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# Taking the road most travelled: Understanding patterns of snake (Colubridae; Storeria) movement and road mortality in a state park

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# Taking the road most travelled: Understanding patterns of snake (Colubridae; *Storeria*) movement and road mortality in a state park

by

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# ABSTRACT

Roadways negatively affect their surrounding ecosystems through the contamination of air, water, and soil resources, the dissection of populations and habitat areas, and the direct mortality of several fauna. My study assessed the significance of a number of variables that might influence the temporal and spatial patterns of road mortality in a population of Midland Brownsnakes (*Storeria dekayi wrightorum*). I utilized passive sampling techniques and road-walking surveys to collect individual snakes from a road during their biannual migrations from lowland activity areas to upland forests where they hibernate. I discovered that sexually biased behavioral and natural history traits impacted an individual's survivorship. Using a GIS, I was able to locate clusters of snake movement where individuals are drawn to cross in association with certain habitat types, topographic cues, or possibly even the scent trails made by other migrating snakes. Overall, this population may require the construction of below-grade ecopassages in order to mitigate mortality.

# INTRODUCTION

In recent decades, road ecology has been identified as a research frontier with the potential to impact a number of ecological subdisciplines. As a consequence of the growing human population, road surfaces have become an inescapable feature in nearly every natural landscape, with 73% of all lands in the United States lying within 800 m of a road (Riitters and Wickham 2003). From an anthropocentric point of view, roadways have been described as "the arteries of life" in reference to their contributions to the transport of citizens and goods on an intercontinental scale (FHWA 2001).

In addition to these familiar services, a road network's beneficial effects include some aspects of landscape ecology. For example, a road's presence reduces the frequency of off-road practices that alter multiple habitats within an ecosystem (Forman 2000). Roadways within conservation areas also allow for public access to recreational and educational activities with a goal of promoting a greater appreciation for the natural environment. Even in agriculturally saturated landscapes, "roadside natural strips"— lengths of native vegetation that run alongside roadways— act as buffers to run-off, and simultaneously sustain bird and small mammal populations where they would have otherwise been extirpated. Despite these positive contributions, road networks generally constitute a harmful presence in the natural landscape. The combined negative impacts of a road network cannot be averted without a proper understanding of the ecological flows they disrupt. My research focuses on the disruptions to migration and dispersion patterns in the presence of road surfaces, with an eye towards direct and indirect influences on vertebrate populations.

## Landscape ecology

Before the ecological influence of a road network can be discerned, it is important to recognize the various contributions of biotic and abiotic systems to the broader spatial context of landscape ecology. A landscape, as defined by Harris *et al*. (1996), consists of "multiple ecosystem types that are spatially differentiated but nevertheless interact through many different energy-flows and ecological processes." Forman (1986) summarized the subject with a list of three characteristics: structure, function, and change. He defined "structure" as the spatial relationship between ecosystems, which includes certain features like the distribution of individuals, materials (*e.g.*, air, water, soil), and energy. "Function" refers to the interactions of individuals, materials, and energy-flow across ecosystem types. Finally, "change" implies a shift in the structure and function of the "ecological mosaic" over time, not barring anthropogenic alteration.

## The road-effect zone

By applying aspects of landscape ecology to research on the impacts of roads, scientists have quantified the extent of environmental damage caused by US roadways. Extensive research has identified ecological factors impacted by the road system (*e.g.*, Forman 1986, 2000). To better grasp the under-studied influences of road networks on US lands, Forman (2000) introduced the idea of a "road-effect zone" to US ecologists. The road-effect zone – developed by Reijnen *et al*. (1995) to study avian populations – is a summation of the negative effects exerted on a natural area by a roadway, generally displayed as an uneven effect-buffer several times the width of a road surface. Numerous studies have identified roadway factors that have negatively influenced several biological processes: nitrogen oxides from car exhausts stymieing lichen abundance (Angold 1997); soil erosion, road salt, and invasive plants impacting drainage, reservoirs, and native plant communities, respectively (Forman and Deblinger 2000); and, noise pollution displacing songbird populations (Reijnen *et al.* 1995; Rheindt 2003).

Using data acquired from several case studies as the basis for his model assumptions, Forman (2000) estimated that the United States' 6.4-million km road network negatively impacts roughly 15-20% of the country's surface area, despite the entire US road system only amounting to 1% of the country's area. The most extensive effect-buffers occur in non-urban areas, including preserved natural areas and state-controlled roads, where the road-effect zone in some sections amounts to nearly one km in each direction (Forman 2000). These data highlight a road network's capacity to impact protected and uninhabitable areas where other forms of human disturbance are atypical (but see Roever *et al*. [2010] for logging road effects).

## Vertebrates and road avoidance

The effects of roadways on vertebrate populations illustrate another aspect of road ecology whose impacts extend far past a distinguishable road-effect zone. In line with the various abiotic systems discussed above, indirect effects on vertebrate fauna are secondary and occur in the surrounding habitat (Andrews and Gibbons 2005). Secondary road effects occur in a number of distantly related vertebrate taxa, including birds (Findlay and Houlahan 1997), mammals (Forman and Deblinger 2000; McGregor *et al*. 2008; Roever *et al.* 2010), amphibians (Eigenbrod *et al.* 2009; Marsh *et al.* 2005; Mazerolle *et al.* 2005), and reptiles (Andrews and Gibbons 2005; Clark *et al*. 2010; Shine *et al*. 2004). For example, Rheindt (2003) discovered that some members within avian communities were more affected by traffic noise than other species. This influenced avian community structure near roadways, but had little effect on population connectivity. The issues associated with road avoidance are not present in bird populations because their movements are not restricted by road surfaces (although, birds may use roads as navigational cues during migration [Forman and Alexander 1998]). However, Road avoidance— an organism's disinclination to come into contact with, or even into close proximity to, a road surface— can fragment terrestrial vertebrate populations. This would decrease levels of genetic heterozygosity (Findlay and Houlahan 1997; Lacy 1987) and increase inbreeding depression within isolated subpopulations, and decrease a population's overall viability through an extinction vortex (Caughley 1994).

