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A COMPARISON OF ELK-VEHICLE COLLISION PATTERNS WITH DEMOGRAPHIC AND ABUNDANCE DATA IN THE CENTRAL CANADIAN ROCKY MOUNTAINS

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16. Abstract

This study looks at the patterns and processes of elk-vehicle collisions in the Central Canadian Rocky Mountains and analyses the demographic structure of the wildlife involved in the collisions. Key findings included: males and subadults were more prone to elk-vehicle collisions; collisions occur more commonly in the fall season; all healthy elk are susceptible to vehicle collisions; the magnitude of elk collision was negatively correlated to traffic volumes, because abundance of elk greatly decreased during the study period; and elk abundance was the primary driver influencing occurrence of collisions over time. Collectively, these results will help inform the design of mitigation measures targeting the most vulnerable demographics of a population, i.e. subadults and male elk in the fall.

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A COMPARISON OF ELK-VEHICLE COLLISIONS PATTERNS WITH DEMOGRAPHIC AND ABUNDANCE DATA IN THE CENTRAL CANADIAN ROCKY MOUNTAINS

FINAL REPORT

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DISCLAIMER

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ABSTRACT

This study looks at the patterns and processes of elk-vehicle collisions in the Central Canadian Rocky Mountains and analyses the demographic structure of the wildlife involved in the collisions. Key findings included: males and subadults were more prone to elk-vehicle collisions; collisions occur more commonly in the fall season; all healthy elk are susceptible to vehicle collisions; the occurrence of elk collisions was negatively correlated to traffic volumes, because abundance of elk greatly decreased during the study period; and elk abundance was the primary driver influencing occurrence of collisions over time. Collectively, these results will help inform the design of mitigation measures targeting the most vulnerable demographics of a population, i.e. subadults and male elk in the fall.

EXECUTIVE SUMMARY

Wildlife-vehicle collisions (WVCs) are a widespread phenomenon that are strongly influenced by the traits of the species, animal population density, local terrain, road design, and traffic volumes. In addition, the mortality rate of different classes of age and sex can buffer or exacerbate how the population responds to collisions. However, the underlying patterns and processes of wildlife-vehicle collisions often are analysed without considering the demographic structure of the wildlife population.

In this study, we looked at the patterns and processes of elk-vehicle collisions in the Central Canadian Rocky Mountains where collisions are a concern among park managers and the public. We found that more females were involved in collisions, but when compared to the age and sex classes of the elk population, males and subadults were more prone to elk-vehicle collisions and this occurs more commonly in the fall season. The condition of elk as measured from percent fat marrow content was greater for road- and rail-killed elk than predator killed elk, indicating that all healthy elk are susceptible to vehicle collisions. The magnitude of elk collisions was strongly correlated to traffic volumes; however, elk abundance was the primary driver influencing occurrence of collisions over time.

Collectively, these results will help inform the design of mitigation measures targeting the most vulnerable demographics of a population, i.e. subadults and male elk in the fall. In addition, declining wildlife-vehicle collision rates with increasing traffic volumes is a good indicator that a population may be declining, and can support implementation of mitigation measures before a population crash occurs. This is meaningful to transportation and natural resource managers because in many cases, traffic volumes and vehicle collision data sets are logistically easier to collect and compile relative to abundance measures.

1. BACKGROUND

Roads are one of the most dominant forms of human-created transformations of the world's terrestrial ecosystems. There are an estimated 21 million km of roads in the world and there may be an additional ~4.7 million km more roads added by 2050 (Meijer et al. 2018). Approximately 56% of the terrestrial surface of the earth is within 5 km of a road (Ibisch et al. 2016). The effects of roads on ecosystems includes mortality from collision with vehicles, the barrier effect created by impeding ecological flows (i.e., the movement of water, organisms, or propagules), and the facilitation of elevated levels of predation, disease, and invasive species (Laurance et al. 2009; Brady & Richardson 2017). Roads facilitate human access to remote areas and instigate rapid land conversion to more urbanized and industrialized practices (Forman et al. 2003). The impacts of roads are thus greater than the footprint of the road surface and extend into surrounding habitats (Reijnen et al. 1996; Shanley & Pyare 2011).

Large mammals create a particularly vexing problem for understanding and mitigating the impacts of roads. Many species of ungulates, for example, are fairly abundant relative to other large mammals and their presence on roads poses a major safety hazard for motorists (Conover et al. 1995; Bruinderink & Hazebroek 1996; Biggs et al. 2004). Huijser et al. (2009) for example estimated the average cost of a collision with a moose, elk, and deer to be US $30,760, $17,483 and $6,617, respectively. The impacts of roads on ungulates can be significant wherever suitable wildlife habitat exists adjacent to major transportation corridors. In this way, roads that bisect protected areas can be significant sources of the barrier and mortality effects of roads on wildlife.

