

## DEMOGRAPHIC PATTERNS OF ACTIVITY AND ROAD MORTALITY FROM A LONG-TERM STUDY OF A WETLAND SNAKE ASSEMBLAGE

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**Abstract.**—Road mortality represents a global threat to animal populations. In many cases, animals vary in their susceptibility to road mortality not only at the species level, but also intraspecifically with respect to age and demography (reproductive class structure in snake populations). Such variations in mortality can be especially pronounced within snake species and are dependent on age and sex-specific movements and ecologies that influence timing and frequency with which different conspecifics encounter roads. Analysis of a data set generated by 617 quantitative road surveys of snakes in southeastern Louisiana, USA, conducted from 31 August 1990 through 31 August 1991, and resumed 31 August 2003 through December 2014 indicated that intraspecific groups experienced differential road mortality risk, which may be influenced by historical processes related to phenology, ontogeny, and reproductive mode (oviparous vs. viviparous; annual vs. biannual). Observations of snakes on the road transect were significantly influenced by phenological and historical phenomena, such as emergence, breeding, parturition, hibernation, and major weather events (e.g., hurricanes, tropical storms, winter storms, and regional flooding), as well as fine-scale changes in environmental conditions (air temperature, road temperature, relative humidity, water stage), the effects of which varied among species and demographic groups.

**Key Words.**—demographics; ontogeny; recruitment; road mortality; seasonal activity; snakes; weather patterns

### INTRODUCTION

Animals, even those within closely related taxa, can exhibit a wide diversity of ecologies, behaviors, morphologies, physiologies, and developmental ontogenies. Historically, environmental pressures shaped these characteristics thereby influencing individual and population fitness, species distributions, and community structures (Pianka 1994). Recently, anthropogenic activities resulting in habitat destruction, pollution, introduction of non-native species, climate change, and direct mortality of individuals have been implicated in global biodiversity loss (Kerr and Currie 1995; Gibbons et al. 2000; Ceballos et al. 2015). Animal species and populations vary in susceptibility to detrimental impacts of anthropogenic perturbations, in large part because of the biological features shaped by natural historical pressures (Webb et al. 2002; Swihart et al. 2003; Davies et al. 2004).

A conspicuous form of anthropogenic disturbance that detrimentally affects animal populations in numerous and surprising ways is road infrastructure (Fahrig et al. 1995, 2009; Foreman et al. 2003; Petranka and Francis 2013). Perhaps the most obvious and well-studied way in which roadways affect animal populations is through road mortality caused by vehicle strikes (e.g., Rosen

and Lowe 1994; Foreman and Alexander 1998; Mumme et al. 2000; Hartmann et al. 2011). Road mortality can differentially affect the persistence of animal populations depending on the demographic or life stage group most affected. For example, concentrated losses of adults, particularly adult females, can skew sex ratios leading to reduced reproductive output and ultimately decreased population size (Munguira and Thomas 1992; Mumme et al. 2000; Aresco 2005; Gibbs and Steen 2005; Row et al. 2007). Alternatively, the preferential loss of juveniles or sub-adult members of animal populations can negatively affect recruitment (Borda-de-Agua et al. 2014). When the loss of individuals outpaces recruitment, road mortality can exacerbate the effects of genetic fragmentation created by the presence of the roadway itself and other forms of regional fragmentation affecting local animal populations. These cumulative effects can result in diminished population viability (Forman et al. 2003; Jackson and Fahrig 2011). Whether animal populations can contend with persistent road mortality depends in part on the demographic group most affected and evolutionary life history constraints imposed on reproduction. Because of ontogenetic differences in ecology, susceptibility to road mortality pressures varies at the species level (Rytwinski and Fahrig 2012, 2013), as well as across demographic groups.

Snakes serve as a good model taxon for comparative demographic studies and as ecological indicators because different species often occupy varying positions in the food web and exhibit a wide range of ecologies, life histories, morphologies, and physiologies (Beaupre and Douglas 2009). Additionally, vulnerabilities to extinction, when faced with anthropogenic impacts, can vary both at the species (Webb et al. 2002; Beaupre and Douglas 2009) and demographic or ontogenetic level, whereby individuals exhibit different trophic, thermal, and behavioral ecologies depending on their age, sex, or life stage (Mushinsky et al. 1982; Lourdais et al. 2002; Shine et al. 2003; Vincent et al. 2007; Mccardle and Fontenot 2016). Furthermore, selection on particular demographic groups can exert differential impacts on communities because the ecological role of individual organisms almost always varies ontogenetically (Nakazawa 2015). Although several studies have shown that snakes as a group tend to be more vulnerable to road mortality than other taxa (Garriga et al. 2017; Brehme et al. 2018; Bastos et al. 2019) and that variation in road mortality risk exists among snake species and sexes within species (Smith and Dodd 2003; Andrews and Gibbons 2008; Hartmann et al. 2011; Rincon-Aranguri et al. 2019; Yue et al. 2019), relatively few biologists also examine differences among demographic groups to make comparisons across species (Bonnet et al. 1999; DeGregorio et al. 2010; Jochimsen et al. 2014).

We used snake observations collected during 617 quantitative road surveys (see Langen et al. 2007) in southeastern Louisiana, USA, between 1990 and 2014, conducted as part of a herpetofaunal monitoring study to evaluate if the number of live and dead snakes found on the road are driven by different intraspecific responses to environmental conditions. We explored whether or not (1) body size and sex, (2) temporal activity, and (3) demographic-specific movements (which may take a snake across a road if one is in the way) affected the number of snakes found on the road. This study, in combination with additional information from our long-term data set (see Mccardle and Fontenot 2016), addresses a significant data gap in road mortality studies of reptiles by identifying demographic distributions of road kills across species and seasons and relating mortality to life-history events and environmental conditions.

### MATERIALS AND METHODS

**Study area.**—The Manchac Land Bridge Area (MLBA) is a 40,273 ha wetland located between Lake Pontchartrain and Lake Maurepas in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA (Keddy et al. 2007). Historically, this area was dominated by old-growth Bald Cypress (*Taxodium*

*distichum*) and Water Tupelo (*Nyssa aquatica*) swamp forests, and the hydrology of the region was defined by periodic flooding and deposition of nutrients and sediments by the Mississippi River (Keddy et al. 2007). The ecological community and hydrology of the MLBA has been severely altered through intensive logging of cypress lumber during the late 1800s to 1950s and channelization of the Mississippi River for flood control (Keddy et al. 2007). The MLBA currently consists of a mosaic of wetland community types (see GIS analysis; Lutterschmidt et al. 2019), including relict and early growth Cypress-Tupelo Swamp Forest, naturally occurring Freshwater Marsh, degraded successional marsh, and disturbed road edge habitats. Despite these changes, the MLBA remains extremely biodiverse and supports a unique herpetofauna (Platt et al. 1989; Schriever et al. 2009) that includes a 15-species snake assemblage. An asphalt-paved, 37-km long segment of U.S. Highway 51 bisects the entire length of the MLBA. This area is subject to extreme weather fluctuations including catastrophic flooding, drought, tropical weather systems, and snow and ice storms. We used this road segment as a survey transect to monitor reptile and amphibian diversity and population characteristics.

**Data collection.**—We conducted quantitative road surveys to collect snake data across the study site following the methodology described in Langen et al. (2007). We slowly ( $\leq 60$  km/h) drove the road transect weekly, beginning approximately 1 h before sunset from the starting point near the town of Ponchatoula, Tangipahoa Parish, Louisiana (30.4070°N, 90.4322°W), to the end point at Frenier Road in LaPlace, St. John the Baptist Parish, Louisiana (30.0961°N, 90.4376°W), and then back to the starting point. Quantitative road surveys usually lasted 2–4 h. The driver (usually only a single observer; the driver conducted the survey) carefully observed the road surface for snakes alive on the road (AOR) and dead on the road (DOR), including both lanes and shoulders (a width of approximately 13 m) adjusting the driving speed if necessary to account for decreased visibility from rain or fog. For each individual encountered, we recorded the species, measured the snout-to-vent length (SVL; to 1 cm) by first placing a string along the length of the snake then measuring the string, and obtained the mass (g) with a Pesola® spring scale (PESOLA Präzisionswaagen AG, Schindellegi, Switzerland). We determined the sex of each individual via manual eversion of hemipenes or visual inspection of tail size and shape in AOR snakes (King 1989) and by dissection in DOR snakes. We collected AOR snakes so we could mark them with a unique scale clip (Brown and Parker 1976) in the lab and released these individuals at their original capture location during the next survey trip. We retained all salvageable DOR snakes in good

condition for dissection. We conducted 617 survey trips from 31 August 1990 through 31 August 1991 (57 survey trips), and 31 August 2003 through 18 December 2014 (560 survey trips) along the transect route (see map in Lutterschmidt 2013). Starting in 2004, we also recorded a suite of environmental measurements at three different times (beginning, turnaround point, and end) of each road survey using an EXTECH® Instruments RH401 digital psychrometer/IR thermometer (FLIR Commercial Systems Inc., Nashua, New Hampshire, USA). We used the extendable air temperature and humidity sensor probe to measure Air Temperature (AT) and Relative Humidity (RH), and we used the infrared laser feature of the unit to measure the temperature of the road surface (RT).

**Statistical analysis.**—Although we encountered all 15 snake species known to occupy the study area, we restricted our analysis to those species with 25 or more individual observations ( $n = 8$ ). We carried out three sets of statistical analyses to test explorations of the data 1–3 described in the Introduction. We conducted two sets of Permutational Multivariate Analysis of Variance (PERMANOVA) models with the software program PRIMER 6 with PERMANOVA+ extension (Clarke and Gorley 2006). PERMANOVA provides a nonparametric hypothesis-testing framework similar to parametric Multivariate Analysis of Variance (MANOVA). MANOVA relies on partitioning variance based on a sum-of-squares calculated from transformed or un-transformed raw data (i.e., counts, biomass), whereas PERMANOVA uses measures of distance or dissimilarity between pairs of individual multivariate observations defined by the user and calculates a probability of the null hypothesis of no between-group difference by randomly permutating observations a specified number of times (Anderson 2001). PERMANOVA, therefore, is more robust to departures from the assumption of a normal distribution to which ecological data rarely conform and is more amenable to analyzing discrete observations and large numbers of zero values typical of ecological data sets (Anderson 2001).