Several experiments have assessed the severity of the "barrier effect" on vertebrate populations within habitats dissected by roads. Studies on small mammals have described an aversion of individuals to cross a road after translocation to the other side (McGregor *et al.* 2008). These trends were not correlated with traffic volumes, and suggest that characteristics of the road surface itself (*e.g.*, reduced canopy and litter cover), and not vehicle traffic (*e.g.*, noise pollution, direct road mortality), restrict movement. Secondary road effects impact amphibian populations to such an extent in some locations that road presence is considered one of the factors driving the global amphibian decline (Puky 2006). One aspect of amphibian physiology that limits road crossing is their vulnerability to desiccation. With highly permeable skin, amphibians are at risk of dehydration when traversing open areas that feature lower moisture levels than are present in the surrounding habitat. Therefore, road surfaces are typically only crossed at night, and following a rainfall event. With this in mind, displacement and homing experiments similar to those in the small mammal studies indicated a 51% reduction in successful homing attempts by salamanders separated from their home range by a road, compared to those in contiguous areas (Marsh *et al.* 2005). Furthermore, Eigenbrod *et al.* (2009) reported that traffic noise and general road presence isolated five of seven amphibian species within a community to pond systems on the same side of a road.

Studying the spatial and behavioral intricacies of reptilian communities allows researchers to investigate road avoidance in a number of species with variable trophic niches and natural history traits (Andrews *et al*. 2008). Sheperd *et al*. (2005b) showed that snakes and box turtles in a moderately dissected habitat were far more likely to avoid crossing a road than would be considered random. Andrews and Gibbons (2005) observed interspecific variation in the propensity of snakes to cross a road, and in the behavioral responses to passing vehicles; in general, smaller species were less inclined to cross, and bulkier species like rattlesnakes or cottonmouths would begin to cross but ultimately would return to their original side.

Using molecular genetics in combination with landscape ethics, Clark *et al*. (2010) discovered that genetic relatedness among hibernating aggregations of Timber Rattlesnakes was significantly affected by road presence. In other words, perceived connectivity (*i.e.*, gene flow) between hibernacula separated by a road surface was significantly less than connectivity of hibernacula in a contiguous landscape. More remarkable, gene flow between two hibernacula separated by a road was comparable, if not greater, than the connectivity of two hibernacula separated by a larger, contiguous distance.

The variable nature of biological responses to indirect road effects is difficult to observe and quantify. In part due to road ecology's relative infancy in the scientific realm, studies done on its behalf are cumbersome to draft and few in overall number (Andrews *et al*. 2006). However, secondary road impacts appear to constrain gene flow in terrestrial vertebrate populations (Forman and Alexander 1998). Factors like road avoidance, although not immediately detrimental to population numbers, can drastically impact population viabilities over the long-term.

## Direct road mortality

Direct road mortality is defined as the infliction of lethal bodily injury to an animal as a result of the construction and/or human-related use of a road surface. Vertebrate road mortality has been documented for nearly a century (Scott 1938), but many early reports were more often anecdotal or based on short-term data collected opportunistically, and often justified only by the concern of the scientists involved for the high occurrence of mortality (Stoner 1925). Standardized experiments with the central intent of examining road influence on wildlife populations have only been undertaken in more recent decades (Andrews *et al*. 2006; Puky 2006). Nevertheless, the rapid turnover of new data following the development of road ecology has facilitated the achievement of many significant conclusions.

Lalo *et al*. (1987) estimated that approximately 1,000,000 vertebrates are killed per day as a result of traffic collisions along the United States' 6.4 million-km road network. Of that total, a small proportion of large vertebrate roadkills (*e.g.*, deer, bears, wolves) is often the focus in the public attention because: 1) the risk of human injury in a collision; and, 2) the charismatic nature of these species (Clevenger *et al*. 2003). These problems are exacerbated where human disturbance in certain areas attracts large species. In a study that examined bear movements with respect to logging roads, Roever *et al*. (2010) discovered that bear movements increased when in close proximity to roads, often resulting in the use of the logging roads as corridors for movement. Bears were also attracted to recently logged areas following the succession of fruit-bearing shrubs and other edible plants. The researchers urged park managers to reduce traffic (especially that of pedestrians) in these areas to limit the chance of lethal encounters between humans and bears.

Although concerns for the safety of both humans and larger vertebrates are warranted, the study and protection of smaller wildlife should be given higher priority, especially in light of the decline of global amphibian and reptile populations (Gibbons *et al*. 2000; Puky 2006). In addition to simply collecting and quantifying roadkill data, researchers have investigated various intrinsic (*e.g.*, behavioral, life history traits) and extrinsic (*i.e.*, anthropogenic, environmental) factors having the potential to influence in-transit survivorship. For example, a roadway can attract wildlife –ultimately increasing the time an organism is on, or near, a road – by its association with an ideal basking surface (*e.g.*, lacertid lizards; Meek 2009), scavengable carrion (*e.g.*, vipers; DeVault and Krochmal 2002) or nesting sites (*e.g.*, pond turtles; Aresco 2005). Road-crossing speed and behavioral responses to passing vehicles vary among snake species having different life histories (Andrews and Gibbons 2005). Crossing speeds were the slowest in bulky (*i.e.*, rattlesnakes) and small-bodied (*i.e.*, ring-necked snakes) species. These types of snakes were also more likely to freeze when faced with an on-coming vehicle, which increases the chances of road mortality.

Extrinsic effects, and their interactions, have been documented as some of the greatest influences to amphibian and reptile road mortality. Subtle variations in nightly traffic intensity have been shown to affect the abundance of dead-on-road (DOR) amphibians, and overall amphibian populations (Fahrig *et al*. 1995) near roads. Gibbs and Shriver (2005) also encountered declines in turtle populations inhabiting areas of increased road density. Smith and Dodd (2003) encountered 623 dead snakes (1.85 snakes/km) in a year-long survey of a Florida roadway – the highest recorded level of snake mortality to date. Road mortality can also be affected by personal opinions about certain species; as a group, snakes are often subject to malicious killing by humans. On-road experiments coupled with personal surveys indicated snakes were more likely to be purposefully run over than other native animals encountered within road boundaries (Langley *et al*. 1989).

