Herpetological Conservation and Biology 14(2):533–545.
Submitted: 12 February 2019; Accepted: 31 July 2019; Published 31 August 2019.

Hot Moments and Hot Spots in the Bayou: Spatiotemporal Patterns of Road Occurrence in a Snake Assemblage in Louisiana, USA

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***Abstract.*—Quantifying temporal and spatial occurrence of road crossing activity by amphibians and reptiles has become increasingly important in conservation efforts. By documenting both the common times (hot moments) and places (hot spots) of individuals, species, and assemblages, effective conservation strategies can help to mitigate road mortality. We conducted a 1-y survey of a snake assemblage on U.S. Highway 51 along the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. We made 78 road-cruising surveys, which allowed us to investigate both the temporal and spatial patterns of snake road crossing activity. We found 409 snakes representing 11 species within two families, Colubridae and Viperidae. Hot moments occurred in late spring or early summer, potentially coinciding with the breeding season and mate-searching behavior in many colubrid species. Hot spots along Highway 51 were detected at the assemblage level and some species-level hot spots were also detected due to large sample sizes. Both peak times and areas of snake activity along U.S. Highway 51 may help to inform potential management efforts for reducing wildlife road mortality.**

Key Words.—activity patterns; reptiles; road ecology; road mortality; wetlands; wildlife-vehicle collisions

Introduction

Numerous studies have addressed and reviewed the conservation issues and ecological impacts of roads on wildlife populations (e.g., Bonnet et al. 1999; Coffin 2007; D'Amico et al. 2015; Santos et al. 2015; Crump et al. 2016). Roads are barriers to movement (Brody and Pelton 1989; Develey and Stouffer 2001; Bhattacharya et al. 2003; Andrews and Gibbons 2005; Shepard et al. 2008a), sources of mortality (Cristoffer 1991; Bernardino and Dalrymple 1992; Mumme et al. 2000; Main and Allen 2002; Smith and Dodd 2003) and even modifiers of behavior (Brody and Pelton 1989; Norling et al. 1992; Kerley et al. 2002; Tigas et al. 2002). Specific movement patterns and high site fidelity, particularly for those species with small home ranges, can result in catastrophic mortality with new road construction or increased traffic patterns along existing roadways (Coffin 2007). Despite particular conservation measures and effective mitigation efforts (e.g., Jaeger and Fahrig 2004; van der Ree et al. 2011; Colley et al. 2017), roads are still major threats to biodiversity.

More recently, studies have highlighted the importance of understanding both species-specific life-history traits (e.g., Roe et al. 2006; DeGregorio et al. 2010; D'Amico et al. 2015) and ecological requirements (e.g., thermal preferences; Mccardle and Fontenot 2016) to understand how they affect the probability of road mortality. Such species-specific differences are evidenced by variation in the frequency of road mortality among species (Ashley and Robinson 1996; Erritzoe et al. 2003; Ford and Fahrig 2007; Barthelmess and Brooks 2010; Cook and Blumstein 2013). Both temporal and spatial variation in road mortality have been documented (Bernardino and Dalrymple 1992; Smith-Patten and Patten 2008; Lagos et al. 2012; Rodríguez-Morales et al. 2013; Meek 2015) and are most likely associated with interspecific seasonal activities and behaviors.

Times when (hot moments) and places where (hot spots) road mortality is greatest vary among species (Mysterud 2004) and are frequently governed by movements associated with the timing of reproductive events (Lutterschmidt et al. 2005; Shepard et al. 2008b; Grilo et al. 2009; Lutterschmidt et al. 2009; Beaudry et al. 2010) and preferred microhabitat use (Tanner and Perry 2007; Gomes et al. 2009; Langen et al. 2009). Because snakes are generally synchronous in the seasonal timing of reproduction (e.g., Olsson et al. 1999), many species within an assemblage may suffer similar high rates of mortality during a particular hot moment. When road mortality is spatially clumped, the factors influencing a hot spot can be identified (Beaudry et al. 2010; Mountrakis and Gunson 2009; Cureton and

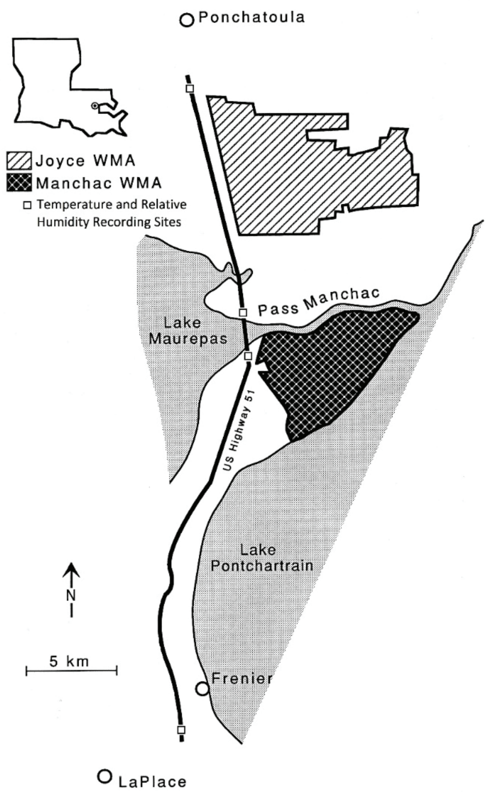

Figure 1. The study area and route showing the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA.

Deaton 2012). Spatially clumped road mortality or hot spots within a snake assemblage, however, may be less common than in other taxa (e.g., turtles) as snakes are generally more solitary and partition microhabitats (e.g., Reinert 1984) or time and food resources (Mushinsky and Hebrard 1977a,b), presumably to reduce competition. This generalization is of course confounded by the potential interaction of times when snakes require a common resource (e.g., communal hibernacula) associated with a particular hot spot.

