

# Influence of ecology and landscape on snake road mortality in a sagebrush-steppe ecosystem

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## Keywords

demography; landscape; snakes; road ecology; road mortality; sagebrush steppe.

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## Abstract

Roads fragment our landscape, posing a severe threat to the persistence of wildlife populations through losses of individuals to direct mortality and decreased connectivity. Although they possess a particular suite of life history characteristics that make them especially vulnerable, snakes tend to be underrepresented in research examining vertebrate road mortality. Here, we report a statistical analysis of snake mortality along a 183-km road circuit in sagebrush-steppe habitat located in southeastern Idaho. We describe differential road mortality across snake species, season, sex and age. We also analyze both fine-scale and broad-scale habitat measurements to identify various habitat and landscape factors associated with snake road mortality. Our results show clearly that snake road mortality is influenced by interactions among demographic, ecological and temporal factors. Vagile species and life stages were particularly vulnerable to road mortality during periods of peak activity. Gophersnakes dominated our road observations, with adult male mortality peaking in spring and high casualties of neonates in the fall. Snake crossings were especially common along roadsides with high vegetative cover, in areas dominated by non-native grasses. These results suggest the potential for snake populations to become fragmented over time, and that habitat conversion and species invasions may be compounding this effect. This study suggests that conservation efforts need to account for inter- and intraspecific differences in road mortality risk and provides guidance for roadside management that may serve to minimize vertebrate mortality on roads.

## Introduction

Despite the range of anthropogenic threats that contribute to the current biodiversity crisis, the excessive number of vertebrate fatalities on roads raises a substantial conservation concern. For some species and regions, animal-vehicle collisions act as a significant source of direct human-caused mortality (Lalo, 1987; Andrews, 1990), and studies report mortality rates sufficient to cause population declines (Boarman & Sazaki, 2006; Ciarniello *et al.*, 2007). Beyond the losses to direct mortality, roads further threaten population viability indirectly through fragmentation (Andrews, 1990; Jaeger & Fahrig, 2004), resulting in decreased gene flow, loss of genetic diversity and, potentially, decreased fitness and increased risk of local extinction (Frankham, Ballou & Briscoe, 2002; Balkenhol & Waits, 2009).

Snakes tend to be underrepresented in road ecology studies, yet members of this taxon possess a suite of life history characteristics that render them vulnerable to road mortality (Jochimsen *et al.*, 2004; Andrews, Gibbons & Jochimsen, 2008). Such traits include the tendency to thermoregulate on road surfaces or edges (Sullivan, 1981a),

activity patterns that coincide with high traffic volumes (Seigel, 1986), slow locomotion (Andrews & Gibbons, 2005) and an elongate body form. In addition, due to negative perceptions, snakes often fall victim to intentional killing on roads (Langley, Lipps & Theis, 1989). Many species have long generation times in addition to low reproductive and adult mortality rates (Ernst & Ernst, 2003); traits that increase population sensitivity to even a few road fatalities. Robust field studies have documented a high number of snake deaths on roads (Bernardino & Dalrymple, 1992; Smith & Dodd, 2003; Andrews & Gibbons, 2008), although the suspected effect that these deaths may have in a population context is often unknown. In several cases, the data provide convincing evidence that losses to road mortality can be detrimental over time (Klauber, 1939; Rudolph *et al.*, 1999) and modeling approaches suggest that even a few road deaths may increase extinction risk for some long-lived species (Row, Blouin-Demers & Weatherhead, 2007).

In addition, snake populations are sensitive to the fragmentary effects of roads, because of their reliance on resources that vary seasonally and are patchily distributed (Ernst & Ernst, 2003). This is especially true in northern

latitudes, where species migrate to and from a communal hibernaculum (overwintering site that supports multiple species) to locate refugia, mates, prey and oviposition or gestation sites (Gregory, Macartney & Larsen, 1987; King & Duvall, 1990). These resources are associated with habitats that possess unique attributes [e.g. hibernacula occur in rocky areas with southern aspects (Doering, 2005)] and individuals exhibit high site fidelity, often retracing the same migratory route biannually (Duvall, King & Gutzwiler, 1985; Rodríguez-Robles, 2003) to attain them. When roads bisect these paths, individuals risk mortality twice per year and population persistence is threatened (Clark *et al.*, 2010).