Direct road mortality rates are highest in vertebrates where the spatial connection among resources across a landscape is compromised by the road surface in question (Andrews *et al*. 2006). Roadways have little direct effect on overarching ecosystem features, such as adjacent habitat types or local climate patterns. Given that a landscape is composed of repeating ecosystem clusters interconnected by a number of nutrient and energy flows, a vertebrate population's intrinsic movement patterns stimulated by environmental variables will persist despite the obstructive and potentially lethal presence of a roadway.

Seasonal movements in amphibian and reptilian populations increase the vulnerability of taxa to road mortality and population decline. Amphibians are known for their explosive migrations to and from aquatic breeding aggregations. Ashley and Robinson (1996) observed over 30,000 amphibian road kills in conjunction with seasonal migratory breeding patterns. Glista *et al*. (2007) suggested these *en masse* migrations put amphibian populations at the highest risk of decline. Several studies have also investigated the effects of road mortality on sex ratios in turtle populations. Generally, female pond turtles make long-distance migrations out of their normal home ranges in order to reach optimal nesting sites (Beaurdy *et al*. 2010). These movements increase the chances of female road mortality, and the resulting shift to a male-biased sex ratio could limit effective population sizes (Gibbs and Steen 2005). Snake populations incur similar mortality, especially during seasonal activity peaks associated with breeding seasons (Bonnet *et al*. 1999; Hartmann *et al*. 2011; Sheperd *et al*. 2008; Shine *et al*. 2004), egg-laying (Bonnet *et al*. 1999), and the ingress and egress periods associated with over-wintering (Seigel and Pilgrim 2002; Shine and Mason 2004).

The general consensus among wildlife biologists is that indirect effects like road avoidance are more detrimental to vertebrate populations than direct road mortality (Andrews and Gibbons 2005; Bonnet *et al*. 1999; Forman and Alexander 1998); scientists especially urge against the use road-kill numbers as an estimator of overall mortality or population trends (Andrews *et al*. 2006; Bonnet *et al*. 1999). It could be argued that direct mortality trends will ultimately promote the selection of road avoidance behavior, however, and the issues of connectivity therein (Sheperd *et al*. 2008b). In situations where a road cannot be avoided, the reduction of certain age or sex class individuals can significantly decrease a population's viability. Row *et al*. (2007) analyzed the mortality rate and total expected number of crossings by a moderately-sized sample of radio-tracked ratsnakes. They reported that a small number of adult mortalities per year were enough to increase extinction risk from 7% to 98% over the next 500 years.

An interaction among two or more negative variables could increase direct mortality rates. Joly *et al*. (2003) used models and GIS overlays to display how increased traffic volumes during explosive amphibian migrations can decrease individual survivorship. Similar results were observed in several field experiments (Fahrig *et al*. 1995; Lode 2000; Sheperd *et al*. 2008).

My experiment assessed the significance of a number of variables influencing the temporal and spatial patterns of road mortality in a population of Midland Brownsnakes (*Storeria dekayi wrightorum*). Individuals of this population utilize two separate habitat types in the span of a year, and therefore must make biannual migrations between summer activity areas and over-wintering sites. However, in order to successfully reach either, snakes must traverse a 2.4-km stretch of paved road. Despite their relatively small size and cryptic nature, Brownsnakes readily cross the road surface during their seasonal migrations. There is no evidence to show that any cohort within this population elicits road avoidance behaviors; on the contrary, road surveys have yielded a substantial representation from all age and sex classes.

My study had two main objectives. First, I determined whether certain intrinsic (*i.e.*, overall body size, gender, behavior) or extrinsic (*i.e.*, temperature, season, traffic volume) variables affected Brownsnake survivorship. Next, I employed a Geographic Information System (GIS) to examine whether snake movements across the road tended to cluster around certain habitat features along the road. I analyzed these data to better inform potential efforts to mitigate road mortality rates in this population.

I expected that size variables like body mass or size would not influence snake mortality for two reasons. First, even the largest recorded Brownsnakes are small enough to be mistaken by a passing motorist for twigs or other road debris. And secondly, Midland Brownsnakes, like other species (Andrews and Gibbons 2005), utilize a freezing defensive behavior when threatened. Adopting this sort of posture while on a road surface increases that individual's risk of death, regardless of the snake body size. I also expected that male snakes would incur higher mortality than females, on account of their propensity to move more in search of mates at certain times of the year (Ernst and Ernst 2003). For this same reason, I suspected that male snakes would be less consistent in their movements across the road, thereby further increasing their chances of mortality. Moreover, I hypothesized that movement direction across the road would be best predicted by the season within the entire activity period.

Because the road and associated edge habitat do not serve either of the purposes of the adjacent ecosystems, I predicted that on-road encounter rates will peak during migration pulses. Next, I hypothesized that temperature and traffic volume will influence snake occurrence and mortality on the road, respectively. If my hypothesis is supported, then days where the temperatures best suited for Brownsnake migration coincide with the highest vehicle traffic will result in the highest mortality rates for Brownsnakes. Finally, I predicted that snakes would choose to cross the road at certain “hotspots”, my term for points along the road associated with certain habitat types or even scent trails laid down previously by other migrating Brownsnakes.

# METHODS

## Study site

Our study was conducted at Fox Ridge State Park (FRSP; Fig.1), located 11 km south of Charleston (Coles County, Illinois). The park is 835 ha in size, and consists of upland oak-hickory forests, lowland old-field and successional forests, and small patches of short-grass prairie. FRSP also contains approximately 8 km of paved, two-lane road. This road network consists of three components. The main road that connects to the park entrance forks near the center of the park, and those two new branches extend and culminate in canoe-launches on the Embarrass River. Our experiments focused on a 2.4-km stretch of road located in the distal portion of the northernmost branch, also called Ridge Lake Road. This stretch of road is unique in that it bisects lowland Brownsnake activity areas to the west from optimal hibernation sites located in the upland ridges to the east.