Since the mid-1970s, collisions between vehicles and large herbivores on the major roads have been a concern for managers in Canada's national parks (Holroyd 1979; Damas & Smith 1982; Banff-Bow Valley Study 1996). Although deer are the largest proportion of collisions with vehicles in the mountain parks, elk contribute to 27% of all wildlife-related accidents within the Central Canadian Rocky Mountains (Gunson et al. 2009). Given their large body size, important ecological role (Hebblewhite & Merrill 2009), and potential for increased damage to vehicles and passengers, resolving elk-vehicle collisions is a priority. For example, Parks Canada initiated the construction of phased wildlife crossing structures and wildlife-exclusion fencing along the Trans Canada Highway (TCH) in Banff National Park in the 1980's (Ford et al. 2010). These measures have proven successful in reducing wildlife-vehicle collisions and reduced collisions with ungulates up to 80% (Woods 1990; Clevenger et al. 2001). Similar measures are currently being planned for and built in neighbouring parks such as Kootenay and Yoho National Parks and the provinces of British Columbia and Alberta.

The impacts of roads on wildlife and the success of mitigation measures will depend, in part, on understanding the spatial and temporal patterns in wildlife-vehicle collisions. Collisions tend to be concentrated in spatial and/or temporal locations, or 'hotspots' (Mountrakis & Gunson 2009). These hotspots are formed through a combination of landscape structure near the road, wildlife population size, and traffic volume (Gunson et al. 2011). Collisions may also disproportionately affect some portions of the animal population – such as migrants and dispersers (Mumme et al. 2000; Clark et al. 2010). Finally, mortality from collisions may not reflect the same patterns of mortality in populations under density-dependent constraints associated with poor nutrition and vulnerability to predators (Hebblewhite et al. 2002; Gervasi et al. 2012; Olson et al. 2014). Restoration of landscapes impacted by roads must consider how these patterns of mortality can more accurately emulate natural processes following mitigation.

To support the design and implementation of mitigation strategies for elk and other wildlife, our primary objective was to describe the demographic groups of elk that are most susceptible to elk-vehicle collisions (EVCs). We then evaluated how abundance and traffic volume collectively and independently may influence EVCs seasonally and annually. Specifically, we developed the following hypotheses to explain patterns in EVCs (Table 1).

Table 1: Hypothesis and predictions tested to explain elk-road interactions in the Central Canadian Rocky Mountains.

Hypothesis	Prediction	Explanation
H_{age}	The proportion of young animals killed in EVCs will be greater than expected by the age structure of the surrounding elk population in the landscape surrounding the road.	Younger elk are inexperienced with roads and traffic.
H_{sex}	The sex ratio of EVCs will be the same as the sex ratio of the elk population in the landscape surrounding the road.	Vehicles are non-selective for sex: males and females are equally vulnerable to mortality from EVCs.
$H_{body\ condition}$	Predator-killed elk have poorer health and are more likely to be subadults than transportation (i.e., road and railway)-killed elk.	Predators are more selective for age and body condition than vehicle mortalities (Huggard 1993)..
$H_{season\text{-}F}$	EVCs are more likely to occur in the fall than other seasons.	Rutting behaviour increases the movement and activity of elk, making them more vulnerable to EVCs, and the addition of the spring calf cohort increases susceptibility of inexperienced individuals to EVCs.
H_{season}-S	EVCs are less likely to occur in the spring than other seasons	After harsh winter conditions, elk numbers are low
$H_{season\text{-}W}$	EVCs are more likely to occur in the winter than other seasons.	Elk have larger home ranges in the winter, making them more likely to encounter a road (Anderson et al. 2005). Adverse driving conditions may also make elk more vulnerable to EVCs in the winter.
$H_{traffic\text{-}neg}$	Traffic volume negatively affects EVC frequency.	Elk avoid roads because of traffic.
$H_{traffic\text{-}pos}$	Traffic volume positively affects EVC frequency.	Elk do not avoid roads and are killed more often with increasing vehicles (van Langevelde & Jaarsma 2004).
$H_{abundance}$	Elk abundance positively affects EVC frequency.	Elk do not avoid roads and are killed more often as elk abundance increases.

