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Snakes on a lane: Road type and edge habitat predict hotspots of snake road mortality

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ABSTRACT

Roads constitute just 1% of the total land in the US, but their impacts on wildlife are significant and far-reaching. Snakes are particularly susceptible to road mortality because many species do not avoid crossing roads, may use the road's surface to thermoregulate, or freeze when approached by a vehicle. We conducted opportunistic surveys to collect road mortality points for snakes in southeastern Ohio over 15 years (2003–2018). We used logistic regression to predict roadkill hotspots and evaluate variables that influence road mortality. The species most frequently found dead on roads were Black Ratsnakes (*Pantherophis spiloides*), Northern Black Racers (*Coluber constrictor*), Eastern Gartersnakes (*Thamnophis sirtalis*), and Rough Greensnakes (*Opheodrys aestivus*). Across the 14 snake species we recorded dead on roads, percent pasture within a 100 m buffer of the roadkill point, township route, county route, and state route were all negative predictors of road mortality. All surveys started in Athens, Ohio, and distance to roadkill locations was a positive predictor for road mortality. These results indicate that high-traffic roads pose a risk to snake populations, but that mortality also occurs on low-traffic roads as well. Our top model showed that low levels of pasture embedded in other land cover types was an important predictor of roadkill, suggesting that edge habitat contributes to snake road mortality. Because road mortality does not seem to be localized, road mortality mitigation structures such as underpasses and fences may have limited benefits for snake populations in our study area. The creation of edge habitat away from roads could provide snakes with necessary habitat without increasing their risk of mortality.

1. Introduction

Roads are one of the most predominant and widespread human landscape modifications (Ibisch et al., 2016; Laurance et al., 2014; Trombulak & Frissell, 2000) with approximately 6.2 million kilometers of public roads covering 1% of the land in the United States. The ecological effects of roads are far reaching (National Research Council, 1997) and are predominantly negative (Forman & Alexander, 1998; Trombulak & Frissell, 2000). These include animal mortality (Gibbs & Shriver, 2005), habitat loss (de Maynadier & Hunter, 2000), reduced habitat connectivity (Shepard, Kuhns, Dreslik, & Phillips, 2008), barrier effects (Bhattacharya, Primack, & Gerwein, 2003), and edge effects (May & Norton, 1996; Findlay & Bourdages, 2000) that may contribute to population declines and extinctions for many species (Forman et al., 2003) and result in ecosystem-wide effects (Vilela et al., 2020). Road mortality has surpassed hunting as the primary cause of vertebrate mortality with as many as 1 million vertebrates killed per day on roads in the United States (Lalo, 1998).

Both invertebrates (Baxter-Gilbert, Riley, Neufeld, Litzgus, & Lesbarrères, 2015; Muñoz, Torres, & Megías, 2015) and vertebrates are heavily affected by road mortality, but reptiles and amphibians are among the most vulnerable species to the effects of roads (Fahrig, Pedlar, Pope, Taylor, & Wegner, 1995; Gibbs & Shriver, 2002). Reptiles are also facing worldwide declines (Gibbon et al., 2000), with roads and road mortality as one of the leading causes (Gibbs & Shriver, 2002, 2005). Reptiles and amphibians are typically slow moving and may not be able to assess the dangers posed by roads (Fahrig et al., 1995), readily crossing paved and unpaved roads during migrations, nest searching, or dispersal (Roe & Georges, 2007); but see Shepard et al. (2008) and Weigand, Wagner, Tonra, and Popescu (2019) on avoidance behavior of high-traffic roads by snakes and turtles. Impacts of roads on turtles and amphibians have been heavily studied, with much less known about

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another declining taxonomic group, snakes. For example, roads that bisect suitable amphibian habitat, such as wetlands, or split overwintering (terrestrial) and breeding (aquatic) habitat, often have high rates of mortality and reduced anuran population densities (Becker, Fonseca, Haddad, & Prado, 2010). Skewed sex ratios in turtles may result from increased female mortality as they cross roads to lay eggs (Steen et al., 2006), contributing to a lack of recruitment (Beaudry, deMaynadier, & Hunter, 2009).

Snakes are heavily affected by road mortality (Smith & Dodd, 2003), with tens to hundreds of millions killed by vehicles in the United States (Rosen & Lowe, 1994). However, far less research has been dedicated to understanding the magnitude of the impacts of roads on snake populations (Kjoss & Litvaitis, 2001). Snakes occupy a wide range of ecological niches, with some species at greater risk of road mortality than others (Ernst & Ernst, 2003). Large-bodied species and individuals do not avoid crossing roads leading to increased mortality (Andrews & Gibbons, 2008; Row, Blouin-Demers, & Weatherhead, 2007). Alternatively, some small-bodied species show strong road avoidance, subjecting them to population fragmentation in areas where roads are abundant (Andrews & Gibbons, 2005). Species that rely on crypsis may freeze rather than flee when approached by a vehicle (Andrews & Gibbons, 2005). Although snakes tend to minimize the distance they must travel by crossing perpendicular to the road's surface, they often cross slowly and present a large target to oncoming vehicles (Rosen & Lowe, 1994). As ectotherms, snakes may be attracted to roads for thermoregulation (Whitford, 1985), or they may use the right-of-way habitat to forage (Andrews & Gibbons, 2005). Snakes are long-lived with delayed sexual maturity, and any increase in adult mortality may contribute to reduced snake population densities and local extinctions (Brooks, Brown, & Galbraith, 1991; Row et al., 2007).

