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Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*)

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ABSTRACT

Roads negatively affect animal populations by presenting barriers to movement and gene flow and by causing mortality. We investigated the impact of a secondary road on a population of black ratsnakes (*Elaphe obsoleta*) in Ontario, Canada by radio-tracking 105 individuals over 8 years. The road was not a significant barrier to movement and none of the reproductive classes examined (male, non-reproductive female, reproductive female) avoided crossing the road. However, the road was a significant source of mortality. From a total of 115 road crossings by radio-implanted snakes, 3 individuals were killed by cars, resulting in a mortality rate of 0.026 deaths per crossing. We multiplied this mortality rate by the total number of expected road crossings by all individuals in the population in an active season (340) to estimate the number of road kills (9 individuals) each year. This estimate was higher than the actual number of road kills found, but half the number estimated from road kill models. Population viability analysis revealed that our estimate of road mortality was enough to increase the extinction probability for this population from 7.3% to 99% over 500 years. Road mortality of more than 3 adult females per year increased the extinction probability to >90%. Our results strengthen the view that road mortality can have a pronounced negative effect on populations of long-lived species.

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1. Introduction

The ecological impact of roads has been estimated to extend to up to 15–20% of the total land area of most nations (Reijnen et al., 1995). Roads affect their surrounding environment in many ways that are detrimental to the neighboring animal populations (Forman and Alexander, 1998). Studies from the emerging field of road ecology have shown that many species of mammals (Dyer et al., 2002; Dickson et al., 2005; Riley et al., 2006), reptiles (Klingenberg et al., 2000; Koenig et al., 2001; Andrews and Gibbons, 2005; Richardson et al., 2006), and invertebrates (Bhattacharya et al., 2003) avoid crossing roads. Roads can therefore act as significant barriers to gene flow, which can ultimately reduce the overall genetic diversity of

populations (Epps et al., 2005) and lead to an increased extinction risk (Saccheri et al., 1998). Furthermore, road networks can also cause heavy mortality (Rosen and Lowe, 1994; Trombulak and Frissell, 2000; Seiler et al., 2004; Mazerolle, 2004) for many species of animals and can alter the demographics of the surrounding populations (Mumme et al., 2000; Aresco, 2005; Gibbs and Steen, 2005).

To our knowledge, very few studies have attempted to examine intraspecific variation in road avoidance. Differences in ecology and behavior (mate searching, nest prospecting) between reproductive classes (males, non-reproductive females, and reproductive females) are reflected in their movement patterns (Blouin-Demers and Weatherhead, 2002), which could alter their tendencies to cross roads. In turn,

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differences in road crossing should lead to differences in road mortality (Bonnet et al., 1999). Increased mortality rates for different reproductive classes can have profoundly different consequences for a population. For instance, increased mortality of gravid females will have a more dramatic demographic impact than increased mortality of males. It is therefore important that studies examine intraspecific differences in risks of road mortality if we are to make accurate predictions about the impacts of road mortality on animal populations.

Most studies documenting the negative impacts of roads estimate the number of road kills using models, or make inferences from the number of road kills found in road surveys. These methods have biases (e.g., road kills being removed by scavengers) and may not accurately represent the total number of road kills. Some studies have tried to circumvent these problems by measuring population parameters in areas with and without roads (Gibbs and Steen, 2005). To our knowledge, however, no studies have directly measured road mortality rates and determined their impact on population viability. Without such studies, it is difficult to evaluate the severity of the effect road mortality has on animal populations.

The general goal of this study is to assess the impacts of a secondary road on a population of black ratsnakes (*Elaphe obsoleta*) in Ontario, Canada. Ratsnakes in our population take 7–9 years to reach maturity and have a maximum lifespan of ~20 years (adapted from Blouin-Demers et al., 2002 using unpublished data), making their populations particularly vulnerable to increases in adult mortality (e.g., through road mortality) (Brooks et al., 1991; Congdon et al., 1994). First, with data from a long-term radio-telemetry study, we examine road avoidance behavior and estimate risk of road mortality for 3 reproductive classes of black ratsnakes. Second, we estimate road mortality rates with three methods (including direct measures) and determine the consequences of this mortality on the population using population viability analysis (PVA).