The objective of this study was to identify the interspecific and intraspecific variation in hot moments and hot spots for a wetland assemblage of snakes. We used the temporal and spatial occurrence of snakes (live and dead) on a roadway in Louisiana to: (1) describe the snake assemblage structure and demographics of road mortality; (2) determine the relationship between snake occurrence, abiotic factors (environmental temperature and humidity), and observed traffic frequency; and (3) determine the hot moments and hot spots for snake occurrence along this road. We then discuss how these spatiotemporal patterns of snake occurrence may help to mitigate against road mortality in wetland assemblages of snakes.

Table 1. The number of surveys (n), total survey mileage (km), number of snakes, and the number of snakes per km encountered from September 1990 to August 1991 on Highway 51 between the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area, Tangipahoa and St. John the Baptist parishes, Louisiana, USA.

Month	n	km	Number of Snakes	Snakes per km
September	9	637.2	30	0.047
October	9	637.2	10	0.016
November	9	637.2	10	0.016
December	4	354.0	2	0.006
January	5	354.0	0	0.000
February	5	354.0	4	0.011
March	5	354.0	28	0.079
April	5	354.0	39	0.110
May	8	566.4	118	0.208
June	7	495.6	92	0.186
July	6	424.8	37	0.087
August	6	424.8	39	0.092
Total	78	5,593.2	409	0.858
Average	6.5	466.10	34.1	0.072

Materials and Methods

Study area and road surveys.—The Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area (Keddy et al. 2007) between Lake Pontchartrain and Lake Maurepas is accessible by U.S. Highway 51 (Fig. 1). This two-lane asphalt highway parallels the elevated interstate highway (I-55) from Ponchatoula to Frenier, Louisiana, USA (35.4 km), and has only slight elevation above the surrounding bayous and canals, providing recreational water access for boating and fishing. We accessed Highway 51 from one of its two-lane access roads in Ponchatoula; the only other access road is located in Frenier.

We sampled Highway 51 an average of 6.5 times per month for one year from September 1990 through August 1991 (Table 1). We surveyed both lanes of the highway while road cruising (e.g., Fitch 1987; Langen et al. 2007; Sosa and Schalk 2016) at approximately 60 km/h twice (traveling south and then north) on each of 78 sampling nights (Lutterschmidt 2013). We started adjacent to the Joyce Wildlife Management Area shortly before dusk with a record of general weather conditions and measures (Hanna Instruments® model-8564 thermo-hygrometer; Smithfield, Rhode Island, USA) of air temperature (T_a), road temperature (T_r), and relative humidity of the air (RH_a) and at the road surface (RH_r). We recorded these measurements at four specific sampling locations along U.S. Highway 51 (Fig. 1; open

Table 2. Diversity and number of snakes from September 1990 to August 1991 on Highway 51 between the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area, Tangipahoa and St. John the Baptist parishes, Louisiana, USA. Live snakes encountered on the road are designated by LOR, while dead snakes are designated by DOR. The abbreviation M = males, F = females, U = sex undetermined, and an asterisk (*) indicates a significant sex ratio ($P \leq 0.05$).

	Sampling Frequency				Sex Frequency			
Taxon	Total	LOR	DOR	LOR:DOR Ratio	M	F	U	Male:Female Ratio
Colubridae								
North American Racer (*Coluber constrictor*)	19	0	19	0:19	10	0	9	10:0*
Red-bellied Mudsnake (*Farancia abacura*)	33	6	27	1:4.5	14	3	16	4.7:1*
Eastern Kingsnake (*Lampropeltis getula*)	4	0	4	0:4	1	1	2	1:1
Mississippi Green Watersnake (*Nerodia cyclopion*)	70	17	53	1:3.1	21	23	26	1:1.1
Southern Watersnake (*Nerodia fasciata*)	114	38	76	1:2	47	35	32	1.3:1
Diamond-backed Watersnake (*Nerodia rhombifer*)	25	4	21	1:5.2	10	5	10	2:1
Gray Ratsnake (*Pantherophis spiloides*)	21	4	17	1:4.2	10	5	6	2:1
Glossy Swampsnake (*Liodytes rigida*)	17	12	5	2.4:1	4	9	4	1:2.2
Dekay's Brownsnake (*Storeria dekayi*)	8	7	1	7:1	2	4	2	1:2
Western Ribbonsnake (*Thamnophis proximus*)	37	9	28	1:3.1	22	3	12	7.3:1*
Viperidae								
Cottonmouth (*Agkistrodon piscivorus*)	44	21	23	1:1.1	6	26	12	1:4.3*
Unidentified	17	12	5	2.4:1	0	0	17	0:0
Total	409	130	279	1:2.1	147	114	148	1.3:1

squares on road) and again during the return north for a total of six independent measurements that we used to calculate mean temperatures and RH for each sampling night. Surveys would typically take 2–2.5 h depending on observed snake activity and associated sampling.

We quantified vehicular frequency during sampling nights using a hand-held counter to record each time a vehicle passed heading either in the same or opposite direction. We used the total number of vehicles per night to investigate potential effects of traffic volume on road mortality. Two investigators participated in each survey with WIL being solely responsible for sighting and sampling snakes, thus avoiding investigator bias. The second investigator recorded all data dictated by WIL and monitored and recorded vehicular frequency.

We captured, determined sex, and measured snakes to the nearest 0.5 cm snout-to-vent length (SVL), and we released snakes found Live on Road (LOR). We also measured, determined sex, and removed snakes found Dead on Road (DOR) to avoid repeated sampling of the carcass. We did not record sex and SVL in instances were individuals eluded capture or road-killed specimens were of poor condition. We conducted Chi-square analyses to test for differences in occurrence of male and female snakes on the road for each of the 11 species (Table 2). We recorded localities of LOR and DOR snakes along the roadway by odometer and mapped them for spatial analyses using Geographic Information Systems (GIS).