In this study, we evaluated the road mortality hotspots for several snake species in southeastern Ohio using 15 years of road surveys. We investigated the effects of landcover and route types on snake mortality to (1) determine landscape and road-level predictors of road mortality for 14 species of snakes identified, separately for the four most frequently encountered species: Black Ratsnakes (*Pantherophis spiloides*), Black Racers (*Coluber constrictor*), Rough Greensnakes (*Opheodrys aestivus*), and Eastern Gartersnakes (*Thamnophis sirtalis*), and (2) predict mortality hotspots across all 18 snake species found in southeastern Ohio. We expected to find high levels of road mortality for routes with high levels of traffic that bisected suitable snake habitat. As all four focal species of our study often use edge habitat for foraging and thermoregulating, we expected increased road mortality in areas dominated by natural vegetation (i.e., forest) interspersed with open canopy habitat that created significant edge habitat near roads. Overall, this study will provide managers with a tool for evaluating the feasibility of implementing wildlife mitigation techniques, as well as to assess the risk to wildlife when improving or building new roads.

2. Methods

2.1. Long-term road mortality data

We conducted opportunistic surveys between April and October to collect road mortality points for snakes in southeastern Ohio over 15 years (2003–2018). Ohio has one of the most dense road networks in the United States, ranking 5th in traffic volume, 10th on the length of its highway network, and has the 4th largest interstate system (Ohio Department of Transportation 2018). While having a high road density and high traffic volumes, as well as having a modified landscape due to agriculture, urbanization, and legacies of past mining and forestry operations, the study area is dominated by natural vegetation (forest) interspersed with open canopy (pastures, grasslands), and is host to 18 snake species. During the study period, we monitored approximately 35,400 km, through 298 surveys spanning twelve counties: Adams, Athens, Gallia, Hocking, Jackson, Lawrence, Meigs, Pike, Ross, Scioto, Vinton, and Washington.

Data were recorded opportunistically, day and night, and included species, latitude, and longitude (via GPS), county, township, date, time, carcass condition, and route type. We removed carcasses from the road to prevent duplication of records. All surveys started from the city of Athens, Ohio (39.32905, 82.10100), and extended up to 114 km (Euclidean distance) from our starting point.

2.2. Road mortality analysis

To ensure that the road environment within suitable snake habitat was accurately represented during analysis, we only included roadkills and roads within counties that had at least three roadkill points (11 counties, hereafter referred to as the "study area").

To measure background variation in landcover, we mapped roadkill occurrences (n = 296) in ArcGIS and generated four times as many random pseudo-absences (n = 1233) throughout the road mortality study area. The number of pseudoabsences was high enough to characterize the overall background variation in landscape characteristics and road network in our study area; we followed guidelines by Barbet-Massin, Jiguet, Albert, and Thuiller (2012) for dealing with presence and pseudo-absence data in a generalized linear model framework (see below) in that using a larger number of pseudo-absences generally provides improved model fit.

To determine predictors of road mortality, we used logistic regression with a binary predictor variable (1 = roadkill and 0 = pseudoabsence). We explored a variety of landscape variables (surrounding land cover) and local road trait variables (route type) for roadkill and pseudoabsences. Land cover data was obtained from the 2011 National Land Cover Database (NLCD) and the most commonly occurring land cover types that were biologically and ecological relevant for our study species were grouped into three categories: deciduous forest, grassland, and pasture. We extracted the proportion of a given land cover type within a 100-m radius from each roadkill and random point. This radius value was chosen because 1) snakes have low vagility, and 2) their presence on the road is affected by landscape composition and configuration within a relatively short distance from the roadkill location (Langen, 2009; Langen, Ogden, & Schwarting, 2009). This small radius also ensured that the resulting buffers did not overlap, thus reducing the risk of pseudo-replication of predictor variables. We also extracted road types (US Route, State Route, County Route, Township Route) from the Ohio Department of Transportation (ODOT) spatial database for 2017 (http://www.dot.state.oh.us) at both roadkill and pseudoabsences

Lastly, we calculated the distance between our starting point of surveys (Athens, Ohio) and each roadkill and pseudo-absence location. Because the multiple routes available to reach any given point, we could not calculate the actual road distance. Instead, we built concentric buffers in 10 km increments focused on our starting location in Athens, Ohio, and extending beyond the farthest location used in the analysis, and extracted the buffer value for each location. By doing so, instead of calculating an Euclidean distance between Athens and each point, we accounted for uncertainty in the route taken to reach any given location. We standardized the variable *distance from Athens* prior to use in the models. We used Pearson *r* pairwise correlations to identify highly correlated variables that could be used in the same model and found that no Pearson *r* values were $>|0.7|$).

Using both land cover and road attributes, we developed suites of 22 models and a null model for (1) all snake species combined, (2) four individual species with >30 roadkill locations (*T. sirtalis, C. constrictor, P. spiloides, O. aestivus*). For each model set, the models contained land cover variables only, road attributes only, and additive combinations of land cover and road attributes that we deemed biologically meaningful for predicting snake road mortality. In addition to additive models, we also tested the predictive power of several interaction terms: 1) route type × deciduous forest, 2) route type × grassland, 3) route type × pasture. We added distance from Athens to all the models to account for

additional variation and potential bias in the road mortality data due to the nature of our surveys (starting from our base in Athens, Ohio). We then used model selection procedures based on the Akaike Information Criterion corrected for small sample size (AICc) to evaluate the best ranking models. We used the Area Under the Curve (AUC) of the Receiver Operating Characteristic to measure the discriminatory power and model fit. A value of 0.5 denoted complete lack of predictive power, and values >0.8 denoted excellent model fit. We calculated the odds ratios for the predictors selected in the top selected model and calculated the probability of mortality at each roadkill location. All analyses were performed in program R version 3.6.2 (R Core Team, 2019)

3. Results

Over 15 years, we recorded 296 cases of snake road mortality comprising 14 of the 18 snake species native to southeastern Ohio (Fig. 1).