2. Methods

2.1. Study area and species

We conducted this study from April 1996 to October 2004 at the Queen's University Biological Station (QUBS), 100 km south of Ottawa, Ontario, Canada. The study area was approximately 2000 ha and comprised mainly of rolling terrain covered with second-growth deciduous forest, intermixed with numerous old fields, rocky outcrops, lakes, and marshes. One secondary road (Opinicon Road) bisects the study area from northeast to southwest and services numerous smaller cottage roads (Fig. 1 in Blouin-Demers and Weatherhead, 2002). Here we consider only the effect of Opinicon Road. Because the road is used principally to access summer cottages, traffic is heaviest during the summer months, coincident with the snakes' active season. The road is approximately 6 m wide including the shoulders, with a narrow (4 m) margin of grass and herbaceous vegetation. Beyond this margin the dominant habitat is mixed deciduous forest. During the study, the road surface was primarily gravel. Although the speed limit was 80 km/h, vehicles generally traveled somewhat

more slowly (~60 km/h) because of the numerous curves and hills.

Our ratsnake population has been studied continuously since 1981 (Weatherhead et al., 2002). Here we refer to the study species as the black ratsnake (*E. obsoleta*), but note that recent genetic analyses (Gibbs et al., 2006) create some uncertainty regarding the eventual taxonomic designation.

Within the study area, we captured individuals opportunistically throughout the active season and at hibernacula during spring emergence (Blouin-Demers et al., 2000; Row and Blouin-Demers, 2006). We implanted radio-transmitters (Model SI-2T, battery life of 24 months at 20 °C, Holohil Systems Inc., Carp, Ontario) in 105 individuals (25 males, 52 non-reproductive females, and 28 reproductive females) for periods ranging from a few weeks to a few years. Individuals with radio-transmitters were located approximately every second day. We recorded the UTM coordinates with a GPS at each location to map the movement paths of individuals.

2.2. Road avoidance

For the road avoidance analyses, we used individuals that were tracked for a complete active season (May–September) only and divided them into 3 groups based on their reproductive status: males ($N = 15$), reproductive females ($N = 17$), and non-reproductive females ($N = 34$). Female ratsnakes rarely reproduce every year. Thus, we considered individuals tracked in multiple years ($N = 14$) independently each year they were tracked. We calculated the degree of road avoidance for each individual by comparing the actual number of road crossings made by the individual to the number of road crossings it would have made if it moved randomly with respect to the road. We determined the number of crossings made by a randomly moving snake by generating 20 'random walk' movement paths for each individual (Klingenberg et al., 2000; Koenig et al., 2001) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). Each random movement path started in the same location as its paired snake movement path and had the same chronological series of distances moved, but we used a randomly determined bearing between each move. For each individual, we took the difference between the mean number of road crossings for the 20 random movement paths and the actual number of road crossings made by the individual. We then compared these values between the reproductive classes. Finally, we determined overall road avoidance for each reproductive class by testing the distribution of differences between real and random crossings against 0.

2.3. Road mortality

We determined the effect of road mortality on this population by 1) determining if the risk of mortality was the same for all reproductive classes, and 2) by calculating the mortality rate of radio-implanted individuals and using this rate to estimate the total number of adult road kills expected each year. We estimated the risk of road mortality for each reproductive class by comparing the total number of road crossings made between classes and months. We used the same classes and individuals as in the road avoidance analysis. The test, how-

ever, was different from our measure of road avoidance because a particular reproductive class may have a greater road mortality risk simply because it moves more. Because we compared the number of road crossings to a paired randomly moving snake in the road avoidance analysis, this greater risk would not have been detected. We expected the road mortality risk to be higher for snakes that hibernated closer to the road and, therefore, measured the distance from each individual's hibernaculum to the road and included it as a covariate in the analysis.