Temporal and spatial analyses of snake occurrence.—We assessed monthly variation and significant differences in the number of snakes sampled per month while controlling for sampling effort in km traveled (snakes/km). We used Kruskal-Wallis and Mann-Whitney U-tests (Zar 2010) to determine differences in temporal variation of overall snake occurrence and for temporal variation among individual snake species ($\alpha = 0.05$). Of the 409 snakes we sampled in this study, we did not record locations of 21 snakes, which left 388 snake locations for spatial analysis.

We investigated spatial distribution and variation with Siriema 2.0 (Coelho et al. 2014) and ArcGIS 10.x; all analyses were conducted in NAD 1983 UTM Zone 15N. We also downloaded a 1996 Louisiana coast digital raster map (https://coast.noaa.gov/ccapftp/#/) with 16 land cover classes within the study area (Fig. 2). We used the Ripley's *K*-function to analyze spatial clustering and dispersion (Ripley 1976; Bailey and Gatrell 1995). Ripley's *K*-function measures statistically significant clustering and dispersion at multiple spatial scales without regard to the shape of the area studied (Conolly and Lake 2006; Sayer and Wienhold 2013) and can be used to analyze locations along a line or in space (Dixon 2002). An index is calculated by measuring the distance from each feature to all other features in the dataset where a mathematical operation (see Bailey and Gatrell 1995) then generates a *K* value. A hypothetical random distribution is generated, and the difference between the observed index value and the index value of the randomly generated features is calculated. The basic formula for the *K*-function is:

$$\lambda K(d) = E$$

where E is the number of events within distance d of a randomly chosen event, λ is the mean number of events per unit area, and $\lambda K(d)$ is the expected number of neighbors in a circle of radius d at a randomly chosen point in the distribution. We then used the common *L*-function transformation:

$$L(d) = \sqrt{\frac{A \sum_{i=1}^{n} \sum_{j=1, j\neq i}^{n} k_{i,j}}{\pi n(n-1)}}$$

where d is distance, n is the number of features, A is total area, and $k_{i,j}$ is any weight given to the features. This transformation results in an expected $L(d)$ always being equal to distance.

Performing a standard two-dimensional Ripley's *K*-function analysis for roadkill can be problematic, due to straight roads being essentially one-dimensional. Therefore, we used a modified Ripley's *K*-function analysis (Clevenger et al. 2003; Mountrakis and Gunson 2009) in Siriema 2.0 to find significant clustering and dispersion. We used radii of 1-km increments up to 36 km; resulting graphs will show both the observed *K* and the 95% confidence limits.

If the observed *K*-function is greater than the upper confidence limit for a particular distance, the distribution of individual localities is more clustered than a random distribution at that distance (i.e., scale of analysis). If the observed *K*-function value is less than the lower confidence limit, the distribution is more dispersed than random or significant over-dispersion is indicated in relation to other snake localities. Therefore, if the observed *K*-function falls outside the upper or lower confidence envelope, spatial clustering or over-dispersion (respectively) for that distance is statistically significant. We ran 999 simulations to avoid a Type I error (Grabarnik et al. 2011).

We identified hot spots of snake occurrence using Siriema 2.0 as described in Coelho et al. (2012), with the difference that our hot spots were linearized for reasons described above. We only identified hot spots for species that exhibited significant clustering as identified by the Ripley's *K*-function analyses. We did not perform hot spot analyses on species that did not exhibit significant clustering, due to the possibility that any identified hot spot could be a hot spot from a sample distribution of uniform probabilities. Hot spots were identified by first dividing the study road into 100-m segments. A circle with a defined radius passes through each snake occurrence, summing the number of snakes.

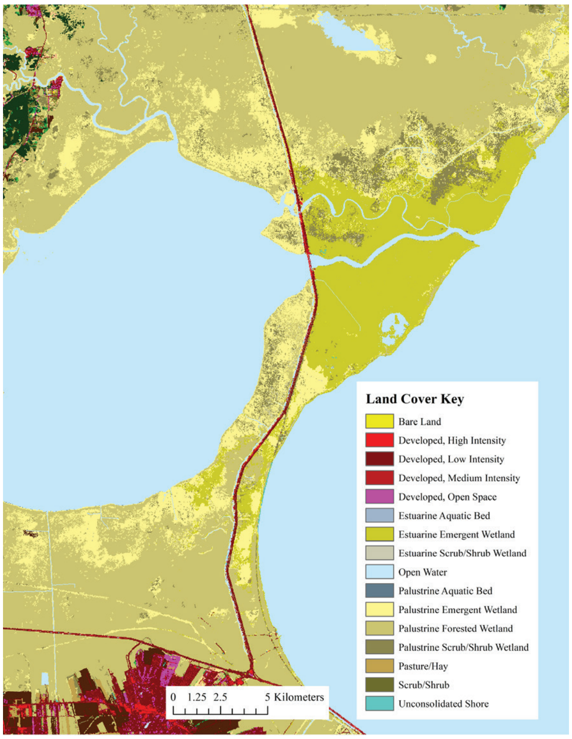

Figure 2. Land cover classes of the study area in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. (From Louisiana digital coast raster map using ArcGIS 10.x and NAD 1983 UTM Zone 15N).

We applied a correction factor that takes into account the length of the road, resulting in aggregation intensity values along the entire length of the road. We ran 999 simulations for each hot spot analysis. Aggregation intensity values above the 95% upper confidence limit indicate significant hot spots of snake occurrence.

