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The influence of thermal biology on road mortality risk in snakes

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ABSTRACT

Road mortality is a significant threat to terrestrial vertebrates in many areas, and the novel thermal environment of black-topped roads may represent ecological traps for some species and demographic groups. We investigated the relationship between ambient temperature and on-road detection in a snake assemblage in southeastern Louisiana by comparing observations of live snakes on a black-topped road, across measurements of air temperature and road temperature on survey days. Analyses indicated on-road detection of snakes was significantly influenced by ambient temperature conditions for five snake species. Additionally, road temperatures, and the difference between air and road temperatures, were strong drivers of on-road snake detections. Permutation analysis methods revealed that significant temperature related group (species or sex) structure exists in occurrences of snakes on the roadway, and that road temperature was the strongest driver of species differences. We also compared how air and road temperatures affected occurrence on the road between sexes in the colubrid snakes *Nerodia fasciata, Nerodia cyclopion, Thamnophis proximus,* and *Pantherophis obsoletus*. Males and females of the viviparous species *N. fasciata, N. cyclopion,* and *T. proximus* diverged significantly in temperature preferences, with females found under warmer conditions, while males and females of the oviparous species *P. obsoletus* did not. Road temperature was also the strongest driver of differences between sexes. Our results indicate that black-topped roads are an ecological trap that is heavily influenced by sex, reproductive condition, and species specific thermoregulatory requirements, particularly for viviparous species.

1. Introduction

Terrestrial ectotherms behaviorally regulate body temperature by selecting suitable time periods for activity, and thermal environments conducive to homeostatic functions (Blouin-Demers et al., 2001; Fitzgerald et al., 2003). For temperate reptiles, thermally suitable climate conditions and microhabitats are important resources with direct implications for survival and fitness (Blouin-Demers et al., 2001; Lelievre et al., 2013). Variation in the thermal features of their environments and the thermoregulatory ability have been shown to be a major driver in evolutionary patterns such as species assemblage structure (Mushinsky et al., 1980), and differential survival, growth rates, and reproductive mode and success in sympatric species (Lelievre et al., 2013).

Over the last 100 years, the public road network has expanded to cover greater than 1% of the total land surface in the continental United States (Foreman et al., 2003). Black-topped roads represent novel thermal environments because they often retain more heat during dawn, dusk, and night, than the surrounding landscape (Shine et al., 2004). Several studies have attributed high road mortality levels and their associated negative population consequences in snakes at least in part to their perceived tendency to rest on warm road surfaces in order to absorb heat during certain seasons or times of day (e.g. Rosen and Lowe, 1994; Andrews and Gibbons, 2005).

While many authors have suggested that the thermal attributes of black-topped roads may partially explain high-numbers of casualties of snakes on these roads, whether snakes actually utilize roads as a thermal resource, and to what extent, has not been empirically investigated. If snakes thermoregulate on black-topped road surfaces, leading to increased susceptibility to road mortality, these roads may act as ecological traps for some species and demographic groups. An ecological trap is defined as a situation where environmental cues that an animal associates with positive survival and fitness outcomes, are present in habitats with diminished survival and fitness quality relative to other habitats available to the animal (Schlaepfer et al., 2002; Robertson and Hutto, 2006). Thus, behavioral responses historically associated with positive survival and fitness outcomes become maladaptive by the presence of the ecological trap.

We used data from a long-term quantitative herpetofaunal monitoring road survey that we conducted in southeastern Louisiana, to address whether a black-topped road can be an ecological trap, by testing the following five hypotheses:

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(1) there is a relationship between temperature and detection of snakes on a black-topped road, (2) that the relationship is influenced by body size, and (3) that these relationships influence likelihood of road mortality. We also test the hypotheses that there are differences among (4) species, and (5) sex.

2. Materials and methods

2.1. Snake mortality survey and temperature data collection

The Manchac Land Bridge Area (MLBA) is a 40,273 ha wetland between Lake Pontchartrain and Lake Maurepas (Keddy et al., 2007). This area is bisected by a 37-km segment of black-topped roadway (U.S. Highway 51), which we used as a transect for monitoring herpetofaunal species diversity, abundance, and road mortality, generally following the procedures outlined in Langen et al. (2007).