For the first set of PERMANOVA models (Model Set 1), we constructed Bray-Curtis Dissimilarity Matrices of the numbers of all snakes found on the road by species, for which SVL and mass measurements were taken, and for which sex was determined. We then included the factors of SVL class, sex, and their interaction to test for any intraspecific differences in presence on roads across each of these factors. To compare the differences in the composition of life-stages within each species, we binned individuals into 10-cm SVL classes (Weatherhead et al. 1995), except for the Gray Ratsnake (*Pantherophis spiloides*), for which we used SVL classes given in

Blouin-Demers et al. (2002). Replicates for the first set of PERMANOVA models was the sampling year.

In the second set of PERMANOVA models (Model Set 2), we constructed Bray-Curtis dissimilarities of numbers of snakes across all survey years for each species, by survey. We then included the factors of year, demographic group, season, and their interactions to test the prediction that temporal structure exists in on-road activity across the demographic groups that compose snake populations. We organized individuals within each species into three demographic groups (i.e., adult female, adult male, and juveniles). We based these divisions on the relationship between SVL and the presence of secondary oocytes in females and vascularization of testes in males of dissected DOR individuals; we classified individuals greater than or equal to the indicated sizes as adults and smaller individuals as juveniles (Table 1). Because of the complexity of timing of snake activity and the dramatic climatic variations experienced within a given year, we diagnosed the factor season using the six ecological seasons characteristic of climates and phenologies within temperate areas (Ryan 2012). These seasons included: prevernal (1 March to 1 May), vernal (2 May to 15 June), estival (16 June to 15 August), serotinal (16 August to 15 September), autumnal (16 September to 1 November), and hibernal (2 November to 28 February).

Finally, we explored the influence of environmental factors on the temporal differences of on-road activity and presumably mortality risk, identified by the second set of PERMANOVA models (Model Set 2). We accomplished this by fitting Generalized Linear Models (GLMs) of five environmental predictor variables, as well as year and season, on the probability of detecting AOR or freshly killed (as diagnosed by residual nerve activity indicating that the snake had been killed during or shortly before the survey trip began) within specific demographic groups for the four most frequently encountered species (Model Set 3). We constructed GLM models in the software program Systat 13 (Systat Software Inc.) based on snake data collected from 2004 to 2014 (578 trips), which overlapped with our environmental measurements. Sampling trips were the replicates for

**TABLE 1.** Minimum size at maturity (snout-vent length; in centimeters) by sex for the four most-commonly encountered snake species on the U.S. Highway 51 Transect in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014.

| Species  | Females | Males |
|--|---------|-------|
| Banded Watersnake ( <i>Nerodia fasciata</i> )      | 50      | 40    |
| Green Watersnake ( <i>Nerodia cyclopion</i> )      | 50      | 40    |
| Western Ribbonsnake ( <i>Thamnophis proximus</i> ) | 45      | 42    |
| Gray Ratsnake ( <i>Pantherophis spiloides</i> )    | 70      | 60    |

the second set of PERMANOVA models (Model Set 2) and the GLMs (Model Set 3).

The environmental predictor variables included: (1) air temperature (AT); (2) road surface temperature (RT); (3) difference between RT and AT (TD); (4) relative humidity (RH); (5) day-of-survey precipitation (Precip); and (6) water stage (WS) within the MLBA. We averaged the three measurements for each survey trip and used these values to construct predictive GLMs. Water stage data for the MLBA was obtained from a weather station located in the western portion of Lake Ponchartrain (30.315°N, 90.281°W), approximately 11 km east of our survey transect, operated by the Louisiana Universities Marine Consortium (LUMCON). Water stage data consisted of 24-h averages of measurements above or below a benchmark water height of 104 cm for the day of each survey. The total precipitation for the study region was obtained from the New Orleans Lake Front Airport Weather Station of the National Oceanic and Atmospheric Administration (NOAA), located 29.9 km east of our survey transect. The response variable was the presence or absence of AOR or fresh DOR snakes, indicating that individuals of a given species and demographic group were active and entering the roadway under the specific environmental conditions of a given survey trip. This was encoded as 1 if at least one AOR or fresh DOR individual of a given species and demographic group was found on a survey trip, or 0 if no individuals of a given species and demographic group were found during a survey trip, and specifying a binomial distribution for the GLMs. We used detection/non-detection (1/0) of AOR or fresh DOR snakes as a metric of on-road activity over the number of AOR or fresh DOR snakes found during a survey trip because of high over-dispersion in GLMs fitted with count data (the variance of count data was usually 5–10 times the variance of detection/non-detection data). This level of dispersion was likely caused by factors not accounted for in the GLMs we fitted, such as processes driving abundance such as water salinity, water flow velocity during storm or flood events, and prey availability, rather than activity and road-entry behavior. We used the corrected Akaike Information Criterion (AICC) to assess model support and the multiple  $r^2$  value to assess relative explanatory power of each model.

## RESULTS

**Model set 1: body size and sex influences.**—We conducted 617 surveys and traveled 43,882 km from 31 August 1990 through 31 August 1991, and 31 August 2003 through 18 December 2014 (see map in Lutterschmidt 2013). We found 2,032 individual snakes representing 15 species. Of all snakes collected, 1,444 (71%) were DOR and 588 (29%) were AOR, giving

a mortality rate of 0.033 DOR snakes per kilometer surveyed for the duration of the study. The Eastern Black Kingsnake (*Lampropeltis nigra*), Rough Green Snake (*Opheodrys aestivus*), Yellow-bellied Watersnake (*Nerodia erythrogaster*), Glossy Crawfish Snake (*Liodytes rigida*), Dekay's Brown Snake (*Storeria dekayi*), and Gulf Salt Marsh Snake (*N. clarkii*) were represented by fewer than 25 individuals and were not included in statistical analyses. We did not record any recaptures of snakes marked by scale-clipping during the study. It is likely that some snakes that we found DOR were too damaged for scale-clip markings to be detected. For all species, we observed more individuals than we could include in the analyses because of excessive damage from repeated vehicle collisions, scavengers, or desiccation for sex and body-size measurements to be accurately determined.

We found a wide range of body sizes (SVL) for snakes found on roads, from very small to large (Fig. 1). To maintain statistical power, we did not include the factor sex in analyses for species with low samples of a particular sex or condition (i.e., Western Mudsnake, *Farancia abacura*, six females; Black-masked Racer, *Coluber constrictor*, only one AOR of nine females). Body size (SVL) was a significant factor for on-road samples of five of the eight species assessed (Banded Watersnake, *N. fasciata*, Green Watersnake, *N. cyclopion*, Western Ribbonsnake, *T. proximus*, Gray Ratsnake, *P. spiloides*, and Diamondback Watersnake, *N. rhombifer*; Table 2). For most species, we observed the middle and larger SVL classes on the road more frequently than smaller SVL classes (Fig. 1; Table 2). The exception was *P. spiloides*, which exhibited peaks at the smallest SVL class (Fig. 1; Table 2). Size distributions of the Western Cottonmouth (*Agkistrodon piscivorus*), *C. constrictor*, and *F. abacura* could not be distinguished from a uniform distribution (Table 2). Generally, the SVL distributions of snakes found on the road tended to be unimodal with different peaks for males and females corresponding largely to previously documented patterns of sexual size dimorphism for each species (Fig. 1). Only two species, *N. fasciata* and *T. proximus*, had a significant SVL  $\times$  sex interaction indicating size distributions of snakes found on the road differed between the sexes.

Three species showed significant differences between sexes in overall snake encounters (Table 2). Overall, we found significantly greater numbers of males (M) than females (F) for *N. fasciata* (M = 300, F = 255), *T. proximus* (M = 103, F = 84), and *P. spiloides* (M = 91, F = 46), but not for *N. cyclopion* (M = 133, F = 113), *N. rhombifer* (M = 48, F = 29), or *Agkistrodon piscivorus* (M = 36, F = 19). There was a significant interaction in the number of snake encounters between SVL and sex for *N. fasciata* and *T. proximus* (Table 1), indicating that