2. RESEARCH METHODS

2.1. Study Area

Our research was carried out in the Central Canadian Rocky Mountains approximately 150 km west of Calgary in southwestern Alberta and southeastern British Columbia (Figure 1). The study area is comprised of the mountain landscapes in Banff, Kootenay, and Yoho National Parks, adjacent Alberta Provincial lands, and in the Treaty 7 area (Figure 1). The climate is continental and characterized by relatively long winters and short summers (Holland and Coen 1983). The roads in the study traversed montane and subalpine ecoregions. Vegetation consisted of open forests dominated by Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), Englemann spruce (*P. englemannii*), aspen (*Populus tremuloides*) and natural grasslands.

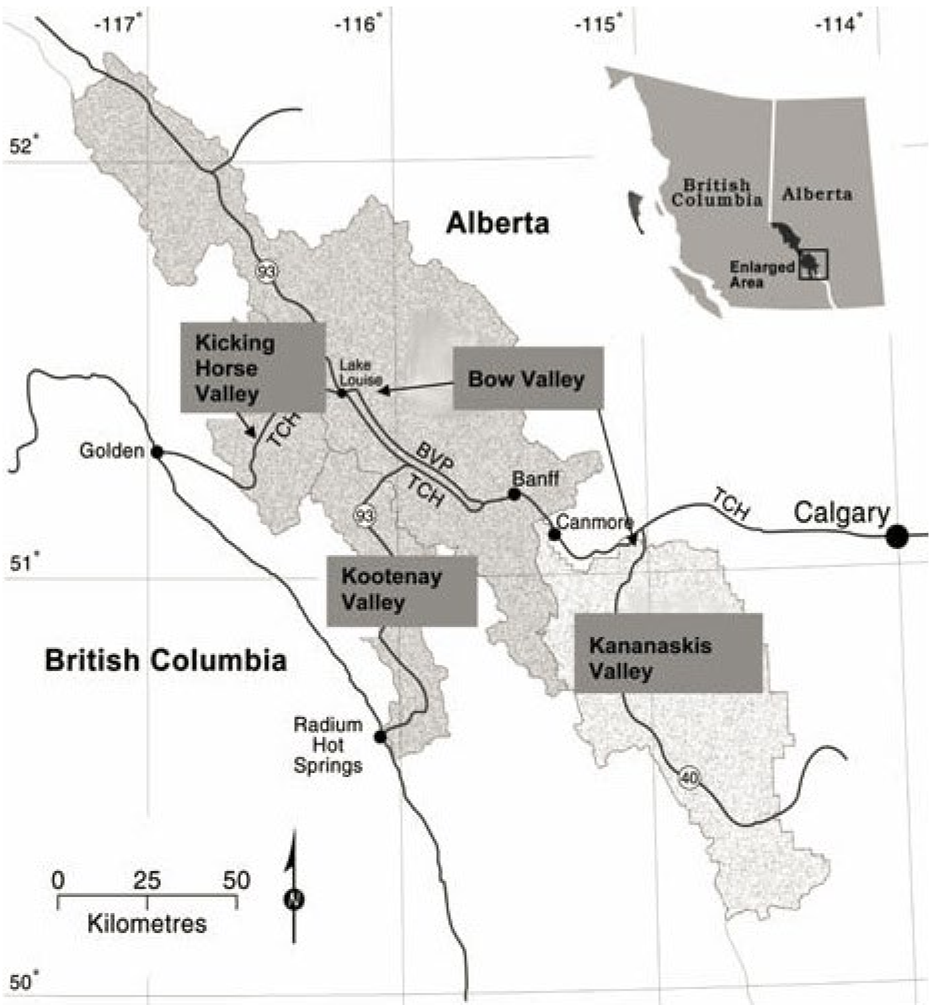

Figure 1: Location of study area and highways used to examine elk-vehicle collisions in the Central Canadian Rocky Mountains.

The geography of the central and eastern portions of the study area is dictated by the geology of the Rocky Mountains. This geography influences the distribution and movement of wildlife in the park. The few large valleys in this area, the Bow Valley being the most prominent, are recognized as critical not only in maintaining the regional-scale east-west movement of large animals (Hebblewhite & Merrill 2009), but also in providing a vital link between the valleys nested among the front ranges of the park.

We selected primary and secondary road segments within Banff, Yoho, and Kootenay National Parks and Alberta adjacent lands where reliable monitoring of EVCs and elk population sizes have occurred for decades (Table 2; Figure 1). The Alberta adjacent lands and Banff and Yoho National Parks are bisected by a nationally significant transportation corridor consisting of the Canadian Pacific Railway and the Trans-Canada Highway (TCH). The TCH lies along the valley bottoms of this mountainous terrain, for approximately 162 km from the intersection of the TCH with Highway 40 to the western boundary of Yoho National Park (YNP). We also used 102.6 km of secondary highway (Highway 93 South) within Kootenay National Park (KNP) and BNP. Annual Average Daily Traffic Volumes (AADTV) on all roads in the study area ranged from 2,000 on Highway 93 South to 16,960 east of Banff National Park (BNP) in the province in 2005 (Table 2; Parks Canada Highway Service Centre and Alberta Infrastructure, unpublished data).