The month with the highest average number of roadkills encountered per survey was September (n = 0.826, Fig. 1). The month with the lowest average number of roadkills encountered per survey was April (n = 0.151, Fig. 1). The year with the highest average number of roadkills encountered per survey was 2011 (n = 1.185, Fig. 2), and the year with the lowest average number of roadkills encountered per survey was 2003 (n = 0.033, Fig. 2). We recorded almost a third of all roadkills (n = 94) on State Routes and recorded our fewest (n = 27) on Township Routes.

The most common snake roadkill fatalities were Black Ratsnakes (*P. spiloides*) (n = 115, Fig. 3), Black Racers (*C. constrictor*) (n = 53, Fig. 3), Rough Greensnakes (*O. aestivus*) (n = 29, Fig. 3), and Eastern Gartersnakes (*T. sirtalis*) (n = 27, Fig. 3). We only recorded one roadkill (Fig. 3) for the Eastern Wormsnake (*Carphophis amoenus*), Queensnake (*Regina septemvittata*), and Smooth Earthsnake (*Virginia valeriae*).

3.1. Predictors of snake road mortality

All Snakes — The top logistic regression model for all snakes had an AUC value of 0.816 and an AICc weight of 0.775, and indicated that proportion of pasture, route type, and distance to Athens were important factors in predicting road mortality (Table 1). The proportion of pasture within a 100 m buffer around each point was negatively associated with roadkill (Fig. 4). Pasture had an odds ratio <1 (0.35), indicating a 6.5 % decrease in the likelihood of a fatal vehicle strike for every 10 % increase in percent pasture (Fig. 4). The distance from Athens to each roadkill point was significant and positively associated with roadkill (Fig. 4). Among route type categories included in the top model, county route, township route, and state route were negatively associated with road mortality, with odds of being struck by a vehicle 0.05 for township routes, 0.23 for county routes, and 0.96 for state routes. State route was not significant with an odds upper 95 % CI > 1 (1.24), indicating a high likelihood of recording roadkill snakes on state routes under certain conditions.

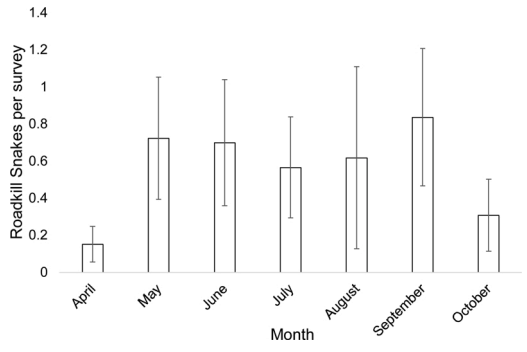


Fig. 1. Number of roadkills per species observed in southeast Ohio between 2003 and 2018 during 298 surveys.

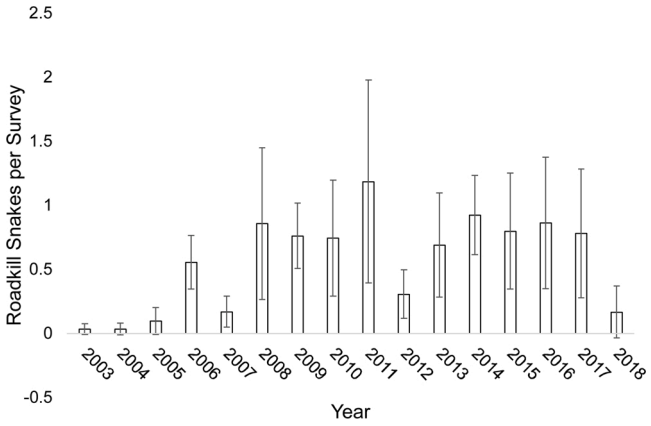


Fig. 2. Number of roadkill snakes per survey per month in southeast Ohio between 2003 and 2018 (N = 298 surveys). Error bars represent 95 % CI.

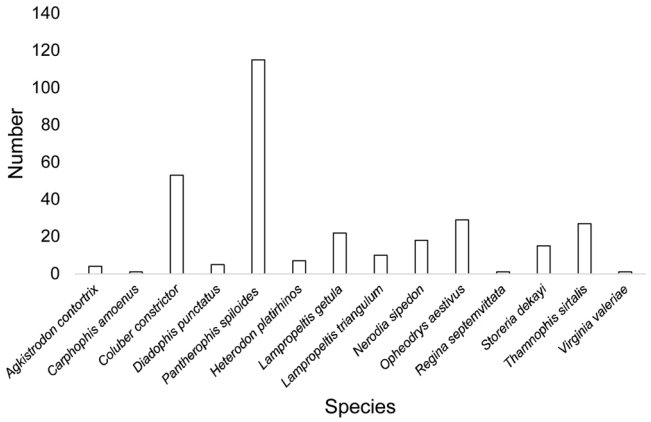


Fig. 3. Number of roadkill snakes per survey per year in southeast Ohio between 2003 and 2018 (N = 298 surveys). Error bars represent 95 % CI.

