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Estimating actual versus detected road mortality rates for a northern viper

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ABSTRACT

Mitigation of adverse effects of roads on wildlife benefits from a fundamental understanding of the number of animals killed by traffic. Road surveys are a key part in quantifying this mortality; however, without accounting for scavenging and observer detection rates, this method only reveals a minimum number of roadkilled animals. We quantified western rattlesnake (*Crotalus oreganus*) road mortality on a two-lane road in the dry interior of British Columbia, Canada. In 2015, 2016 we repeatedly surveyed 11.7 km of this road by walking, driving, and cycling. We determined the rate of carcass removal by scavengers and observer detection probability during walking surveys using planted snake carcasses. Fifty-two percent of carcasses were removed from the road by scavengers in two days, while 11% remained for >14 days. The mean observer detection probability was 0.76 for a team of two observers conducting surveys by walking. The mean road mortality rate, which accounts for scavenging and observer detection during walking surveys, was 0.06 rattlesnake deaths/km/day or 124 rattlesnake deaths/year based on mean rattlesnake active season duration. The estimated number of rattlesnake deaths was 2.7times the number of dead rattlesnakes detected through all surveys and incidental observations combined. Overall, walking surveys detected only 8% of the estimated rattlesnake deaths. Incidental observations of carcasses made while driving at other times in the study area were numerous, however the detection rate per kilometer was very low compared to more rigorous survey methods. The results highlight the magnitude of snake road deaths that can occur on a two-lane road with just 350 vehicles per day bisecting a wildlife reserve, the importance of standardized surveys and accurate assessments of sources of error in road mortality research, and the value of a model that can be used to calculate detection rates of roadkilled wildlife by trained observers.

1. Introduction

The fragmentation of ecosystems inevitably results in movements of animals across roads to reach habitats or other resources. Some animals even may be attracted to the roads themselves (e.g. nesting habitat – Aresco, 2005; scavenging – Schwartz et al., 2018) and there is often a high density of roads located in naturally productive areas (Ibisch et al., 2016) that

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support high biodiversity (Luck, 2007), exacerbating the rate of wildlife-vehicle encounters. More often than not these confrontations with roads have negative results for animals (Fahrig and Rytwinski, 2009; Trombulak and Frissell, 2000). The most visible effect of roads on wildlife is direct mortality from traffic collisions, an event that likely has repercussions on populations beyond just the death of an individual. Direct road mortality also may be closely tied to the barrier effect, when animals are prevented from crossing a road through either severe mortality or road avoidance. This in turn effectively fragments populations and leads to genetic isolation (Andrews et al., 2008; Shepard et al., 2008). The compounding of all these effects may culminate in even greater impacts at the population or community levels, and thus accurate estimates of road mortality rates are imperative when assessing conservation threats to populations.

Unfortunately, efforts to quantify road mortality rates are hampered by several sources of error (Bishop and Brogan, 2013; Boves and Belthoff, 2012; Smallwood, 2007) and experimental evaluations of survey errors involving terrestrial vertebrates show that actual mortality rates are at least two times higher than rates determined empirically without adjustment for sources of error (Kline and Swann, 1998; Santos et al., 2016; Slater, 2002; Teixeira et al., 2013). To date, four main sources of potential error inherent in conventional survey methods have been identified (Bishop and Brogan, 2013; Boves and Belthoff, 2012; Smallwood, 2007): 1) scavenger-removal, 2) observer detection error, 3) crippling bias (when injured animals leave the roadside before dying) and 4) habitat bias.

The greatest amount of uncertainty in road mortality rates comes from scavenger-removal and observer detection error (Loss et al., 2014). In particular, road mortality rates for rare and cryptic species, such as snakes are difficult to accurately evaluate and hence often are under-reported. Santos et al. (2011) suggested that road surveys for snakes should be conducted on a daily basis to avoid missing significant numbers of carcasses before they are removed by scavengers. Degregario et al. (2011) determined that 50% of snake carcasses were removed by scavengers after only 8 h on the road, a pattern further supported by Enge and Wood (2002) who determined 70% of snake carcasses were removed within one day. Rapid removal is particularly evident on paved roads (Hubbard and Chalfoun, 2012) where snakes are easily detected by scavengers (Antworth et al., 2005). Furthermore, human observer detection rates during reptile roadkill surveys, including those for snakes, are generally low: Gerow et al. (2010) and Santos et al. (2016) found detection rates of only four and six percent, respectively. Small-sized carcasses are most commonly overlooked (Santos et al., 2016), leading to data biases for species, sexes, and age classes (Hartmann et al., 2011).

