Seasonal Activity and Species Habitat Guilds Influence Road-Kill Patterns of Neotropical Snakes

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Research Article

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Abstract

Animal road mortality is the product of multiple factors. We sought to examine the impact of roads on Bolivian biodiversity by quantifying road mortality in a community of tropical snakes and examine variation in road-kills in the context of extrinsic (seasonal effects) and intrinsic factors (habitat guild, sex). From 2007 to 2011, we surveyed the old Santa Cruz-Cochabamba highway and local dirt roads in Florida Province, Santa Cruz Department, Bolivia. We observed 1,444 snake road-kills comprised at least 32 species from 21 genera and 4 families. Nearly one fifth (18.4%) of road-killed species are endemic to the region. A temporal peak in road mortality was observed in February in the middle of the rainy season and was lowest in July coinciding with the dry season. Male snakes were more frequently killed than females and male mortality peaked during the mid to late rainy season. Habitat guild had a significant influence on the species occurrence during the road surveys; road-kills of terrestrial snakes were observed more frequently compared with fossorial, arboreal, semi-arboreal, and semi-aquatic species. The impact of roads on Bolivian biodiversity, including snakes, is expected to increase, as road networks in the region continue to expand. Documenting additional interspecific and intraspecific variation in vulnerabilities to road mortality is needed to better understand the long-term impacts of roads on population persistence as well as inform the design and implementation of mitigation efforts.

Keywords

Bolivia, hot moment, reptiles, road ecology, road mortality, South America, tropics, wildlife–vehicle collisions

Introduction

Demand for expanding road networks has been concomitant with mass production of automobiles, and the pervasiveness of impacts of roads on biodiversity has long been recognized (Coffin, 2007; Stoner, 1925, 1936). Roads fragment the landscape by creating edge effects and inhibiting dispersal or movement and expose animals to traffic collisions and mortality as well as alter assemblage composition (Coffin, 2007; Laurance, Goosem, & Laurance, 2009; Maynard, Aall, Saenz, Hamilton, & Kwiatkowski, 2016). This in turn can affect ecological and evolutionary dynamics by reducing effective population size, skewing sex ratios, and reducing genetic diversity (Balkenhol & Waits, 2009).

Nonrandom vulnerabilities for animals to road mortality emerge from interactions of extrinsic and intrinsic factors. Extrinsic factors that influence vulnerability to road mortality can be both spatial (e.g., habitat types) and temporal (e.g., weather patterns; Crawford, Maerz, Nibbelink, Buhlmann, Norton, & Albeke, 2014; Patrick, Schalk, Gibbs, & Woltz, 2010). Intrinsic factors that influence vulnerability to road mortality are attributed to life-history traits associated with reproduction, foraging behavior, or physiology (Andrews, Nanjappa, &

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Riley, 2015; Barthelmess & Brooks, 2010; Bonnet, Naulleau, & Shine, 1999; Gibbs & Steen, 2005; Rodda, 1990). The interaction of these extrinsic and intrinsic factors, in turn, create nonrandom spatial concentrations (i.e., hot spots) and temporal concentrations (i.e., hot moments) of road mortality (Andrews et al., 2015; Crawford et al., 2014).

Ecological, evolutionary, and environmental conditions affect vagility and dispersal behavior of animals (Matthysen, 2005; Schalk & Luhring, 2010; Whitmee & Orme, 2013); however, ectotherms are particularly influenced by environmental factors with activity often linked to seasonal or ontogenetic factors (Bonnet et al., 1999; Gravel, Mazerolle, & Villard, 2012; Lillywhite, 2014; Schalk & Saenz, 2016). Behavioral patterns of ectotherms lead to interactions with roads for various reasons, including utilization of roads for thermoregulation (Bernardino & Dalrymple, 1992; Sullivan, 1981) or individuals having to cross roads that have been established within migratory routes to nesting or breeding sites (Bonnet et al., 1999; Crawford et al., 2014; Gibbs & Steen, 2005; Steen & Gibbs, 2004). Reptiles, especially small-bodied and slow moving species, are particularly vulnerable to impacts by roads (Andrews et al., 2015). Attributes of snakes, such as their cryptic behaviors and irregular activity patterns, makes them one of the most difficult group of reptiles to study and are particularly challenging for the design and implementation of conservation strategies (Durso, Willson, & Winne, 2011; Parker & Plummer, 1987; Turner, 1977), which makes the assessment of snake population trends, conservation status, or threat mitigation extremely difficult.

In the United States, ecological effects of roads are extensive, affecting nearly one fifth of the country (Forman & Deblinger, 2000). Compared with North America and Europe, far fewer studies have examined the impacts of roads on South American biodiversity, despite expanding road networks in many regions across the continent (Freitas, Sousa, & Bueno, 2013). Bolivia lies in the center of the South American continent and harbors high biodiversity, yet as development continues, almost nothing is known on the impact of roads on Bolivian biodiversity.

There are at least 306 reptile species documented in Bolivia, with snakes being the most species-rich group of at least 169 species, yet many aspects on their ecology and conservation status are lacking (Cortez, 2009). Quantifying the magnitude of mortality, while accounting for the extrinsic and intrinsic factors that influence variation in animal vulnerability to road mortality is necessary for mitigation efforts to be successful. In studies of Neotropical road-kills, snakes often comprise a higher proportion of road-kills compared with other faunal groups, suggesting that they are more prone to vehicle-induced mortality (Gumier & Sperber, 2009; Quintero, Osorio, Vargas, & Saavedra, 2012; Souza, Pires, Borges, & Eterovick, 2015; Vargas, Delgado, & López, 2011), yet there are large gaps in our knowledge on the impacts of roads across the South American continent.