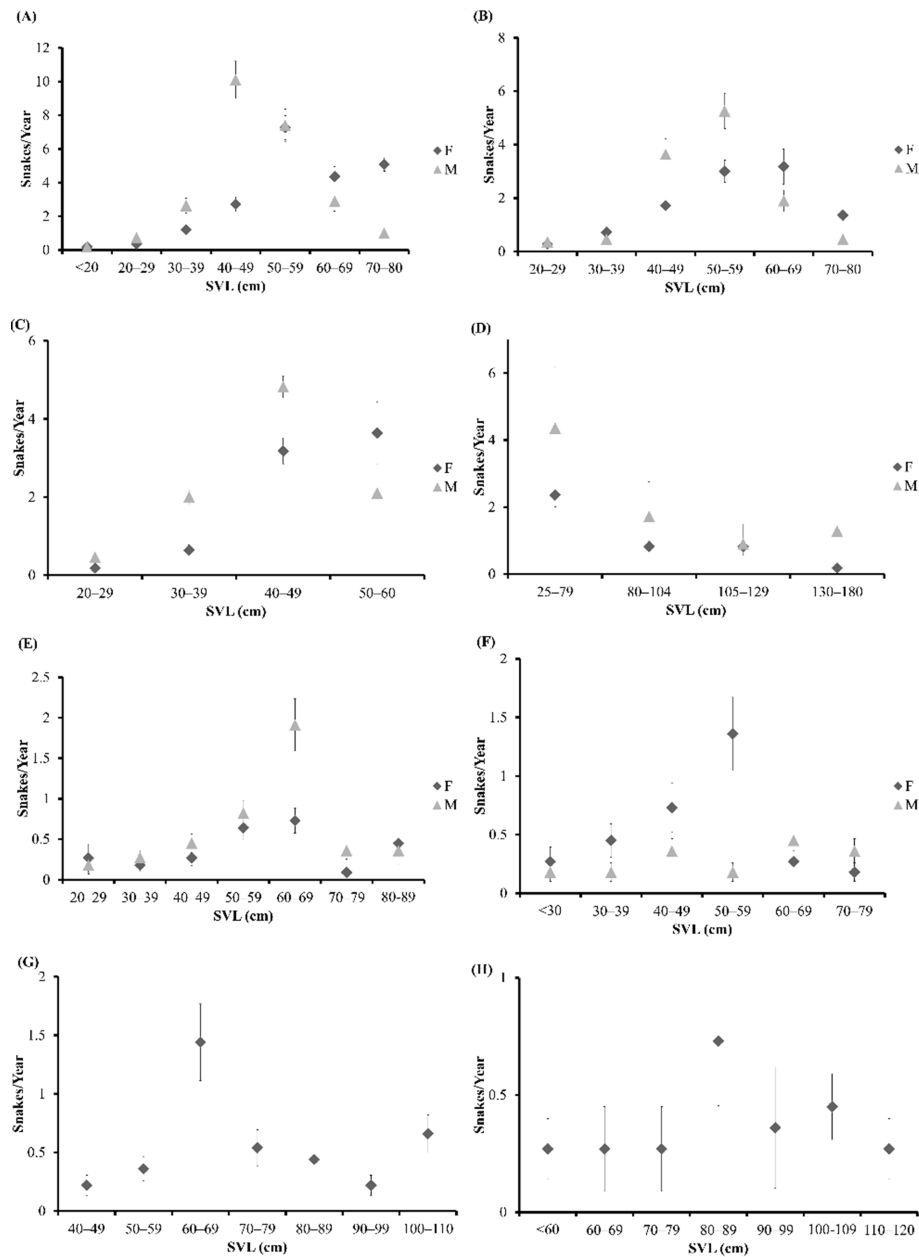


FIGURE 1. Snout-vent length distributions (mean  $\pm$  standard error) for the eight most commonly encountered snakes on the road transect through the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Species are (A) Banded Watersnake (*Nerodia fasciata*); (B) Green Watersnake (*N. cyclopion*); (C) Western Ribbonsnake (*Thamnophis proximus*); (D) Gray Ratsnake (*Pantherophis spiloides*); (E) Diamondback Watersnake (*N. rhombifer*); (F) Western Cottonmouth (*Agkistrodon piscivorus*); (G) Western Mudsnake (*Farancia abacura*); (H) Black-masked racer (*Coluber constrictor*).

the sex difference is body size-specific. Among small individuals, we found males on the road more often, but among large individuals, we encountered females more often than males (Fig. 1).

**Model set 2: temporal patterns.**—We compared variation in on-road activity and road mortality over seasons and years within the five snake species with

sample sizes amenable to analysis. Road observations of each of these species varied significantly over seasons and years (Figs. 2–5). Demographic groups within these species, however, often varied in the level and timing of activity and mortality.

*Nerodia fasciata.*—We encountered this species most commonly on road transects. Both seasonally and yearly, we encountered more adult females (mean



**TABLE 2.** Results from PERMANOVA models testing the effects of snout-vent length (SVL), sex, and their interaction on numbers of snakes detected on the road transect for eight species in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. PERMANOVA tests were run with 1,000 permutations. Values in **bold** indicate  $P$ -values  $< 0.05$ .

| Species  | Source    | df  | Pseudo- $F$ | $P$ -value   |
|--|-----------|-----|-------------|--------------|
| Banded Watersnake<br>( <i>Nerodia fasciata</i> )<br>n = 555        | SVL       | 6   | 4.050       | <b>0.001</b> |
|  | Sex       | 1   | 3.389       | <b>0.004</b> |
|  | SVL x Sex | 6   | 2.135       | <b>0.002</b> |
|  | Residuals | 14  |             |              |
|  | Total     | 27  |             |              |
| Green Watersnake<br>( <i>Nerodia cyclopion</i> )<br>n = 246        | SVL       | 5   | 2.062       | <b>0.010</b> |
|  | Sex       | 1   | 1.146       | 0.358        |
|  | SVL x Sex | 5   | 0.957       | 0.541        |
|  | Residuals | 12  |             |              |
|  | Total     | 23  |             |              |
| Western Ribbonsnake<br>( <i>Thamnophis proximus</i> )<br>n = 187   | SVL       | 3   | 14.92       | <b>0.001</b> |
|  | Sex       | 1   | 6.001       | <b>0.009</b> |
|  | SVL x Sex | 3   | 2.227       | 0.056        |
|  | Residuals | 168 |             |              |
|  | Total     | 175 |             |              |
| Gray Ratsnake<br>( <i>Pantherophis spiloides</i> )<br>n = 137      | SVL       | 3   | 11.27       | <b>0.001</b> |
|  | Sex       | 1   | 8.274       | <b>0.010</b> |
|  | SVL x Sex | 3   | 0.799       | 0.541        |
|  | Residuals | 168 |             |              |
|  | Total     | 175 |             |              |
| Diamondback Watersnake<br>( <i>Nerodia rhombifer</i> )<br>n = 77   | SVL       | 6   | 4.588       | <b>0.001</b> |
|  | Sex       | 1   | 2.325       | 0.134        |
|  | SVL x Sex | 6   | 1.070       | 0.382        |
|  | Residual  | 272 |             |              |
|  | Total     | 285 |             |              |
| Western Cottonmouth<br>( <i>Agkistrodon piscivorus</i> )<br>n = 55 | SVL       | 5   | 1.110       | 0.346        |
|  | Sex       | 1   | 2.123       | 0.125        |
|  | SVL x Sex | 5   | 1.861       | 0.081        |
|  | Residuals | 252 |             |              |
|  | Total     | 263 |             |              |
| Black-masked Racer<br>( <i>Coluber constrictor</i> )<br>n = 29     | SVL       | 6   | 0.708       | 0.631        |
|  | Residuals | 63  |             |              |
|  | Total     | 69  |             |              |
| Western Mudsnake<br>( <i>Farancia abacura</i> )<br>n = 27          | SVL       | 4   | 1.539       | 0.186        |
|  | Residuals | 85  |             |              |
|  | Total     | 89  |             |              |

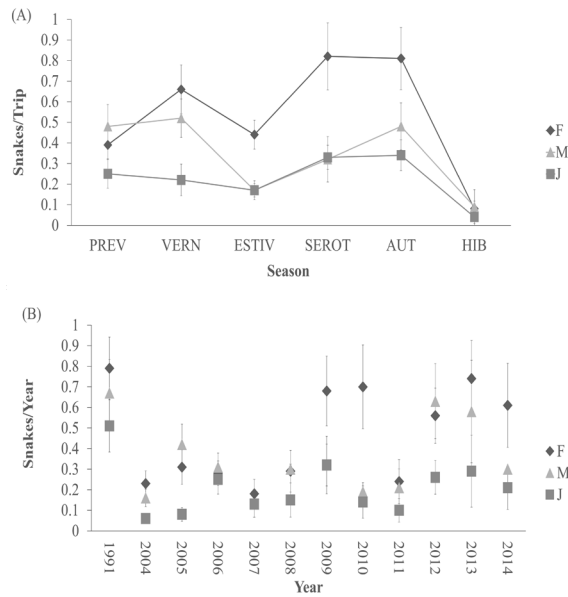
encounter rate of individuals per survey trip [MER] = 0.36) than either adult males ( $t = 4.17$ ,  $P < 0.001$ ) or juveniles ( $t = 6.68$ ,  $P < 0.001$ ). We encountered adult males (MER = 0.32) more often than juveniles (MER = 0.28;  $t = 2.35$ ,  $P = 0.018$ ). There was a significant overall effect of season on snake activity for this species (pseudo- $F = 14.19$ ,  $P < 0.001$ ). There was a significant interaction between season and demographic group for this species (pseudo- $F = 2.29$ ,  $P = 0.010$ ) indicating intraspecific variation in seasonal activity,

where observations of females increased during the vernal season, relative to observations of adult males following emergence and mate-seeking movements during the prevernal period (Fig. 2). Observations of all demographic groups decreased during the estival season. The second peak in adult female activity occurred in the serotinal season and relatively high female activity continued into the autumnal season. The second peak of adult male activity occurred later, in the autumnal season. Juvenile activity followed a similar pattern to that of adult females, but with fewer observations per survey (Fig. 2). Observations of *N. fasciata* also varied significantly among years (pseudo- $F = 7.06$ ,  $P < 0.001$ ; Fig. 2).

*Nerodia cyclopion*.—In comparisons of on-road occurrences between demographic groups within *N. cyclopion*, we encountered adult male snakes (MER = 0.19) on the road transect more frequently than either adult females (MER 0.13;  $t = 2.22$ ,  $P = 0.028$ ) or juveniles (MER = 0.09;  $t = 4.06$ ,  $P = 0.001$ ). Adult females were encountered more frequently than juveniles ( $t = 1.96$ ,  $P = 0.048$ ). *Nerodia cyclopion* exhibited strong overall seasonality in numbers of encounters (pseudo- $F = 12.78$ ,  $P = 0.001$ ). There was also significant interaction between year, season, and demographic group in this species (pseudo- $F = 2.11$ ,  $P = 0.001$ ), where encounters with females increased between the vernal and serotinal periods relative to adult males and juveniles in years where this snake was most frequently encountered, and adult male activity was bimodal in the vernal and autumnal seasons (Fig. 3). Observations varied significantly among years (pseudo- $F = 15.48$ ,  $P = 0.001$ , Fig. 3).