Table 2: The location, general characteristics, and elk-vehicle collision rate from 1986 to 1996 on the four highways compared in this study.

Highway	**Region**	**Road length (km)**	**Traffic volume (AADT V[a,b])**	**No. lanes**	**Posted vehicle speed (km/hr)**	**Mean EVCs/km ± standard deviation**
Trans-Canada Highway	Alberta, east of Banff National Park (BNP)	35.1	16,960	4	110	7.26±7.86
Trans-Canada Highway (unfenced west zone)	BNP, Alberta	54.4	8,000	2	90	3.73±11.57
Trans-Canada Highway	Yoho National Park, British Columbia	45.6	4,600	2	90	2.06±4.20
Highway 93 South	Kootenay National Park, British Columbia and BNP (10 km)	102.6	2,000	2	90	1.26±9.21

[a]2005 annual average daily traffic volume. Data from Parks Canada Agency, Banff National Park and Alberta Transportation, Edmonton, Alberta.

[b]The 1999 summer average daily traffic volume. Data from Alberta Transportation, Edmonton, Alberta

2.2. Data Collection

We used EVC records collected year-round by Parks Canada (Banff, Yoho, Kootenay National Parks) and Alberta Natural Resources Service from 1986-2000 (n=812) that occurred on unmitigated sections of highway. Therefore, within BNP, only EVCs that occurred along the TCH west of the Banff townsite to the western boundary (TCH-west zone) where no mitigation (fencing or wildlife crossing structures) was present at the time of the collision were used. This section of highway corresponds to the ‘west zone’ as defined by Hebblewhite et al. (2002) and Phases 3A and 3B during the highway construction periods (Figure 1; Clevenger & Barrueto 2014).

The site of each accident was visited and the location, date, sex, and age were recorded for each animal mortality unless the condition of the animal was too poor to determine these characteristics. We estimated elk ages by cementum analysis in conjunction with tooth eruption patterns for ungulates (Larson & Taber 1980). The location of the mortality was plotted as a Universal Transverse Mercator (UTM) coordinate to $\pm$100 m on a 1:50,000 scale topographic map.

We obtained AADTV data on national park roads from Parks Canada (Table 2; Parks Canada Highway Service Centre, unpublished data) and on provincial roads from the Province of Alberta (Table 2; Alberta Infrastructure, unpublished data).

We used elk relative abundance estimates from annual classified ground counts in the national parks (KNP and BNP) conducted consistently in spring and fall for BNP and fall-only for KNP between 1986 and 1996 (Woods 1991; Woods et al. 1996; Parks Canada, unpublished data). Definitions of each variable used in the analysis, its source and the number of records are given in Table 3.

We analyzed data using Microsoft Excel, Statistica™ kernel release 5.5 statistical package (Statsoft® 2000) and SPSS v13.0 (SPSS Inc, 2004) for all statistical analyses. We screened all data for outliers and normality prior to each analysis.

Table 3: Definition and description of variables used in the elk-vehicle collision (EVC) analysis, 1986 to 2000.

Variable name	Definition	Source	Year
Region	Geographical location of EVCs: Banff National Park (BNP), Yoho National Park (YNP), Kootenay National Park (KNP), and Alberta Province (province)	Geographic coordinate from EVC records	1986-2000
Road[a]	Trans-Canada highway (TCH)-province = provincial highway with 4-6 lanes of high volume traffic and TCH-west (BNP, west of town of Banff to Lake Louise: phases 3a and 3b) and TCH-YNP = national park highway with 2 lanes of moderate-to-high volume traffic; Highway 93 = KNP national park highway with 2 lanes of moderate traffic volumes	Parks Canada and Alberta province mortality database and matching EVC geographical references to digital road system layer	1986-2000
Year	Year of EVC record	Parks Canada and Alberta province mortality database	1986-2000
Season	Seasons defined as: spring = March-May; summer = June-August; autumn = September-November; Winter = December-February	Parks Canada and Alberta province mortality database	1986-2000
Sex	Male, Female, Unknown	Parks Canada and Alberta province mortality database	1986-2000
Age	As recorded in database or classified into: adult = >2 years old; subadult = yearling and young-of year; yearling = $\geq$1 and $\leq$ 2 years old; young-of-year = <1 year old. Ages were estimated during necropsy analysis, or by personnel upon carcass recovery	Parks Canada and Alberta province mortality database	1986-2000
Condition	Percent marrow fat content in femur as measured by Neiland (1970)	Parks Canada mortality database	1990-1998
Mortality Type	Highway, Railway or Predation	Parks Canada mortality database	
Road length	The total length of a road on a particular section	Taken from North American Datum 83 maps and measured using ArcView 3.2 (ESRI 1999)	1986-2000

