles 2002). A study summarizing the feeding ecology of gophersnakes based on geographic regions reported that specimens collected from the Great Basin Desert consumed a greater proportion of small mammals compared to those from three other regions (California Province, Arid Deserts, and Great Plains) (Rodríguez-Robles 2002). Several studies report lower abundance of mammal species in cheatgrass and crested wheatgrass habitat (Brandt and Rickard 1994, Gipzen et al. 2001), and one study conducted in the Birds of Prey Area, Idaho (BOPA), found a negative association with ground squirrel burrow densities and cheatgrass (Yensen et al. 1992). Furthermore, capture data of small mammals on the INL suggests that grazing and invasive grasses negatively affect their abundance (C. Jenkins, unpublished data). Because radiotelemetry studies report that individuals spend a considerable proportion of their time underground (47 – 90%) (Grothe 1992, Rodríguez-Robles 2003) both burrow and prey density within a given habitat should influence surface activity. Increased surface activity through unsuitable habitat exposes individuals to highway surfaces.

The presence of basalt piles within 100 m of the roadside influences where snakes cross roads, most likely because of their dependence on these habitat features. When snakes begin their shedding cycle (ecdysis), it is common for them to seek refugia. They may retreat underground for days at a time or congregate in rocky areas (Grothe 1992, Rodríguez-Robles 2003). I have observed shed skins from gophersnakes in basalt piles across the study area. Several studies also report that females may undergo egg-laying migrations and nest communally in these habitats (Parker and Brown 1980, Ernst and Ernst 2003). This association may also be tied to the fact that this species is capable of overwintering in basalt piles. I discovered three new den sites along Hwy 26 that were created by farmers moving basalt rocks to the edge of their field. These areas may serve as temporary refugia or hibernacula.

The number of snake crossings decreased as the mean distance to surrounding hibernacula within 10 kilometers decreased. Surveys conducted in the Intermountain West document that gophersnakes co-occur with other snake species at communal den areas (Hirth et al. 1969, Koch and Peterson 1995). Capture data from the INL and the increased likelihood of occurrence farther from dens suggest that gophersnakes may be overwintering in hibernacula that are not yet documented across the study area, or possibly in small mammal burrows, as observed in Indiana (Schroder 1950). Alternatively, populations within closer vicinity of roadsides may be decimated by traffic mortality (Enge and Wood 2002, Smith and Dodd 2003). Studies suggest that movements of this species are philopatric (Fitch 1958, Rodríguez-Robles 2003), and Parker and Brown (1980) captured individuals within the same general locations across years. Therefore, if there is a genetic component to direction of movement, selection may be acting to remove individuals in a den that consistently cross roads. The closer a den is to a road, the more likely this is to occur. Research should be conducted to further investigate the relationship between roads and hibernacula, as we lack movement data on gophersnakes at this study site.

Roadside topography (slope) was included in the majority of best models (6 of 8) as a factor explaining where snakes cross roads. As a parameter, slope was marginally significant (around $P = 0.11$), but because I specified raised roadbed (slope 1) as the reference class, locations associated with a sunken roadbed were calculated as significant ($P < 0.05$) with a positive relationship with snake presence. Perhaps flat surfaces offer less resistance to movement than do raised surfaces, similar to the logistic regression models presented by Clevenger et al. (2003) that predicted small fauna were less likely to be road-killed on raised sections of roads relative to those that are level.

Although not a major predictor of snake occurrence, solar radiation was included in seven of the eight best models. As ectotherms, snakes require warm areas for thermoregulation and digestion, and are, therefore, attracted to such areas. Gophersnakes may control the amount of solar radiation they are exposed to through behavioral adjustments (Pough et al. 2001). For example, several studies report instances of increased road mortality when snakes are observed basking on road surfaces during cooler temperatures (McClure 1951, Klauber 1939, Sullivan 1981). In addition, one study noted that gophersnakes might preferentially expose the stomach region to sunlight following ingestion of large prey (Ashton 1998), a behavior referred to as regional heterothermy. I have observed this behavior on the INL along roadsides on several occasions.

Conservation Implications

In conclusion, this research has estimated the magnitude of road mortality on snake species in the upper Snake River Plain and provides insight into how roads with vehicles differentially affect snake species and demographic groups within snake species. Understanding these impacts is critical when determining the appropriate conservation strategy for these species and what consequences this might have on a population level. The loss of these individuals affects the population in two ways. Adults are required for successful reproduction, and males actively seek out the females during the mating season. Over time, if road mortality removed more adult males than are replaced, the population could decline if there are too few males to seek out the females or through inbreeding effects. The dispersal of juveniles is critical to gene flow across the landscape, and the roads could, therefore, be isolating certain den populations when road mortality of juveniles is high near these locations. This research augmented the monitoring methods currently employed by the ISU Herpetology Laboratory of the snake populations on the INL, to include road surveys in addition to hand and drift fence surveys at major hibernacula. Additionally, I recommend that research designed to examine the habitat relationships (including effect of invasive grasses) and movements (using radio-telemetry) of gophersnakes is needed on the site. Although this species is widespread across the United States, with their distribution extending from south-western Canada to northern Mexico and east from the Pacific Coast to the Great Plains and Great Lakes regions (Rodríguez-Robles and Jesús-Escobar 2000, Stebbins 2003), the magnitude of road mortality of this genus should not be overlooked because population-level effects are not yet understood. Finally, this research has implications for the mitigation of road effects.

High levels of mortality coincided with seasonal activities specific to different age and sex classes, and there appears to be landscape characteristics that influence where mortality occurs. Methods designed to ameliorate the road mortality of snakes should, therefore, coincide with these activity periods to be effective and should be placed in areas with high proportions of invasive vegetative cover and near basalt piles. However, the question of proper placement of mitigation efforts needs to be studied further based on the data I have collected. It may be difficult to estimate high-risk areas for snake road mortality without measuring parameters at both small and large scales. Although estimates of habitat cover across various spatial scales using a GIS are important, focal studies that measure small-scale attributes should be conducted to effectively identify snake-crossing zones. Further research is needed to investigate the possibility that habitat conversion may be increasing this species' susceptibility to road mortality.

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(officially December, 2005). She has eight years of research experience with reptiles and amphibians, including survey and laboratory work. Main interests include the field of road ecology, specifically regarding herpetofauna, and disease. In the future, she is interested in continuing research on the INL site focusing on the population effects of roads on snakes and mitigation placement.

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