Mitigation measures (e.g. road closures, faunal tunnels) can minimize road impacts (see examples in Jochimsen *et al.*, 2004), but interspecific and demographic vulnerabilities must be assessed to best direct conservation actions. The frequency and type of snake movement varies seasonally and differs between species, sexes, ages and reproductive classes (Ernst & Ernst, 2003). As mortality risk increases with greater vagility (Bonnet, Naulleau & Shine, 1999; Whitaker & Shine, 2000), research that aims to identify temporal pulses of movement can help determine when mitigation efforts are most needed. Such studies could also offer insight into the potential population-level consequences of road mortality. For instance, adult female survival is often the key demographic for maintaining population growth for long-lived species with low reproductive rates (Caughley & Sinclair, 1994; Greene, 1997). In addition to proper timing, the identification of movement corridors could help ensure the proper placement of mitigation measures. Yet, few studies have quantitatively described the spatial pattern of wildlife casualties along a road network or examined how landscape variables are associated with collisions (e.g. Clevenger, Chruszcz & Gunson, 2003; Ramp *et al.*, 2005; Malo, Suárez & Diezand, 2004).

Here, we analyze snake mortality on roads within a sagebrush-steppe ecosystem. We designed this study to (1)

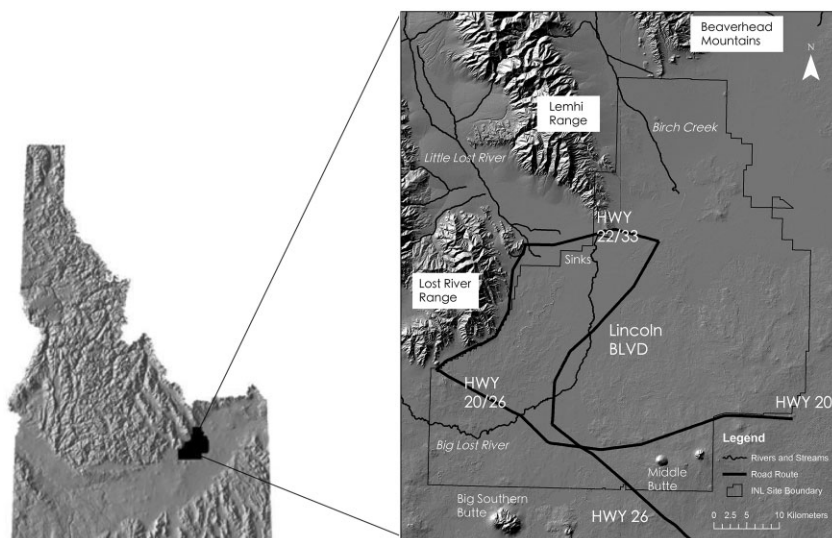
quantify the magnitude of road mortality on snake species in sagebrush steppe, (2) explain variation in road mortality with respect to species, season, sex and age, and (3) evaluate the importance of various habitat and landscape factors associated with snake road mortality.

## Materials and methods

### Study area and species

We conducted surveys along a 183-km road circuit, composed of six road sections, on the upper Snake River Plain in southeastern Idaho, USA (Fig. 1). All roadways are two-lane (approximately 10 m wide) and paved with speed limits posted at 104 km·h<sup>-1</sup> (with the exception of Lincoln Boulevard at 56 km·h<sup>-1</sup>). Road sections vary with respect to traffic volume, with annual average daily traffic estimates ranging between 300 and 2200 vehicles per day (average = 1123), with pulses of high traffic volumes during commuting hours.

The survey route traverses the Idaho National Laboratory (INL), a Department of Energy facility that encompasses the largest contiguous reserve of sagebrush-steppe ecosystem (2305 km<sup>2</sup>). Public access onto the INL is restricted, thereby limiting the amount of anthropogenic disturbance. In contrast, grazing, agriculture and low levels of urbanization occur along the periphery of the INL, which is managed by the Bureau of Land Management and private owners. Native vegetation consists predominantly of a sagebrush-grass community characterized by a shrub overstory with a perennial grass and forb understory (Anderson & Inouye, 2001; Forman, Hafla & Blew, 2013). Although shifts in abundance and distribution of plant species have occurred in response to wildfire, soil disturbance, drought and invasive species [including crested wheatgrass (*Agropyron spp.*) and cheatgrass, *Bromus tectorum*], the native community remains largely intact (Forman *et al.*, 2013).