The individual species predictions reflected the general trend for all snakes combined with slight differences, with the top models for Gartersnakes containing only route type attributes.

Black Ratesnakes — The top logistic regression model for Black Ratsnakes had an AUC value of 0.849 and an AICc weight of 0.479 and indicated that proportion of pasture, route type, and distance to Athens were important factors in predicting road mortality (Table 1). For the top model, proportion of pasture within a 100 m buffer around each point was negatively associated with roadkill (Fig. 4); odds ratio was 0.30, indicating a 7% decrease in the likelihood of a fatal vehicle strike for every 10 % increases in percent pasture (Fig. 4). The distance from Athens to each roadkill point was significant and positively associated with roadkill (Fig. 4). Among route type categories included in the top model, county route and township route were negatively associated with road mortality. Only state route was positively associated with road mortality with odds of being struck by a vehicle 0.04 for township routes and 0.22 for county routes. State route had the only odds >1 (1.26), with an upper upper 95 % CI of 1.9, indicating that Black Ratsnakes were almost twice as likely to be found dead on state routes).

Black Racers — The top logistic regression model for Black Racers had an AUC value of 0.881 and an AICc weight of 0.309 and indicated that proportion of pasture, route type, and distance from Athens were important factors in predicting road mortality (Table 1). For the top model, proportion of pasture within a 100 m buffer around each point was negatively associated with roadkill (Fig. 4), however, the 95 % confidence interval overlapped value 1. Pasture had an odds ratio <1

Table 1
Top models (within 2 AICc units) and null model for each group of logistic models considered here: all species combined, and individual species with >30 roadkill observations.

Species	Model	df	logLik	AICc	delta	weight	AUC
All Snakes	Route Type + Pasture + Distance	5	−577.3	1164.7	0.00	0.775	0.810.
	Route Type*Pasture + Distance	7	−577.1	1168.2	3.54	0.132	0.817
	Null	1	−744.7	1491.5	326.8	0.00	0.5
Black Ratsnake	Route Type + Pasture + Distance	5	−191.8	393.7	0.00	0.479	0.849
	Route Type*Pasture + Distance	7	−190.8	395.8	2.05	0.171	0.851
	Route Type + Distance	4	−194.0	396.2	2.47	0.139	0.840
	Route Type + Grassland + Distance	5	−193.4	397.3	3.64	0.078	0.843
	Deciduous*Route Type + Distance	7	−199.9	397.6	3.86	0.069	0.847
	Null	1	−268.6	407.9	145.4	0.00	0.50
Black Racer	Route Type + Pasture + Distance	5	−82.5	175.3	0.00	0.309	0.881
	Route Type + Distance	4	−83.6	175.3	0.04	0.303	0.876
	Deciduous + Route Type + Distance	5	−83.4	177.0	1.77	0.127	0.875
	Route Type + Grassland + Distance	5	−83.6	177.4	2.08	0.109	0.876
	Route Type* Grassland + Distance	7	−82.0	178.5	3.27	0.060	0.881
	Deciduous*Route Type + Distance	7	−82.2	178.9	3.61	0.051	0.878
	Null	1	−123.1	248.3	72.99	0.00	0.50
Eastern Gartersnake	Route Type	3	−48.1	102.4	0.00	0.184	0.819
	Route Type*Grassland	6	−45.0	102.7	0.38	0.152	0.835
	Route Type + Pasture	4	−47.3	102.9	0.57	0.139	0.841
	Route Type*Pasture	6	−45.4	103.4	1.01	0.111	0.852
	Route Type + Distance	4	−47.7	103.6	1.26	0.098	0.829
	Route Type* Pasture + Distance	5	−46.9	104.3	1.92	0.070	0.842
	Deciduous + Route Type	4	−48.1	104.4	2.09	0.065	0.832
	Route Type + Grassland + Distance	7	−44.8	104.5	2.11	0.064	0.844
	Route Type*Grassland + Distance	7	−45.1	105.0	2.64	0.049	0.851
	Deciduous + Route Type + Distance	5	−47.6	105.7	3.32	0.035	0.836
	Null	1	−63.6	129.2	26.81	0.00	0.50
Rough Greensnake	Deciduous + Route Type + Distance	5	−59.4	129.2	0.00	0.222	0.766
	Route Type + Distance	4	−60.5	129.4	0.14	0.207	0.742
	Route Type + Pasture + Distance	5	−59.8	130	0.73	0.154	0.765
	Route Type* Grassland + Distance	7	−57.6	130	0.82	0.147	0.770
	Route Type + Grassland + Distance	5	−60.5	131.4	2.17	0.075	0.746
	Deciduous + Route Type + Distance	7	−59.8	132.1	2.9	0.052	0.769
	Route Type	3	−57.6	132.6	3.36	0.041	0.686
	Null	1	−70.3	142.6	13.36	0.000	0.50

(0.27), indicating a 7.3 % decrease in the likelihood of a fatal vehicle strike for every 10 % increase in percent pasture (Fig. 4). The distance from Athens to each roadkill point was significant and positively associated with roadkill (Fig. 4). Among route type categories included in the top model, county route, township route, and state route were negatively associated with road mortality, with odds of being struck by a vehicle of 0.04 for township routes, 0.15 for county routes, and 0.75 for state routes. State route was not significant with an odds upper 95 % CI > 1 (1.5).