Results

Road survey results.—Across the 12 month survey period, we conducted 78 surveys that totaled 5,593 km traveled with a total of 0.858 snakes/km (average = 6.5 surveys/month; average = 466.1 km/month; average = 0.07 snakes/km/month; Table 1). The 409 snakes we observed comprised at least 11 species (17 observations were unidentified; Table 2) from two families with dead snakes being encountered nearly twice as often as live snakes (Table 2). We found vehicular frequency to be a significant predictor of road mortality ($F_{1,44} = 4.52$; $P = 0.039$) but it only explained 9.3% of the variation in the number of DOR snakes observed (Fig. 3). We found that when vehicular frequencies reach 24 cars, increased traffic generally results in similar road mortality. For example, vehicular frequencies of 24, 32, 45, 50, 66, and 81 all resulted in 10 or 11 DOR snakes. We also found that vehicular frequency did not differ among months

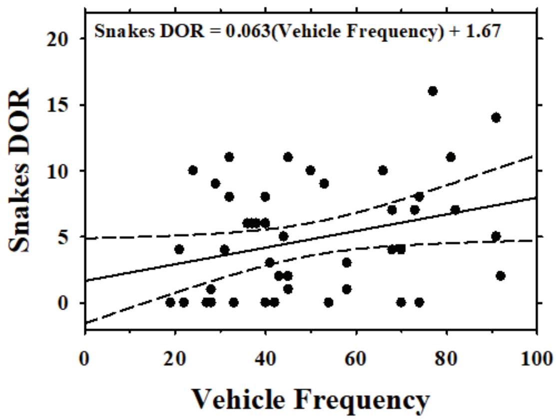

Figure 3. Relationship between vehicle frequency and the number of snakes observed dead on the road (DOR) in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. Dashed lines show the 95% confidence limits of the regression line.

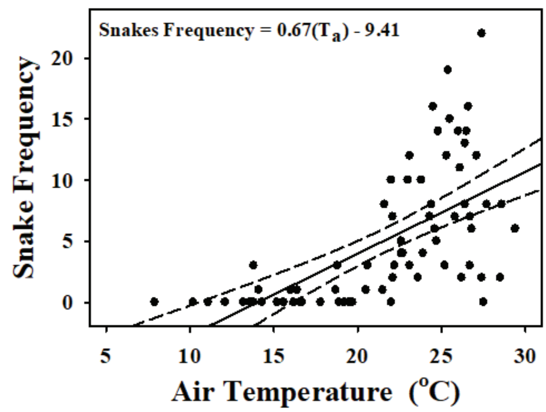

Figure 4. Relationship between Ta and the number of snakes observed (r^2 = 0.396) in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. Dashed lines show the 95% confidence limits of the regression line.

($F_{1,11}$ = 1.48; P = 0.199), unlike the monthly differences in DOR snakes observed.

Of the snakes examined, more snakes were male than female (147 males versus 114 females; Table 2) but this difference was not significantly different (χ^2 = 2.09, df = 1, P = 0.148). Only the North American Racer, *Coluber constrictor* (χ^2 = 6.67, df = 1, P = 0.010), Red-bellied Mudsnake, *Farancia abacura* (χ^2 = 3.88, df = 1, P = 0.049), and Western Ribbonsnake, *Thamnophis proximus* (χ^2 = 8.32, df = 1, P = 0.004), of the 11 species had significantly skewed sex ratios with a greater number of males observed (Table 2). Only the Northern Cottonmouth, *Agkistrodon piscivorus*, had significantly more females observed than males (χ^2 = 6.93, df = 1, P = 0.008).

Occurrence of snakes.—Snake occurrence (number of snakes/km) differed among months (H = 32.81, df = 11, P < 0.001). Such temporal variation in activity is likely related to differences in monthly temperature (H = 51.39, df = 11, P < 0.001). We found a significant relationship between T_a and the number of snakes observed on the road ($F_{1,72}$ = 47.2; df = 1, 72; P < 0.001) with T_a explaining 39.6% of the variation (Fig. 4). Other measures of temperature (T_r) and relative humidity (RH_a and RH_r) were correlated with T_a; however, a multiple regression model indicated that only T_a (P = 0.039; Coef. = 1.45, SE = 0.69) and RH_r (P = 0.048; Coef. = 0.47, SE = 0.24) were significant predictors of snake frequency.

For eight of the nine species examined, the highest road occurrences were in late spring/summer and the lowest occurrence in winter (Fig. 5). The three species of watersnakes (Genus *Nerodia*) were detected on the road over the longest periods of time and were detected every month beginning in February-March until October-November (Fig. 5). Each species differed in their peak of temporal activity, however, with Mississippi Green Watersnakes (*N. cyclopion*) peaking in May (H = 27.2, df = 11, P < 0.001; Fig. 5), Southern Watersnakes (*N. fasciata*) peaking in July (H = 33.84, df = 11, P < 0.001; Fig. 5), and the peak of activity for Diamond-backed Watersnakes (*N. rhombifer*) occurring in April (H = 12.74, df = 11, P < 0.010; Fig. 5).

We detected *Farancia abacura* from April to July and peaked in May (H = 27.2, df = 11, P < 0.001; Fig. 5). Similarly, Glossy Swampsnakes (*Liodytes rigida*) peaked in May (H = 12.8, df = 11, P < 0.001) but were detected on the road from March to June (Fig. 5). *Thamnophis proximus* were detected from April to September and peaked in June (H = 11.14, df = 11, P < 0.040; Fig. 5). *Agkistrodon piscivorus* were detected on the road from April to November with the highest occurrence in June (H = 23.71, df = 11, P < 0.001; Fig. 5). Gray Ratsnakes (*Pantherophis spiloides*) were detected from April to September with a peak in June (H = 12.89, df = 11, P < 0.010; Fig. 5). *Coluber constrictor* were found from March to September but were the only species to not exhibit significant temporal variation (H = 8.11, df = 11, P < 0.070; Fig. 5). Additionally, the monthly activity of road occurrence observed between males and females shows no overall trends in sex-dependent activity within species.