*Thamnophis proximus*.—The number of *T. proximus* encounters among demographic groups did not differ significantly (pseudo- $F = 0.82$ ,  $P = 0.436$ ), nor was there a significant interaction between season and demographic group (pseudo- $F = 1.29$ ,  $P = 0.255$ ). A significant overall seasonal pattern to activity, however, existed (Pseudo- $F = 8.69$ ,  $P = 0.001$ ; Fig. 4). There was also a significant three-way interaction of year, season, and demographic group (pseudo- $F = 1.69$ ,  $P = 0.001$ ), where observations of adult females and juveniles increased relative to observations of adult males during serotinal and autumnal periods of years in which this species was more frequently observed, which were predominantly years of or following flooding from tropical weather events (Fig. 4) such as in 2005–2006 (hurricanes Katrina and Rita), 2008–2009 (hurricanes Ike and Gustav), and 2012–2013 (Hurricane Isaac). Overall observations varied significantly among years (pseudo- $F = 7.71$ ,  $P < 0.001$ ; Fig. 4).

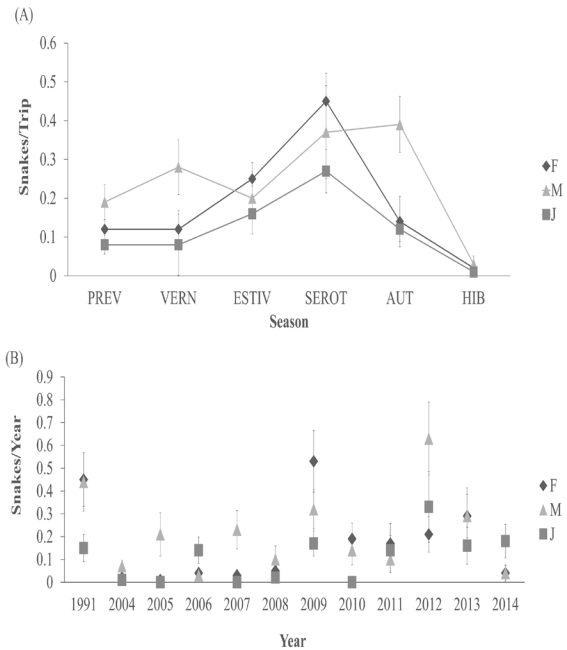
*Pantherophis spiloides*.—For the oviparous colubrine, *P. spiloides* (previously *P. obsoletus* in this area; Powell et al. 2016), adult females were encountered



**FIGURE 2.** (A) Seasonal (mean  $\pm$  standard error) and (B) annual (mean  $\pm$  standard error) road encounter rates of the Banded Watersnake (*Nerodia fasciata*) demographic groups on the transect through the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Abbreviations are PREV = prevernal, VERN = vernal, ESTIV = estival, SEROT = serotinal, AUT = autumnal, and HIB = hibernal.

less frequently (MER = 0.03) than either juveniles (MER = 0.09;  $t = 2.38$ ,  $P = 0.017$ ), or adult males (MER = 0.09;  $t = 3.25$ ,  $P < 0.0001$ ). Demographic groups within *P. spiloides* exhibited similar seasonal patterns of activity (Fig. 5), and there was no significant interaction between season and demographic group (pseudo- $F = 1.51$ ,  $P = 0.133$ ), nor was there a significant interaction between year and demographic group (pseudo- $F = 1.49$ ,  $P = 0.090$ ). There was, however, a three-way interaction of season, year, and demographic group in this species (pseudo- $F = 1.29$ ,  $P = 0.038$ ). This interaction occurred during the serotinal period of 2007 where observations of adult females increased relative to observations of adult males and juveniles (Fig. 5).

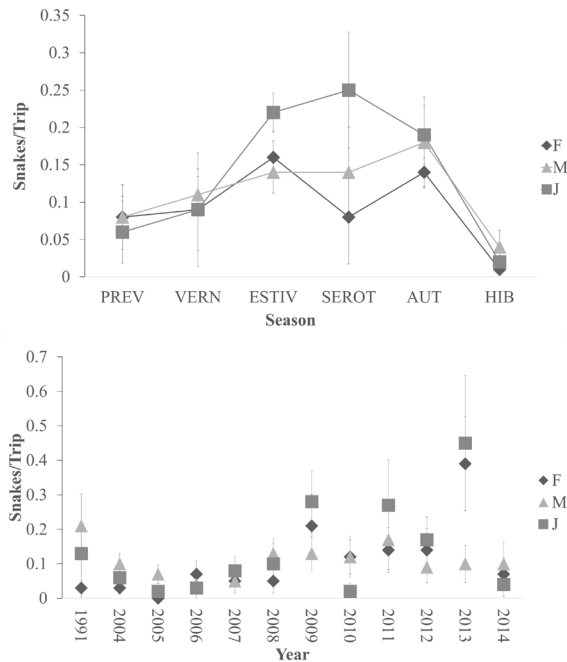
*Nerodia rhombifer*.—Because we found relatively few individuals of the viviparous natricine *N. rhombifer*, we only included two levels (male and female) in the demographic group factor for this species to retain a sample size robust enough for the PERMANOVA analysis. Most individuals were  $> 50$  cm SVL (Fig. 1), indicating that adult snakes made up the majority of the sample. Overall, encounters varied significantly among both years (pseudo- $F = 4.64$ ,  $P = 0.001$ ) and seasons (pseudo- $F = 7.08$ ,  $P = 0.001$ ; Fig. 6). The only significant demographic comparison was the three-way interaction of sex, season, and year (pseudo- $F = 1.59$ ,  $P = 0.011$ ), where



**FIGURE 3.** A) Seasonal and B) annual (mean  $\pm$  standard error) road encounter rates of Green Watersnake (*Nerodia cyclopion*) demographic groups on the transect through the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Abbreviations are PREV = prevernal; VERN = vernal; ESTIV = estival; SEROT = serotinal; AUT = autumnal; HIB = hibernal.

there were increased observations of males relative to females in the vernal and estival periods of 2005, 2007, 2010, 2012, and 2013 (Fig. 6).

**Model set 3: environmental and phenological predictors.**—To explain temporal patterns detected by PERMANOVA analyses, we further explored the relative influence of potential environmental and phenological predictors on snake detection using GLMs that tested detection probabilities of demographic groups across seven potential explanatory variables. The relative importance of the environmental and phenological predictors varied among species and demographic groups (Appendix Table 1). Patterns revealed by this analysis include: (1) pronounced differences in encounter probability among years across species and demographic groups; (2) the association between warmer road temperature regimes (RT, TD) and increased encounter probability in adult females of viviparous species (*N. fasciata*, *N. cyclopion*, and *T. proximus*); (3) increased detection of adult male snakes and juveniles for *N. fasciata*, *N. cyclopion*, and *P. spiloides* in response to higher relative humidity; and (4) increased encounter probability of snakes associated with increased water height, particularly less frequently observed species and demographic groups, such as

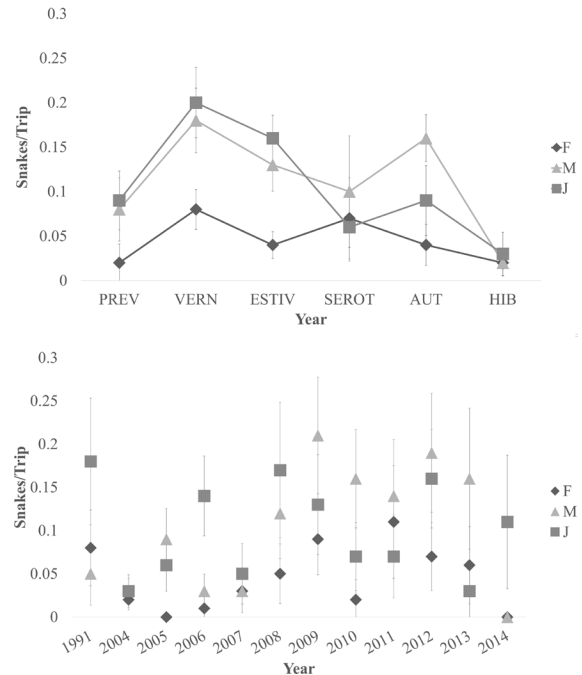


**FIGURE 4.** A) Seasonal and B) annual (mean  $\pm$  standard error) road encounter rates of Western Ribbonsnake (*Thamnophis proximus*) demographic groups on the transect through the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Abbreviations are PREV = prevernal; VERN = vernal; ESTIV = estival; SEROT = serotinal; AUT = autumnal; HIB = hibernal.

adult female *P. spiloides* and juvenile watersnakes (*N. fasciata* and *N. cyclopion*; Fig. 7, Appendix Table 1). In species and demographic groups for which the amount of precipitation on the day of the survey was a significant predictor, the models indicate a complex relationship. In the strongest and second strongest model for adult female *N. cyclopion*, the maximum likelihood estimate (MLE) for precipitation ( $\pm$  standard error) was  $-0.016 (\pm 0.007)$  and  $-0.015 (\pm 0.006)$ , respectively. This indicates that AOR adult female *N. cyclopion* were less likely to be observed on survey days where rainfall occurred in the study region. Similarly, precipitation was negatively associated with observations of AOR adult male *N. cyclopion* (MLE  $\pm$  standard error for the strongest models =  $-0.020 \pm 0.006$ ,  $-0.020 \pm 0.006$ , and  $-0.016 \pm 0.007$ , respectively). Conversely, precipitation on the day of the survey was significantly positively correlated with observations of AOR adult female *T. proximus* (MLE  $\pm$  standard error for the strongest models =  $0.036 \pm 0.006$ ,  $0.037 \pm 0.006$ , and  $0.036 \pm 0.006$ , respectively).