## Study organism

Midland Brownsnakes (*Storeria dekayi wrightorum*) are one subspecies within the *dekayi* complex. The distribution of the entire species ranges eastern United States, eastern Canada, and parts of Mexico and Central America (Ernst and Ernst 2003). Midland Brownsnakes are live-bearing, nonvenomous natricine snakes that are considered a member of the leaf-litter snake guild—an assemblage of small, fossorial snakes (but see Neill [1948] for arboreal behaviors) that feed mostly on snails, worms, and other soft-bodied invertebrates (Ernst and Ernst 2003). Brownsnakes have been known to reach 52.7 mm total body length (TBL), although individuals usually average 20.0-40.0 cm TBL. Breeding activities generally occur in mid-April at these latitudes. After an average gestation period of 74 (observed range: 14-113) days, females isolate themselves from conspecifics and give birth to about 13 (observed range: 3-41) young.

Despite their commonality across much of eastern North America, the cryptic nature of Brownsnakes and their relatives makes this entire group difficult to detect and study. Therefore, the amount of work done assessing the natural history and ecology of this guild in general is relatively scant (Clausen 1936; Neill 1948; Noble and Clausen 1936; Pisani 2009). Thus, my study site is novel in that a large proportion of one entire population can be opportunistically encountered and captured during highly synchronous migrations.

### Data collection

I surveyed the 2.4-km stretch of Ridge Lake Road by two methods. First, I installed nine 100-m drift fences at 170-m intervals along the entire uphill (east) side of the road. Drift fences and pitfall trap arrays are effective methods to passively survey small snake species in a large area. The fences were constructed from 45-cm rolls of silt fencing stapled to 30 cm wooden stakes. I augmented each fence with pitfall traps and rubber covermats. I used 19-L plastic buckets at 33-m intervals along the uphill side of the fence, and three 1-L buckets at 25-m intervals along the downhill side of the fence. Four pairs of covermats, each approximately 3 $m^2$, were placed evenly along the length and on each side of each fences.

To supplement the passive sampling efforts of the fences, I completed road-walking surveys to collect both live and dead snakes directly off of the road surface. During periods of high snake movement, I walked the road twice daily. Generally, the use of vehicles for transport between fences was only allowed when snake encounter rates were low enough that the vehicle 1) did not impair the accuracy of locating snakes on the road, and that it 2) did not add to the observed mortality data. If either of these criteria were broken, then I began road-walking surveys.

Upon encountering a snake, I first noted whether it was alive, or DOR (*i.e.*, dead or dying from a collision. Next, I gathered orientation data. Orientation was defined as the direction a snake was moving in prior to being disturbed. Therefore, if I encountered a snake on the road and facing the fence, it was considered to be moving "up". If I captured a snake on the uphill side of the fence, it was assumed that the snake was attempting to reach the lowland habitat, and so I considered it to be moving "down". The opposite was true for snakes encountered on the downhill side of the fence. Orientation data could not be collected either from individuals in any of the fences' end buckets, or from dead or dying individuals, since the force of a collision could have disturbed them from there original positions. Next, I recorded the GPS location of where all live and DOR snakes were first sighted. If a snake was located in a bucket or under a coverboard, I gathered that object's location code as well. In order to identify recaptured snakes, I uniquely branded all live individuals using a medical cauterizer. Winne and colleagues (2006) identified these medical cauterizers as a field-portable and inexpensive means of marking small-bodied snakes. The marks have also been shown to last two years, or more in some species. To conserve battery life, we marked DOR individuals with a round-tipped permanent marker; however, we did not mark or take morphometric data from DOR individuals that were too desiccated to provide accurate measurements.

All live snakes and DOR snakes in good condition were brought to the lab for further processing. There, I measured mass (±0.01 g), snout-vent length (SVL) and tail length (±1 mm). I palpated all snakes to determine the presence of stomach contents; females were also palpated to determine gravidity. Finally, I determined gender via cloacal probing. It should be noted that I took measurements in the order of increasing level of stress put on the animal in order to minimize stress throughout the entire procedure. I collected all possible accurate measurements from DOR individuals (*e.g.,* flattened snakes still provided SVL and/or TL data, but not data for mass or gender).

I collected daily traffic volume data from an Illinois Department of Transportation (IDoT) car counter installed at the start of the 2.4 km study stretch. All live specimens were captured under the authorization of IDNR permits, and were handled in accordance with IACUC guidelines.

Prior to any hypothesis testing, I ran the appropriate normality tests (PROC UNIVARIATE, SAS) on all response variables. Due to the absence of normality in the majority of my variables ($p<0.001$ in Kolmogorov-Smirnov tests), all statistical analyses in my study were done using non-parametric analyses. I used a Kruskal-Wallis test (PROC NPAR1WAY, SAS) to determine whether body size variables (*i.e.*, SVL, TL, mass) had an effect on snake survivorship, orientation when crossing a road surface, and overall activity season. Next, I used Chi-Square analyses (PROC FREQ, SAS) to investigate the differential effects of mortality across sexes, orientation across sexes, and overall orientation across seasons. Finally, a Kernel-density function within ArcGIS visualized the spatial clustering of snake movements across the road, and variation in clustering across seasons.

# RESULTS

Since October 2010, 1885 Midland Brownsnakes have been collected from Ridge Lake Road and associated drift fence arrays. Of those snakes, 1184 (62.8%) were DOR individuals. It should be noted that my lab group and I have captured an additional 11 snake species either on or adjacent to the road surface at FRSP. These species include: Gray Ratsnake (*Pantherophis spiloides*), Blue Racer (*Coluber constrictor foxii*), Prairie Kingnsnake (*Lampropeltis c. calligaster*), Red Milksnake (*Lampropeltis triangulum syspila*), Eastern Milksnake (*Lampropeltis t. triangulum*), Eastern Hog-nosed Snake (*Heterodon platirhinos*), Northern Watersnake (*Nerodia sipedon*), Rough Greensnake (*Opheodrys a. aestivus*), Common Gartersnake (*Thamnophis s. sirtalis*), Northern Ring-necked Snake (*Diadophis puntatus edwardsii*), and Northern Red-Bellied Snake (*Storeria o. occipitomaculata*).