We calculated road mortality rate by dividing the total number of radio-tracked individuals that were killed by vehicles by the total number of road crossings for all 105 individuals (including individuals not tracked for a full active season). We then estimated the expected number of road kills each year by multiplying the road mortality rate by the expected number of road crossings for all adults in the population. To determine if our estimate of the total number of road kills was reasonable, we compared the results of our calculations with the actual number of road kills found on the road each year. In all years, the whole length of the road within our study area (10 km) was usually driven at least once a day in both directions and any road kill encountered was collected, but we did not quantify search effort formally. The exception was 1997 when an extensive road kill study was conducted and the road was driven slowly once a day and biked once a week.

For comparative purposes, we also calculated the mortality rate with the equation $P_{\text{killed}} = 1 - e^{-Na/v}$ developed by Hells and Buchwald (2001). This equation attempts to determine the probability of an individual being killed (P_{killed}) while crossing the road, given the traffic intensity N (vehicles/lane/min), the kill zone a (m), and the velocity of the individual v (m/min) while crossing the road. This equation has been used to estimate road mortality for amphibians (Hells and Buchwald, 2001), turtles (Gibbs and Shriver, 2002, 2005), and snakes (Roe et al., 2006). Although the validity of this equation has been verified for amphibians (Gibbs and Shriver, 2005), no validation has been conducted for reptiles or larger-bodied animals.

We determined traffic intensity by counting the number of vehicles that passed per minute (in either lane) at different time periods each day based on a mean of 80 min/day of observation, evenly distributed across daylight hours (ratsnakes are diurnal in our population) throughout the active season (May–September) of 1997. Because this road has 2 lanes, we divided the number of vehicles/min by 2. We used a 2-way ANOVA to determine if traffic intensity varied significantly between months.

Although we did not measure the velocity of ratsnakes in our population, Andrews and Gibbons (2005) tested the behavioral response of snakes to roads for a variety of species. In their study, black ratsnakes had an average speed of 7.4 cm/sec (4.44 m/min) while crossing the road. Lastly, we calculated the kill zone as the width of two tires (2×0.25 m) plus the average SVL of adult ratsnakes (1.2 m) used in this study, under the assumption that the snake would be killed if any part of its body was struck.

2.4. Population effects

To determine the effects of road mortality on the population, we used Vortex 9.5 (Lacy et al., 2003) to perform a population viability analysis (PVA) with and without road mortality included. For simplicity and because snakes have very small energetic requirements, we considered the population within our study area to be one population with an unlimited carrying capacity. It is noteworthy that the PVA results were relatively insensitive to carrying capacity, however. Individuals from numerous hibernacula were used in this study, but these hibernacula populations are not genetically differentiated (Lougheed et al., 1999) and individuals from different hibernacula regularly mate with each other (Blouin-Demers and Weatherhead, 2002; Blouin-Demers et al., 2005). The life history parameters included in the PVA were taken directly from published research (from the QUBS population) in all but a few cases. The values and literature used (if applicable) are listed in Table 1. The adult population of black ratsnakes within our study area has been estimated to be 400 (Blouin-

Table 1 – Life history parameters used in Vortex 9.5 (Lacy et al., 2003) to execute a population viability analysis (PVA)

Parameter	Value	Literature
<i>Reproductive system</i>		
Age at maturity	Males – 8 years Female – 8 years	Adapted from Blouin-Demers et al. 2002 using unpublished data ^a
Maximum age of reproduction	20 years	Adapted from Blouin-Demers et al. (2002) using unpublished data ^a
Maximum # of progeny	17	Blouin-Demers et al. (2004)
Sex ratio at birth	1:1	Blouin-Demers et al. (2004)
<i>Reproductive rate</i>		
% Adult females breeding	41.5 ± 8.5%	Blouin-Demers and Weatherhead (2002)
# Offspring/female	10 ± 2	Blouin-Demers et al. (2004)
<i>Mortality rates</i>		
0–7 years	30.5–20.5 ± 5%	See Section 2
>8 years (adult)	18.5 ± 5%	See Section 2
<i>Mate monopolization</i>		
Mean #mates/sire	2.15	Blouin-Demers et al. (2005)

^a Recent data added to the growth models used in Blouin-Demers et al. (2002) modified the published estimates slightly.