Variable name	Definition	Source	Year
Traffic volume	Annual Average Daily Traffic Volume (two lanes of traffic)	Parks Canada Highway Service Centre and Alberta province traffic counter data	1986-1996
Elk relative abundance	Estimated elk relative abundance in BNP (west zone) during spring and fall; fall-only KNP	Parks Canada classified elk ground survey data	1986-1996
Standardized elk abundance	Relative elk abundance (fall-only) divided by number of km's of road surveyed (elk/km)	Parks Canada classified elk ground survey data	1986-1996

[a] All unmitigated highway sections, i.e. no fence or wildlife crossing structures.

2.3. Age (H_{age}) and Sex (H_{sex}) Patterns in EVCs

We tested for independence of sex and age (adult, subadult) classes in EVCs using Chi-squared analyses. Subadults were defined as young-of-the-year (YoY) and yearlings which was denoted in the database, while adults were considered 2 years or older. We used the complete EVC data set where sex and age were described from all regions between 1986-2000 (Table 2). We performed three tests, one each for sex (2x2), age (2x2), and a combined analysis (4x4) and assumed a 1:1 ratio among classes.

We compared the sex and age of EVCs with the adjacent elk population in the 'west zone' of BNP where both spring and fall elk ground counts occurred. We used a Chi-squared analysis to compare observed frequencies of EVCs for each sex and age class with expected frequencies derived from an average of spring and fall elk ground counts from 1986 to 2000. The average of spring and fall elk ground counts would take into account differences in elk demographics from the elk herd migrating between the east and west zones of Banff National Park. Although individuals move between zones (east and west of the town of Banff) movements are not permanent (McKenzie 2001).

From the ground counts, we used elk classified as YoY and spike (also known as yearling males) as subadults and therefore only YoY and yearling males were included in the observed counts for EVCs. In order to account for population fluctuations, we grouped the EVC records into three five-year periods from 1986 to 2000 and did a separate analysis for each period and again for all years.

2.4. Seasonality of EVCs (H_{fall}, H_{spring})

We calculated the proportion of total, male, female and unknown EVCs for each month. We then calculated the seasonal mean and standard deviation and tested for differences using a Kruskal-Wallis Analysis of Variance (ANOVA) test followed by a Tukey's range test. Autumn began in September, which is typically the start of the rut. To test whether sex and age influenced EVCs differently seasonally, we used a Chi-square test to compare observed EVCs in the spring and fall with each respective seasonal elk ground count in the BNP west region. (Figure 2)