**Figure 1** Shaded relief map of Idaho, USA with the Idaho National Laboratory (a Department of Energy site) denoted in black and an inset of the study area located on the upper Snake River Plain. The inset includes prominent landscape features of the study area, with the 183-km road circuit composed of six different highway segments represented in black.

Six snake species occur on the study site: North American racer (*Coluber constrictor*), desert nightsnake (*Hypsiglena chlorophaea*), striped whipsnake (*Masticophis taeniatus*), gophersnake (*Pituophis catenifer*), terrestrial gartersnake (*Thamnophis elegans*) and western rattlesnake (*Crotalus oreganus*). These species overwinter in communal hibernacula from which they migrate seasonally, yet they differ with respect to certain ecological characters that could potentially influence their susceptibility to road mortality (e.g. foraging mode, vagility, time of peak activity and body size).

## Data collection

In 2003, we conducted surveys for live and road-killed snakes by slowly driving (48 km·h<sup>-1</sup>) the complete route circuit. We drove a minimum of 3 days per week (average = 4) during snake egress from hibernacula (May–June) and a minimum of 1 day per week from July through early October to monitor summer activity and ingress (the return of snakes to hibernacula). We alternated the start time [morning (07:00–10:00 AM), evening (05:00–08:00 PM) and afternoon (12:00–04:00 PM)] and the direction traveled along the circuit for successive surveys. We visually scanned both sides of the pavement and the gravel edges for snakes. The duration of each survey ranged from 4 to 8 h depending on traffic volume and the number of snakes encountered.

We stopped the vehicle each time we observed a snake and noted species, sex, whether the snake was alive or dead, the observation time and the location using a hand-held global positioning system (GPS) receiver (GeoExplorer II, Trimble Navigation Ltd, Sunnyvale, CA, USA). We measured both the total length and snout-vent length when possible and used snout-vent length measurements to estimate the age class (subadult or adult; Diller & Wallace, 1996; Parker & Brown, 1980). Finally, we marked carcasses with a biodegradable paint and left them on the road for identification during subsequent surveys.

We recorded fine-scale habitat data associated with each snake locality. We noted how many sides of the road were raised or sunken with respect to the road surface to describe roadside topography (Clevenger *et al.*, 2003). We estimated the percentage of cover and dominant cover type (shrub, grass or forbs) within a 10-m radius of the location for each roadside. We also searched these areas for mammal burrows, as an index of prey and refugia availability, and assigned a score of 1 to a location if each roadside had  $\geq 5$  burrows. We noted the presence of basalt outcrops within 100 m of each location by recording a 1 (present) or 0 (absent); snakes use these features for overwintering, ecdysis (shedding) and cover.

We used a geographic information system (GIS) database to attain supplementary habitat variables for each snake observation at a broad scale. We measured the vegetative composition at three spatial scales on a land-cover raster layer produced by the Idaho Gap Analysis Project (Scott *et al.*, 2002) with a spatial resolution of 30 m<sup>2</sup>, and calculated the percentage of each cover type within buffer radii of 50, 100 and 500 m of each observation. We then used the

POINTDISTANCE command in ArcInfo on a coverage denoting the location of known snake hibernacula (Doering, 2005) to measure the minimum distance from each location to the nearest known hibernacula within 10 km (the maximum migration distance). We also computed a solar radiation index for each locality (continuous variable between 0 and 1) based on aspect (Roberts & Cooper, 1989).

Finally, we generated a set of 251 random locations (equivalent to the number of snake observations) using a Poisson point process (SANET version 1.2; Okabe, Okunuki & Funamoto, 2003) to describe available habitat along the route. To account for GPS error, we ensured that these locations were separated by a minimum distance of 30 m, in addition to being at least 30 m from any snake observation. We measured the same fine-scale habitat data, and used the GIS database to calculate the same broad-scale data described above for the snake locations.