Clusters of snakes.—In addition to using moving averages to investigate snake occurrence along Highway 51 (Fig. 6), we also used the Ripley's *K*-function to test if snakes exhibited patterns of spatial clustering or dispersion. Of the total 409 snakes and 11 species observed, 21 observations were missing

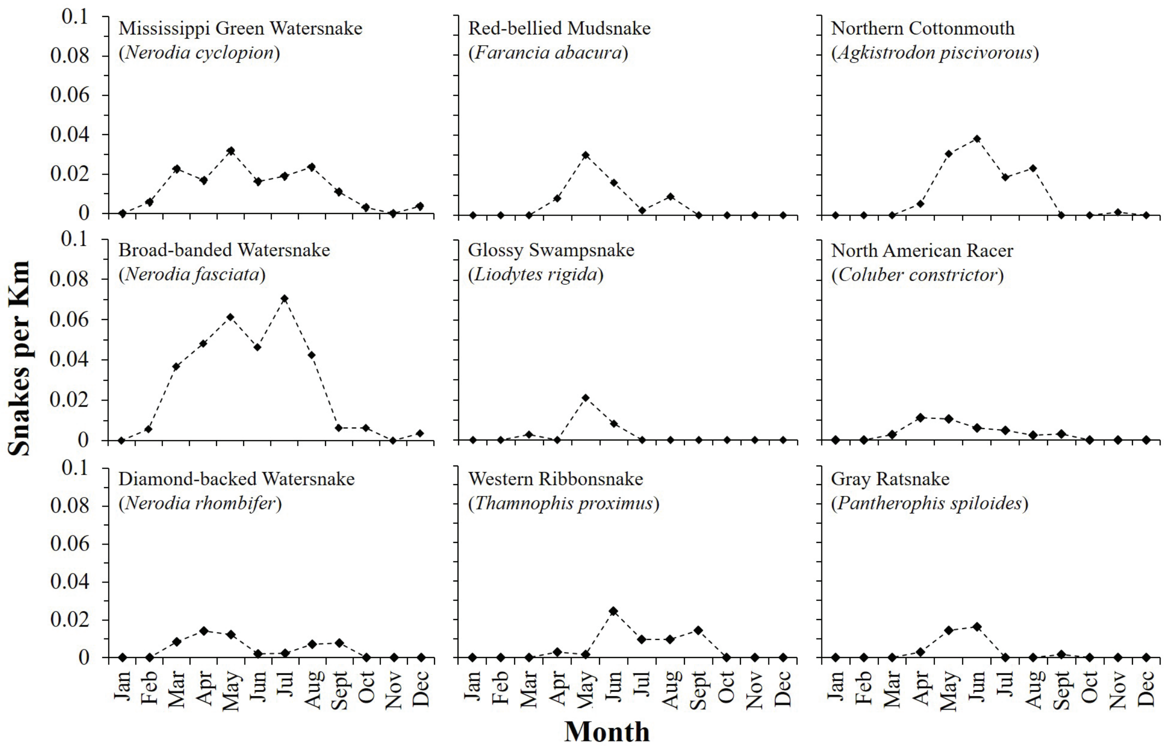

Figure 5. Average monthly variation in snake road occurrence measured as snakes encountered per km detected from September 1990 through August 1991 in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area, Louisiana, USA. Snakes occurrence included individuals that were found live on the road (LOR) and dead on the road (DOR). We only plot species where 10 or more individuals were encountered.

records of locality. Of the remaining 388 records, we used only the nine species (see Figs. 7 and 8) that had at least 14 recorded road localities for interspecific comparisons of the Ripley's *K*-function. Aggregating the locality records of these nine species (n = 357 observations of the 388) revealed an overall pattern (Fig. 7) of clustering at small distances, but as distance increased, they exhibited a pattern of over-dispersion. *Nerodia cyclopion* were clustered at small distances and exhibited over-dispersion at greater distances, while *N. fasciata* exhibited clustering up to moderate distances, and *N. rhombifer* were over-dispersed at moderate and large distances (Fig. 8). *Farancia abacura* exhibited a pattern of clustering at small distances, over-dispersion at moderate distances, and clustering at greater distances (Fig. 8). *Agkistrodon piscivorus* were clustered at almost every distance (Fig. 8). *Liodytes rigida* were clustered at small distances, and *T. proximus* were clustered up to moderate distances (Fig. 8). *Pantherophis spiloides* were clustered at small distances, while *C. constrictor* did not exhibit any nonrandom pattern of dispersion (Fig. 8).

Generally, the activity of the nine snake species was concentrated at the beginning, middle, and end of Highway 51, with land cover primarily consisting of palustrine forested wetland, estuarine emergent wetland, and palustrine emergent wetland (Fig. 9). Hot spots were only identified for seven of the nine species, as well as the nine species aggregated together. These seven species (and the nine species aggregated together) exhibited clustering at small distances, so we used a 3-km radius for our hot spot analysis. *Nerodia fasciata* was primarily concentrated in the southern half of Highway 51 and was mainly associated with palustrine forested wetland and palustrine emergent wetland (Fig. 9). Activity of *F. abacura* and *N. cyclopion* were both concentrated on the northern portion of Highway 51 occurring in habitats primarily consisting of palustrine forested wetland (Fig. 9). Interestingly, *A. piscivorus* activity was also associated with palustrine forested wetland, but their localities were concentrated on the southern end of Highway 51. Activity of both *T. proximus* and *P. spiloides* were concentrated in the middle section of Highway 51 and were mainly associated with estuarine emergent wetland and palustrine emergent wetland (Fig. 9). A hot spot for *L. rigida* activity was located in the mid-southern end of Highway 51 and was associated with estuarine emergent wetland and palustrine forested wetland.