Neither SVL (K-W statistic = 0.12, p = 0.74) nor TL (K-W statistic = 0.17, p = 0.68) were effective predictors of road mortality. Live snakes had greater mass than DOR individuals (K-W statistic = 14.4, p = 0.0002). Females had longer SVL, shorter TL, and larger masses than male snakes ($p < 0.0001$).

Male snakes suffered higher mortality than females ($\chi^2 = 16.38$, p< 0.0001; Fig. 2); in spite of that fact, male and female snakes were equally likely to, in any season, cross the road in both directions (Spring: $\chi^2 = 0.85$, p= 0.36; Summer: $\chi^2 = 0.00$, p =1.00; Autumn: $\chi^2 =3.50$, p= 0.06; Fig. 3). Snakes migrating into the lowland habitat were less numerous than the number of snakes present in the Autumn migration (K-W statistic = 28.69, p <0.0001; Fig. 4, 5).

# DISCUSSION

My results indicate that a number of intrinsic and extrinsic ecological factors relate to the overall negative influence of roadways on this population of Midland Brownsnakes. First, I discovered that body mass, but no other size factor, influenced the probability of snake mortality. Brownsnakes have a diminutive profile that makes them difficult to identify and avoid along a road surface, even among drivers inclined to do so. It is very likely that what is an improvement in size, in reality, might have very little biological influence on the snake's overall size or ability to flee from predators. When threatened, a brownsnake will often elicit a freezing defensive behavior. A common occurrence among small or cryptic species, this behavior is selected for in a natural context where predators often rely on visual cues to detect prey. In the foreign context of a road surface, freezing behaviors increase the amount of time a snake resides on the roadway, thereby increasing the chances of a vehicle collision (Andrews and Gibbons 2005).

In road avoidance tests, Andrews and Gibbons (2005) observed nearly absolute road avoidance in Ring-necked Snakes (*Diadophis punctatus*), another small-bodied species. They conclude that behavioral and natural history traits might have more explanatory power in discerning patterns of inter-individual survivorship. Such insights could streamline conservation decisions that have to do with road planning in sensitive areas.

The direction of brownsnake movement was dependent on season, with snakes entering the lowland habitat in the Spring, and migrating to the upland forests in the Autumn (Fig. 3). In the Spring, snakes descend from the upland ridges and enter lowland areas containing wetlands and old fields, where substantial snail and worm populations sustain breeding adults and newborn individuals. Pisani (2009) reported similar findings for a population that hibernated in forest edge habitat, then migrated to grassier and prairie habitats in the Spring. Brownsnakes at

FRSP benefit from the utilization of two distinct habitat types in the course of a single year. The innate drive to make migrations (Pisani 2009) across a fragmented landscape might have originated at a time when no road barrier was present, which would explain their willingness to traverse an exposed road surface (thereby subjective themselves to both natural and anthropogenic mortality risk; Bonnet *et al.* 1999).

Shine and Mason (2004) introduced the idea that mortality risk during periods of inactivity can dwarf the risk associated with predation or roadkill during migratory periods. They estimated mortality of a population of Red-Sided Gartersnakes (*Thamnophis sirtalis parietalis*) to > 60,000 animals following freezing and flooding events in three large dens. Seigel and Pilgrim (2002) reported on the factors (*e.g.*, habitat alteration due to flooding, or direct road mortality) had greater influence on the shift in migratory behavior they observed in a population of Masassaugas (*Sistrurus c. catenatus*). They hypothesized that the population was composed of migrating and non-migrating individuals, and that a factor (or factors) reduced numbers of the migrating individuals. The semi-annual flooding that occurs in the lowland areas of FRSP could explain the persistence of annual migrations of brownsnakes towards upland hibernacula. Because these flooding events only inundate parts of brownsnake activity areas during the early spring, drastic population losses (*e.g.*, Shine and Mason 2004) would not be expected. Thus, direct road mortality is the most obvious threat to migrating brownsnakes at FRSP.

Generally, snake-road interactions are negative; for those snakes that survive a road crossing, the tongue and oral mucosa of scent-trailing individuals can become irritated by road particulate (Andrews and Gibbons 2005; Shine *et al.* 2004). In contrast, however, snakes sometimes sit motionless and prostrate on warm road surfaces for extended periods (Ashley and

Robinson 1996). Andrews and Gibbons (2005) argued that these are simply exaggerated freezing defensive behaviors in the presence of incoming vehicles or people.

Snake encounter rates were higher in the Autumn than in other seasons (Fig. 5). One explanation for this pattern is that the young-of-year individuals migrating for the first time raised the total number of snakes encountered at that time. Female *T. s. parietalis* typically approach hibernacula using preferred migratory corridors, while dispersal during egress occurs in all compass directions (Shine *et al.* 2001). It is possible that Brownsnakes at FRSP display similar dispersal responses prior to their migration into the lowland habitat. This type of behavior may allow females to acclimate to climatic conditions before mating or dispersing further. Further research in this system should attempt to identify Brownsnake over-wintering sites in FRSP so that patterns of post-emergence dispersal could be better understood.

Male Brownsnakes incurred higher road mortality than their female counterparts (Fig. 2). In general, this pattern is explained by male snakes having increased vagility when searching for mates, and therefore in greater risk of encountering a predator or other threat. Bonnet *et al.* (1999) and Hartmann *et al.* (2011) examined various mortality risks dependent on the amount of movement. They observed that snakes were at highest risk during long-distance movements outside of their home ranges. Sedentary snakes, therefore, were least threatened by natural or anthropogenic threats. Similarly, in the weeks preceding birth, gravid Brownsnakes will isolate themselves and immobilize (Clausen 1936). As has been shown in other snakes (Waldron *et al.* 2013), female brownsnakes that produced offspring in a given year might be at higher risk of over-wintering mortality than individuals that were not gravid in the same year. The sampling regime of my study could not quantify this possibility.