Demers et al., 2002). Using this adult population, we estimated the total initial population size (including juveniles) to be 2500 based on a stable age distribution.

Using unpublished raw data from Weatherhead et al. (2002), we calculated the survival rate of ratsnakes to be 0.68 ± 0.17 . This rate included the effect of road kills, however, and we wanted to start with a population not affected by road mortality. Also, applying this mortality rate to a cohort of 1000 adults, no individuals survived from maturity (8 years) to the oldest age class (20 years) estimated by growth models (adapted from Blouin-Demers et al., 2002 using unpublished data). Therefore, we adjusted the mortality rate to allow 10% of 1000 adults to survive from maturity to the oldest age class. We also had no estimates of juvenile mortality, so we similarly adjusted the mortality rate to allow 10% of 1000 juveniles to survive until adulthood (8 years), but also required that survival increased with age (~2% increase in each age class) (Blouin-Demers et al., 2002).

2.5. Statistical analysis

We compared the degree of road avoidance (the difference between the number of actual road crossings and the number of road crossings estimated for randomly moving snakes) between the reproductive classes using a Kruskal–Wallis test. A Kruskal–Wallis test is the same as a one-way ANOVA except the data have been ranked. To test for overall differences between actual and random number of road crossings, we tested the distribution of the degree of road avoidance (number of actual road crossings – number of road crossings by random movements) against 0 using a Wilcoxon–signed rank test.

We used a permutation 3-way analysis of covariance (ANCOVA) to determine if there were differences in the total number of road crossings (risk of road mortality) between the reproductive classes and between different months of the active season, while controlling for the distance of each individual's hibernaculum to the road. The permutation ANCOVA reshuffled the dataset 1000 times and calculated an F-value from the ANCOVA for each permutation. Significance was determined by calculating the percentage of time that the F-value from a reshuffled ANCOVA was greater or less than the actual F-value.

All statistical analyses were performed with R (R Development Core Team, Vienna, Austria) or JMP version 5.0.1 (Statistical Analysis Systems, Cary, North Carolina). We reported all means \pm one standard error and accepted significance of tests at $\alpha = 0.05$.

3. Results

3.1. Road avoidance

Contrary to our prediction, there was no significant difference in the degree of road avoidance between any of the reproductive classes ($R^2 = 0.02$, $F_{2,65} = 0.66$, $p = 0.52$) and therefore we pooled them. Snakes crossed the road an average of 0.85 ± 0.20 times per season (maximum number of crossings = 8), whereas randomly moving snakes crossed the road an average of 0.93 ± 0.09 times per season (maximum number

of crossings = 11). A Wilcoxon–signed rank test showed that the difference between actual and random number of road crossings, pooled over reproductive classes, was not significantly different from 0 (Signed-Rank₆₅ = 200, $p = 0.14$).

3.2. Road mortality

Although there was an indication of a potential interaction between reproductive class and month (Fig. 1), all the interactions in the total number of road crossings (road mortality risk) model were non-significant and were removed. In the reduced model, there was no significant difference in the total number of road crossings between the reproductive classes ($F_{2,395} = 2.38$, $p = 0.09$) or months ($F_{5,395} = 1.73$, $p = 0.14$), and the effect of distance from hibernacula to the road was non-significant ($F_{1,395} = 0.87$, $p = 0.37$).

Adult radio-implanted snakes crossed the road 115 times and 3 were killed by cars, resulting in a mortality rate of 0.026 deaths per crossing. Because of the small number of road kills, we could not compare differences in road mortality between reproductive classes. Because there was no significant difference in the number of road crossings, however, we assumed that road mortality would be equal for the different reproductive classes. Given the estimated adult population size (400) (Blouin-Demers et al., 2002) and road crossing frequency (0.85 ± 0.20 times per season), the total number of road crossings expected by adults in a given season is 340. With a 0.026 chance of mortality per road crossing, there would be approximately 9 adults killed each year. The actual number of adult road kill ratsnakes found each year (mean = 3.25 ± 0.73) was lower than this estimate every year (Fig. 2).