Discussion

Road mortality of wildlife populations has received great attention because of its potential to reduce effective population size (Fahrig et al. 1995) and genetic

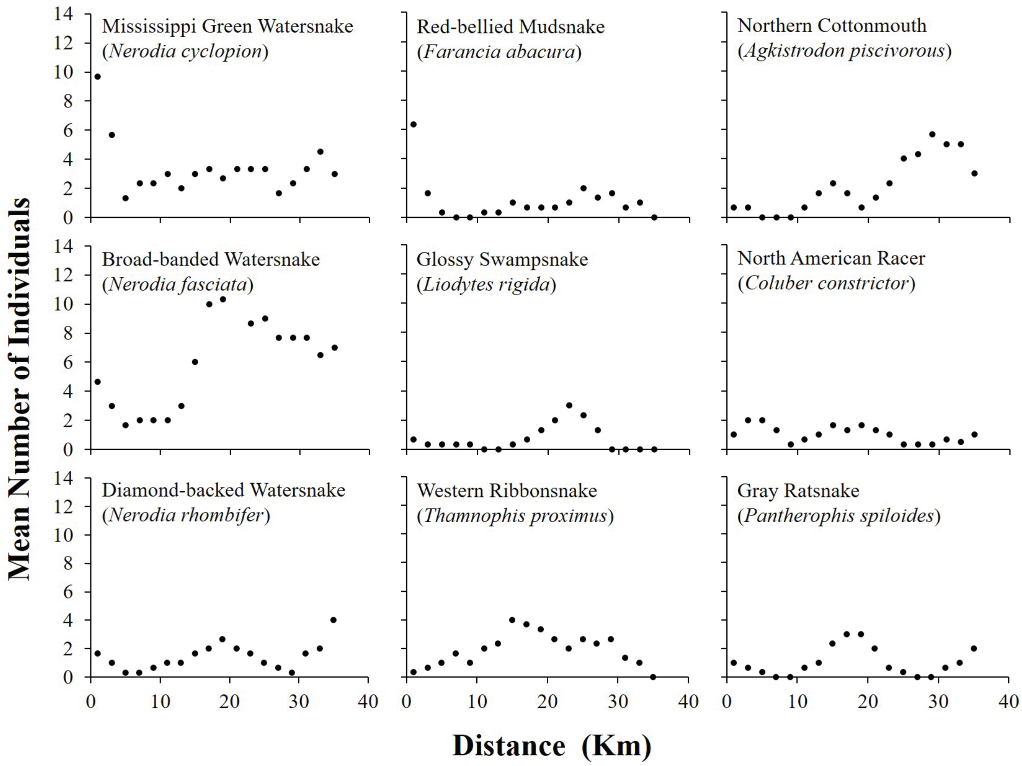

Figure 6. Moving averages of snake occurrence along the 35.4 km of Highway 51 in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area, Louisiana, USA, September 1990 through August 1991. We only plot species where 10 or more individuals were encountered.

diversity (Noël et al. 2007), and to alter sex ratios (Gibbs and Steen 2005) due to sex-dependent differences in activity patterns and home-range size. Road mortality is spatially and temporally clumped, which must be considered in conservation planning. We found more than twice the number of DOR snakes (n = 279) as LOR snakes (n = 130). *Nerodia fasciata* suffered the greatest road mortality (n = 76) followed by *N. cyclopion* and *T. proximus*. Of the 11 species observed in this survey, we observed two species (*L. rigida* and *Storeria dekayi*) with a greater occurrence of LOR than DOR snakes. This may be due to their small body size and potentially lower probability of being struck by vehicles. Of the 37 smaller-bodied (≤ 35 cm SVL) juvenile or sub-adult snakes (representing seven species) detected during our surveys, 24 individuals (65%) were found LOR. Unfortunately, intentional killing of snakes by motorists has been documented (Langley et al. 1989; Ashley et al. 2007; Secco et al. 2014), but with their small size and less conspicuous appearance on a roadway, smaller snakes may have a lower potential for road mortality. The lower proportion of smaller-bodied DOR snakes, however, may also be a result of scavengers (DeGregorio et al. 2011; Hubbard and Chalfoun 2012). Smaller carcasses on roads persist for shorter periods of time due to removal by scavengers and thus may be underestimated during surveys.

We found male-biased sex ratios in *C. constrictor*, *F. abacura*, and *T. proximus*. This result is most likely associated with the larger home ranges of males in some snake species (e.g., Putman et al. 2013; Bauder et al 2016). Interestingly, we found female-biased sex ratio in *A. piscivorus* even though this species also demonstrates the same trend for larger male home-range

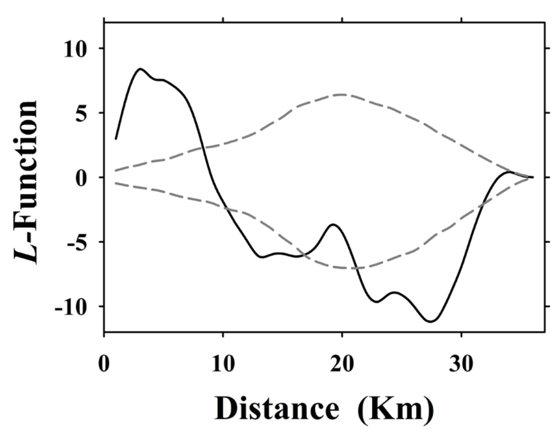

Figure 7. Ripley's *K*-function graph for all snake occurrences (n = 357) for the aggregated nine species of snakes in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. Solid line shows observed *K* and dashed lines indicate the upper and lower limits of the 95% confidence envelope.