Road surveys provide snapshots of the density of dead animals on the road. At any given time, this density is determined by the interaction of the mortality rate (which adds dead animals to the road) and the rate at which carcasses are removed by scavengers; therefore, an indirect way to calculate the road mortality rate is by measuring the removal rate and the observed density (Teixeira et al., 2013). However, sources of error in road mortality estimates are not consistent across geographic locations or habitats (DeGregorio et al., 2011; Slater, 2002), nor clades of species (Santos et al., 2016, 2011; Teixeira et al., 2013), and therefore must be assessed within a given region. Since road mortality affects a wide variety of animals, scavenging and detectability studies often simultaneously monitor a broad range of species and then group animals by class (Gerow et al., 2010; Santos et al., 2016; Teixeira et al., 2013). Given the distinct morphological traits possessed by snakes compared to other reptiles, this is likely an inadequate approach for this taxon. Unfortunately, studies specific to snakes often independently consider separately either scavenger-removal or observer error, rather than a combination of these errors. Because many snake species are 'at risk' (Lesbarrères et al., 2014), accurate estimates of threats such as road mortality are essential to assessments of population viability and the implementation of recovery actions.

We assessed road mortality rates and associated sources of error for a population of western rattlesnakes (*Crotalus oreganus*) in an arid grassland ecosystem in British Columbia, Canada. Dead rattlesnake detections on a two-lane road were quantified along with scavenger-removal and observer detection rates. We predicted that, after accounting for these factors, the actual number of rattlesnake deaths would be higher than the number of rattlesnake carcasses detected.

2. Methods

2.1. Study area

The study was conducted in 2015 and 2016 in the White Lake Basin (latitude 49°N, longitude 119°W) in the South Okanagan region of British Columbia, Canada (Fig. 1) during April–October when rattlesnakes were active. This basin consists of forested, rolling hills and steep bluffs surrounding open shrub-steppe and grassland habitat, predominantly characterized by Bluebunch Wheatgrass (*Agropyron spicatum*), Big Sagebrush (*Artemisia tridentata*) and Ponderosa Pine (*Pinus ponderosa*) (Meidinger and Pojar, 1991). The Nature Trust of British Columbia (TNTBC) manages the area with the objective to "integrate livestock management with conservation of habitat for species at risk" (TNTBC, 2018).

A paved, undivided two-lane road (BC Class 5 highway) with an unposted speed limit of 80 km/h traverses the basin bottom (elevation 500 m). Through April–October of our study years, the average daily maximum traffic volume passing through the 11.7 km study area of the road (Fig. 1) was 350 vehicles as measured by traffic counters provided by BC Ministry of Transportation and Infrastructure. During this time [hereafter referred to as 'the active season'] the rattlesnakes in the basin migrated to and from overwinter hibernacula (den sites) among other activities, including hunting and mating. Within this area we have detected at least 26 rattlesnake hibernacula located within 1.4 km of the road, with some as close as 5 m (Winton, 2018). Vegetation along the road shoulder was maintained in each year of the study by annual mowing to a height of

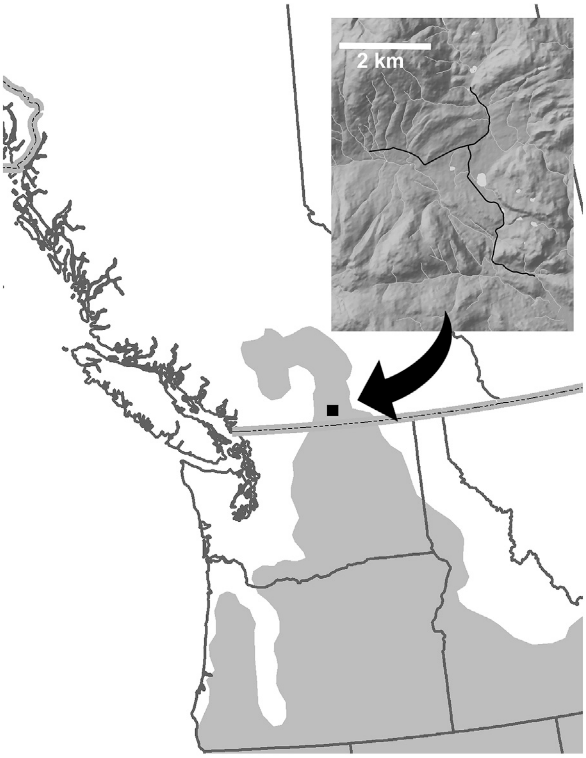

Fig. 1. Location of the study site within the range of Western Rattlesnakes (*Crotalus oreganus*) in western North America and an inset of the survey route in the White Lake Basin, BC, Canada.

less than 0.5 m for a distance of 1.8 m from the road edge. A barbed wire fence was located approximately 5 m from the road edge along the entire survey route.