## Data analysis

We used general linear models with a Poisson link function to test for the effects of species, season, age, sex and their interactions on the number of snakes observed per sampling route in R 2.9.0 (R Development Core Team, 2009). We analyzed compiled counts for all snakes, separated by age and sex, recorded in each 2-month period (May–June, July–August and September–October). We identified the route as the experimental unit to account for uneven sampling across seasons. We sequentially added terms to this model using a forward selection–backward elimination procedure starting with main effects (e.g. age, sex) followed by two-way and higher interactions (e.g. age  $\times$  sex). At each step, we retained the term that resulted in the greatest decrease in Akaike information criterion (AIC) score (Burnham & Anderson, 1998). When all new terms increased the AIC score, we checked the final model using backward elimination, removing any variables whose elimination resulted in a decrease in AIC score.

We used multinomial logistic regression to model the probability of snake occurrence on roads as a function of fine-scale habitat and landscape variables using the global test package (Goeman *et al.*, 2004) in R 2.9.0. Response variable categories included random points ( $n = 251$ ), and snake-crossing points grouped by species ( $n = 233$ ). We used only rattlesnake and gophersnake points, both live and dead; other species were excluded because of low sample sizes. We included 42 explanatory variables, all with pairwise correlation coefficients  $\leq 0.6$ , transformed for normality when appropriate. Six categorical variables described fine-scale habitat: slope raised, slope sunken, burrow, basalt, shrub cover and grass cover. Slope raised and slope sunken relate to road shoulder topography with values of 0, 1 or 2 to identify the number of roadsides at a location that fit each category. We recorded shrub and grass cover categories in a similar fashion with a 0, 1 or 2 to denote the number of roadsides with shrub or grass as the major cover type. Burrow and basalt were binomial variables (described above). The remaining 36 continuous variables included:

percentage cover within 10 m, GIS 50 m, GIS 100 m, GIS 500 m, distance to den and solar radiation index. To calculate the percent cover variable, we averaged the percent cover data estimated in the field for both roadsides and then arcsine square root transformed these values. GIS 50 m included 10 cover categories, GIS 100 included nine cover categories and GIS 500 included 14 cover categories. We logged +1 the GIS cover data and logged the distance to the nearest den. We used a forward selection–backward elimination procedure to build models and used AIC to evaluate model fit. We used *P*-values to evaluate the significance of explanatory variables and associated coefficients following Menard (2002).

## Results

We conducted 56 road surveys between 13 May and 12 October 2003 and traveled a total of 10 248 km. We observed 251 snakes, and the total number of individuals encountered per survey ranged between 0 and 16 (average = 4.5). We rarely observed live snakes; we discovered 93.2% of individuals dead on the road, yielding an overall mortality rate of 0.023 snakes per km traveled.

We found evidence for effects of species, age, sex and season influencing snake counts. Gophersnakes comprised the majority of road observations (74.5%), with rattlesnakes (18.3%) more common than either gartersnakes (6.4%) or whipsnakes (0.8%). Although previous surveys report the occurrence of racers and nightsnakes, we did not observe these species. We mainly encountered adults (63.3% of the records) and males (64.9%). In terms of seasonality, snake counts exhibited a bimodal distribution, with peaks in the spring (average = 4.7, *SD* = 4.0) and fall (average = 7.0, *SD* = 5.5). High mortality events ( $\geq 10$  snakes) were spread across the entire spring season, while those occurring in the fall were concentrated over a 15-day period.

Beyond the main effects discussed above, our analysis identified a pair of two-way interactions (season  $\times$  age and season  $\times$  sex) that influenced snake counts common to all of our best models. The season by age interaction reflects the bimodal pattern of adult activity, with a greater number of records in the spring, and the predominance of subadult encounters in the fall (Fig. 2a). The season by sex interaction reflects increased detection of males during spring and fall, while female observations remained relatively low and constant until peaking slightly in the fall (Fig. 2b). There was also weak support for a species by age interaction (improved model fit by 1.2 AIC units), where the percentage of adults and subadults varied by species (Fig. 2c), and a species by season interaction (improved model fit by 0.6 AIC units). Rattlesnake observations peaked in the spring, followed by a lower but equal number of individuals in the summer and fall, while counts of gophersnakes and gartersnakes both followed a bimodal pattern, with a significant peak in gophersnake observations in the spring compared with fall and equal numbers of gartersnakes during spring and fall (Fig. 2d).