Here, we present results from 4 years studying road-kills in a tropical snake community of Bolivia. To our knowledge, these results are the first to examine the impact of roads on Bolivian biodiversity. Specifically, we sought to (a) quantify road mortality of snakes on our study roads, (b) examine whether there was a temporal concentration in road-kills during a specific time of year (i.e., hot moment; Beaudry, Demaynadier, & Hunter, 2010), (c) determine if there was a difference in the number of road-kills between male and female snakes, and (d) determine if species belonging to different habitat guilds were more prone to road mortality. We hypothesized that road-kills would peak in the rainy season with peak snake activity (i.e., foraging and reproduction), and that males are overall more at risk of road mortality. Furthermore, we hypothesized that terrestrial snakes would experience greater numbers of road kills compared with species from other habitat guilds.

Methods

Study Site

The study area covers the Samaipata (18°10′S, 63°52′W), Mairana (18°7′S, 63°57′W), and Pampagrande (18°5′S, 64°6′W) municipalities in Florida Province, Santa Cruz Department, Bolivia (Figure 1). Surveys were conducted on the primary and secondary roads via the old road Santa Cruz-Cochabamba highway from kilometer markers 65 to 206 km (Figure 1; Cole, 1958). The study area consists of a mixture of Yungas Forest, Bolivian Tucumano Forest, Chaco Serrano Forest, and Inter-Andean Dry Forest. The region, particularly the Inter-Andean Dry Forests, possesses a high number of endemic species, including at least five reptiles (Reichle & Embert, 2005). Regional weather patterns consist of warm, wet summers (November–April), and cool, dry winters (May–October). Mean annual temperature for this region is 20.9°C (range: 0°C–30°C) and mean annual precipitation for this region 575 mm (range: 500–700 mm; Navarro & Maldonado, 2002).

Road Surveys

We surveyed two types of roads (primary and secondary). The primary road is a two-lane asphalt highway that has a width of 10 m, and the section surveyed in this study measured approximately 141 km total. This highway is used by various vehicle types, including buses and heavy transport trucks. The primary road has a higher