2.2. Road surveys

Three different types of survey methods were conducted on different days along the same 11.7 km route: walking, driving, and cycling (Table 1). For walking surveys, two observers scanned for dead and alive rattlesnakes in both road lanes as well as the 1.8 m vegetation control zone of the road shoulder as they walked along opposite edges of the road. Walking surveys were conducted on average 4.7 days since the last survey in 2015 and 3.1 days in 2016. Driving surveys were conducted by vehicle, travelling at 20 km/h or less, again with two observers, the driver and the passenger, scanning the road and the shoulder. For driving surveys conducted after sunset, high-beam headlights were used as well as a high-powered spotlight that was used in a back and forth scanning pattern across the road and shoulder. Bicycle surveys were conducted wherein only one observer cycled along the edge of the road while scanning the road and shoulders. Walking and cycling surveys were only conducted during daylight hours due to safety concerns. The road survey area was driven and cycled in both directions to ensure the two lanes were surveyed completely. The results of these two directional surveys were combined but individual roadkills were counted only once. The starting point and direction of travel were varied between surveys, the start and end times for each survey were recorded (Table 1), and the exact length of the transect on each occasion was measured with GPS. Overall, road surveys were conducted on average 2.4 days apart or three times per week.

All detections of dead or alive rattlesnakes on the survey route were noted whether during surveys or at other times. Detection points for rattlesnakes were recorded $\pm$5m with a handheld GPS (Garmin 72H). Live rattlesnakes were captured, measured, and tagged with Passive Integrated Transponder (PIT) tags as part of an overarching mark-recapture study on the rattlesnake population (Winton, 2018). After, captures were released at the fence line in the direction that the snake had been travelling, or if that was not obvious, the side of the road closest to the capture location. Carcasses were identified to species and scanned for the presence of PIT tags. The carcass was removed and, when possible, measured and weighed.

Incidental detections of roadkill (i.e. detections made when road surveys were not being conducted) were a common occurrence when working within the survey route. We were not actively surveying at these times, however, any carcasses we observed were documented in the same manner as detections made during surveys. Although the kilometers driven outside of survey times were not recorded daily, we were able to approximate the minimum distance based on our records of travel in the area. While the focus of this study was western rattlesnakes, detections of all vertebrates on the road including other

Table 1
Timeframe and survey effort per road survey method in the White Lake Basin, BC, Canada, 2015, 2016. Date format is MM/DD.

Survey method	Time of day	Survey start time ranges		Dates		Number of surveys		Total km surveyed	
		2015	2016	2015	2016	2015	2016	2015	2016
Walk	Day	6:00–11:55	6:41–10:32	05/12–08/27	04/29–08/28	23	28	116.2	253.5
Drive	Day	6:00–14:30	8:50–13:25	05/05–10/02	04/11–09/18	6	5	62.4	51.6
Drive	Night	20:30–23:38	18:17–22:30	05/16–09/03	04/12–09/29	25	22	233.3	257.4
Bike	Day	8:00–13:40	7:10–12:00	08/08–10/03	04/15–09/28	9	16	53.1	129.9
Incidental (Drive)	Day + Night	–	–	04/09–10/03	04/05–10/11	–	–	1633.8	2382.4

snake species were recorded (Appendix A; Table A1). Any detections of rattlesnakes made along the road in the greater study area of the White Lake Basin but outside of the survey route were also recorded (Appendix A; Table A2).

2.3. Scavenging and observer error experiments

We evaluated scavenger-removal and observer detection error as the probable main sources of bias in estimating snake road mortality in this area. To date, habitat and crippling biases have not been quantified in this region for snakes. However, we assumed these biases were likely negligible due to the homogeneity of roadside habitat maintenance.

Experiments were conducted to examine the rate of carcass removal from the road by scavengers and the detection probability of snake carcasses on the road by trained observers. The experiments involved using snake carcasses that had been previously collected off-site and were then thawed from storage. Because the supply of rattlesnake carcasses alone was insufficient, carcasses of all six species of snake native to the area were used: western rattlesnake, Great Basin gopher snake (*Pituophis catenifer*), western yellow-bellied racer (*Coluber constrictor*), rubber boa (*Charina bottae*), western terrestrial garter snake (*Thamnophis elegans*), and common garter snake (*T. sirtalis*). In addition to recording species, we also categorized carcasses by size (small, medium, large).