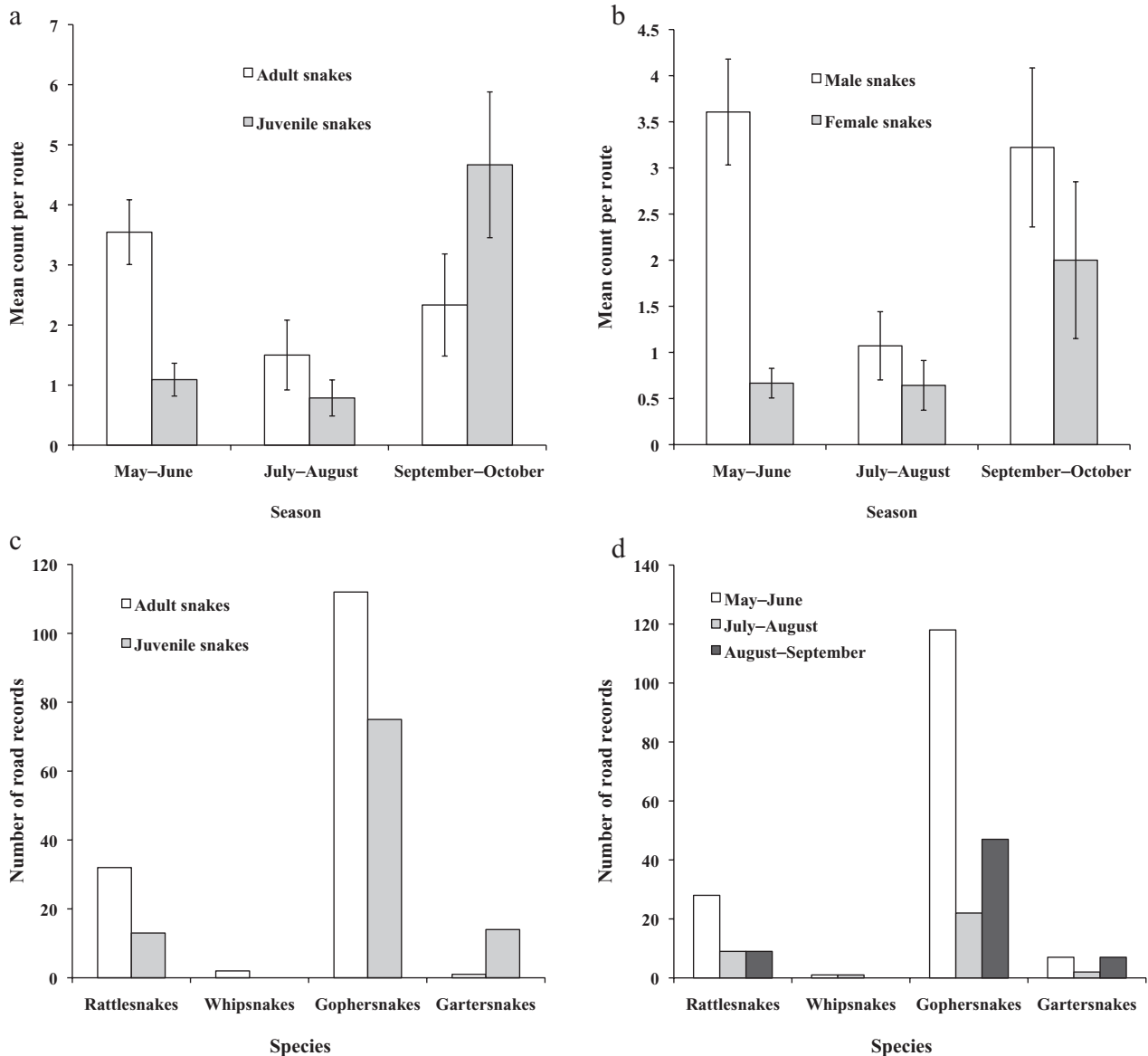
Multinomial logistic regression revealed associations of nine environmental variables with random points and snake localities (Table 1). Five of the variables (mean percentage cover within 10 m, grass and shrub cover as dominant vegetation, the presence of basalt outcrops within 100 m and the presence of five or more burrows on both roadsides) reflected roadside habitat, while the remaining four described the landscape at a broader scale (percentage of urban cover within 100 m, the percent of juniper cover within 500 m, the percent of riparian shrub cover within 500 m and distance to the closest hibernacula; Table 1).