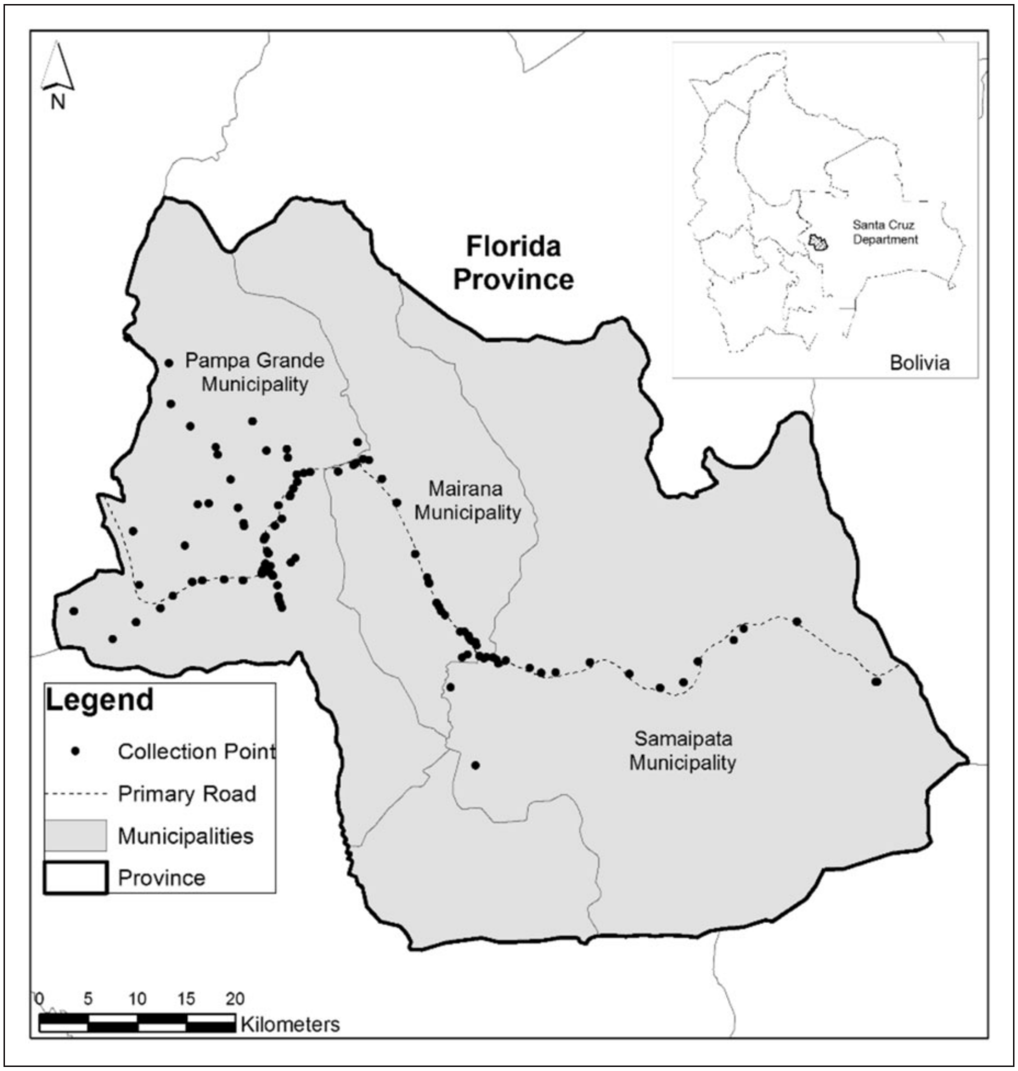

Figure 1. Map of the study area in the municipalities of Pampa Grande, Mairana, and Samaipata in Florida Province, Santa Cruz Department, Bolivia. A road-killed snake is represented by a collection point along the primary road and secondary roads.

traffic volume compared with secondary roads in this region (Sosa, pers. obs.). The secondary roads ($n = 9$) are a series of local roads measuring a total distance of approximately 118 km. Secondary roads range in width from 5 to 8 m and are unpaved, and in some sections, rugged terrain. These roads are not suitable for large, heavy vehicles and are primarily used by light transport vehicles. In the rainy season, some secondary roads become impassable because they are flooded by rivers and poorly maintained. Because of the poor maintenance, the roads are not used regularly by local communities during the rainy season.

Driving road surveys were conducted from March 2007 to May 2011. In total, we conducted 675 surveys (primary road = 548; secondary roads = 127; Table A1). Survey effort averaged 8.2 surveys per month on the primary road and 2.6 surveys per month on the secondary roads (monthly range for both road types 0–27; Table A1). Vehicular surveys were conducted at both day (generally from 0600–0900 hr) and night (generally from 2000–2300 hr) and consisted of a single observer driving a 4 × 4 all-terrain vehicle at 30 to 40 km/hr. All road-killed individuals were collected to avoid counting the animal twice. When specimen conditions allowed, we identified individuals to the lowest taxonomic category possible (taxonomy follows, Uetz & Hošek, 2015). Furthermore, the sex of individuals was identified and species were assigned to one of the following habitat guilds: fossorial, terrestrial, arboreal, semi-arboreal, or semi-aquatic guild. Species were assigned to habitat guilds from Cei (1993), Cortez (2009), Dixon, Wiest, and Cei (1993), Embert and Reichle (2008), Gonzales, Embert, and Montaño (2004), Köhler (2003), and Sosa (unpublished data).

Statistical Analyses

We generated curves for species richness estimates using EstimateS Richness Estimator Program, Version 9.1.0 (Colwell, 2013). We compared the estimated number of species (S(est)) to the abundance-based coverage estimator of species richness (ACE; Chao, Ma, & Yang, 1993). Abundances were pooled as the total number of individuals per species. One hundred randomizations and 10 abundance classes were included in the analysis. To compare the observed distribution of road-kills by habitat guild, we used the proportion of species in the assemblage that fall into each habitat guild to generate expected values and applied Chi-square goodness of fit tests (Barthelmess & Brooks, 2010; Zar, 1996). We conducted a Chi-square analysis to compare total number of road-killed male and female snakes across all species. We used ANOVA and Tukey's HSD to compare variation in snake mortality by comparing the monthly variation in the number of road-killed snakes found per survey. Data were pooled for all surveys conducted within each month during the entire sampling period (2007–2011). Snake mortality per survey was analyzed separately for the primary road and secondary roads. Prior to conducting the ANOVA, we log transformed all data to meet assumptions of normality. Analyses were conducted in PAST (Hammer, Harper, & Ryan, 2001).

Results

We found 1,444 snake road-kills comprised at least 32 species from 21 genera and 4 families (Tables 1, A2). Nearly one fifth (18.4%) of road-killed species are endemic to the region (Table 1). One species, *Apostolepis multicincta*, is considered to be Near Threatened by the IUCN, 7 species are classified as least concern, and 24 species have not been evaluated by the IUCN (Table 1; IUCN, 2015). According to the criteria by Cortez (2009), five species are classified Vulnerable (*Clelia langeri*, Bock's Ground Snake, *Atractus bocki*, *Tomodon orestes*, *Micrurus serranus*, and *Apostolepis multicincta*) and two species are classified as Near-Threatened (Neotropical Snail-eater [*Dipsas chaparensis*] and Andean Lancehead [*Bothrops* cf. *andianus*]), but five of these seven species have not been evaluated by the IUCN (Table 1; IUCN, 2015). The estimated number of species (S(est)) curve did not reach a steady asymptote, suggesting an inadequate sampling effort (Figure 2). The abundance-based coverage estimator of species richness (ACE) produced a prediction of 39 species (Figure 2). This was highlighted by our failure to detect seven species recorded by Embert (2002): Jonathan's Lancehead (*Bothrops jonathani*), Wagler's Sipo (*Chironius scurrulus*), Thin Ground Snake (*Liophis taeniurus*), Blind Ground Snake (*Liophis typhlus*), Lichtenstein's Green Racer (*Phlilodryas olfersii*), Patagonia Green Racer (*Philodryas patagoniensis*), Coastal House Snake (*Thamnodynastes* cf. *strigatus*). However, we recorded nine species that were not previously recorded by Embert (2002): *Atractus bocki*, Brown Sipo (*Chironius fuscus*), Mussurana (*Clelia Clelia*), *Dipsas chaparensis*, Aesculapian False Coral Snake (*Erythrolamprus aesculapii*), Blunthead Tree Snake (*Imantodes cenchoa*), Jan's Green Racer (*Philodryas varia*), *Tomodon orestes*, and False Lancehead (*Xenodon rhabdocephalus*). Bolivian Tree Snake (*Sibynomorphus turgidus*) was the most common species killed (29.7% of road-kills), followed by Günther's Green Racer (*Philodryas psammophidea*; 8.9% of road-kills), *Bothrops mattogrossensis* (6.3% of road-kills), *Clelia langeri* (6.1% of road-kills), Neotropical Snail-eater (*Dipsas bucephala*; 5.9% of road-kills), and Amazon False Coral Snake (*Oxyrophus rhombifer*; 5.8% of road-kills; Table 1).