Brownsnake mortality on the road surface at FRSP was highest during the Autumn migration – likely caused by the combined influences of temperatures promoting snake occurrence on the road and traffic volume on mortality (Fig. 5, 6). Previous studies have demonstrated that snake mortality is correlated with summer temperatures that spurred snake movements, or the interactions of temperature with traffic volume and habitat type (Ciesiołkiewicz *et al.* 2006; Sheperd *et al.* 2008). My experiments indicated that Brownsnake mortality within the Autumn increased when traffic volume was highest, during during the weekends. Although high traffic volume occurring during large migration pulses can exacerbate mortality, its localized nature also offers opportunities to mitigate roadkills through various means.

Patterns of road mortality in my study system were shaped by topography and habitat formations on either side of the roadway. In FRSP, snake movements in the spring associated with a fair proportion of the drift fences. I expect that the optimal microhabitat found beneath coverboards made this passive sampling method most effective at that time period. During the Autumn migration, however, movement clusters have shifted from the drift fences to areas associated with valleys or temporary streambeds that form a pathway of low-slope topography. It is likely that brownsnakes follow these streambeds into the upland habitat, where they find appropriate microhabitat in which they hibernate. It is also worth noting that one of the two snake movement clusters along the FRSP road was more closely associated with some riparian habitat near the Embarrass River than any other section of road. Amphibian and reptile corridors often overlap with wetland habitats (Glista *et al.* 2007; Langen *et al.* 2007). At FRSP, brownsnakes may be utilizing wetter areas to feed on soft-bodied invertebrates prior to fall migrations.

Corridors between two suitable parcels of habitat are typically installed as culverts that allow animals to pass underneath a road.  These structures range in size and design, depending on the type of road and taxa involved, and might also be constructed as bridges passing over a road. Corridors have reduced mortality in a number of herpetofaunal communities (Aresco 2005b; Dodd *et al.* 2004; Jackson 2003; Patrick *et al.* 2010). Installing such culverts in locations that harbor the highest occurrence of snake movements within FRSP might reduce the overall mortality rate in this population.

My study has identified a number of factors – including seasonal, spatial, and sexual components – that influence road mortality in a little known species of leaf-litter snake. As a result of gender-driven variation in movement, male brownsnakes incurred greater mortality than their female counterparts. Snake encounter rates on the road as a whole varied with season, with periods of higher movement frequency occurring in the Autumn, and in association with topographic cues. Because of their dependence on distinct habitat features, this population of Midland Brownsnakes traverses a road surface despite high mortality risk. After almost three activity seasons, 63% of snake encounters have been DOR individuals. Further investigation will determine whether this population can sustain itself in the face of large, annual mortality events. These findings might also apply to similar systems involving species of greater conservation concern in Illinois, such as Kirtland's Snakes (*Clonophis kirtlandii*). Furthermore, where they occur in proximity to roads, future studies involving small-bodied snake should consider road-related factors in their experimental design.

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# FIGURES

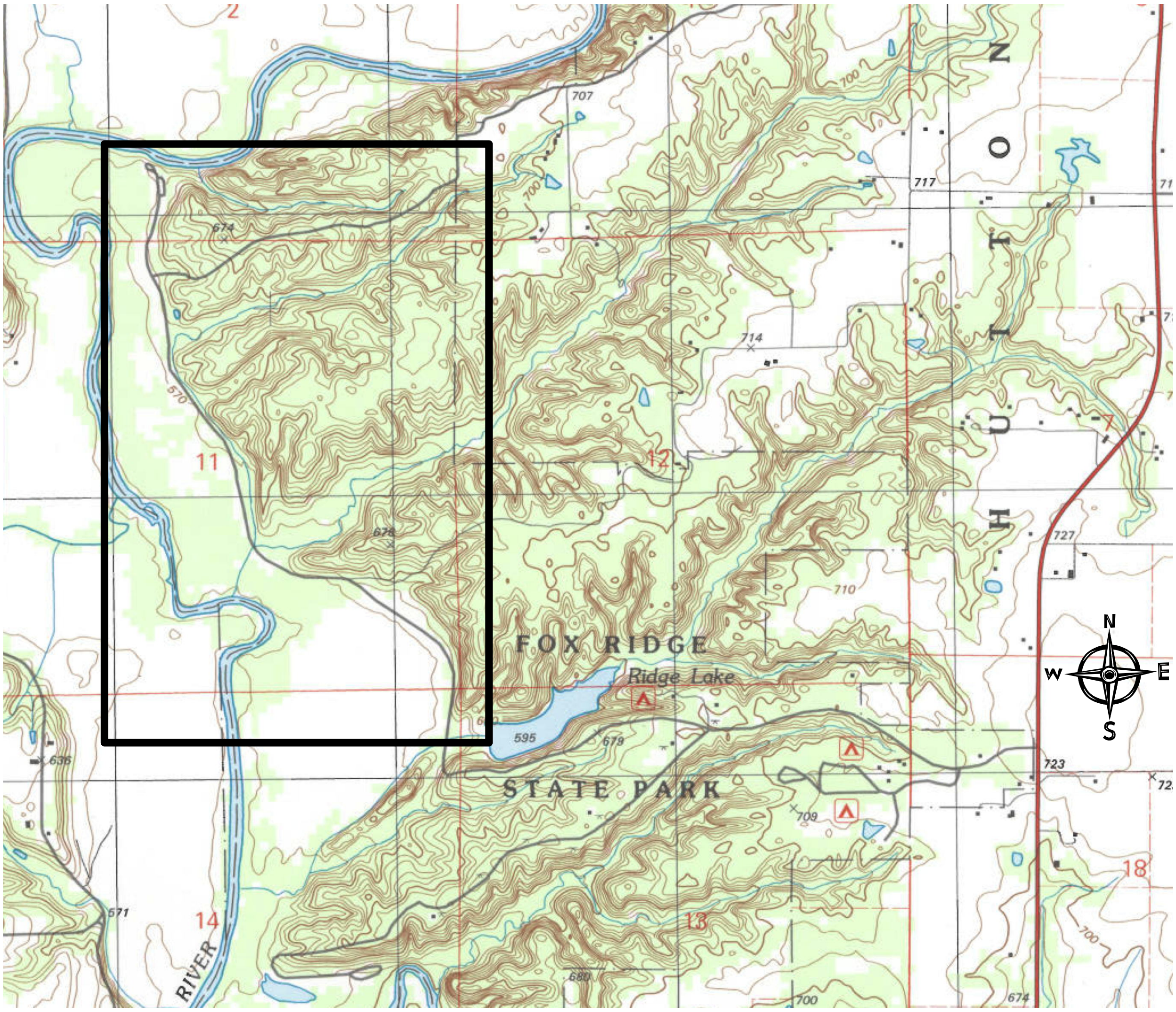

Fig. 1. Topographic map of Fox Ridge State Park (FRSP; Coles Co., Illinois). The rectangular box identifies the 2.4-km study road running along the ecotone between lowland areas to the west and upland forests to the east.