The importance of these variables varied by point type and species. Random points were negatively associated with the percentage of roadside cover, areas dominated by grass cover, the percent of juniper cover within 500 m and the presence of basalt within 100 m (Table 1). In addition, these non-crossing points were positively associated with areas dominated by shrub cover and distance to the nearest den (Table 1). The most important predictors of rattlesnake crossings included areas with a high percentage of roadside cover, juniper cover within 500 m, areas dominated by grass cover, the percent of urban cover within 100 m and areas in close proximity to dens (Table 1). The most important variables associated with gophersnake crossings included the dominance of grass cover along roadsides, the presence of basalt within 100 m, areas lacking shrub cover, low burrow densities and the percentage of juniper cover within 500 m (Table 1).

## Discussion

### Road mortality on the Snake River Plain

The high incidence of road mortality reported here suggests that roads pose a potential conservation threat to regional snake populations. However, we would like to emphasize that the following interpretations of the trends we detected are based on only one year of survey data, potentially limiting their ability to be representative of patterns across a broader time period. Although the number of dead snakes per km traveled is similar to those reported in comparable ecosystems (Klauber, 1939; Fitch, 1949; Sullivan, 1981b; Mendelson & Jennings, 1992), the striking difference is that our observations consisted primarily of two species. Furthermore, the proportion of road-killed snakes that we encountered (93.2%) ranks among the highest reported for systematic surveys (Jochimsen, 2006; Andrews & Gibbons, 2008; Andrews *et al.*, 2008). The long distance of the road circuit and time required to complete surveys could have inflated this value, as we may have missed successful crossings. However, intensive surveys conducted in 2004 along a 10-km segment during periods of peak activity showed that 73.7% of snake records were casualties (Jochimsen, 2006), which still ranks high compared with other studies, with a mortality rate (0.079 snakes per km traveled) much greater than that reported here.



**Figure 2** Main and interacting effects influencing the occurrence of snakes along a 183-km road circuit on the upper Snake River Plain in Idaho, USA revealed by general linear models. (a) Mean number of adult and juvenile snakes of four species, with one standard error above and below the mean, observed per survey across seasons over 56 surveys conducted in 2003. The 2-month time periods correspond to spring, summer and fall. (b) Mean number of male and female snakes of four species, with one standard error above and below the mean, observed per survey across seasons over 56 surveys conducted in 2003. The 2-month time periods correspond to spring, summer and fall. (c) Number of adult and juvenile individuals that comprised road observations for four species collected over 56 surveys in 2003. (d) Seasonal distribution of road observations for four species collected over 56 surveys in 2003.

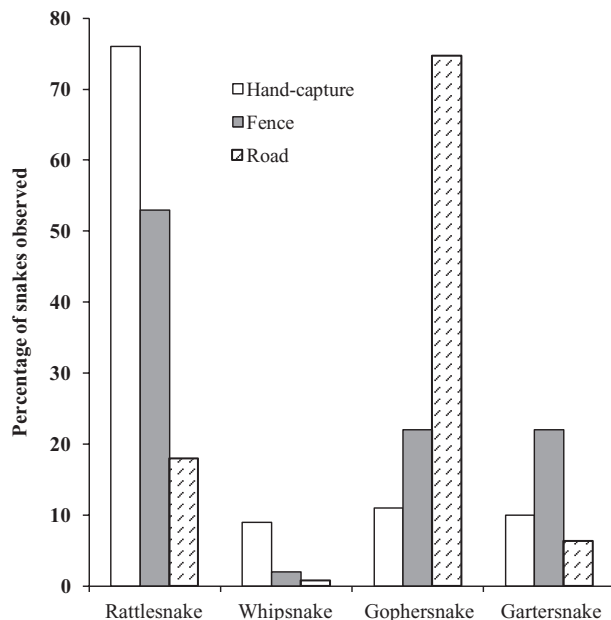
**Main factors driving variation in road mortality**