Greensnakes — The top logistic regression model for Greensnakes had an AUC value of 0.766 and an AICc weight of 0.222 and indicated that proportion of deciduous, route type, and distance from Athens were important factors in predicting road mortality (Table 1). For the top model, proportion of deciduous within a 100 m buffer around each point was positively, but not significantly associated with roadkill (Fig. 4); the odds ratio was 3.78 indicating a dramatic increase in the likelihood of a fatal vehicle strike with increased percent deciduous forest (Fig. 4). However, deciduous was not significant with a odds lower 95 % Ci <1 (0.68). Among route type categories included in the top model, county route, township route, and state route were negatively associated with road mortality, with odds of being struck by a vehicle of 0.06 for township routes, 0.09 for county routes, and 0.53 for state routes. State route was not significant with an odds upper 95 % CI > 1 (1.3), indicating a high likelihood of finding dead Rough Greensnakes on this type of route under certain conditions (Fig. 4).

Gartersnakes — The top logistic regression model for Gartersnakes had an AUC value of 0.819 and an AICc weight of 0.184 and indicated that route type was an important factor in predicting road mortality (Table 1). None of the land cover types we considered in our study were predictive for Gatersnake roadkill. Among route type categories included in the top model, county route, township route, and state route were negatively associated with road mortality, with odds of being struck by a vehicle of 0.02 for Township routes and 0.20 for County routes (Fig. 4). State route was positive but not significantly associated with roadkill, with an odds upper 95 % CI > 1 (1.9), indicating a high likelihood of finding dead Eastern Gartersnakes on this route type of route (Table 2).

We mapped spatial vehicle strike hotspots (for all snakes only) in the study area by interpolating (using kriging interpolation with K = 5 neighbors) the predicted mortality probability yielded by the best model across both roadkill and randomly-generated points (Fig. 5). This procedure highlighted high-risk areas associated with high traffic roads throughout the study area, including in regions not well covered by our surveys, suggesting that the combination of suitable snake habitat and high-traffic roads lead to high prevalence of roadkill (Fig. 5).

4. Discussion

Our study documenting snake road mortalities has implications for the management and conservation of herpetofauna in Ohio. We observed increases in snake road mortality in May and September, consistent with increased movement to and from hibernacula (Jochimsen, Peterson, & Harmon, 2014).

While we did not find strong land cover predictors of road mortality for snakes in southeastern Ohio, our results support the hypotheses that snake roadkills are positively related to the presence of edge habitat and high-traffic, high-speed roadways. Specifically, we showed that (1) Route Type was highly predictive of snake roadkill and highlights the risk posed by high traffic roads, such as State Routes (in our study area, the median annual average daily traffic for State Routes was 3270 vehicles per day (Bencin, Prange, Rose, & Popescu, 2019); (2) percent pasture within a 100 m buffer around a snake roadkill had a negative