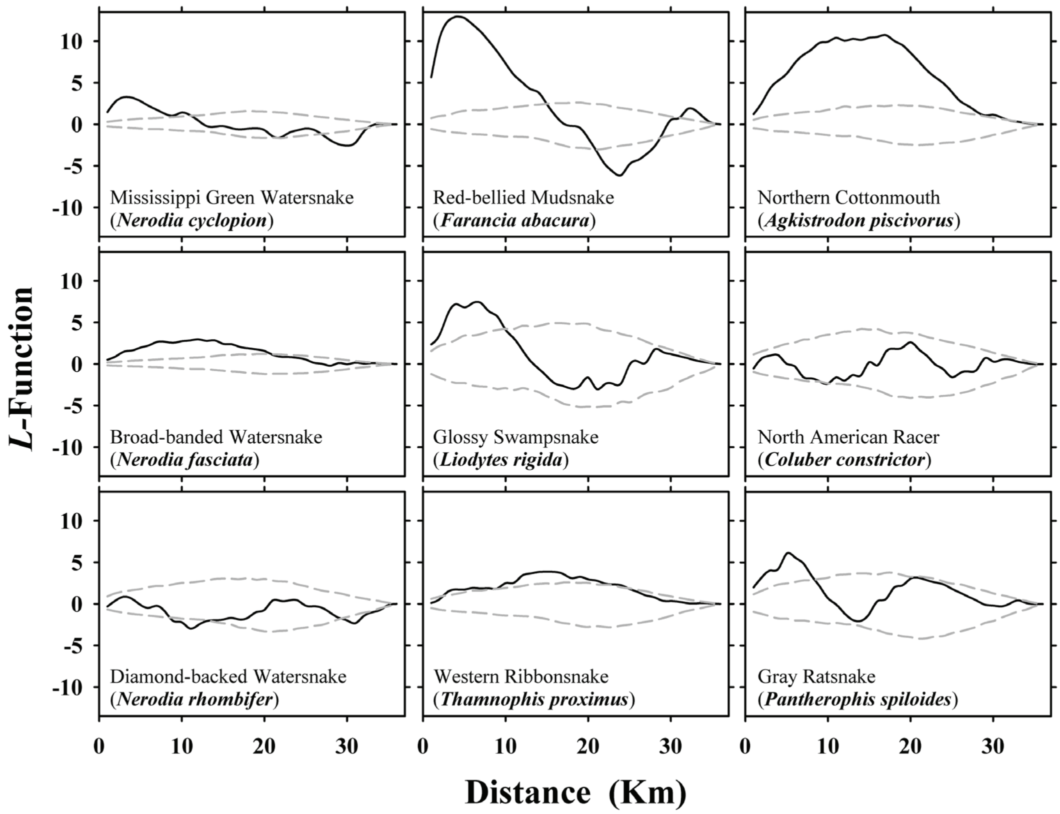

Figure 8. Ripley's *K*-function graphs for each of the nine species with at least 14 observations of locality in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. Solid lines show observed *K* and dashed lines indicate the upper and lower limits of the 95% confidence envelope.

size (Roth 2005). It is possible that these females, if reproductive, may have had increased association with the roadway as a thermoregulatory source (Mccardle and Fontenot 2016).

Road crossing activity.—Temporal aggregations of road crossing activity are the result of multiple interacting factors operating across different temporal scales. Across smaller temporal windows (e.g., days) road crossing activity of ectotherms is more strongly affected by environmental conditions (i.e., temperature and humidity). Across a broader temporal window (i.e., months/seasons), we observed spring and summer peaks in road crossing activity. Temporal peaks in road crossing activity usually coincide with the annual reproductive cycle of a species or increased foraging activity. For example, annual peaks in road crossing activity for turtles are a result of females making forays into the terrestrial environment to nest (Beaudry et al. 2010). For the snakes in this assemblage, breeding usually coincides with the spring and summer months (e.g., Lutterschmidt et al. 2005). During the breeding season, male snakes often traverse greater distances compared to females as they engage in mate searching behavior (Bonnet et al. 1999). This increased activity in mate searching behavior increases the probability of a male snake crossing a road and increases their risk of vehicular mortality and ultimately their greater proportion of DOR snakes (Bonnet et al. 1999; Shepard et al. 2008a; Sosa and Schalk 2016). Overall, when all snakes were pooled, we observed a similar trend of male-biased DOR snakes in this assemblage; however, DOR snakes of only three species were significantly biased towards males. Many of the species in this assemblage are primarily aquatic or semi-aquatic and may concentrate mate searching in aquatic habitats and make fewer forays into the terrestrial environment, thus reducing their exposure to traffic and resulting in an unbiased sex ratio for the majority of species.

Clustering in road crossing activity.—Our hot spot analysis revealed as a whole that the beginning, middle, and end of Highway 51 were noticeable hot spots for the nine species aggregated together. The shortest distance between Lake Pontchartrain and Lake Maurepas occurs in the middle of the highway where many hot spots were located. Snakes may be utilizing habitats at both Lake Maurepas and Lake Pontchartrain and may