The number of snake road-kills differed between months on the primary road (ANOVA; $F(11, 39) = 9.40$, $p < .001$) and the secondary roads (ANOVA; $F(11, 38) = 6.97$, $p < .001$). On the primary road, road-kills peaked in February at the middle of the rainy season and were lowest in July, which coincided with the dry season (Figure 3). On the secondary roads, road-kills peaked at the start of the dry season in May but declined to their lowest values in the middle of the dry season (July–September; Figure 3). Road-kills on secondary roads also dipped to low levels in December, which was in the middle of the rainy season (Figure 3). Pooling across species, males experienced higher mortality than females ($\chi 2 = 19.89$, $df = 11$, $p < .05$) with male mortality peaking during the mid to late rainy season (February–April, Figure 4).

Comparing total road mortality across habitat guilds revealed that terrestrial snake species incurred greater casualties (71.6% of road-kills) compared with semi-arboreal snakes (8.2% of road-kills), arboreal species (3.7% of road-kills), fossorial species (2.5% of road-kills), and semi-aquatic species (0.4% of road-kills). Habitat guild influenced the distribution of species impacted by road-mortality observed during the road surveys (Figure 5). For both primary and secondary roads, there were more terrestrial snakes observed, and fewer fossorial, arboreal, semi-arboreal, and semi-aquatic snakes observed than expected based on the proportion of the species in their respective habitat guilds (primary road: $\chi^2 = 79.25$, $df = 4$, $p < .001$; secondary roads: $\chi^2 = 7.57$, $df = 3$, $p = .05$).

Discussion

Vulnerability to road-mortality in Neotropical snakes arises from both extrinsic and intrinsic factors.

Table 1. Diversity and Number of Snake Road-Kills in Florida Province, Santa Cruz Department, Bolivia From March 2007 to May 2011.

Family	Vernacular name	Scientific name	Number of individuals	RBVB	IUCN	Habitat guild
Colubridae	Linnaeus' sipo	*Chironius exoletus*	30		NE	Ar
	Brown sipo	*Chironius fuscus*	2		NE	SAr
		Chironius sp.	17			
	Western indigo snake	*Drymarchon corais*	1		LC	T
	Black-headed snake	*Tantilla melanocephala*	6		NE	T
Dipsadidae		*Apostolepis multicincta**	6	VU	NT	F
	Bock's ground snake	*Atractus bocki**	1	VU	NE	F
	Mussurana	*Clelia clelia*	2		NE	T
		*Clelia langeri**	88	VU	NE	T
	Neotropical snail-eater	*Dipsas bucephala*	85		LC	SAr
	Catesby's snail-eater	*Dipsas catesbyi*	29		LC	T
		*Dipsas chaparensis**	21	NT	LC	A
		Dipsas sp.	14			
	Aesculapian false coral snake	*Erythrolamprus aesculapii*	1		NE	T
		Erythrolamprus ceii	6		LC	SAq
		Erythrolamprus sp.	4			
	Blunthead tree snake	*Imantodes cenchoa*	1		NE	Ar
	Banded cat-eyed snake	*Leptodeira annulata*	32		NE	SAr
		Oxyrhopus guibei	4		NE	T
	Amazon false coral snake	*Oxyrhopus rhombifer*	84		NE	T
		Oxyrhopus cf *niger**	4			T
		Oxyrhopus sp.	4			T
	Brazilian green racer	*Philodryas aestiva*	1		NE	Ar
	Günther's green racer	*Philodryas psammophidea*	120		LC	T
		Philodryas sp.	10			
	Jan's green racer	*Philodryas varia*	1		LC	T
	Bolivian tree snake	*Sibynomorphus turgidus*	429		NE	T
	Jan's forest snake	*Taeniophallus occipitalis*	6		NE	T
		*Tomodon orestes**	1		NE	T
	Wagler's snake	*Xenodon merremi*	51		NE	T
	False lancehead	*Xenodon rhabdocephalus*	1		NE	T
	Ringed hognose snake	*Xenodon semicinctus*	10		NE	F
		Unknown Colubridae/Dipsadidae spp.	65			
Elapidae		*Micrurus serranus**	63	VU	NE	T
Leptotyphlopidae		*Epictia striatula*	19		NE	
Viperidae	Andean lancehead	*Bothrops* cf. *andianus*	2	NT	NE	T
		Bothrops mattogrossensis	91		NE	T
		Bothrops sp.	17			T
	Neotropical rattlesnake	*Crotalus durissus*	23		LC	T
		Unknown Viperidae	2			
Unknown family		Unknown snake	180			

Note. Conservation status of the snakes detected according to the Red Book of Vertebrates in Bolivia (RBVB; Cortez, 2009) and the International Union for Conservation of Nature (IUCN; 2015). NE = not evaluated; LC = least concern; NT = neat threatened; VU = vulnerable. Habitat guild classifications T = terrestrial; F = fossorial; Ar = arboreal; SAr = semi-arboreal; SAq = semi-aquatic. Species endemic to the region are marked with an asterisk (*).