The road transect was driven weekly, slowly ($\leq$45 kph), beginning approximately one hour before sunset, from the starting point near Ponchatoula, LA to the end point near Frenier Road in LaPlace, LA and then from the end point to the starting point while the driver observed the road surface carefully for alive on road (AOR) and dead on road (DOR) snakes. Each time this procedure was performed was considered a “survey trip”. A total of 657 survey trips was conducted from September 2003 through December 2014, with survey trips occurring in all seasons. Most survey trips were conducted by a single observer/driver, and usually lasted between 2 and 4 h depending on the amount of herpetofauna being encountered. For snakes detected AOR, individuals were captured (the survey vehicle was stopped usually within 20 m of the snake, and the snake was captured by hand or using a snake hook) and transported to the behavioral ecology laboratory at Southeastern Louisiana University. The majority of AOR snakes ($>$90%) detected were successfully captured, as many remained immobile in response to the survey vehicle and other passing vehicles. In the lab, snout-to-vent (SVL), and mass (g) measurements of each snake were taken. Sex of each individual was determined by manual eversion of hemipenes in juveniles, and visual inspection of tail shape and size in adults (Shine et al., 2001). Individuals that could not be reliably sexed were omitted from sex comparisons. Presence of eggs or developing embryos was determined by palpation of adult females. Live snakes were given a unique scale-clipping and released on the following survey trip. Snakes that were encountered DOR were also recorded and the carcasses were collected if not too damaged to be salvaged, and taken to the lab. The same measurements were conducted on DOR individuals, and sex was determined via dissection to examine the reproductive organs.

To determine the influence of ambient temperatures on per survey trip snake detections (as indicated by presence or absence of AOR or freshly killed snakes on the road transect), and to correlate snake presence with specific temperature ranges, in 2004 we began collecting air and road temperature measurements at the beginning, turn-around point, and end of each survey trip using an EXTECH® Instruments RH401 infrared thermometer equipped with a laser for measuring road surface temperature. The three air temperature measurements were averaged for each trip, and this number was considered the ambient air temperature (AT) for the survey.

Similarly, the three road temperature measurements were averaged to give the ambient road temperature (RT) for the survey.

2.2. Test for the influence of ambient temperature on snake detections

We used logistic regression to model the influence of ambient temperatures on on-road observations of AOR or freshly killed snakes from survey trips conducted from 2004 and afterward (577 survey trips). Explanatory variables were RT, AT, and the difference between RT and AT (TD). Unpaired two-sample *t*-test indicated that RT was significantly higher than AT ($t=27.75$, $p=0.0000$) in most cases. Therefore, TD was considered to be an indicator of use of the road surface as a thermoregulation medium for snakes. The dependent variable for each logistic regression model was detection/non-detection of live or freshly killed (killed the day of the survey in which they were collected) snakes of a given species on the road transect during a survey trip (a “1” was entered if at least one AOR or freshly killed individual of a species was detected during the survey trip, and a “0” was entered if no AOR individual of that species was encountered). Each DOR snake was examined for the presence of residual nerve activity and the degree of desiccation and decomposition to determine whether freshly killed. DOR snakes with no obvious nervous activity were not included in the logistic regression analysis. Detection/non-detection was favored as a metric of road entry for snakes over abundance (number of individuals per survey) because road observations of snakes may not be a reliable indicator of abundance within the surrounding landscape (Bonnet et al., 1999). Pearson's correlation analysis indicated that RT and AT were highly correlated (Pearson's correlation score$=$0.92) and that RT and TD were highly correlated (Pearson's correlation score$=$0.64). Therefore, each logistic regression model included a single explanatory variable in order to avoid potential suppression effects due to correlated variables (Ludlow and Klein, 2014). Correlation between the explanatory variables may confound the interpretation of their effects for the species that exhibit significant relationships (i.e., are snakes found on the road because they are utilizing the black-top as a thermoregulatory substrate, or are they being found because of increased activity associated with favorable air temperature?). Therefore, each single explanatory variable model was assessed for goodness of fit and ranked by calculating the corrected Akaike Information Criterion (AIC_C) score.

2.3. Test for temperature driven group structure in on-road snake detections (species and sex differences)

Our objective was to determine whether different species, and sexes within species, were detected on the road transect under different ambient temperature conditions. Because survey trips were conducted year-round in most cases, including inactive periods for snakes (winter), and immediately following extreme weather events (e.g., hurricanes, tropical storms) which leads to pronounced variation in the numbers of snakes found on the road transect during individual survey trips, we selected statistical tests with minimal assumptions. A series of permutation based analyses was performed with the community analysis program PRIMER 6 (PRIMER-6 Ltd., United Kingdom). We constructed data matrices from the air and road temperatures associated with each observation of AOR/freshly killed snakes on the road for all species with at least 10 AOR/freshly killed samples. We then calculated resemblance matrices of Euclidean distances of AT and RT. The Euclidean distance is calculated by the formula:

$$D_{X,Y} = \sum_{J=n}^{J} \sqrt{(X_J - Y_J)^2}$$

where “*J*” is the number of variables (air temperature and road temperature) and “*X*” and “*Y*” are samples (either species or sexes within a species) (McCune and Grace, 2002). We tested the null hypothesis that there was no difference in AT or RT between species or sex, by one way analysis of similarity (ANOSIM) permutation tests on the Euclidean distances (Clarke et al., 2008). ANOSIM tests for differences in group (species or sex) composition by calculating a statistic *R* (Clarke et al., 2008). The *R* statistic was