Eleven scavenger-removal trials were conducted during May–September 2016. Each carcass was placed at a previously recorded snake roadkill location (10–15 carcasses/trial, 127 carcasses total) and monitored on a daily basis until it was no longer present or up to 14 days after placement (which exceeded the longest amount of time between subsequent surveys). At least 200 m separated each carcass in each trial to reduce scavenger overlap. Motion-activated wildlife cameras were placed by 26 of the snake carcasses to observe scavenger species.

Three trials measuring observer detection probability were run by placing snake carcasses at locations unknown to the two observers in the study. The observers then proceeded with a walking road survey following the previously outlined procedure; after this, all placement sites were revisited immediately following the survey (within approx. 30 min) to confirm whether each carcass had been detected or missed during the survey. Observer detection probability (p) was calculated as the mean of the three trials.

Results were compared across size classes using the N-1 χ^2 statistic for observer detection probabilities, and using Kruskal-Wallis One-Way ANOVA for scavenger-removal times. Statistical analyses were performed in SigmaPlot version 13.0 and $\alpha = 0.05$ was used to interpret significance.

2.4. Road mortality rate model

The density of dead rattlesnakes on the road, $D(t)$ (dead rattlesnakes/km), was estimated from the number of dead rattlesnakes detected (N) per km surveyed (x), and corrected for observer detection error based on the mean probability of detection (p) determined from the experimental trials:

$$D(t) = N(t)/xp \tag{1}$$

The proportion of carcasses remaining on the road over time from scavenger-removal trials (P) was fit to the following equation:

$$P(t) = P_0 + (1 - P_0)e^{-at} \tag{2}$$

where P_0 accounts for the proportion of carcasses that remained on the road for longer than 14 days and were not scavenged.

To estimate the road mortality λ (deaths/km/day) from our survey data, we used the following model that accounts for the effects of observer error, scavenging, time period between surveys, and our removal of snake carcasses at each survey. The model is drawn from Texeira et al. (2013) but modified to account for our observation that a proportion P_0 of snake carcasses were not scavenged.

We treat each snake death on the road as contributing to one of two distinct groups of carcasses: a fraction (P_0) of all deaths add to a group of carcasses that are never scavenged; the remaining fraction (1- P_0) contributes to a separate group that are scavenged. The scavenged carcasses are removed from the road (by scavengers) at a fractional rate a, while the non-scavenged carcasses remain on the road to decay on a time-scale that we assume is much longer than both our sampling period and the characteristic scavenging time $1/a$. Under these assumptions the densities of non-scavenged and scavenged carcasses (Dn and Ds) can be modeled by the equations:

$$\frac{D_n}{dt} = P_0\lambda \tag{3}$$

$$\frac{D_s}{dt} = (1 - P_0)\lambda - aD_s \tag{4}$$

where t is the time since the last survey was conducted. Since we removed all snake carcasses at each survey, these equations are supplemented by the initial conditions:

$$D_n(0) = D_s(0) = 0 \tag{5}$$

Solving equations (1)–(3) gives:

$$D_n(t) = P_0\lambda t \tag{6}$$

$$D_s(t) = \frac{(1 - P_0)\lambda}{a}\left(1 - e^{-at}\right) \tag{7}$$

Each of our surveys resulted in all detected carcasses being removed from the roads; thus, we did not distinguish between those carcasses that would have been scavenged versus those that would have persisted indefinitely. These two groups of carcasses therefore were aggregated to determine overall carcass density, using the equation:

$$D(t) = D_n(t) + D_s(t) = P_0\lambda t + \frac{(1 - P_0)\lambda}{a}\left(1 - e^{-at}\right) \tag{8}$$

Solving this equation for λ gives the final equation we used to estimate the road mortality rate,

$$\lambda = \frac{N(t)/xp}{P_0 t + \frac{1}{a}(1 - P_0)\left(1 - e^{-at}\right)} \tag{9}$$

where we have used $D(t) = N(t)/xp$ as the estimate of carcass density, compensating for observer error.

Equation (9) determines a road mortality rate for each survey based on the density of dead rattlesnakes observed on the road per km surveyed, corrected for observer error, and the proportion of non-scavenged carcasses, the time between surveys, and the characteristic scavenging time. Mean road mortality rates for rattlesnakes calculated from walking survey results were compared between years using a Mann-Whitney Rank Sum Test. The mean mortality rates were used to calculate the number of rattlesnake deaths within the 11.7 km of the study area based on the length of the active season for each year. The length of each active season for rattlesnakes was based on when rattlesnakes commenced egress from their overwinter den (first observations at den sites in the spring) and when return ingress was completed (last day of rattlesnake observations at the dens in the fall or found on the roads). The number of estimated rattlesnake deaths were divided proportionally among the different survey methods to produce adjusted densities that reflect what would be expected if all rattlesnake deaths were detected.