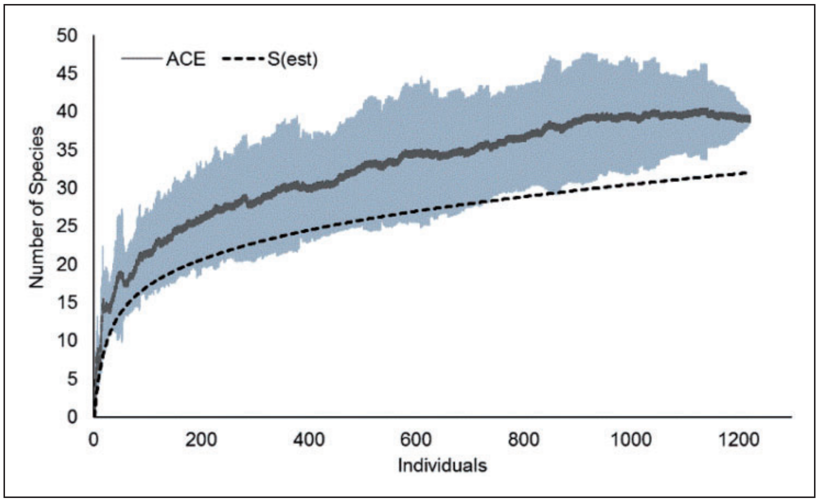

Figure 2. Expected number of species (S(est); dashed line) and mean (±*SD*) abundance coverage-based estimator of species richness (ACE; solid line) for snakes detected during road-kill surveys conducted on both the primary road and secondary roads in the municipalities of Pampa Grande, Mairana, and Samaipata, Florida Province, Santa Cruz Department, Bolivia.

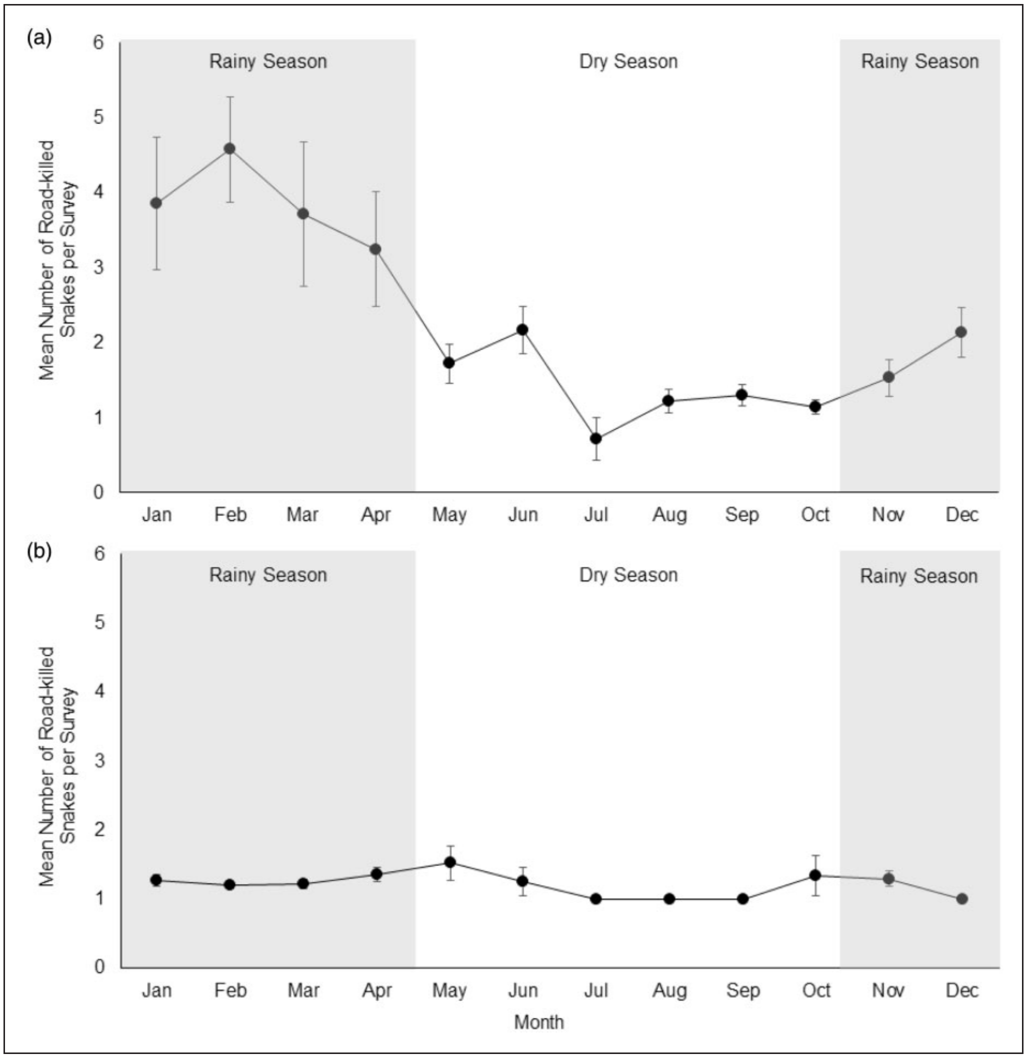

Figure 3. Average (±*SE*) monthly variation in snake road-kills measured as animals killed per survey detected from March 2007 to May 2011 on the (a) the primary road and (b) the secondary roads in Florida Province, Santa Cruz Department, Bolivia.