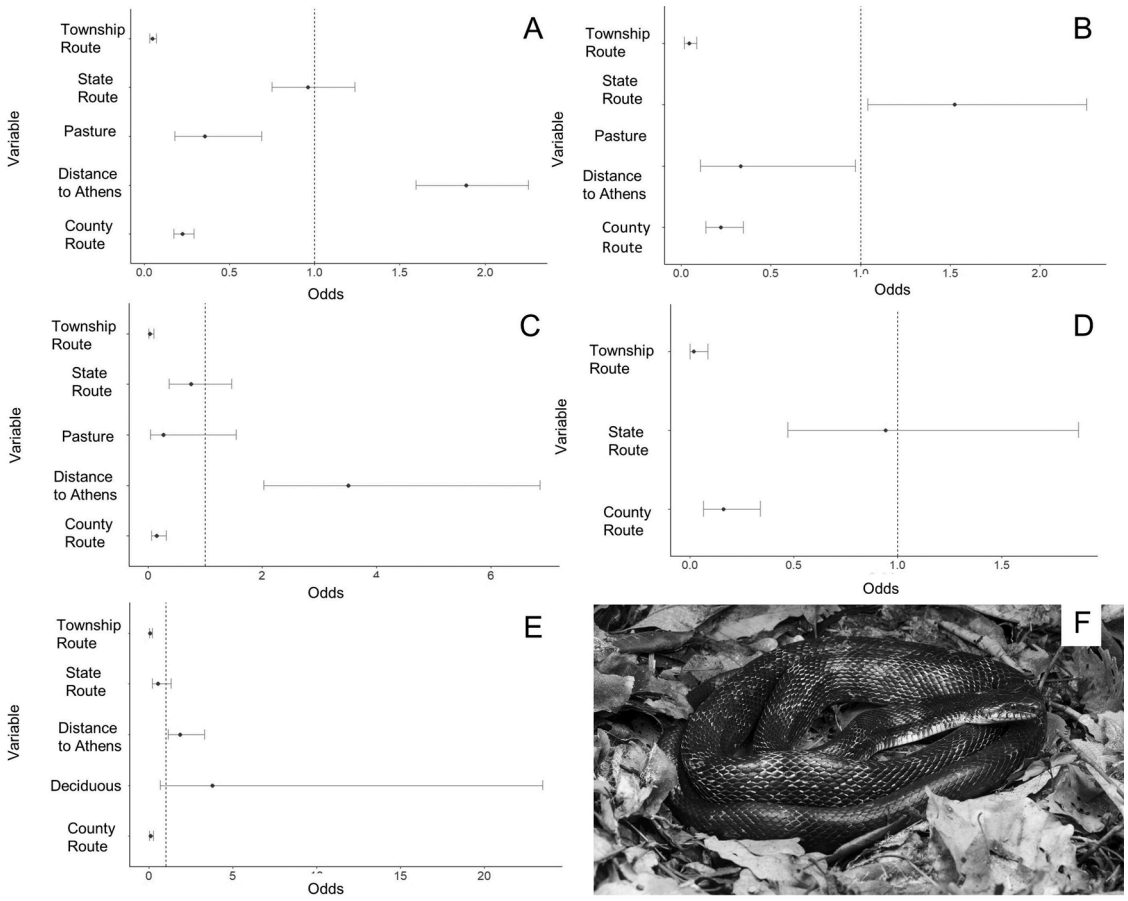


Fig. 4. Odds ratios for variables in the top models across the five model sets considered here: (A) all snakes; (B) Black Ratsnakes; (C) Black Racers; (D) Eastern Gartersnakes; and (E) Rough Greensnakes. (F) Live Black Ratsnake recorded in the study area.

Table 2
Top predictors of snake road mortality in southeast Ohio based on the top models from each model set.

Speceis	Distance to Athens	Land cover Type		Route Type		
		Pasture	Deciduous	Township Route	County Route	State Route
All Snakes	+*	-*		-*	-*	+
Ratsnakes	+*	-*		-*	-*	+
Racers	+*	–		-*	-*	+
Greensnakes	+*		+	-*	-*	–
Gartersnakes				-*	-*	–

"*"denote significant predictors.

associate with roadkills and suggests that increasing amounts of edge habitat is a significant predictor of snake road mortality; and (3) distance from the start of the surveys, Athens, Ohio is positively associated with our roadkill observations.

4.1. Predictors of road mortality

The logistic regression analysis of landscape and local predictors of road mortality, based on a 15-year dataset (2003–2018), identified several positive and negative predictors of mortality that are consistent with known patterns of snake road mortality and habitat use. In our survey areas in SE Ohio, pasture was often embedded in a forested landscape context suggesting that heterogeneous landscapes including open and closed canopy, forming edge habitats are important for predicting hotspots of snake road mortality. Many Ohio snakes, including our four focal species, use edge habitat (Carfagno & Weatherhead, 2006; Weatherhead & Charland, 1985; Zappalorti & Mitchell, 2008) to thermoregulate and to forage (Durner & Gates, 1993; Zappalorti & Mitchell, 2008). Use of edge habitat near roads is known to increase the frequency of road crossings, resulting in a greater risk of road mortality (Andrews & Gibbons, 2005; Jochimsen et al., 2014). Concomitantly, higher snake densities in edge habitat may expose a greater percentage of the population to road mortality (Siers, Reed, & Savidge, 2016).

Township and County Routes were strong negative predictors of road mortality for all snakes combined, Black Ratsnakes, Black Racer, Rough Greensnakes, and Eastern Gartersnakes. These route types typically have low traffic volumes in our study area, with median annual average daily traffic of 158 and 970 vehicles per day, respectively (Bencin et al., 2019; https://gis.dot.state.oh.us/tims). State routes were a significant positive predictor of snake road mortality for Black Ratsnakes and a negative, though not significant, predictor of snake road mortality for All Snakes, Black Racers, Rough Greensnakes, and Eastern Gartersnakes.. High traffic roads such as State Routes (in SE OH, the median vehicle traffic is 3270 vehicles per day) have been shown to cause increased mortality rates in herpetofauna (Carr & Fahrig, 2001; Gibbs & Shriver, 2005) and are likely to contribute to local declines in snake populations (Andrews