### DISCUSSION

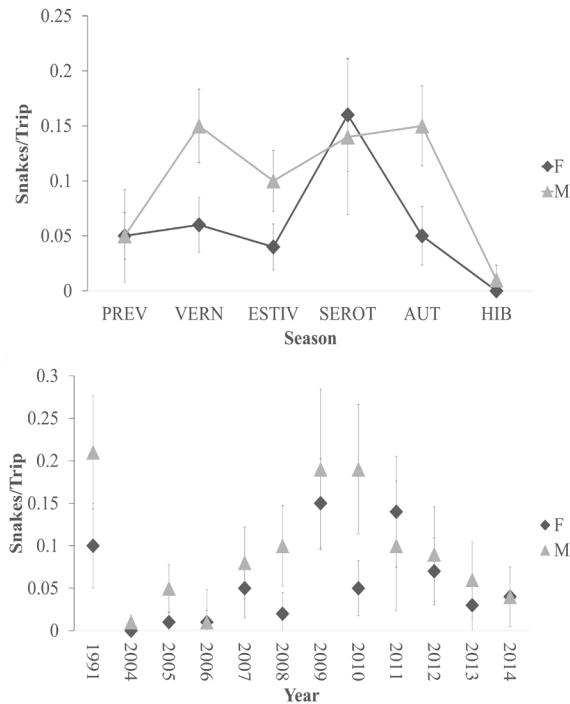
From the results of our study, we infer that road mortality was unequally distributed among demographic



**FIGURE 5.** A) Seasonal and B) annual (mean  $\pm$  standard error) road encounter rates of Gray Ratsnake (*Pantherophis spiloides*) demographic groups on the transect through the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Abbreviations are PREV = prevernal; VERN = vernal; ESTIV = estival; SEROT = serotinal; AUT = autumnal; HIB = hibernal. F = female; M = male; J = juvenile.

or life stage groups within and among snake species. Unequal demographic distributions may be caused by natural pressures such as predation and competition, or through anthropogenic pressures including road mortality, collecting, or hunting (Rosen and Lowe 1994; Brooks et al. 2007; Row et al. 2007). It is possible that bias in the survey methodology resulted in some degree of detection error for certain species, demographic groups, or life stage groups because of variation in behavior and natural history, or the decreased likelihood of detecting smaller individuals. Juvenile snakes are notoriously difficult to detect, leading to the belief that these cohorts experience high annual mortality. Evidence indicates, however, that juvenile snakes experience relatively high annual survivorship, particularly in viviparous species and those that have relatively large neonate and juvenile stages, and that the underrepresentation of these demographic stages in studies is likely caused by sampling bias (Pike et al. 2008). The long-term nature of our study and large number of sampling trips we made likely mitigated these inherent biases that accompany the road-cruising sampling method as evidenced by the size range of individuals we encountered. Furthermore, as we only conducted surveys in the evenings and at night, diurnal snakes were more likely to be found DOR



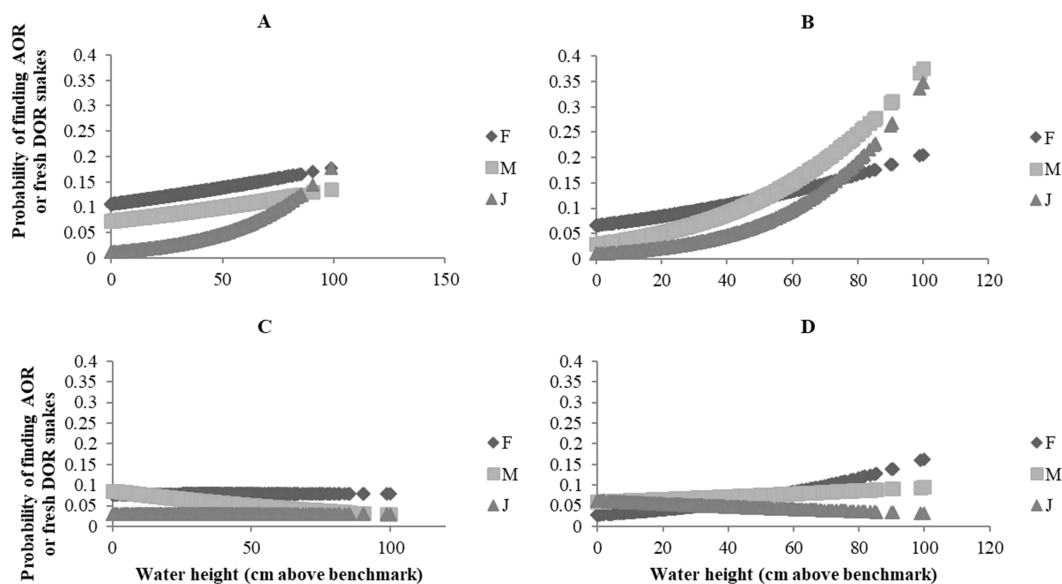


**FIGURE 6.** A) Seasonal and B) annual (mean  $\pm$  standard error) road encounter rates of Diamondback Watersnake (*Nerodia rhombifer*) demographic groups on the transect through the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Abbreviations are PREV = prevernal; VERN = vernal; ESTIV = estival; SEROT = serotinal; AUT = autumnal; HIB = hibernal. F = female; M = male.

than crepuscular or nocturnal species. For example, we only documented DOR specimens for *C. constrictor* (DeGregorio et al. 2014) and *L. nigra* (Howze and Smith 2012), both diurnal species.

We chose a simplified two or three group system (adult female, adult male, juvenile) in an attempt to make biologically meaningful comparisons, and to provide a rough framework for understanding relative road mortality rates of demographic or life stage groups. Analysis of size distributions of the samples of snakes collected from this roadway and several other studies (e.g., Mushinsky et al. 1982; Houston and Shine 1993; Vincent et al. 2007), however, indicate that the process of recruitment is much more complex, with individuals passing through life stages that require specific ecological resources before entering the adult population. There is substantial variation among and within species in age at maturity, generation time, life-stage specific survival rates, recruitment rate, and susceptibility to negative population consequences of anthropogenic perturbations (Blouin-Demers et al. 2002; Webb et al. 2002). Road mortality was concentrated in adults in most species in this study, except *P. spiloides*.

Our study and others assess an effect that suggests that body size influences the probability that snakes will enter roadways in complex ways. In a study where previously captured snakes were released in a road margin, Andrews and Gibbons (2005) found that although greater body size (SVL) was correlated with road-crossing attempts across snake species,



**FIGURE 7.** The influence of water height on detection probability of alive on road (AOR) or fresh dead on road (DOR) individuals of different demographic groups within four snake species: (A) = Banded Watersnake (*Nerodia fasciata*); (B) = Green Watersnake (*N. cyclopioides*); (C) = Western Ribbonsnake (*Thamnophis proximus*); (D) = Gray Ratsnake (*Pantherophis spiloides*).

body size was not a significant predictor of road-entry behavior when within-species comparisons were made. Conversely, for aquatic and semi-aquatic species (*Nerodia*, *Thamnophis*, *Agkistrodon*, and *Farancia*), the body-size distributions of snakes found on the road were similar to those of other studies that assessed body-size distributions via funnel-trap sampling in off-road natural or semi-natural habitats, where larger individuals are observed more frequently than smaller individuals (Andrews and Gibbons 2008; Willson et al. 2008; Rose et al. 2013). These findings suggest that larger individuals of these species have greater vagility, which increases their likelihood of detection by sampling methods that rely on animal movement, such as funnel trapping or road surveying, and therefore their risk of on-road mortality compared to less mobile body-size classes or demographic groups. Of the 37 smaller-bodied ( $\leq 35$  cm SVL) juvenile snakes we observed (representing seven species) during our surveys, we found 24 individuals (65%) alive on the road (AOR). 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 because of removal by scavengers and thus may be underestimated during surveys. Additionally, observers are less likely to see a small flattened stationary snake than a 3-dimensional live one that may offer a bigger and more distinct moving visual target. In addition to challenges in detecting smaller snakes on the road surface, there is also evidence that smaller snakes heat faster and therefore spend less time on thermoregulating on asphalt roads, making them less vulnerable to road mortality than larger snakes (Mccardle and Fontenot 2016).

In addition to body size, sex and reproductive condition can influence road-entry behavior and risk of mortality in snakes. Our findings differ with some of those of Bonnet et al. (1999), which indicate that body size does not influence mortality risk for adult female snakes in a study that examined mortality (including road mortality) in relation to dispersal in several snake species. The proposed explanation for this finding was that body size should not influence the duration of gestation for live-bearing female snakes, presumably because the body size of a gestating snake will not influence vagility associated with movements to basking/thermoregulatory sites or post-birth foraging activity. In our study, larger females of viviparous species (*Nerodia*, *Thamnophis*,

and *Agkistrodon*) were found on the road significantly more often than smaller individuals. Although body size is not known to be related to duration of gestation in live-bearing reptiles, larger body size is associated with greater numbers of egg follicles, larger litter sizes, and larger offspring birth size (Ballinger 1973; Barron and Andraso 2001; Lourdais et al. 2003; Shine 2003). These fitness constraints of viviparity impose unique energetic requirements on female snakes including increased need to forage, including foraging into the fall/autumnal season (Madsen and Shine 1993; Barron and Andraso 2001; Gregory et al. 2006), and increased thermoregulatory requirements, such as increased basking activity and selection of warmer microsites (Tu and Hutchinson 1994; Gregory et al. 1999; Rock et al. 2000; Crane and Green 2008; Pattishall and Cundall 2009). Foraging movements and the unique thermal characteristics of asphalt roads (Barron and Andraso 2001; Mccardle and Fontenot 2016) potentially play a role in increased road mortality of larger viviparous snakes.