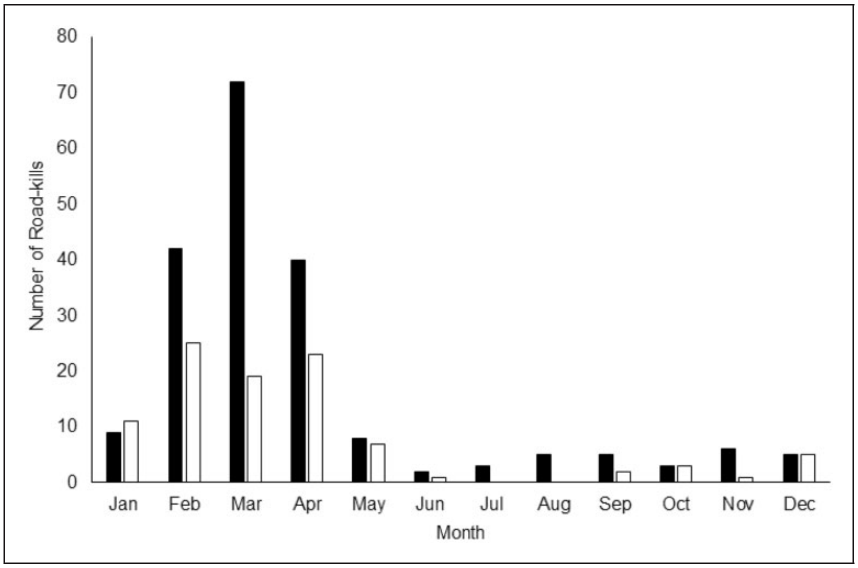

Figure 4. The number of road-killed male (filled bars) and female (open bars) snakes detected per month from March 2007 to May 2011 in Florida Province, Santa Cruz Department, Bolivia. Road-kills were pooled across all species and both road types.

We observed 84% of the total snake species in this region of Bolivia dead on roads as a consequence of collisions with vehicles. Hot moments in road mortality peaked during the rainy season on the primary road, which coincide with reproduction and foraging activity of the snakes in this region (Embert, 2002). In the Brazilian Pantanal, de Souza, da Cunha, and Markwith (2015) observed that peaks in road mortality were linked to seasonal flood pulses that drove animals to seek refuge on highway embankments, which also coincides when snakes are most active and with the breeding season. We observed that the road-kills observed were disproportionally biased toward male snakes, especially during the rainy season. Adult male snakes are at higher risk as they make large forays outside their home ranges in an effort to search for mates which in turn, increases the likelihood of crossing a road and exposure to vehicular traffic (Bonnet et al., 1999; Hartmann, Hartmann, & Martins, 2011).

The primary (i.e., asphalt) road had higher number of road-kills per survey when compared with the secondary (i.e., dirt) roads, especially during the rainy season. The primary road also did not exhibit seasonal variation in traffic volume compared with the secondary roads (Sosa, pers. obs.). Many sections of the secondary road are impassable during the rainy season, and overall traffic volume is lower compared with the primary road (Sosa, pers. obs.), limiting interactions between snakes and vehicles. Furthermore, vehicles traversing secondary roads must travel at a slower speed than vehicles on the primary road because of the differences in road quality, which may give snakes on the road a longer opportunity to detect oncoming vehicles and move to safety. However, as development and improvement in road quality (i.e., increased number of paved roads) continues in Bolivia, impacts of roads on snakes and other taxa will presumably increase as well. de Souza et al. (2015) proposed that targeted mitigation efforts (e.g., reduced speed limits) during the peak road-kill season could reduce the magnitude of road-kills by up to one third. Similarly, in our study area, management that links short-term mitigation efforts to the rainy season, when mortality is most intense for these snakes, especially on the primary roads, may be an effective measure to reduce the magnitude of road-kills.