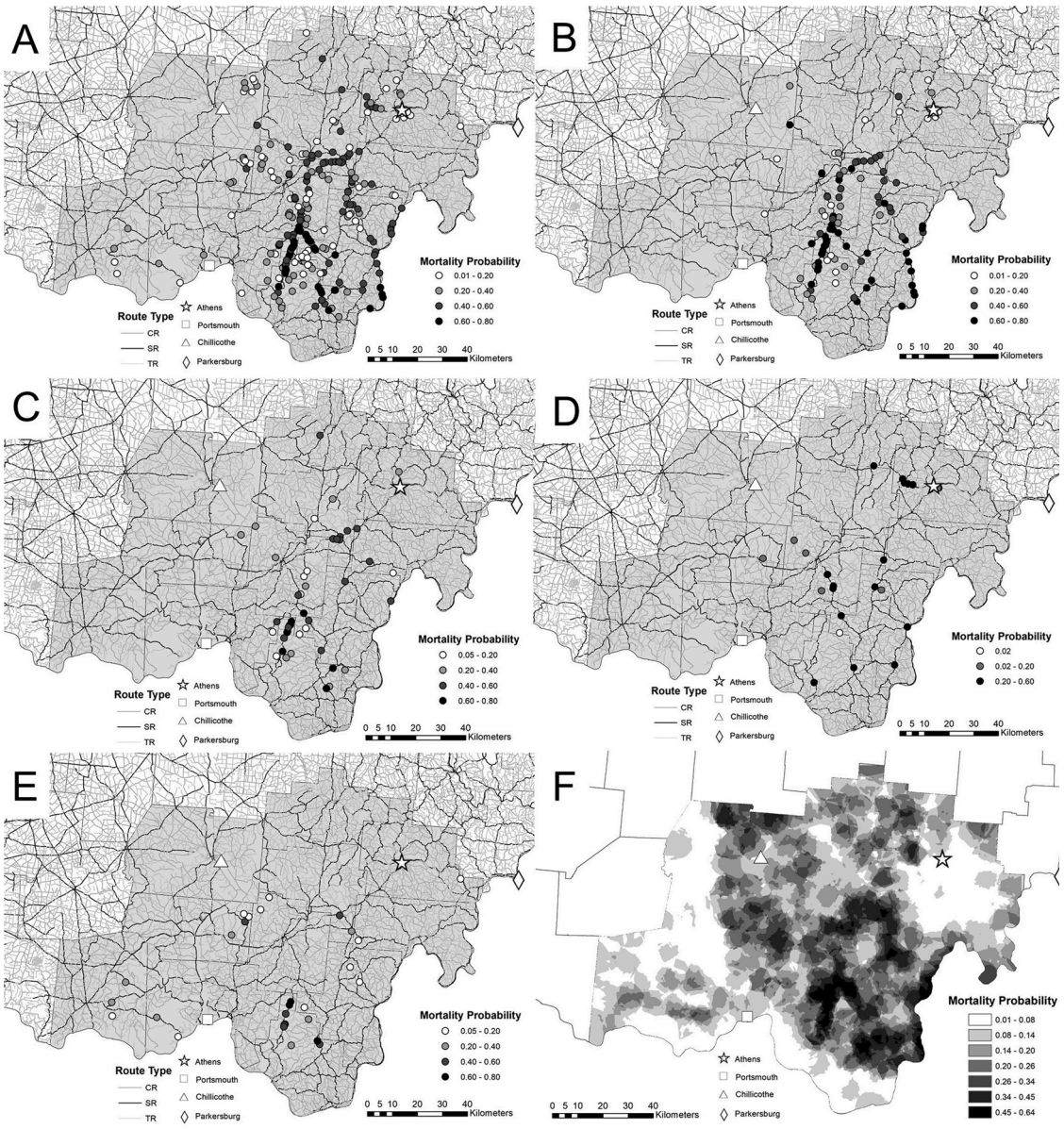


Fig. 5. Predicted road mortality probabilities at observed roadkill locations based on the best logistic regression model for (A) all snakes. (B) Black Ratsnakes. (C) Black Racers. (D) Eastern Gartersnakes. (E) Rough Greensnakes. (F) Kriging interpolation of the predicted mortality probability yielded by the best model for all snakes across both roadkill and pseudoabsence.

& Gibbons, 2008).

Larger, more mobile snake species have a greater likelihood of being killed, and this may explain why Black Ratsnakes and Black Racers (the longest species in our study area) were so commonly found dead on roads (Enge & Wood, 2002). Rudolph, Burgdorf, Conner, and Schaefer (1999) found that large snake species in Texas can experience declines of 50 % or more near roads and concluded that increased road mortality was the primary contributor to Timber Rattlesnake (*Crotalus horridus*) local extinctions and a significant additive form of mortality for the Louisiana Pine Snake (*Pituophis ruthveni*). Black Racers have home ranges between 15 and 25 ha (Carfagno & Weatherhead, 2008; Kjoss & Litvaitis, 2001), and move on average 50–77 m per day (Carfagno & Weatherhead, 2008). Peak movement occurs by June and July as activity increases during the summer (DeGregorio, Weatherhead, Ward, & Sperry, 2016). Black Ratsnakes have home ranges between 3.5 and 6.2 ha (Carfagno & Weatherhead, 2008) (although some studies suggest home ranges as small as 1 ha and as large as 93 ha (Blouin-Demers & Weatherhead, 2002), and move on average 29–36 m per day (Carfagno & Weatherhead, 2008). Peak movement occurs during early spring as individuals disperse from the hibernacula in late March and mate in late May and early June (DeGregorio et al., 2016). Movement declines later in the season (DeGregorio et al., 2016) with a second peak as snakes move back to hibernacula in fall (Blouin-Demers & Weatherhead, 2002). As such, road mortality is likely to be time-sensitive, and our survey data corroborates this finding (Fig. 2).

Small snakes have smaller home ranges and move shorter distances, reducing their likelihood of encountering a road (Andrews & Gibbons, 2005). Small snake species may actively avoid crossing roads, reducing direct mortality, but contributing to population fragmentation (Andrews & Gibbons, 2005). Life history may also contribute to the likelihood of road mortality. Several of the species represented by low sample sizes are fossorial or semiaquatic and may not regularly encounter roads. Variation in daytime activity may also reduce the likelihood of mortality if peak activity coincides with reduced traffic, such as during the night (Hels & Buchwald, 2001). In general, ~24 % of daily traffic occurs during evenings and night times (between the hours of 18:00 and

06:00), thus nighttime-active species may be at lower risk of road mortality.

Along with large home ranges and movements that lead to snakes encountering and crossing roads (especially in road dense areas such as southeastern Ohio), snake behavior likely contributes to increased mortality. While longer snakes can move faster across the road surface (Enge & Wood, 2002), Black Ratsnakes, Black Racers, and Rough Greensnakes tend to become immobile when threatened by an approaching vehicle (Andrews & Gibbons, 2005; Kjoss & Litvaitis, 2001; Plummer, 1981). This is likely a cryptic response to avoid predators, and this response with regard to approaching vehicles will likely increase the probability of road mortality. Species with a higher crossing rate are more likely to be killed (Seiler & Helldin, 2006) and Blouin-Demers, Bjorgan, and Weatherhead (2007) showed that Black Ratsnakes did not actively avoid crossing roads. Row et al. (2007) found that a mortality rate of 0.026 deaths per crossing was enough to increase the extinction probability of a population of Black Ratsnakes to 99 % over 500 years.