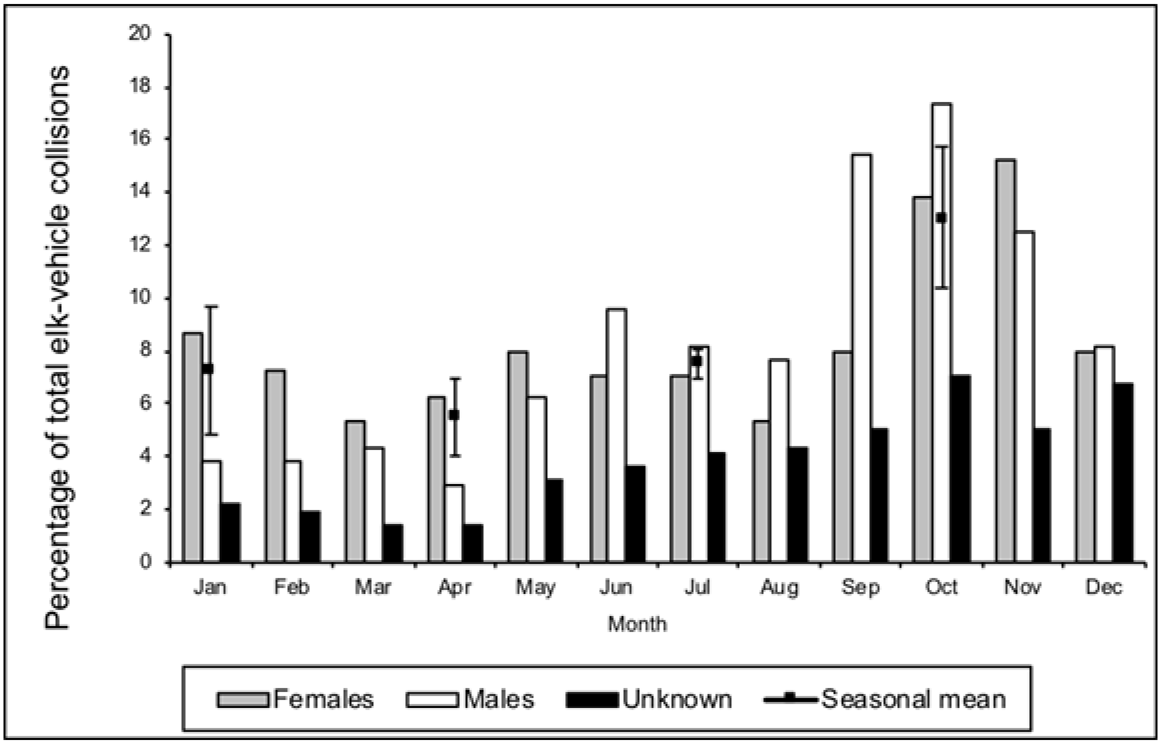

Figure 2: The percentage of female, male, and unknown elk-vehicle collisions occurring in each month and the total seasonal mean with standard errors on the Trans-Canada Highway and Highway 93 S in the Canadian Rocky Mountains, from 1986 to 2000 (n = 812).

2.5. Condition of Elk Killed on Highways, Railways and by Predators ($H_{predation}$)

We tested for differences in the body condition of elk killed on highways, railways, and by predators in BNP. Predator-killed elk were confirmed by park researchers, wardens and veterinary personnel. Femur marrow was assayed to measure percent fat content following Neiland (1970); however, we used a dehydrator instead of an oven. We used a Kruskal-Wallis test to determine if percent marrow fat content can be explained by a mortality type and month-class interaction.

2.6. Traffic Volume ($H_{traffic-neg}$, $H_{traffic-pos}$) and Elk Abundance ($H_{abundance}$)

Elk-vehicle collision rates (EVC per km) were compared between roads from 1986 to 2000 for each highway [TCH-province, TCH-west zone, TCH-YNP, and Highway 93 (KNP only); Table 2] using a Kruskall-Wallis ANOVA. We then compared the rates of EVCs with traffic volumes using a Pearsons Correlation test.

To evaluate how both elk abundance and traffic volume influence EVCs, we conducted a more detailed examination on the TCH in the west zone and Highway 93 where annual elk ground counts (fall only) were available from 1986 to 1996. We used an analysis of covariance (ANCOVA) test to evaluate the influence of elk abundance and traffic volume separately on EVC rate using road-type as our categorical variable. Traffic volume was log transformed so it was normally distributed (Zar 1999).

Elk abundance and traffic volume were significantly negatively correlated to each other on the two roads combined (Spearman's rank correlation, both $r>-0.80$, $p<0.05$; Figure 3). Therefore, to evaluate the influence of elk abundance independent of traffic volume on EVC rates, we used an ANCOVA test with fall and spring as the categorical variable on the TCH in the west zone. This controls for the influence of traffic volume on EVC occurrence because traffic volumes are similar during the spring and fall periods (t-test, $p>0.05$, 1996-2000). Seasonal elk counts were only available for the TCH-west zone from 1986 to 2000, so frequencies of EVCs were used instead of rates.