Traffic intensity (vehicles/lane/min) on Opinicon Road varied significantly by month ($R^2 = 0.01$, $F_{4,1254} = 4.14$, $p = 0.005$; Fig. 3). We therefore determined the expected number of road kills separately for each month using the equation: $P_{killed} = 1 - e^{-Na/v}$. The average SVL of individuals tracked throughout this study was 1.2 m. This was added to the width

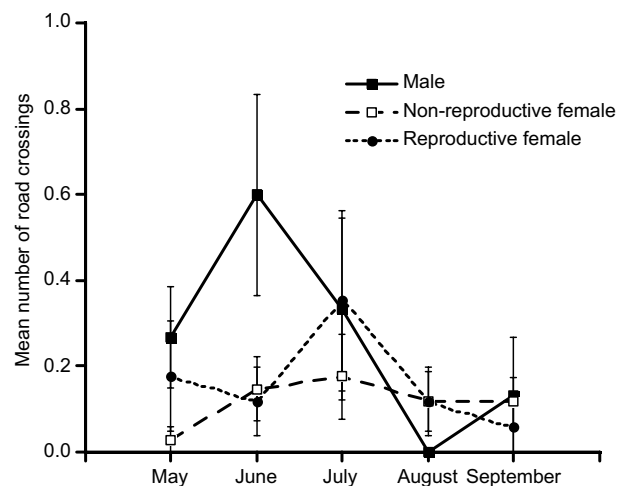


Fig. 1 – Mean number of road crossings (\pm SE) across months and between reproductive classes for black ratsnakes in eastern Ontario.

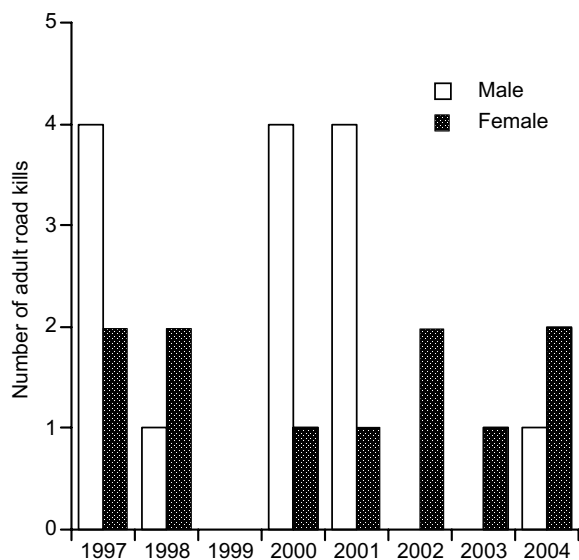


Fig. 2 – Total number of adult black ratsnake road kills found on Opinicon Road within the Queen’s University Biological Station study area from 1997 to 2004.

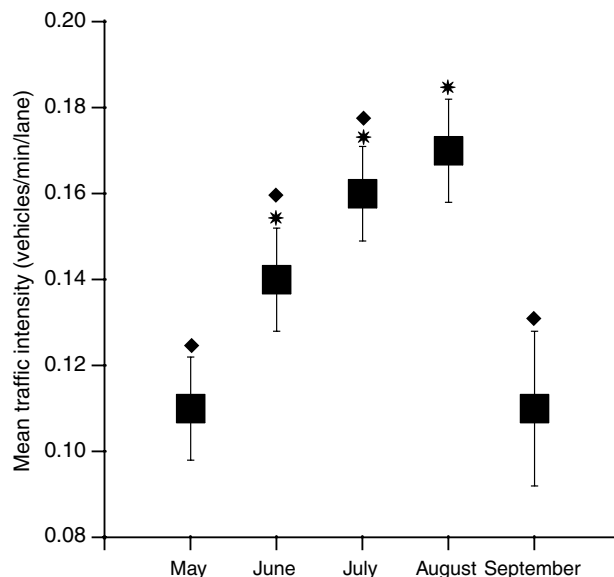


Fig. 3 – Mean traffic intensity ± SE on Opinicon Road across months. Means with the same symbol are not significantly different from one another at $p = 0.05$.

of 2 tires ($0.25\text{ m} \times 2$) to give a kill zone of 1.7 m. Therefore, the probability of a snake being killed while crossing the road for May, June, July, August, and September is 0.042, 0.053, 0.061, 0.064, and 0.042, respectively. All of these estimates are higher than our observed mortality rate (0.026). To determine the expected number of road kills using this equation, we determined the mean traffic intensity for the full active season (0.14) and used this value in the equation. This gave a mortality rate of 0.053 deaths per crossing. Given this mortality rate

and our calculated 340 total road crossings annually, this equation predicts that 18 adult ratsnakes will be killed crossing the road each year.