For *Pantherophis spiloides*, we encountered smaller, younger individuals more often than larger, older individuals, suggesting that juveniles experience more road mortality than adults. For northern populations of North American rat snakes, age at maturation has been estimated at 7–9 y (Blouin-Demers et al. 2002; Row et al. 2007), while age at maturation for many natricines in the mid latitudes in North America has been estimated at 2–4 y (Brown and Weatherhead 1999; Stanford and King 2004; Roe et al. 2013). This indicates that patterns of road mortality observed in these species are likely related to development, where the populations of rat snakes are skewed toward juveniles due to their longer maturation time, and populations of natricines are skewed toward adults due to the relatively early onset of reproductive maturity. In a study on the comparative demography of populations of the Black Ratsnake (*Pantherophis obsoleta*) in Ontario, Canada, and Maryland, USA, larger size classes (80–180 cm SVL) dominated samples of opportunistically captured snakes (Blouin-Demers et al. 2002), whereas in our study, smaller and younger snakes (25–79 cm SVL) made up most on-road encounters. It is unclear whether or not the differences in these sample-wise demographic distributions are attributable to demographic-specific movements that result in juveniles and subadults entering the road more frequently or variation in demographic structure between populations. Effects of road mortality, therefore, would presumably be to limit reproductive opportunities and reproductive output in the natricines by applying mortality pressure to the adult cohort (particularly females), while limiting recruitment in the rat snake by introducing an added mortality pressure to the sub-adult cohort.

*Pantherophis spiloides* is a relatively long-lived species (approximately 20 y; Blouin-Demers et al. 2002; Row et al. 2007) with presumably low natural adult mortality and reduced hatching success (relative to viviparous species), whereas natricines are extremely fecund with large litter sizes (Weatherhead et al. 1998; Bronikowski and Arnold 1999). Fortuitous births or dissections revealed maximum litter sizes of 23, 14, and 17 young for *N. fasciata*, *N. cyclopion*, and *T. proximus*, respectively, for samples of these species found on the road transect. Adult females of natricines are thought to make a significant metabolic investment in both litter size and neonate size (Stewart et al. 1989; Barron and Andraso 2001; Van Dyke and Beaupre 2011). Conversely, in *P. spiloides*, a metabolic investment (greater growth from birth to maturity, older age at maturity than *Nerodia* or *Thamnophis*) is made in adult survivorship, and therefore increased long-term reproductive opportunities (Blouin-Demers et al. 2002). These findings suggest that natricines occupy a relatively *r*-favored, while *P. spiloides* occupies a relatively *K*-favored, position on the *r*-*K* selection continuum (Pianka 1994). We did not quantify demographic- or population-level consequences of road mortality within these snake populations. Evidence indicates, however, that relatively few annual road mortality deaths of adult female *P. spiloides* can dramatically increase the likelihood of population extinction over a 100-y period (Row et al. 2007). Additionally, road mortality has been shown to significantly imperil population persistence in a vagile water snake species in isolated habitats bisected by roads (Roe et al. 2006). For snake populations to persist with unmitigated road mortality may require large tracts of contiguous habitat that support populations large enough to ameliorate road mortality.

Several studies have documented male bias in snake road mortality (e.g., Andrews and Gibbons 2008; Shepard et al. 2008; Keogh 2007; Hartmann et al. 2011), as did we for *T. proximus*, *P. spiloides*, and *N. fasciata*, as well as mortality associated with demographic group-specific movements (e.g., Bonnet et al. 1999; Hartmann et al. 2011; Jochimsen 2014). In our study, although we found males generally on the road more often than females, a closer examination of demographic-specific observations and seasonality seems to indicate more complicated patterns. High adult male mortality in the prevernal and vernal periods associated with mate-seeking movements (Bonnett et al. 1999) are complemented by increases in adult female mortality presumably associated with increased foraging activity and thermoregulation behavior later in the active season in viviparous species (Madsen and Shine 1993; Barron and Andraso 2001; Gregory et al. 2006), or migratory movements to egg-laying habitats for oviparous species (Bonnet et al. 1999; Jochimsen et al. 2014). Increased

energy requirements for growth and maturation, and a demographic skew toward sub-adult segments of the populations of the large, slow-maturing *P. spiloides* may contribute to the high road mortality of juveniles in this species (relative to other species examined). Our findings indicate that road mortality affects snake populations at different demographic levels depending on species, growth rate, and reproductive strategy, and therefore, it may not be appropriated to generalize population-level consequences across species.

We found that demographic groups within snake populations vary in the conditions under which they enter the roadway, suggesting that road mortality risk is not randomly distributed among life stages of species. Individuals within snake populations use resources differently within heterogeneous landscapes based on their body-size, sex, and other life-stage specific phenotypes. For example, Shine et al. (2003) documented significant differences in habitat use within the Turtleheaded Seasnake (*Emydocephalus annulatus*) attributable to the effects of sex, body size, and coloration. Ontogenetic changes in ecology for several of the species considered in our assemblage are well documented (e.g., Mushinsky et al. 1982; Savitzky and Burghardt 2000). For example, Mushinsky et al. (1982) found that the importance of frogs (relative to fish) in the diet of *N. fasciata* increased as individuals grew to over 50 cm SVL. This shift in prey importance is presumably associated with increased terrestrial activity in *N. fasciata*, which have been observed feeding on large breeding aggregations of the Gulf Coast Toad (*Incilius nebulifer*) in water-filled depressions and ditches adjacent to the roadway (pers. obs.). There is also a clear non-random relationship between on-road snake activity or mortality and ambient temperatures (D'Amico et al. 2015; Mccardle and Fontenot 2016). There is a growing preponderance of evidence suggesting that ontogenetic, phenological, and environmental pressures make live-bearing snakes particularly vulnerable to road mortality. In cases where available habitat is limited, or in fragmented or small populations, roads may function as significant population sinks that imperil long-term fitness (Roe et al. 2006; Roe et al. 2013).

One important finding of our study was the effect of water height on road occurrence and mortality in this snake assemblage. Throughout coastal Louisiana, inundation events caused or exacerbated by coastal land loss and erosion, tropical weather events, and increasingly common catastrophic precipitation events create problematic conditions (Barras et al. 2004; Keddy et al. 2006). In the Manchac Land Bridge region, flood events dramatically increase numbers of snake road mortalities, and prolonged periods of high water further increase the likelihood of road mortality for species and demographic groups that do not typically

enter the roadway. Flooding from tropical weather events in this region can severely decrease abundance and diversity within herpetofaunal communities (Schriever et al. 2009), which has also been linked to increased road mortality for snakes by destruction of suitable hibernacula in other regions (Tucker 1995). Besides simply limiting or destroying the amount of non-inundated terrestrial habitat available to snakes in flood-prone regions, flood events can have complex and non-intuitive effects on snake ecology and life-history events that potentially contribute to vulnerability to road mortality. In a study in southeast Texas, flooding and flood suppression affected prey diversity and overlap in *N. fasciata*, *N. erythrogaster*, and *T. proximus* (Hampton and Ford 2007). Dietary overlap between *N. fasciata* and *T. proximus* doubled in years in which flooding occurred compared to years in which flooding was suppressed, with frogs being the most important component of the diet for both species. This suggests that flooding results in increased competition for a more terrestrial (compared to fish and crayfish) prey items, which, during flood events in the MLBA likely means not only added trophic competition between to frog-eating species, but also increased spatial competition because of the reduced amount of non-inundated land, of which the road and road shoulder are the primary component during flood events. Increased foraging movements related to increased competition along a limited portion of high ground which features an exotic mortality pressure may contribute to higher road mortality during flood events for these species.

Species and demographic groups within this assemblage varied markedly in the relative importance of seasonal, climate, and weather drivers of on-road observations. Many of the variables we considered, including humidity (Daltry et al. 1998), temperature (Mccardle and Fontenot 2016), and season (Bernardino 1990), influence snake activity. Brown and Shine (2002) suggested that although weather and climatic variables are correlated with variation in reptile activity, the explanatory power of these types of variables was relatively low. Similarly, although our study detected several potentially important variables, the overall amount of variation explained by our models was low, indicating that variation between species and demographic groups was influenced by factors unaccounted for in our analysis. Brown and Shine (2002) and our study documented significant synchrony of activity among closely related taxa. Our study further revealed, however, that many species exhibit significant intraspecific demographic variation in timing of activity as well.

Generalized Linear Models were intended to explore temporal differences in on-road observations between demographic groups by examining behavioral drivers of

on-road activity at the individual level (i.e., removing the effects of abundance by considering only a binary presence or absence variable rather than counts of snakes per trip and modeling fine scale presence/absence with same day environmental conditions). Annual and seasonal variation in snake observations both between and within species, however, were quite pronounced in many instances and may be better explained at the population rather than the individual (behavioral) level. Processes that influence abundance, such as variation in rainfall between years, drought, and prey availability, can be dramatic on the MLBA. Two likely important variables that we did not consider include rainfall and salinity variation within the study area. Monthly rainfall totals obtained from Global Historical Climatological Network weather station USW000 12916 located at the New Orleans International airport, 18.65 km southwest of the southern terminus of the survey transect, indicated that rainfall in the year 1991 (mean monthly rainfall = 21.67 cm) was higher than any other survey year, and higher than the average (13.49 cm) for all survey years. The year 1991 also saw the greatest number of overall on-road snake observations. Fluctuations in snake abundance in relation to rainfall are well documented (e.g., Willson et al. 2006; Brown and Shine 2007). Rainfall can influence snake populations in various ways. For anuran-eating snakes (several species in our study), wetter conditions that increase anuran abundance are correlated with increased fecundity (Brown and Shine 2007). In a study of a snake assemblage similar to our own (Willson et al. 2006), snake species varied considerably in response to drought, ranging from declining dramatically or even becoming extirpated (*N. fasciata* and *N. cyclopion*) to faring relatively well by migrating to areas with more favorable hydrological conditions (*A. piscivorus*) or aestivating (*Seminatrix pygaea*). Although cumulative rainfall appears to be associated with increased snake activity and potentially abundance overall in our study area, the relationship between rainfall on the day of the survey and snake activity is more complex and apparently varies across species and demographic groups. For example, day-of-survey precipitation was negatively associated with adult female and male *N. cyclopion* encounter probability, but it was positively associated with activity of adult female *T. proximus*. Possible explanations for this difference may be related to differences in preferred prey between these species.