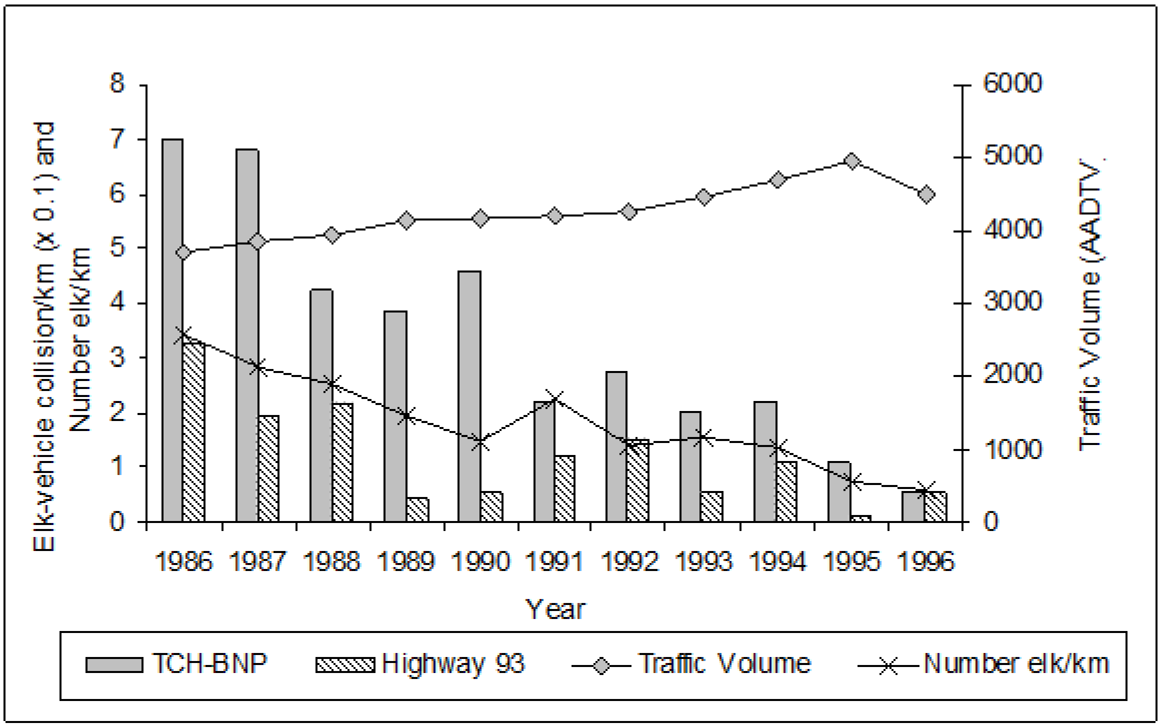

Figure 3: Standardized number of elk-vehicle collisions (EVC) annually, with annual average daily traffic volume (AADTV) for both highways and estimated standardized elk abundance along Highway 93 and Trans-Canada Highway-BNP, in the Central Canadian Rocky Mountains, 1986-1996.

3. RESULTS

3.1. Age (H_{age}) and Sex (H_{sex}) Patterns in EVCs

There were significantly more female EVCs (n=292) than male EVCs (n=146) on all four roads ($\chi_1^2 = 25.0$, $n = 438$, $p < 0.0001$) but sex did not influence EVCs for subadults (Table 4). Furthermore, there were significantly more adult elk (n=329) involved in EVCs than subadults (n=109) ($\chi_1^2 = 72.8$, $n = 438$, $p < 0.0001$, Table 4). The male:female ratio among adult EVCs was 0.45:1 as opposed to 0.68:1 in subadult EVCs (Table 4). When taking the sex ratio of the elk population in the TCH-west zone into account, there was a greater proportion of male EVCs than female EVCs during each of the 5-year periods (all $\chi^2_1 \geq 10.8$, all $p < 0.05$; Table 5) and the overall 15-year period ($\chi^2_1 = 68.2$, $n = 374$, $p < 0.0001$; Table 5).

The total number of adult and subadult EVC occurrences were similar in the TCH-west zone (Table 6). However, when taking the distribution of age classes in the local population into account, there was a significantly greater frequency of subadult road mortality during both periods: 1986 to 1990 and 1991 to 1995 (both $\chi^2 \geq 12.5$, $p < 0.01$), whereas no significant difference was found in 1996-2000 ($p = 0.369$; Table 6). Over the entire duration of the study (1986 to 2000) significantly more subadult elk were killed in EVCs than adults ($\chi^2_1 = 18.3$, $n = 291$, $p < 0.0001$; Table 6).

Table 4: The number of elk-vehicle collisions by sex and age class in the Canadian Rocky Mountains from 1986-2000.

Age	Males	Females	Total	Sex ratio EVCs (M:F)	χ^2_1[b]
Adult	102	227	329	0.45:1	24.6***
Subadult	44	65	109	0.68:1	2.04
Total	146	292	438	0.50:1	25.0***

[b] *: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 5: The number of elk-vehicle collisions by males and females compared to the expected frequencies from ground counts averaged for the spring and fall periods (Parks Canada, unpublished data) in the TCH-west zone of Banff National Park, from 1986-2000.

Year sequence	Males		Females		X^2[a]
	Observed	Expected	Observed	Expected	
1986-1990	44	23	65	86	24.3***
1991-1995	28	10	26	44	47.5***
1996-2000	10	4	14	20	10.8*
Total period	82	37	105	150	68.2***

[a] Denotes a sex ratio significantly different with the following probability values.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 6: The number of elk-vehicle collisions involving subadults and adults on the in the TCH-west zone of Banff National Park, 1986-2000

Year sequence	Subadult		Adult		$X^{2\,a}$
	Observed	Expected	Observed	Expected	
1986-1990	65	31	59	113	27.7***
1991-1995	26	15	28	63	12.5**
1996-2000	7	6	20	30	0.8
Total period	98	18	107	68	18.3***

[a] Denotes a subadult-adult ratio significantly different with the following probability values. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

3.2. Seasonality of EVCs (H_{fall}, H_{spring})

The monthly incidence of EVCs among female and male elk was relatively constant among winter, spring, and summer, but higher during the fall (Kruskal-Wallis test, $F_{3,44} = 3.48$, $p = 0.025$; Figure 2). There were significantly more EVCs in fall compared to spring and winter (Tukey's HSD test, $P = 0.0030$ and $P = 0.0100$ respectively; Figure 2).