Relative abundance of species may also influence mortality rates. Much of our study area is characterized by highly fragmented habitats such as patches of forest interspersed with open herbaceous habitat, and to a lesser extent, agricultural land. Small, cryptic species of snakes may be excluded from an area if the habitat patch is too small (Kjoss & Litvaitis, 2001), which may explain why some smaller-bodied species were only found sporadically. The prevalence of edge habitat in our study area may explain why our samples were dominated by a few species. Disturbed habitat along roads is known to be used by Black Ratsnakes, Black Racers, Eastern Gartersnakes, Rough Greensnakes for improved thermoregulatory, foraging, and refuge opportunities (Howey, Dickinson, & Roosenburg, 2016; Zappalorti & Mitchell, 2008).

Our study used a long-term data set to analyze trends in snake road mortality. However, the data collection was opportunistic, and not meant for a systematic study to test specific hypotheses for roadkill predictions. There was sparse data for some species, and variation in effort from month to month and year to year. However, while limited in its scope, these data and analysis can inform management and conservation not only about species occurrence, but also about potential risks to population persistence. The long-term, broad-scale nature of this study allowed us to apply our models to a large geographic region on a scale that only few other studies have attempted (Langen et al., 2009). Despite these limitations, our study corroborated increases in snake road mortality during late spring and early fall, as individuals move to and from hibernacula (Jochimsen et al., 2014). The roadkill predictors also corroborate evidence of snake habitat use (Howey et al., 2016; Zappalorti & Mitchell, 2008), suggesting that open or grassy habitats are correlated with higher numbers of snake crossings (Jochimsen et al., 2014). We effectively used landscape and road features to predict hotspots of snake road mortality in Ohio (Patrick, Gibbs, Popescu, & Nelson, 2012) and established that increased traffic (Carr & Fahrig, 2001) and suitable habitat near roads (Langen, Gunson, Scheiner, & Boulerice, 2012) contribute to increased mortality. Lastly, the distance from the start of our surveys (Athens, Ohio) and roadkill locations was a positive predictor of roadkill. While the expectation was that higher roadkill would be recorded closer to the start location of our surveys, due to the inherent bias that some routes closer to Athens would be driven more frequently to reach the farther locations in our study area, we found the opposite. As such, we consider that adding the distance component accounted for more variation in the data (AUC values were higher for models that included this variable), and thus we were better able to detect roadkill locations away from Athens despite the lower effort in some marginal areas of the study.

Follow up systematic surveys to validate the accuracy of our model are necessary (Patrick et al., 2012). Importantly, our study does not identify hotspots where populations have already declined due to increased road mortality (Findlay & Bourdages, 2000). Localized radio telemetry studies may be able to reveal such hotspots (Langen et al., 2009) as well as where species are deterred from crossing (Shepard et al., 2008), but likely on a much smaller spatial extent. As such, future studies should standardize sampling effort and roadkill detectability (Langen et al., 2009). Variation in road type (i.e. gravel vs paved), traffic volume, and speed limit greatly influence the longevity and detectability of roadkill snakes. Roadkill surveys can be used to compare abundance of certain species across different habitats, but bias towards larger-sized individuals should be considered. Without recording important demographic data such as size class or sex, the full impacts of road mortality on population persistence will remain elusive (Rouse, Willson, Black, & Brooks, 2011).

4.2. Implications for management and conservation

Snake populations separated by roads have reduced genetic diversity and increased risk of extinction (Clark, Brown, Stechert, & Zamudio, 2010). Snakes are known to have similar ranging behavior and habitat use to terrestrial testudines, and a 2–3 % annual additive adult mortality has been shown to cause population declines in turtles (Macartney, Gregory, & Larsen, 1988). Large snake species are prone to declines of 50 % or more near roadways (Rudolph et al., 1999). Roadkill studies are important for conservationists because they indicate areas with large, healthy populations (Hels & Buchwald, 2001) or areas in need of mitigation where populations may be at risk of declining (Fahrig et al., 1995). Our study indicates that high traffic roadways and edge habitat are high risk areas for snakes. Removing habitat directly adjacent to roads, such as by maintaining mowed grass boarders (Durner & Gates, 1993) and by providing open habitat away from roads, such as with controlled burns (Howey et al., 2016), are possible management strategies to reduce snake road mortality.

Studies that encompass large areas and time spans could be effective for planning mitigation strategies. Our study revealed that snake mortality hotspots are widespread, making mitigation difficult, thus corroborating other reptile roadkill studies (Bank et al., 2002; Bissonette & Cramer, 2008; Evink & Erickson, 2002; Forman et al., 2003; Glista, DeVault, & DeWoody, 2009). We did, however, determine brief periods of time during the active season when snakes are moving to and from hibernacula when mitigation efforts may be more feasible. These 'hot moments' (Beaudry, Demaynadier, & Hunter, 2010) have been used to establish reduced speed limits, exclusionary fencing, and zonal signage (Kenneth Dodd, Barichivich, & Smith, 2004) during times of the year when turtles, amphibians, and snakes are active and at increased risk of road mortality (Beaudry et al., 2010). While road mortality for widely dispersed, low density reptiles such as snakes may be difficult to mitigate in a region with dense road networks, without specific measures focused both temporally and spatially on high value areas, populations will likely continue to decline and go locally extinct.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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