Long-term studies are increasingly important to conservationists for documenting anthropogenic impacts upon and changes within cryptic animal populations. A short-term (one-year) study of snake and road interactions in the same area as the current study did not document significant differences in road activity between sexes for most species (Lutterschmidt



et al. 2019). Another long-term study (over a 21-y period) using a road survey to monitor changes in snake populations showed that species were dissimilar in whether they declined or increased over the study period, and that drivers of population changes were complex and enigmatic and are likely related to land use changes (Mendelson and Jennings 1992; Croshaw et al. 2019). Further investigation is clearly needed to elucidate the influence of biotic, abiotic, and anthropogenic pressures on snake activity and population dynamics on the MLBA and globally. It is also important to consider data on demographic differences in certain population viability modeling procedures that use road mortality data to estimate snake densities, population parameters, and extinction risks (e.g., Row et al. 2007; Willson et al. 2018).

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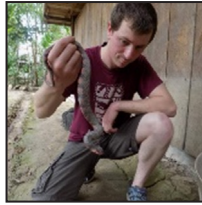
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**APPENDIX TABLE.** Ranked predictive Generalized Linear models of detection probability of demographic groups within four snake species across six predictor variables in the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Relative model support was assessed using the AICC score. Models shown are the three best supported for each demographic group.

| Species  | Group    | Model                                   | Component | df    | F-ratio | <i>P</i> | <i>r</i> <sup>2</sup> | AIC <sub>c</sub> | ΔAIC <sub>c</sub> |
|--|----------|---|-----------|-------|---------|----------|-----------------------|------------------|-------------------|
| Banded Watersnake<br>( <i>Nerodia fasciata</i> ) | Female   | detection ~ 1 + WS + RT                 | WS        | 1     | 2.138   | 0.033    | 0.07                  | 324.8            | 0                 |
|  |          |   | RT        | 10    | 3.386   | < 0.001  |                       |                  |                   |
|  |          |   | Error     | 594   |         |          |                       |                  |                   |
|  |          | detection ~ yr + RT + yr × RT           | RT        | 1     | 33.919  | < 0.001  | 0.111                 | 386.5            | 61.7              |
|  |          |   | yr × RT   | 10    | 3.555   | < 0.001  |                       |                  |                   |
|  |          |   | Error     | 603   |         |          |                       |                  |                   |
|  |          | detection ~ szn + yr + AT + szn × AT    | szn       | 5     | 4.509   | < 0.001  | 0.138                 | 386.8            | 62                |
|  |          |   | yr        | 10    | 2.732   | 0.003    |                       |                  |                   |
|  |          |   | szn × AT  | 5     | 3.374   | 0.005    |                       |                  |                   |
|  | Male     | detection ~ RH +szn + yr + WS + yr × WS | RH        | 1     | 5.925   | 0.015    | 0.098                 | 226.4            | 0                 |
|  |          |   | szn       | 5     | 4.074   | 0.001    |                       |                  |                   |
|  |          |   | yr × WS   | 10    | 2.654   | 0.003    |                       |                  |                   |
|  |          | detection ~ RH + szn × AT + yr × WS     | RH        | 1     | 7.196   | 0.008    | 0.097                 | 226.5            | 0.1               |
|  |          |   | szn × AT  | 5     | 4.056   | 0.001    |                       |                  |                   |
|  |          |   | yr × WS   | 11    | 2.597   | 0.003    |                       |                  |                   |
| detection ~ szn × AT + yr × WS                   | szn × AT | 5                                       | 3.603     | 0.003 | 0.087   | 231.8    | 5.4                   |                  |                   |
|  | Error    | 560                                     |           |       |         |          |                       |                  |                   |

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**APPENDIX TABLE (CONTINUED).** Ranked predictive Generalized Linear models of detection probability of demographic groups within four snake species across six predictor variables in the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Relative model support was assessed using the AICC score. Models shown are the three best supported for each demographic group.

| Species  | Group  | Model  | Component                                | df      | F-ratio | <i>P</i> | <i>r</i> <sup>2</sup> | AIC <sub>c</sub> | ΔAIC <sub>c</sub> |      |
|--|--|--|--|---------|---------|----------|-----------------------|------------------|-------------------|------|
| Green Watersnake<br>( <i>Nerodia cyclopion</i> ) | Juvenile   | detection ~ WS + YR × WS + szn × RH              | yr × WS                                  | 11      | 3.145   | 0.000    |                       |                  |                   |      |
|  |  |  | Error                                    | 561     |         |          |                       |                  |                   |      |
|  |  |  | WS                                       | 1       | 6.126   | 0.014    | 0.065                 | 353.3            | 0                 |      |
|  |  |  | yr × WS                                  | 10      | 2.300   | 0.009    |                       |                  |                   |      |
|  |  |  | szn × RH                                 | 5       | 4.323   | 0.001    |                       |                  |                   |      |
|  |  |  | Error                                    | 598     |         |          |                       |                  |                   |      |
|  |  | detection ~ WS + RT + yr × WS                    | WS                                       | 1       | 9.578   | 0.002    | 0.065                 | 360.2            | 6.9               |      |
|  |  |  | RT                                       | 1       | 6.576   | 0.011    |                       |                  |                   |      |
|  |  |  | yr × WS                                  | 11      | 2.644   | 0.003    |                       |                  |                   |      |
|  |  |  | Error                                    | 602     |         |          |                       |                  |                   |      |
|  |  |  | detection ~ WS + yr × WS                 | WS      | 1       | 12.549   | 0.000                 | 0.055            | 364.2             | 10.9 |
|  |  |  |  | yr × WS | 11      | 2.838    | 0.001                 |                  |                   |      |
|  | Female   | detection ~ WS + Precip + yr × WS + szn × AT     | WS                                       | 1       | 12.909  | 0.000    | 0.276                 | 107.7            | 0                 |      |
|  |  |  | Precip                                   | 1       | 5.891   | 0.016    |                       |                  |                   |      |
|  |  |  | yr × WS                                  | 11      | 2.250   | 0.000    |                       |                  |                   |      |
|  |  |  | szn × AT                                 | 5       | 4.736   | 0.000    |                       |                  |                   |      |
|  |  |  | yr × AT                                  | 11      | 4.739   | 0.000    |                       |                  |                   |      |
|  |  |  | Error                                    | 586     |         |          |                       |                  |                   |      |
|  |  | detection ~ yr + szn+ Precip + WS + TD + yr × WS | yr                                       | 11      | 2.986   | 0.001    | 0.264                 | 120.0            | 12.3              |      |
|  |  |  | szn                                      | 5       | 2.392   | 0.037    |                       |                  |                   |      |
|  |  |  | Precip                                   | 1       | 4.925   | 0.027    |                       |                  |                   |      |
|  |  |  |  | 1       | 7.851   | 0.005    |                       |                  |                   |      |
|  |  |  | WS                                       | 1       | 6.361   | 0.012    |                       |                  |                   |      |
|  |  |  | TD                                       |         |         |          |                       |                  |                   |      |
|  |  |  | yr × WS                                  | 11      | 2.488   | 0.005    |                       |                  |                   |      |
|  |  |  | Error                                    | 586     |         |          |                       |                  |                   |      |
|  |  |  | detection ~ yr + szn + WS + TD + yr × WS | yr      | 11      | 2.848    | 0.001                 | 0.258            | 123.0             | 15.3 |
| szn  | 5  | 2.268  |  | 0.046   |         |          |                       |                  |                   |      |
| WS   | 1  | 6.462  |  | 0.011   |         |          |                       |                  |                   |      |
| TD   | 1  | 7.186  |  | 0.008   |         |          |                       |                  |                   |      |
| yr × WS  | 11   | 2.470  |  | 0.005   |         |          |                       |                  |                   |      |
| Error  | 586  |  |  |         |         |          |                       |                  |                   |      |
| Male   | detection ~ RH + WS + Precip + szn × AT + yr × WS + szn × RT | RH   | 1  | 6.488   | 0.011   | 0.195    | 92.0                  | 0                |                   |      |
|  |  | WS   | 1  | 11.117  | 0.001   |          |                       |                  |                   |      |
|  |  | Precip   | 1  | 9.547   | 0.002   |          |                       |                  |                   |      |
|  |  | szn × AT   | 5  | 2.587   | 0.025   |          |                       |                  |                   |      |
|  |  | yr × WS  | 11                                       | 5.659   | 0.000   |          |                       |                  |                   |      |
|  |  | szn × RT   | 5  | 2.656   | 0.022   |          |                       |                  |                   |      |
|  | detection ~ RH + WS + Precip + szn × RT + yr × WS            | Error  | 554                                      |         |         |          |                       |                  |                   |      |
|  |  | RH   | 1  | 5.157   | 0.024   | 0.177    | 94.6                  | 2.6              |                   |      |
|  |  | WS   | 1  | 11.240  | 0.001   |          |                       |                  |                   |      |
|  |  | Precip   | 5  | 9.540   | 0.002   |          |                       |                  |                   |      |
|  |  | szn × RT   | 10                                       | 4.145   | 0.001   |          |                       |                  |                   |      |
|  |  | yr × WS  | 11                                       | 5.834   | 0.000   |          |                       |                  |                   |      |



**APPENDIX TABLE (CONTINUED).** Ranked predictive Generalized Linear models of detection probability of demographic groups within four snake species across six predictor variables in the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Relative model support was assessed using the AICC score. Models shown are the three best supported for each demographic group.