3. Results

3.1. Road surveys

Including results from all survey types and incidental observations, 92 dead rattlesnakes were detected on the road during the study (2015: 36, 2016: 56; Table 2) compared to 17 live rattlesnakes (2015: 13, 2016: 4). A high amount (39%) of roadkill detections were made incidentally, outside of road survey times (2015: 14, 2016: 22). Eight dead rattlesnakes were discovered on the road shoulder (2015: 2, 2016: 6), and accounted for 8.7% of all detections; the carcasses were detected up to a maximum distance of 2.13m from the edge of the road, and five of these road-shoulder detections were made during walking surveys. Overall, rattlesnakes were detected on the road from May 8 to October 1, 2015, and from April 20 to October 11, 2016. We conducted 137 road surveys by walking (51), driving (day: 11, night: 47), or cycling (25) and traveled 5210 km in total over the two years (Table 2).

Table 2
Detections of dead western rattlesnakes (*Crotalus oreganus*) and densities per km surveyed (unadjusted and adjusted for observer error or scavenging rates) by road survey method in the White Lake Basin, BC, Canada, 2015, 2016.

Survey method	Time of day	Total km surveyed		Number of dead rattlesnakes detected		Unadjusted dead rattlesnake density (dead rattlesnakes/km)		Adjusted dead rattlesnake density (dead rattlesnakes/km)	
		2015	2016	2015	2016	2015	2016	2015	2016
Walk	Day	116.2	253.5	6	13	0.052	0.051	0.130	0.143
Drive	Day	62.4	51.6	3	4	0.048	0.078	0.120	0.218
Drive	Night	233.3	292.5	12	9	0.051	0.031	0.128	0.087
Bike	Day	53.1	129.9	1	8	0.019	0.062	0.048	0.174
Surveys total		465	727.5	22	34	0.047	0.049	0.118	0.137
Incidental		1633.8	2382.4	14	22	0.009	0.009	0.023	0.025
Surveys + Incidental		2098.8	3109.9	36	56	0.017	0.018	0.043	0.050

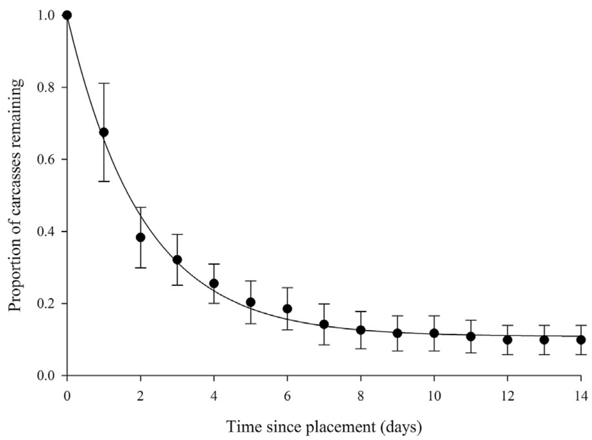

Fig. 2. Mean proportion of snake carcasses remaining on a paved road over time in experimental scavenger-removal trials (n = 11; error bars = 95% confidence intervals; $R^2 = 0.99$) in the White Lake Basin, BC, Canada in 2016.

3.2. Scavenger-removal and observer detection probability

The characteristic scavenging time for snake carcasses was 2.05 days ($a = 0.49$ day^{-1}; Fig. 2), and 52% of the carcasses were removed in this time. The proportion of carcasses remaining on the road after 14 days was $P_0 = 0.11$. Size class did not play a role in the length of time a carcass remained on the road (H = 1.857, df = 2, p = 0.395). Camera traps detected four scavengers (*Canis latrans, Pica hudsonia, Cathartes aura,* and *Homo sapiens*), but missed recording more than half of the scavenging events. In five cases, the snake carcass disappeared from one photo to the next (time interval of 1–60 min) and no scavengers were captured in the photos, possibly indicating aerial scavengers.

The mean detection probability (p) was 0.76 (±0.06 SE) among three trials for two observers conducting walking surveys (trial 1: 18/22 carcasses detected, trial 2: 18/21, trial 3: 11/18). Larger snakes were more readily detected ($\chi^2 = 5.7$, df = 2, p = 0.057).