Roads can act as barriers to movement of reptiles (Andrews & Gibbons, 2005; Koenig, Shine, & Shea, 2001). Our results suggest that while the study roads appear to be less of a barrier to terrestrial and semi-arboreal snake species, despite various numbers of road kills, the relatively few observations of road-killed fossorial and arboreal guild members indicate that these roads may act as a more effective barrier to these guilds. The demographic traits of individuals and mobility are the best predictors of local population persistence in road networks (Gibbs & Shriver, 2002). For example, in mammals, body size and diet influenced susceptibility to road mortality, with large herbivores detected more frequently than smaller species or carnivores (Barthelmess & Brooks, 2010). While fewer road-kills of the fossorial and arboreal guilds were observed when compared with terrestrial guild species, movement of individuals in the fossorial and arboreal guilds may still be inhibited, but whether the long-term impacts roads on limited movement individual on the population persistence of these guilds is not known. Snakes more vulnerable to vehicle-induced mortality tend to be active foragers with greater

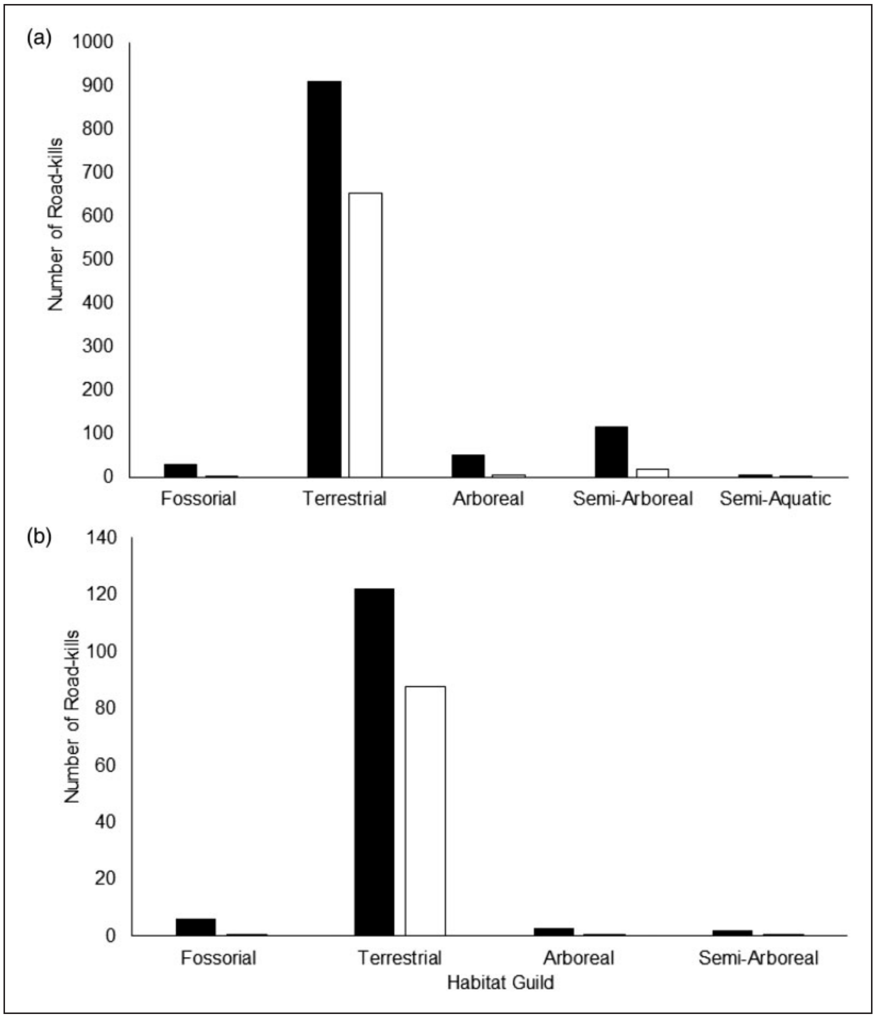

Figure 5. The observed (filled bars) and expected (open bars) distribution of road-kills between habitat guilds for snakes detected on (a) the primary road and (b) the secondary roads in Florida Province, Santa Cruz Department, Bolivia. No semi-aquatic species were detected on the secondary roads. Note the differences in the range of values on the *y* axes for (a) and (b).

mobility, utilize a broad range of microhabitats, and have smaller body sizes (Hartmann et al., 2011). Roads intersect with microhabitats commonly utilized by terrestrial species increasing their encounters with roads and in turn increasing their vulnerability. Species belonging to the terrestrial guild followed by the semi-arboreal habitat guild were the most frequently observed road-kills. Semi-arboreal guild members utilize a broader range of microhabitats, which include terrestrial microhabitats, thereby increasing their likelihood of road encounters relative to arboreal guild species. Other species exhibit strong affinities with certain landscape features (e.g., aquatic habitats), which affect their encounter rate on roads (Patrick et al., 2010). For example, *Erythrolamprus ceii*, the only semi-aquatic snake species in the community, was only encountered on the asphalt road. While we did not examine habitat features (e.g., streams) associated with occurrence in this study (*sensu* Patrick et al., 2010), future efforts that examine this could provide insights as to the existence of corridors where hotspots of road mortality of certain habitat guilds or species coincide with certain habitat features.