Although gophersnakes dominated our road observations, long-term survey data collected at three focal dens by hand, trap or along drift fence arrays suggest that rattlesnakes are by far the most abundant species on the site (Fig. 3). This discrepancy could be due to biases in the long-term survey methodology; for example, if gophersnakes overwinter in

hibernacula not yet documented (Schroder, 1950) or occur in lower densities at the focal dens we have underestimated their abundance. However, we view this as unlikely, and suggest that road mortality risk is inherently greater for some species, and is likely a byproduct of ecological or behavioral tendencies. Relative to population density, species exhibiting frequent movements experience higher mortality rates compared with sedentary ones (Bonnet *et al.*, 1999; Carr & Fahrig, 2001). Although a shorter

**Table 1** Multinomial logistic regression results of fine-scale habitat and landscape variables associated with observation points gathered in 2003 along a 183-km road circuit on the upper Snake River Plain in Idaho, USA. The model was run in R 2.9.0 (R Development Core Team, 2009) using the global test package (Goeman *et al.*, 2004) and mlogit function. Asterisks indicate the significance levels of associations (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ) and the signs indicate the direction of the relationship

Variable	Observation type		
	Random	Rattlesnake	Gophersnake
Intercept	1.15	-1.79	0.64
Burrow	0.92	-0.33	-0.59*
Basalt	-1.84**	0.57	1.28***
Percentage cover	-5.07***	3.49***	1.58
Shrub cover	1.83***	-0.78	-1.05***
Grass cover	-1.69***	0.89**	0.79***
Den distance	0.56**	-0.36*	-0.2
Urban cover GIS 100	-0.56	0.52*	0.04
Juniper cover GIS 500	-1.33***	0.91***	0.42*
Riparian shrub cover GIS 500	14.43	13.62	-28.05



**Figure 3** Comparison of the relative proportion of observations for four species gathered during annual surveys (methodology includes hand capture and drift fence arrays with traps) conducted between 1989 and 2003, at three focal hibernacula on the Idaho National Laboratory and road surveys conducted during this study in 2003 along the upper Snake River Plain, in Idaho, USA.

distance separates hibernacula from feeding grounds for gophersnakes, they are more vagile and active than rattlesnakes (Fitch, 1949; Diller & Wallace, 1996). The differences in movement frequency are tied to feeding ecology, as gophersnakes actively seek their prey, while rattlesnakes ambush them (Ernst & Ernst, 2003). In addition, gophersnakes are habitat generalists, whereas rattlesnakes exhibit preferences for rocky areas and shrubs (Diller & Wallace, 1996). Consequently, gophersnakes may be more

evenly dispersed across the site or willing to traverse a greater area. Interspecific differences in willingness to traverse roads and crossing behavior (Andrews & Gibbons, 2005) could also influence mortality rates. Live gophersnakes tended to remain stretched out and immobilized for a short time in response to vehicles, while rattlesnakes tended to coil. Furthermore, as gophersnakes are longer-bodied snakes, they create a more conspicuous target when stretched across the road. We did observe motorists purposely swerving to kill snakes on the road surface during our surveys, a phenomenon reported in the literature (e.g. Langley *et al.*, 1989; Row *et al.*, 2007).

The remaining main factors influencing snake counts (age, sex and season) are likely tied to movement tendencies as well. The predominance of adult males on roads is likely a consequence of their extensive vagility compared with females and subadults (Parker & Brown, 1980; Grothe, 1992; Bonnet *et al.*, 1999; Whitaker & Shine, 2000; Andrews & Gibbons, 2008). Furthermore, increased vagility during the mating season would serve to increase the likelihood of encountering females, but also that of crossing roads; we observed a higher proportion of adult males on roads than at hibernacula, suggesting an increased mortality risk for this demographic group. The seasonal peaks in snake counts suggest that, in general, individuals experience greater susceptibility to road mortality during egress and ingress from hibernacula.

### Interacting factors driving variation in road mortality

Our survey data reveal a bimodal pattern of snake activity on roads; however, the specific timing of extensive movement and consequently road mortality risk varies by demographic group. The prevalence of adult male snakes in spring (Fig. 2a and 2b) is presumably due to increased activity associated with mate searching (colubrid species on our study site) or movement toward foraging grounds (Bonnet *et al.*, 1999). Mate searching behavior compounds