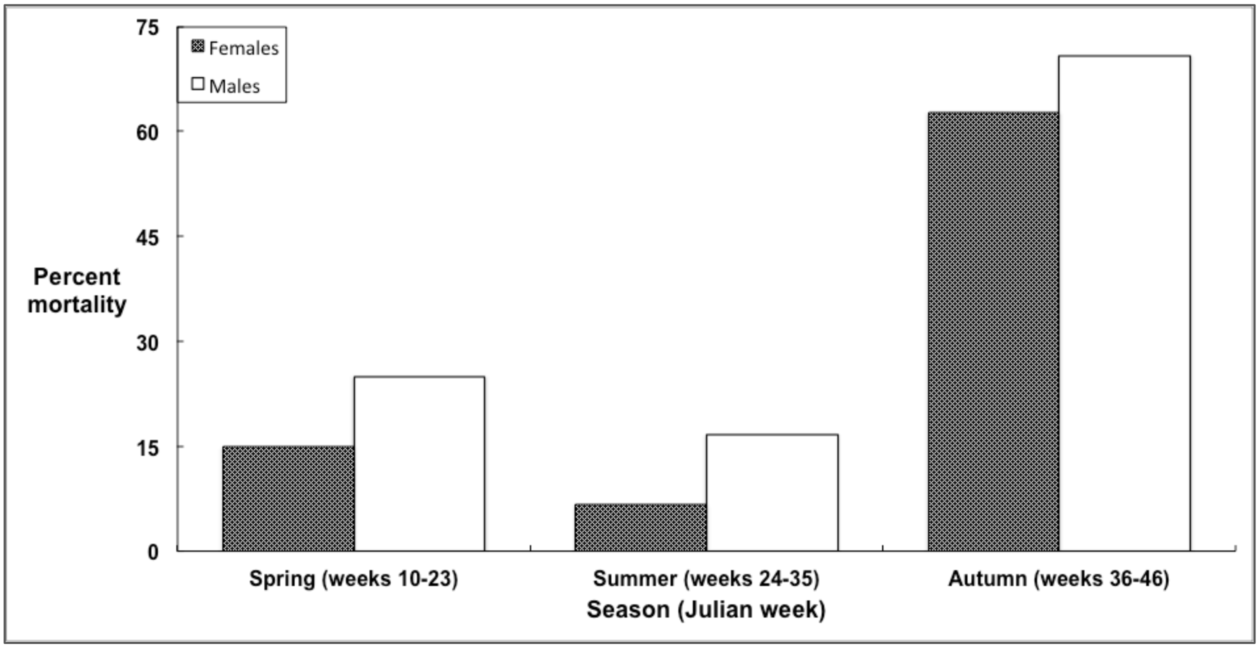

Fig. 2. The percentage of female and male Midland Brownsnakes (*Storeria dekayi wrightorum*) found dead-on-road (DOR) across three seasons.

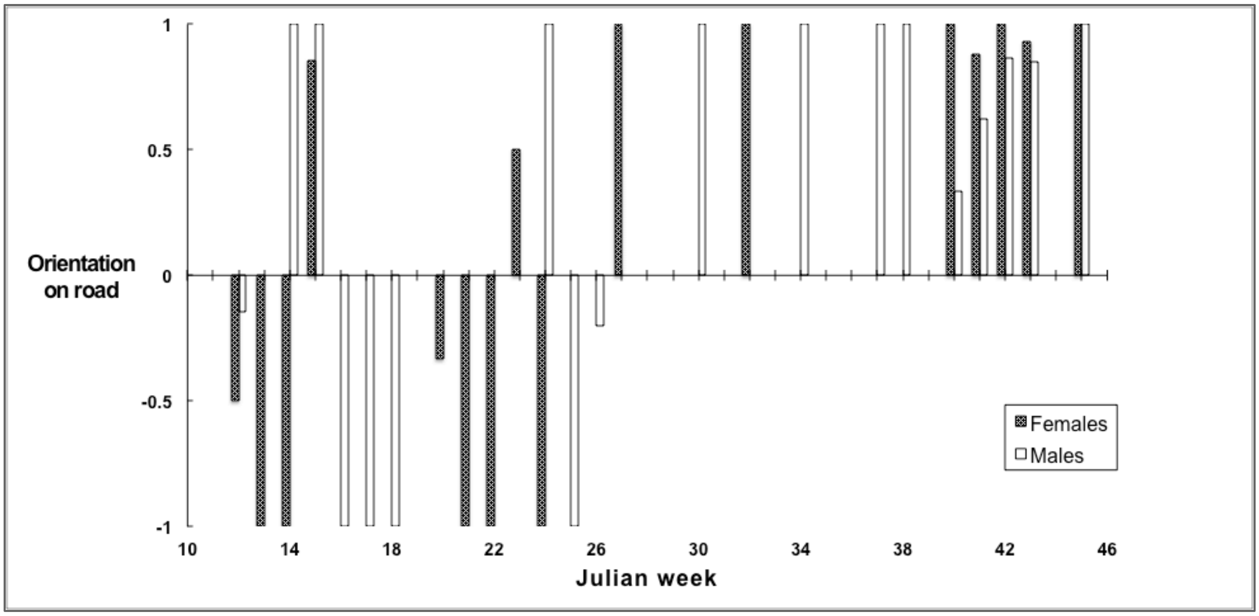

Fig. 3. Weekly orientation trends for all live female and male Midland Brownsnakes (*Storeria dekayi wrightorum*). Bars with a value above zero indicate that snake movements were generally towards upland habitats, while negative values indicate snakes focused movements into lowland areas.