3.3. Population effects

Using the parameters presented in Table 1, the extinction risk for 1000 population simulations over 500 years was 7.3% and the mean instantaneous population growth rate (r) averaged

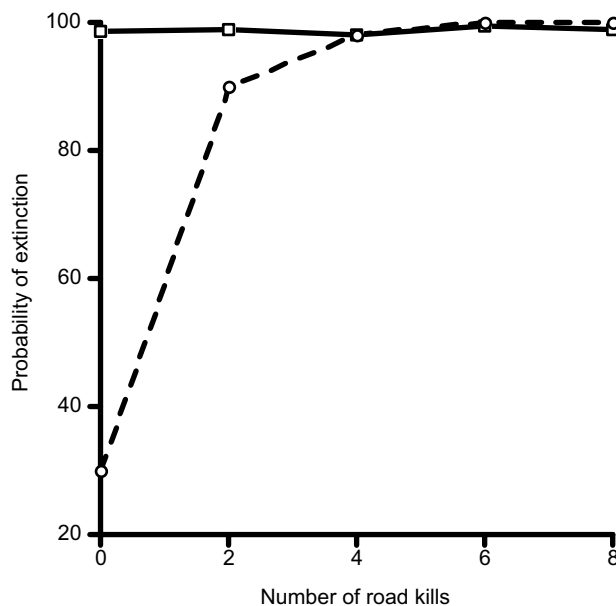


Fig. 4 – Extinction probability over 500 years for a population of black ratsnakes in eastern Ontario as a function of male and female road mortality. The dashed line and open circles reflect the probability of population extinction for variable levels of annual female road mortality with male mortality held constant at 4, and the solid line and squares reflect probability of extinction for variable levels of male annual road mortality with female mortality held constant at 4.

over all years was -0.0020 ± 0.0001 . When we included additional mortality due to roads of 4 adult males and 4 adult females, the extinction rate increased to 98.9% and r was reduced to -0.0370 ± 0.0003 . We conducted a sensitivity analysis for each sex by varying the number of road kill between 0 and 8 while holding the other sex's mortality constant at 4. Whereas the extinction risk was very sensitive to the number of additional females killed, the number of additional males killed had little effect on the extinction probability (Fig. 4).

4. Discussion

Many studies have documented road avoidance in reptiles, establishing the potential for roads to divide populations and reduce gene flow (Klingensbock et al., 2000; Koenig et al., 2001; Andrews and Gibbons, 2005; Richardson et al., 2006). In contrast to these studies, black ratsnakes in Ontario did not avoid crossing a secondary road. Larger snakes are less likely to avoid crossing roads (Andrews and Gibbons, 2005), which could account for ratsnakes differing from other species that have been studied. In an experimental study, however, Andrews and Gibbons (2005) found that black ratsnakes avoided crossing roads. This difference could have resulted from their experimental design biasing the snakes' behavior. They released snakes at a road margin and recorded the direction they moved. A stressed snake in an unfamiliar setting seems more likely to seek cover than to move into the open. Whatever the explanation, it was clear that ratsnakes in our study did not avoid crossing the secondary road.

We had predicted that males and reproductive females should be more likely to cross roads during the mating and nesting season, respectively. Although observed rates of crossing were qualitatively consistent with this prediction, we did not find a significant difference in the number of road crossings across months or between reproductive classes. The willingness of reproductive snakes to cross roads reduces the barrier effect of roads, but also increases the chance of mortality for these classes. It would be useful to determine if this lack of difference between reproductive males and females is similar for other species, particularly those that demonstrate some avoidance of roads.