Implications for Conservation

Our study demonstrates that Neotropical snakes exhibit nonrandom patterns of vulnerability to vehicular mortality, but the influence of additional interspecific and intraspecific factors in behavioral responses to roads is not known. Some snakes demonstrate avoidance behaviors when encountering roads (Andrews & Gibbons, 2005). Experimental approaches will provide insights to the encounter rate and to understanding the individual behavioral responses (Andrews & Gibbons, 2005; Shine, Lemaster, Wall, Langkilde, & Mason, 2004). Using behavior can, in turn, help inform strategies to mitigate road mortality by optimizing design of road crossing structures to individual species preferences (Patrick et al., 2010; Woltz, Gibbs, & Ducey, 2008). However, this starts with gathering basic and fundamental data on the ecologies of these species. Of the at least 32 species documented during this study, 75% have not been evaluated by the IUCN, making it difficult to determine how much of a threat road mortality might be for population persistence. Efforts should target gathering data on foraging ecology (Bonnet et al., 1999; Sosa, Braga, Schalk, & Pinto Ledezma, 2012, 2013a, 2013b; Sosa, Schalk, Braga, & Langer, 2015) and vagility (Roe, Gibson, & Kingsbury, 2006) to understand probability of a species encountering a road. In addition, efforts should gather data on life-history traits (e.g., time to maturity, fecundity) to understand the consequences and long-term dynamics of population persistence as movement of individuals continues to be inhibited. Even though this study was conducted across 4 years, we failed to detect seven species that are known to occur in the region as documented by Embert (2002). However, we did detect nine additional species that were not found by Embert (2002), but curve for the estimated number of species still failed to reach an asymptote at the conclusion of our surveys and the richness estimator produced a higher prediction of species that we detected, highlighting the low detectability and infrequent encounters of many of these tropical species. Furthermore, accounting for biases of detection and carcass persistence will provide a more accurate assessment road-kills in this region (Santos, Carvalho, & Mira, 2011; Teixeira, Coelho, Esperandio, & Kindel, 2013). This study focused on opportunistic salvage of road-killed individuals, but a more proactive approach, such as the deployment of traps (Durso et al., 2011) or documentation of live snakes found on roads, may provide a clearer picture as to the species and individuals that are encountering roads more frequently.

The impact of roads on Bolivian biodiversity, including snakes, is expected to increase as the demand for better road networks in Bolivia is increasing. From 1997 to 2009, Bolivia has observed a strong increase in road access, and this is highlighted by the increased accessibility to the Inter-Oceanic Highway which spans from Brazil to Peru (Zenteno, de Jong, Zuidema, & Boot, 2014). Previous recommendations to mitigate road mortality for reptiles have included posting signage or reduction in speed that coincide with peak crossing periods in certain habitats or across certain timeframes (Crawford et al., 2014). In Bolivia, snakes are often targeted by motorists when observed on roads (Sosa, pers. obs.), as documented in other regions (Crawford & Andrews, 2016), thus these mitigation efforts may not be the most effective measures at this time. Educational campaigns that aim to change local perceptions and attitudes of snakes is the first step to mitigate road mortality in this region. Only then additional mitigation efforts (e.g., culverts, signage) may be effective.

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Declaration of Conflicting Interests

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Table A1. Number of Snake Road-Kill Surveys Conducted per Month From March 2007 to May 2011 on the Primary Road and Secondary Roads in the Samaipata, Mairana, and Pampagrande Municipalities in Florida Province, Santa Cruz Department, Bolivia.

Road type	Month	2007	2008	2009	2010	2011	Total
Primary	January		16	20	12	14	62
Primary	February		21	22	14	19	76
Primary	March	14	9	21	20	27	91
Primary	April	15	4	19	17	25	80
Primary	May	10	8	16	9	16	59
Primary	June	8	5	3	5		21
Primary	July	2	N/S	8	2		12
Primary	August	5	6	6	2		19
Primary	September	6	3	6	4		19
Primary	October	6	3	6	7		22
Primary	November	7	11	11	6		35
Primary	December	16	16	14	6		52
Secondary	January		7	5	3	4	19
Secondary	February		4	5	2	7	18
Secondary	March	1	N/S	4	3	8	16
Secondary	April	4	N/S	2	7	10	23
Secondary	May	4	3	1	4	5	17
Secondary	June	2	N/S	N/S	1		3
Secondary	July	N/S	N/S	1	1		2
Secondary	August	1	3	1	N/S		5
Secondary	September	1	N/S	N/S	1		2
Secondary	October	1	1	2	N/S		4
Secondary	November	2	2	3	2		9
Secondary	December	2	3	3	1		9

Note. N/S indicates that there was no survey conducted for that month during the study period.

Table A2. Number of Road-Killed Snakes Detected per Month From March 2007 to May 2011 on the Primary Road and Secondary Roads in the Samaipata, Mairana, and Pampagrande Municipalities in Florida Province, Santa Cruz Department, Bolivia.

Road type	Month	2007	2008	2009	2010	2011	Total
Primary	January		26	62	56	22	166
Primary	February		61	71	48	83	263
Primary	March	29	13	63	70	134	309
Primary	April	29	7	45	29	94	204
Primary	May	8	7	40	9	18	82
Primary	June	16	12	7	5		40
Primary	July	2	N/S	10	1		13
Primary	August	4	5	6	2		17
Primary	September	6	3	10	4		23
Primary	October	7	2	4	8		21
Primary	November	7	13	18	5		43
Primary	December	38	26	27	6		97
Secondary	January		7	9	3	5	24
Secondary	February		4	5	3	9	21
Secondary	March	1	N/S	6	3	11	21
Secondary	April	4	N/S	2	10	20	36
Secondary	May	5	10	1	4	5	25
Secondary	June	3	N/S	N/S	1		4
Secondary	July	N/S	N/S	1	1		2
Secondary	August	1	3	1	N/S		5
Secondary	September	1	N/S	N/S	1		2
Secondary	October	2	1	2	N/S		5
Secondary	November	2	3	5	2		12
Secondary	December	2	3	3	1		9

Note. N/S indicates that there was no survey conducted for that month during the study period.