3.3. Mortality rates

Road mortality rates calculated from walking surveys did not differ significantly between years (U-statistic = 313, p = 0.838); therefore, the mean road mortality rate on White Lake Road from 2015 to 2016 was 0.06 rattlesnake deaths/km/day or an average of 124 deaths per year (Table 3). From that mortality rate, which takes into account scavenger-removal and observer error, 2.7 times as many rattlesnake deaths were estimated to have occurred compared to those actually detected (as dead animals) overall. Otherwise stated, all detections of dead rattlesnakes, including those made during surveys and incidentally, account for 37% of the estimated rattlesnake deaths. Dead rattlesnakes detected during walking road surveys specifically accounted for only 8% of the estimated number of deaths. There was an increase in the density of dead rattlesnakes from the unadjusted to adjusted values for all survey methods (Table 2).

Table 3
Road mortality rates (λ), that account for scavenger-removal and observer error, calculated using Equation (4), and associated number of western rattlesnake (*Crotalus oreganus*) deaths based on walking survey results during the active season (April—October) in the White Lake Basin, BC, Canada, 2015, 2016.

	2015	2016	Mean (2015—2016)
Mean mortality rate (±SE) (rattlesnake deaths/km/day)	0.044 (0.019)	0.070 (0.030)	0.058 (0.018)
Active season length (days)	176	188	182
Calculated rattlesnake deaths per year	91	154	124
Correction factor (calculated rattlesnake deaths/detected dead rattlesnakes)	2.5	2.8	2.7

Overall, at White Lake in 2015—2016, the unadjusted rates of rattlesnakes found dead on the road by walking, driving, and cycling surveys, was consistent between years at 0.047/km in 2015 and 0.049/km in 2016. The adjusted rates (0.118/km in 2015 and 0.137/km in 2016), which take into account removal of carcasses by scavengers and observer error, were similar but much higher in total. We also found that simply driving roads repeatedly and covering more than 1000 km incidentally detected the most dead rattlesnakes compared to walking, cycling, or driving less than 300 km while looking for snakes in any year. However, while the rates for incidental observation between years were also very consistent, the rates per km of incidental observations of dead rattlesnakes were at least two times less than careful and slow walking, driving, and cycling surveys whether they were adjusted or unadjusted rates (0.009/km or 0.024/km).

4. Discussion

Consistent with our prediction, the estimated number of deaths was substantially greater (2.7 ×) than the actual number of dead rattlesnakes found on the road during all surveys and incidental observations. Furthermore, road surveys conducted by walking detected only a small proportion of the estimated actual rattlesnake deaths (8%), although our detection probability rate was high (76%). Our scavenger-removal trials also revealed that 52% of snake carcasses were removed within two days and that 11% of the carcasses were never scavenged, suggesting multiple mechanisms beyond scavenging, such as damage due to vehicles or ultimately decomposition, that underlie the removal of roadkilled snakes. Overall, our results emphasize the need to conduct standardized surveys and account for scavenger-removal and observer detection error when calculating road mortality rates to avoid underestimating the actual number of animals killed on the road.

The correction factor of 2.7 × determined in this study is consistent with studies on other taxa and for reptiles where road mortality rates were corrected for scavenger-removal and observer error. Correction factors can be quite high (e.g. 12—16 × - Slater, 2002) with broad ranges across various taxa, including amphibians, birds, mammals and reptiles (e.g. 2—10 × - Santos et al., 2016; 2—39 × - Teixeira et al., 2013). However, studies examining reptiles show relatively lower correction factors than those for other groups of animals. Kline and Swann (1998) determined reptile mortality to be 5 × that observed in Arizona, and Teixeira et al. (2013) estimated a correction factor of 2 × in Brazil. Rosen and Lowe (1994) did not account for sources of error by experimental methods; however, they noted the limitations of their study and corrected their road mortality estimates for snakes in Arizona with a conservative value of 1.7 × .

Our calculated rattlesnake road mortality rate is not easily compared to previous work on snake road mortality, since the majority of these studies have not made corrections for sources of error, reported collective rates on multiple species, or included encounters of live animals (Baxter-Gilbert et al., 2015; Borczyk, 2004; DeGregorio et al., 2010; Enge and Wood, 2002; Gonçalves et al., 2018; Hartmann et al., 2011; Jochimsen et al., 2014; McDonald, 2012; Mendelson III and Jennings, 1992; Shepard et al., 2008; Sullivan, 2000; Tucker, 1995). When we compare the density of dead rattlesnakes detected, without error corrections (0.018 dead rattlesnakes/km traveled in this study), to studies on rattlesnake species in comparable habitats, similar densities were found (0.004/km - Jochimsen et al., 2014; 0.006—0.008/km - Mendelson and Jennings, 1992; 0.031/km - Sullivan, 2000). Slight variation in these results could potentially indicate site, range, or species differences for rattlesnakes in Western North America; however, the values are not vastly different when compared to other areas with different snake species compositions (e.g.<0.001/km - Enge and Wood, 2002; Shepard et al., 2008).