4.1. Road mortality

Although many studies have documented or modeled substantial reptile road mortality, none of those studies has calculated an actual mortality rate (as opposed to modeled or inferred rates). Using an actual mortality rate and the expected number of road crossings each year, we estimated that 9 snakes would be killed on the road annually, which was slightly higher than the actual number of road kills found in any year. Some road kills are probably removed quickly by scavengers, however, and thus never found. Moreover, we found several ratsnakes that had been hit by cars that subsequently died in the lab several hours later (G. Blouin-Demers, personal observation). Injured ratsnakes are probably capable of crawling off the road, resulting in them not being seen when they died. In fact, two of the three radio-implanted ratsnakes that were killed by vehicles were not found on the

road, but in the ditch beside the road. Without radio-telemetry, it is extremely unlikely that the carcasses would have been found. If we assume, based on this observation, that 2 of every 3 road kills are not found, then our mean of 3.25 individuals found each year suggests an annual total of 10 road kills, which is very close to our estimate obtained using the road mortality rate.

The ability to predict road mortality rates from more easily measured life history characteristics and traffic intensity information would be invaluable to biologists and developers attempting to minimize the impacts of road development on animal populations. Because of the small number of snakes killed by vehicles each year, a long (>9 years) and labor-intensive (>100 individuals radio-tracked) study was needed to estimate road mortality accurately. We therefore compared our road mortality estimate to the estimate obtained using the equation $P_{\text{killed}} = 1 - e^{-Na/v}$ developed by Hells and Buchwald (2001). The road mortality rate estimated from this equation was roughly double that measured empirically with telemetry data.

The over estimation of the road mortality from Hells and Buchwald's (2001) equation could be related to our incorrect estimation of one of the parameters. Our kill zone and traffic intensity estimates are likely to be accurate. The road crossing speed, however, could be incorrect because of how it was measured. Andrews and Gibbons (2005) released snakes in unfamiliar habitat before their speed was calculated. Therefore, the speed may not accurately represent the actual crossing speed of an individual that naturally comes across a road. The only way to get an unbiased estimate of road crossing speed would be to observe snakes that encounter and cross roads as a result of natural activity. Even using telemetry this would be extremely difficult. Another possible reason for the overestimation could be that the model does not account for driver behavior. Adult black ratsnakes are long (>1 m) and vehicles on Opinicon Road travel at relatively slow speeds (~60 km/h). Therefore, in most cases drivers probably see snakes well in advance and the drivers' behavior could drastically influence the number of snakes killed either positively (avoiding the snake) or negatively (aiming at the snake). For smaller animals (e.g., frogs) driver behavior may not influence mortality risk. Studies of amphibians have shown that the model accurately predicts road mortality (Gibbs and Shriver, 2005).

4.2. Population effects

Long-lived species with delayed sexual maturity are particularly vulnerable to increases in adult mortality (Brooks et al., 1991; Congdon et al., 1994). Many reptiles are long-lived and therefore road mortality can severely impact their populations. However, few studies have estimated the impact of road mortality (using a relatively accurate estimate of road mortality rate) on populations of long-lived species. In this study, we determined that the current number of adult ratsnakes killed on roads (~9 per year) is enough to increase the extinction probability of an otherwise stable population to 99% over 500 years and road mortality of as few as 3 adult females per year increases the extinction probability to >90%. Each year juveniles and neonates are also killed on the road. These

were not included in the PVA and although their effects would likely be less than those of adult mortality, they would still be negative and therefore further increase the extinction risk. Because a large portion of our study area is in protected, undeveloped habitat, road densities outside our study area are much higher. Thus, the populations outside our study area are likely at greater risk of extinction. Given the observed road mortality in a relatively undeveloped area, it seems unlikely that immigration from populations surrounding our study area will negate the effects observed in this study. These results strengthen the view that road mortality can have a significant impact on populations of long-lived species. If no measures are taken to decrease road mortality, it is probable that many populations of long-lived species in close proximity to roads will go extinct or at least experience significant declines.

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