| Species   | Group                     | Model   | Component          | df     | F-ratio | <i>P</i> | <i>r</i> <sup>2</sup> | AIC <sub>c</sub> | ΔAIC <sub>c</sub> |
|---|---------------------------|---|--------------------|--------|---------|----------|-----------------------|------------------|-------------------|
| Western Ribbonsnake<br>( <i>Thamnophis proximus</i> )     | Juvenile                  | detection ~ WS + Precip + yr × WS + szn × AT              | WS                 | 1      | 16.182  | 0.000    | 0.169                 | 98.5             | 6.5               |
|   |                           |   | Precip             | 1      | 6.758   | 0.010    |                       |                  |                   |
|   |                           |   | yr × WS            | 10     | 6.458   | 0.000    |                       |                  |                   |
|   |                           |   | szn × AT           | 5      | 4.361   | 0.001    |                       |                  |                   |
|   |                           |   | Error              | 597    |         |          |                       |                  |                   |
|   |                           | detection ~ WS + RT + yr × WS + yr × Precip               | WS                 | 1      | 16.753  | 0.000    | 0.157                 | -377.5           | 0                 |
|   |                           |   | RT                 | 1      | 3.247   | 0.072    |                       |                  |                   |
|   |                           |   | yr × WS            | 11     | 6.575   | 0.000    |                       |                  |                   |
|   |                           |   | yr × Precip        | 11     | 1.751   | 0.059    |                       |                  |                   |
|   |                           |   | Error              | 591    |         |          |                       |                  |                   |
|   |                           | detection ~ AT + yr × WS                                  | AT                 | 1      | 7.405   | 0.007    | 0.105                 | -366.7           | 10.8              |
|   |                           |   | yr × WS            | 11     | 5.743   | 0.000    |                       |                  |                   |
|   |                           |   | Error              | 603    |         |          |                       |                  |                   |
|   |                           | detection ~ AT + yr × WS + yr × Precip                    | AT                 | 1      | 6.983   | 0.008    | 0.134                 | -363.1           | 14.4              |
|   |                           |   | yr × WS            | 11     | 5.145   | 0.006    |                       |                  |                   |
|   | yr × Precip               |   | 11                 | 1.770  | 0.056   |          |                       |                  |                   |
|   | Error                     |   | 592                |        |         |          |                       |                  |                   |
|   | Female                    | detection ~ RT + Precip + yr × WS + yr × Precip + yr × AT | RT                 | 1      | 24.4885 | 0.000    | 0.248                 | 29.6             | 0                 |
|   |                           |   | Precip             | 1      | 15.888  | 0.000    |                       |                  |                   |
|   |                           |   | yr × WS            | 11     | 2.901   | 0.001    |                       |                  |                   |
|   |                           |   | yr × Precip        | 11     | 3.483   | 0.000    |                       |                  |                   |
|   |                           |   | yr × AT            | 11     | 3.428   | 0.000    |                       |                  |                   |
|   |                           |   | Error              | 580    |         |          |                       |                  |                   |
|   |                           | detection ~ AT + Precip + yr × WS + yr × AT + yr × Precip | AT                 | 1      | 20.629  | 0.000    | 0.242                 | 33.9             | 4.3               |
|   |                           |   | Precip             | 11     | 15.964  | 0.000    |                       |                  |                   |
|   |                           |   | yr × WS            | 11     | 3.017   | 0.001    |                       |                  |                   |
|   |                           |   | yr × AT            | 11     | 4.076   | 0.000    |                       |                  |                   |
|   |                           |   | yr × Precip        | 11     | 3.601   | 0.000    |                       |                  |                   |
| Error   |                           |   | 580                |        |         |          |                       |                  |                   |
| detection ~ TD + Precip + yr × WS + yr × TD + yr × Precip |                           |   | TD                 | 1      | 9.025   | 0.003    | 0.231                 | 43.0             | 13.4              |
|   | Precip                    | 1   | 16.658             | 0.000  |         |          |                       |                  |                   |
|   | yr × WS                   | 11  | 2.907              | 0.001  |         |          |                       |                  |                   |
|   | yr × TD                   | 11  | 3.036              | 0.001  |         |          |                       |                  |                   |
|   | yr × Precip               | 11  | 3.661              | 0.000  |         |          |                       |                  |                   |
|   | Error                     | 580   |                    |        |         |          |                       |                  |                   |
| Male  | detection ~ yr            | yr  | 11                 | 5.984  | 0.000   | 0.098    | 2.7                   | 0                |                   |
|   |                           | Error   | 604                |        |         |          |                       |                  |                   |
|   |                           | detection ~ yr + RT                                       | yr                 | 11     | 5.015   | 0.000    | 0.128                 | 8.2              | 5.5               |
|   | RT                        |   | 1                  | 20.434 | 0.000   |          |                       |                  |                   |
|   | detection ~ yr + szn × AT | yr  | 11                 | 5.470  | 0.000   | 0.127    | 16.9                  | 14.2             |                   |
|   |                           | szn × AT  | 5                  | 3.997  | 0.001   |          |                       |                  |                   |
|   | Error                     | 604   |                    |        |         |          |                       |                  |                   |
|   |                           | Juvenile  | detection ~ 1 + AT | AT     | 1       | 8.824    | 0.003                 | 0.013            | -329.7            |
|   | Error                     |   | 614                |        |         |          |                       |                  |                   |
|   | detection ~ 1 + RT        | RT  | 1                  | 8.402  | 0.005   | 0.011    | -328.9                | 0.8              |                   |

# Herpetological Conservation and Biology

**APPENDIX TABLE (CONTINUED).** Ranked predictive Generalized Linear models of detection probability of demographic groups within four snake species across six predictor variables in the Manchac Land Bridge Area in Tangipahoa and St. John the Baptist parishes in southeastern Louisiana, USA, 1990–1991 and 2003–2014. Relative model support was assessed using the AICC score. Models shown are the three best supported for each demographic group.

| Species   | Group                                   | Model                    | Component                | df     | F-ratio | <i>P</i> | <i>r</i> <sup>2</sup> | AIC <sub>c</sub> | ΔAIC <sub>c</sub> |  |
|---|---|--------------------------|--------------------------|--------|---------|----------|-----------------------|------------------|-------------------|--|
| Gray Ratsnake<br>( <i>Pantherophis spilloides</i> ) | Female                                  | detection – yr           | Error                    | 604    |         |          |                       |                  |                   |  |
|   |   |                          | yr                       | 11     | 2.072   | 0.020    | 0.036                 | -323.1           | 6.6               |  |
|   |   |                          | Error                    | 604    |         |          |                       |                  |                   |  |
|   | Female                                  | detection – WS + yr + TD | WS                       | 1      | 6.703   | 0.010    | 0.061                 | -131.4           | 0                 |  |
|   |   |                          | yr                       | 11     | 2.736   | 0.002    |                       |                  |                   |  |
|   |   |                          | TD                       | 1      | 5.348   | 0.021    |                       |                  |                   |  |
|   |   |                          | Error                    | 603    |         |          |                       |                  |                   |  |
|   |   |                          | detection – WS + yr + RT | WS     | 1       | 3.937    | 0.048                 | 0.058            | -131.1            |  |
|   |   |                          |                          | yr     | 11      | 2.153    | 0.015                 |                  |                   |  |
|   |   |                          |                          | RT     | 1       | 5.093    | 0.024                 |                  |                   |  |
|   |   |                          | detection – WS + yr      | Error  | 602     |          |                       |                  |                   |  |
|   |   |                          |                          | WS     | 1       | 5.808    | 0.016                 | 0.050            | -128.0            |  |
|   | yr                                      | 11                       |                          | 2.736  | 0.002   |          |                       |                  |                   |  |
|   | Male                                    | detection – RT + yr × WS | Error                    | 603    |         |          |                       |                  |                   |  |
|   |   |                          | RT                       | 1      | 22.415  | 0.000    | 0.089                 | -35.8            |                   |  |
|   |   |                          | yr × WS                  | 11     | 3.067   | 0.001    |                       |                  |                   |  |
|   |   | detection – TD + yr × WS | Error                    | 565    |         |          |                       |                  |                   |  |
|   |   |                          | TD                       | 1      | 17.561  | 0.000    | 0.082                 | -31.0            |                   |  |
|   |   |                          | yr × WS                  | 11     | 2.057   | 0.026    |                       |                  |                   |  |
|   | detection – AT + yr × WS                | Error                    | 603                      |        |         |          |                       |                  |                   |  |
|   |   | AT                       | 1                        | 14.504 | 0.000   | 0.077    | -28.0                 |                  |                   |  |
| yr × WS   |   | 11                       | 3.589                    | 0.000  |         |          |                       |                  |                   |  |
| Juvenile  | detection – yr + yr × Precip + szn × AT | Error                    | 603                      |        |         |          |                       |                  |                   |  |
|   |   | yr                       | 11                       | 2.178  | 0.014   | 0.114    | -84.9                 |                  |                   |  |
|   |   | yr × Precip              | 11                       | 2.139  | 0.016   |          |                       |                  |                   |  |
|   | detection – RH + yr + yr × Precip       | szn × AT                 | 5                        | 3.325  | 0.006   |          |                       |                  |                   |  |
|   |   | Error                    | 588                      |        |         |          |                       |                  |                   |  |
|   |   | RH                       | 1                        | 5.356  | 0.021   | 0.097    | -82.1                 |                  |                   |  |
|   | detection – RH + yr                     | yr                       | 11                       | 2.281  | 0.010   |          |                       |                  |                   |  |
|   |   | yr × Precip              | 11                       | 2.263  | 0.011   |          |                       |                  |                   |  |
|   |   | Error                    | 592                      |        |         |          |                       |                  |                   |  |
| detection – RH + yr                                 | RH                                      | 1                        | 5.621                    | 0.018  | 0.059   | -80.2    |                       |                  |                   |  |
|   | yr                                      | 11                       | 2.647                    | 0.003  |         |          |                       |                  |                   |  |
|   | Error                                   | 603                      |                          |        |         |          |                       |                  |                   |  |