road mortality risk beyond that associated with egress, particularly when movement and traffic overlap. For example, gophersnakes mate throughout spring, while rattlesnakes do not initiate mating until summer (Ernst & Ernst, 2003) in this study region. In spring, snakes are active during commuting hours, while in summer, activity is restricted to cooler temperatures, when traffic volume decreases. Although adult snakes are susceptible to road mortality during ingress, the risk is less than that experienced during spring, likely because of the relationship between activity and traffic discussed above. Previous research detected snakes returning to hibernacula as early as August (Cobb, 1994), when temperatures are such that snakes become crepuscular. This is not the case for subadults, as their mortality risk spikes dramatically in fall (Fig. 2a). This pattern was due to an intense mortality event of gophersnake neonates (both sexes) over a 2-week period. These neonates were likely dispersing from hatching sites, as adult female gophersnakes lay eggs at sites distant from hibernacula (Parker & Brown, 1980), and mortality was high because individuals were moving during peak traffic hours. These dispersal events likely explain the predominance of subadult observations for gophersnakes compared with those of live-bearing species that remain within close vicinity of the hibernacula (Fig. 2d).

### Landscape factors associated with snake crossings

The degree and type of roadside cover are important predictors of rattlesnake and gophersnake presence on roads. In particular, snake observations were highly associated with grass cover (Table 1). Although the native sagebrush and perennial grass community remains largely intact on the site, surveys report shifts in the abundance and distribution of cheatgrass and crested wheatgrass (Forman *et al.*, 2013), invasive species that outcompete sagebrush in areas of disturbance. These grasses were intentionally seeded on INL roadsides to reduce erosion, but have spread, particularly along roadside areas where we measured microhabitat data. The association of snake crossings with grass presence could suggest that individuals occur more often in grassland habitat. Studies that have investigated snake habitat use report uniform distributions of gophersnakes across all habitat types (Diller & Wallace, 1996; Cossell, 2003), while rattlesnakes show preference for shrub cover and rocky areas (Diller & Wallace, 1996), suggesting that this explanation is unlikely. Alternatively, individuals may perceive this habitat as unsuitable. In fact, studies have reported negative responses of rattlesnakes (Jenkins, 2007) and gophersnakes (Hall, Mull & Cavitt, 2009) to cheatgrass cover. Research has detected lower abundance of mammal species (Brandt & Rickard, 1994; Gitzen, West & Trim, 2001; Jenkins, 2007) and decreased burrow densities (Yensen *et al.*, 1992) in cheatgrass habitat. Such reductions in prey availability and refugia

could lead to increased surface activity and wider foraging, thereby increasing snake exposure to road surfaces and traffic.

### Conservation implications

The results of this study have conservation implications for snake populations, and the trends we observed could apply to other small vertebrates and should therefore be considered in future studies examining road effects. First, road surveys should be used in combination with other sampling techniques when assessing species occurrence and abundance (Bonnet *et al.*, 1999; Andrews & Gibbons, 2008). As discussed in this manuscript, road surveys reveal which species comprise the majority of road fatalities, but to determine if these species are truly more susceptible to road mortality, abundance data need to be considered. Road surveys may be particularly suited to detect cryptic species with high vagility that may be difficult to detect with other survey methodology. When long-term data are lacking, road studies that reveal the timing and types of losses to mortality may offer insight into potential population effects. For instance, in this study, the preferential loss of adult males during the breeding season may not seem as consequential as adult female deaths, yet male movement ensures connectivity of den populations and maintains genetic diversity. The continued loss of these individuals could severely reduce population persistence over time (Frankham *et al.*, 2002). Effects would be similar for other species that exhibit such a mating system or metapopulation dynamics. However, if seasonal pulses of movement can be identified, methods designed to ameliorate road mortality could overlap with such time periods. In addition, the association of snakes with particular habitat types and features suggests that alterations to land practices could help minimize the number of road fatalities. Non-native grasses should not be planted in association with construction projects. We also recommend that landowners not pile rocks or debris near roadside areas. Many of the basalt piles associated with gophersnake crossings (Table 1) were manmade features that snakes used for denning, ecdysis and temporary refugia. The placement of habitat features near roadsides could serve as an attractant to a variety of species, and should be avoided. Finally, although further research is needed to investigate the possibility that habitat conversion may be increasing snake susceptibility to road mortality, these data provide evidence that habitat restoration measures should be taken. Such conversion is common across the intermountain west and could have similar impacts for a variety of species dependent on sagebrush habitat.

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