Observer detection probability (0.76) as calculated in our study was considerably higher than that reported elsewhere for reptiles (0.04 - Gerow et al., 2010; 0.06 - Santos et al., 2016) and snakes (0.23 - Gonçalves et al., 2018). This is likely due to differences in methodologies. Other studies determined analogous values by comparing detections made while driving to those made while walking with the assumption that the detection probability was 1.0 when surveying on foot (Gerow et al., 2010; Santos et al., 2016; Teixeira et al., 2013). However, in our study planted carcasses were used to assess detection probability while walking and the outcome strongly indicated the assumption of perfect detection did not hold. Thus results obtained from walking surveys may produce the maximum number of roadkill detections but not necessarily all carcasses on the road. Detection probability of driving surveys will invariably be less than walking surveys (Baxter-Gilbert et al., 2017; Langen et al., 2007). Since we could only examine observer detection probability for walking surveys and not other survey methods (driving, cycling), our results represent a conservative estimate of observer detection error. The inclusion of the road shoulder as part of our survey area increased overall detections by 9.5% and, given that the majority of road shoulder detections were made during walking surveys, this adds further credibility to our detection survey methods.

The scavenger-removal rate of snakes estimated for our study site was lower than rates reported in warmer regions and latitudes, such as Portugal and the southern United States (Antworth et al., 2005; DeGregorio et al., 2011; Enge and Wood, 2002; Santos et al., 2011). This may be due to global patterns of biodiversity that increase the density of scavengers and the intensity of competition for carcasses (DeVault et al., 2003). However, another study conducted in the more northern, temperate climate of Wyoming, USA, reported a 75% removal rate within 60 h (Hubbard and Chalfoun, 2012) similar to our results of 52% removal within 49 h. Our scavenger-removal trials revealed a portion of carcasses (11%) that remained on the road for an extended period of 14 days, something that, to our knowledge, has not previously been addressed. Either those particular carcasses were not removed by scavengers when they were fresh (then reaching a state of decomposition that was undesirable to scavengers), or the carcasses became so damaged (possibly by multiple vehicle collisions) that they were unrecognizable to scavengers. The non-scavenged carcasses remained on the road until they appeared to be mostly decomposed. Interestingly, most of the carcasses that persisted were initially placed on the road shoulder compared to carcasses placed on the road surface that usually disappeared quickly or, if not, were gradually pushed to the road edge probably due to traffic (Winton, pers. observ.). This could be a relevant factor when habitat near to roads is dense and could obscure observation of these carcasses.

Although we determined the true number of rattlesnakes killed on the road using our equation, we did not detect all of these deaths leading to a lack of additional information on sex, age, and reproductive status of the individuals as well as surrounding habitat, time of day, season, and weather conditions under which road mortality occurs. Alternative methods could be explored to improve the efficiency of road kill detection and eliminate potential biases, e.g. drone surveys (Sykora-Bodie et al., 2017), or trained dogs (Arnett, 2006). Based on the high number of incidental observations made in our study, travelling the route many times over a long period each year, therefore, could increase the total number of observations made but would require increased surveyor effort (i.e. rates detected per km will be very low). This is a possible outcome if observer detection probability is low due the speed of the vehicle and observations are only incidental. Costa et al. (2015) indicated frequent surveys (once per week) during times of high activity for reptiles increases the efficacy of roadkill sampling. Still, the total number of dead animals detected in our study both during formal surveys and incidentally was 2.7 $\times$ less than the estimated number of deaths occurring each year; clearly, even with all of our survey effort we are falling well short of 100% detection efficiency, and error corrections must be factored in.

Our results highlight the importance for methodical and rigorous assessments of roadkill in any situation where the true magnitude of roadkill impacts needs to be quantified in order to trigger management actions. A consistent trend, supported by our results that road mortality rates are significantly higher than what is reported either through simple, opportunistic observations or even structured road surveys alone, indicates that accuracy largely may depend on quantifying observer detection probability and scavenger-removal rates. Ideally, intensive surveying, similar to our methods, should be conducted; however, the equation developed herein for road mortality rate can be applied to less frequent surveys, as long as survey effort, time between surveys, carcass persistence time, and observer detection probability all are taken into account. We recommend that researchers conducting road mortality studies, particularly on smaller species, evaluate scavenger-removal and observer error for each study, and that observer detection probability be determined using planted carcasses to accurately assess this source of error for a given survey method. Studies such as ours will assist conservation practitioners in accurately determining rates of road mortality, which will be of particular importance for populations of at-risk animals when the loss of only a few individuals has a significant effect (Colley, 2015; Row et al., 2007).