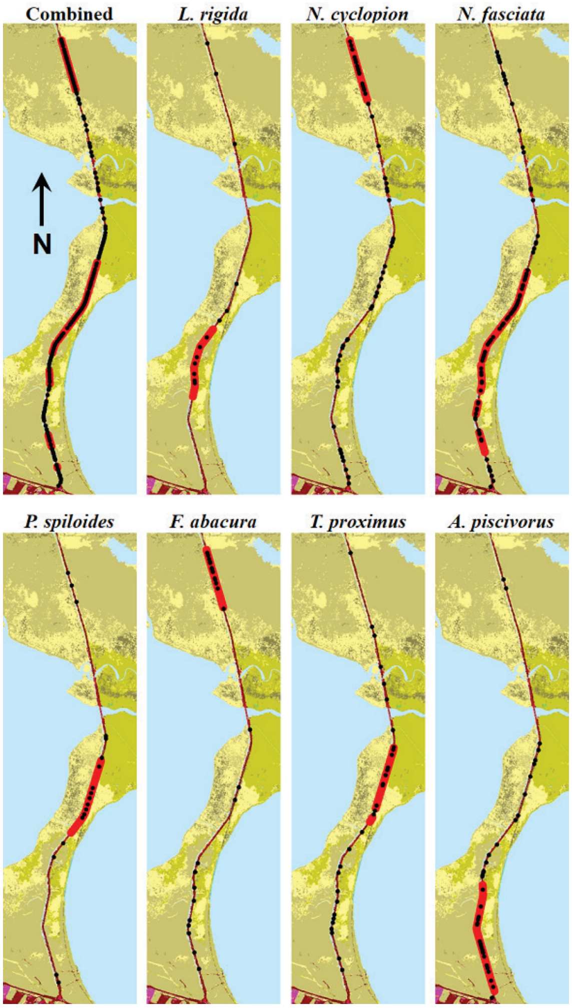

Figure 9. Clusters (hot spots) of occurrence for the nine snake species combined and Glossy Swampsnakes (*Liodytes rigida*), Mississippi Green Watersnakes (*Nerodia cyclopion*), Southern Watersnakes (*N. fasciata*), Gray Ratsnakes (*Pantherophis spiloides*), Red-bellied Mudsnakes (*Farancia abacura*), Western Ribbonsnakes (*Thamnophis proximus*), and Northern Cottonmouths (*Agkistrodon piscivorus*) in the Joyce and Manchac wildlife management areas and the Manchac Land Bridge Area between Lake Pontchartrain and Lake Maurepas, Louisiana, USA. Red areas of the road indicate hot spots with 95% confidence. Eastern Kingsnakes (*Lampropeltis getula*) and Dekay's Brownsnakes (*Storeria dekayi*) were excluded because of low sample size; North American Racers (*Coluber constrictor*) and Diamond-backed Watersnakes (*N. rhombifer*) were excluded because their spatial dispersion patterns were indistinguishable from random.

be crossing over the shortest distance between these two lakes. Some species appeared to be concentrated in areas of just one or two dominant land-cover types, and the hot spots of some species were in areas with the same land cover type but located at different parts of the road (e.g., *A. piscivorus, F. abacura,* and *N. cyclopion*). Our hot spot analysis was conducted at a fairly broad spatial scale, so the interspecific variation in hot spot location may be attributed to other biological factors that are important at finer spatial scales. Additional factors that affect the spatial ecology and subsequent road crossing activity may include microhabitat preference or prey availability. For example, although *N. cyclopion* has been noted for its ability to use a diversity of habitats (Gibbons and Dorcas 2004), it has been closely associated with aquatic habitats that contain low vegetation while avoiding open marshes and grass flats (Mount 1975; Hebrard and Mushinsky 1978). *Farancia abacura* has been noted for its highly aquatic nature (Lutterschmidt et al. 2006) and high prey specificity for aquatic salamanders (Steen et al. 2013; but see Durso et al. 2013) but has also been known to make considerable overland movements (up to 1,288 m from the nearest wetland; Steen et al. 2013). Regardless of whether their spatial concentration at the north end of the highway is a result of concentrations of food resources or preferred microhabitats, mitigation measures could be concentrated in this habitat to divert or minimize road crossings and in turn reduce road mortality.

Nerodia fasciata had several hot spots of occurrence throughout the length of the road that spanned more than one type of land cover. The generalist nature of *N. fasciata* has been well-documented (Gibbons and Dorcas 2004), including in Louisiana, where Hebrard and Mushinsky (1978) found *N. fasciata* to be common across all habitats surveyed. These results highlight the challenge of designing mitigation measures for generalist species that occur in local species assemblages. If resources are not limited, installing culverts, fences, or other barriers across multiple habitat types may be the most effective way to ensure their use by both specialists and generalists. If resources are limited, however, mitigation efforts may be more effective if they are implemented in habitats where the probability of use by specialists is higher and road crossings are more predictable. Hot spots of occurrence can show both stability (Langen et al. 2009; Crawford et al. 2014) or variability over time (Garrah et al. 2015). Although these data were collected nearly 30 y ago, this highway remains relatively unchanged and a site for continued investigation by colleagues (e.g., Mccardle and Fontenot 2016). Resurveys of this site could elucidate whether the hot spots we identified exhibit stability or variability over time to better understand the predictability of snake road-crossing locations.

Conclusions.—Our results demonstrated that species within this snake assemblage exhibit nonrandom patterns in road occurrence across both space and time. In turn, these nonrandom patterns can be used to evaluate and inform mitigation efforts (e.g., Rudolph et al. 1999; Gunson et al. 2009; Robinson et al. 2010; Proppe et al. 2017) to reduce exposure of snakes to vehicular traffic. Complementary mitigation efforts that incorporate both spatial and temporal patterns will be most effective in reducing the exposure of snakes to traffic. If these hot spots exhibit long-term stability, road managers can capitalize on this aspect and install fences or culverts that may reduce or divert individuals from passing over the road (Dodd et al. 2004; Patrick et al. 2010; Colley et al. 2017). Installation of signage that alerts drivers or a temporary reduction in speed limits during peak weeks of road crossing activity can also be an effective means to reduce road mortality (Shepard et al. 2008b; Crawford et al. 2014). Unfortunately, motorists exhibit little remorse when hitting a snake with their vehicle and often swerve to hit them (Ashley et al. 2007; Crawford and Andrews 2016). Educational campaigns that inform drivers on the value and conservation of snakes will increase the likelihood of success of any additional mitigation efforts towards reducing snake vehicular mortality (Crawford and Andrews 2016).

Acknowledgments.—We give special thanks to Richard A. Seigel, Clifford L. Fontenot, and the late Harold A. Dundee for their comments and advice regarding all aspects of this study. We also thank Tom A. Blanchard, Riccardo A. Fiorillo, Jeremiah T. Llewellyn, and Kelley R. Smith for assisting WIL during road surveys and their repeated willingness to take meticulous notes while WIL drove. We acknowledge support from Gary W. Childers and the Department of Biological Sciences at Southeastern Louisiana University for support and use of departmental equipment and vehicles. Amphibians and reptiles were sampled under a scientific collecting permit (#LNHP-92-50) issued to WIL (1990–1992) by the Louisiana Department of Wildlife and Fisheries. Lastly, we acknowledge the support of Sam Houston and Stephen F. Austin State Universities for their financial support of all collaborative efforts involved in preparing this manuscript for publication.

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