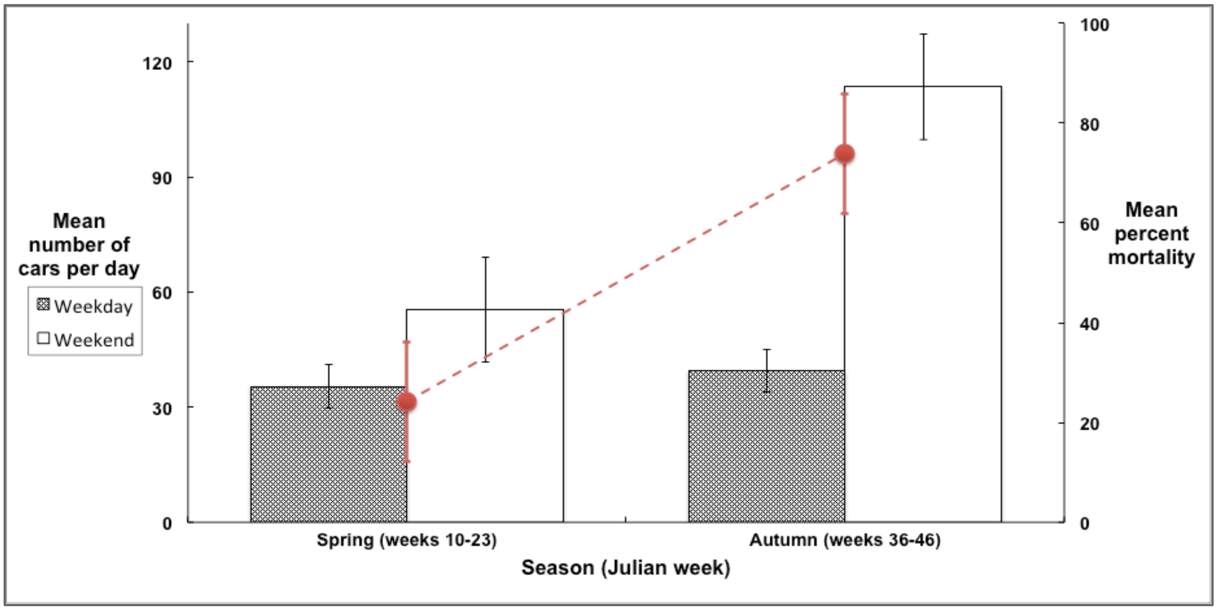

Fig. 4. Average daily traffic volumes (±1 SE) and mortality rates (solid points; ±1 SE) for Midland Brownsnakes (*Storeria dekayi wrightorum*) across Spring and Autumn seasons.

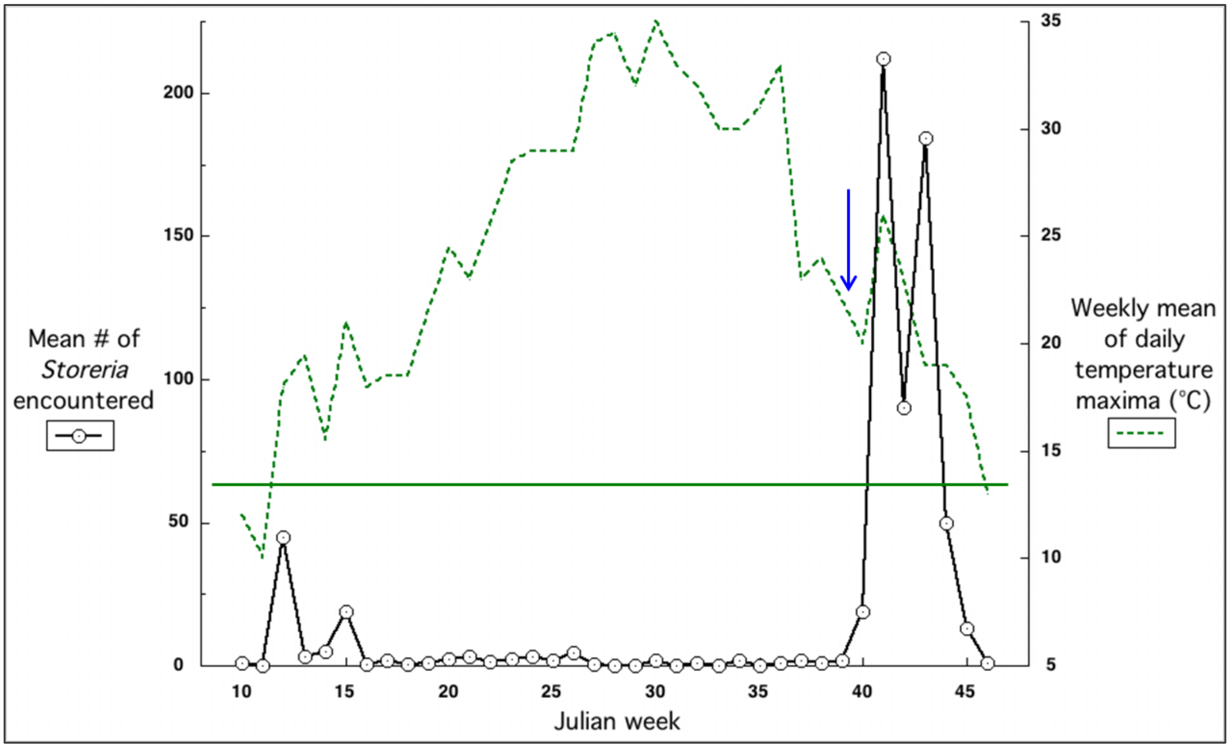

Fig. 5. Weekly mean encounter rates for Midland Brownsnakes (*Storeria dekayi wrightorum*) and weekly mean of daily high temperatures plotted over time. The horizontal line indicates the minimum temperature threshold for snake encounters. The arrow indicates a steep temperature decline that appears to stimulate snake movements.