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2018.e00476.

Appendix A. Road mortality in the White Lake Basin

Table A1
Frequency of roadkill detected for vertebrate species (not adjusted for observer error or scavenging rates) during surveys and incidentally in the White Lake Basin, BC, Canada, 2015, 2016.

Common name	Scientific name	N
Amphibians		
Pacific Tree Frog	*Pseudacris regilla*	114
Great Basin Spadefoot[a]	*Spea intermontana*[a]	44
Long-toed Salamander	*Ambystoma macrodactylum*	23[b]
Western Tiger Salamander[a]	*Ambystoma mavortium*[a]	13
Reptiles		
Western Yellow-bellied Racer[a]	*Coluber constrictor*[a]	128
Western Rattlesnake[a]	*Crotalus oreganus*[a]	92
Great Basin Gopher Snake[a]	*Pituophis catenifer*[a]	84
Common Garter Snake	*Thamnophis sirtalis*	20
Rubber Boa[a]	*Charina bottae*[a]	19
Western Terrestrial Garter Snake	*Thamnophis elegans*	9
Painted Turtle[a]	*Chrysemys picta*[a]	2
Unidentified	–	21
Birds		
Vesper Sparrow	*Pooecetes gramineus*	23
California Quail	*Callipepla californica*	12
Brewer's Blackbird	*Euphagus cyanocephalus*	5
Eastern Kingbird	*Tyrannus tyrannus*	4
Western Bluebird	*Sialia mexicana*	4
Chipping Sparrow	*Spizella passerine*	3
Common Nighthawk	*Chordeiles minor*	2
Gray Catbird	*Dumetella carolinensis*	2
Western Meadowlark	*Sturnella neglecta*	2
American Goldfinch	*Spinus tristis*	1
American Robin	*Turdus migratorius*	1
Bullock's Oriole	*Icterus bullockii*	1
Common Poorwill	*Phalaenoptilus nuttallii*	1
Dark-eyed Junco	*Junco hyemalis*	1
Gray Partridge	*Perdix perdix*	1
Lark Sparrow[a]	*Chondestes grammacus*[a]	1
Lazuli Bunting	*Passerina amoena*	1
Mallard	*Anas platyrhynchos*	1
Mountain Bluebird	*Sialia currucoides*	1
Northern Flicker	*Colaptes auratus*	1
Pine Siskin	*Spinus pinus*	1
Ruffed Grouse	*Bonasa umbellus*	1
Sage Thrasher[a]	*Oreoscoptes montanus*[a]	1
Song Sparrow	*Melospiza melodia*	1
Spotted Towhee	*Pipilo maculatus*	1
Tree Swallow	*Tachycineta bicolor*	1
Sparrow sp.	–	12
Galliform sp.	–	10
Hummingbird sp.	–	3
Wren sp.	–	1
Unidentified	–	53
Mammals		
Great Basin Pocket Mouse[a]	*Perognathus parvus*[a]	43
North American Deer Mouse	*Peromyscus maniculatus*	7
Yellow-pine Chipmunk	*Tamias amoenus*	4
American Red Squirrel	*Tamiasciurus hudsonicus*	2
Bushy-tailed woodrat	*Neotoma cinerea*	2
North American Porcupine	*Erethizon dorsatum*	2
Yellow-bellied Marmot	*Marmota flaviventris*	2
Bobcat	*Lynx rufus*	1
Coyote	*Canis latrans*	1
Meadow Vole	*Microtus pennsylvanicus*	1
Mule Deer	*Odocoileus hemionus*	1
Northern Pocket Gopher	*Thomomys talpoides*	1
Mouse sp.	-	4
Bat sp.	-	3
Unidentified	–	14

[a] Species-at-risk.
[b] many more long-toed salamanders were likely killed; however, to prevent accidentally killing more individuals by driving or walking on them, surveys were stopped when high amounts of salamanders were encountered and thus counts are known to be underestimates.

Table A2
Detections of dead and alive western rattlesnakes (*Crotalus oreganus*) on the road within and outside of the survey route in the White Lake Basin, BC, Canada, 2015, 2016.

	Dead	Alive	Total
Outside survey route (3.3 km)	13	5	18
Survey route (11.7 km)	92	17	109
Total (15 km)	105	22	127

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