There was a significant interaction between the sex ratio of adult EVCs and season, when compared to the spring and fall population counts ($\chi^2_3 = 6.77$, $n = 64$, p = 0.079). In the fall there were more male adult EVCs occurring than female adult EVCs as compared to the population ($\chi^2_2 = 3.81$, $n = 47$, p = 0.051). There was a significant difference in the ratio of subadult:adult EVCs compared to the expected age ratio from the population during the spring and fall ($\chi^2_3 = 29.28$, $n = 133$, p < 0.0001). The ratio of subadult:adult EVCs in the fall was 300% greater than in the spring.

3.3. Condition of Elk Killed on Highways, Railways and by Predators ($H_{predation}$)

Between 1990 and 1998, 397 elk carcasses were collected in BNP from mortalities associated with highways ($n = 102$), railway ($n = 133$), and by predators ($n = 162$). There was a significant effect of elk condition on the three types of mortality (Kruskal-Wallis test, $F_{2,397} = 9.45$, $p < 0.0001$). Percent marrow fat content of highway and railway killed elk was not significantly different, but both had a significantly greater percentage fat content than predator-killed elk (Tukey's HSD test, $p < 0.05$).

3.4. Traffic Volume ($H_{traffic\text{-}neg}$, $H_{traffic\text{-}pos}$) and Elk Abundance ($H_{abundance}$)

EVC rates were significantly different between each road type (Kruskal-Wallis test, $H_{3,60} = 14.99$ $p = 0.001$; Table 2) and were positively correlated to traffic volume (Pearson's correlation = 0.99). The mean EVC rate ± SD from highest to lowest for all 4 roads was TCH-province (7.26±7.86); TCH-west zone (3.73±11.57); TCH-YNP (2.06±4.20) and Highway 93 South, 1.26±9.21 (Table 2). In a more detailed analysis, an opposite relationship was found between traffic volume and EVC occurrence. Both EVCs and elk population counts decreased on the TCH-west zone and Highway 93 combined, by 89% and 83% respectively, while traffic volume increased by 22% between 1986 and 1996 (Figure 3).

Both ANCOVA models evaluating elk abundance ($p<0.0001$, $R^2=0.75$) and traffic volume ($p<0.0001$, $R^2=0.82$) independently on EVC rate on Highway 93 and TCH-BNP were significant (Table 7). As elk abundance decreased, EVCs significantly decreased and this relationship was not different between roads (Table 7, Figure 4). As traffic volumes increased EVC rate significantly decreased and this relationship was more evident on Highway 93 than on TCH-west zone (Figure 5).

We found a significant positive influence of elk abundance on EVC occurrence in the seasonal model (Table 7; $p<0.0001$) when traffic volume remained constant in the TCH-west zone. There was a significant interaction between season and elk abundance on EVC frequency (Table 7; $p=0.0001$). More specifically, EVCs increased at a greater rate during the fall season when elk abundance numbers were significantly higher ($t=-2.09$, $n=16$, $p=0.045$; Figure 6).

Table 7: Analysis of covariance of elk abundance and traffic volume (continuous variable), and season and road (categorical variables) on elk-vehicle collision (EVC) rate on the TCH-west and Highway 93

Source	**d.f.**	**Type III SS**	**F Value**	**Pr. Type I error**
Elk abundance model (see Figure 4); N=22 observations; model $R^2=0.75$				
Road	1	4.0	0.04	0.8514
Abundance	1	2728.0	24.64	0.0001
Road * Abundance	1	395.0	3.57	0.7515
Traffic volume model (see Figure 5); N=22 observations; model $R^2=0.82$				
Road	1	853.8	10.53	0.0045
Log (traffic volume)	1	3203.1	39.51	0.0000
Road * Log (traffic volume)	1	576.6	7.11	0.0157
Season (see Figure 6); N=30 observations; model $R^2=0.79$				
Season	1	22.5	2.88	0.1014
Abundance	1	194.8	25.01	0.0000
Season * Abundance	1	153.3	19.67	0.0001

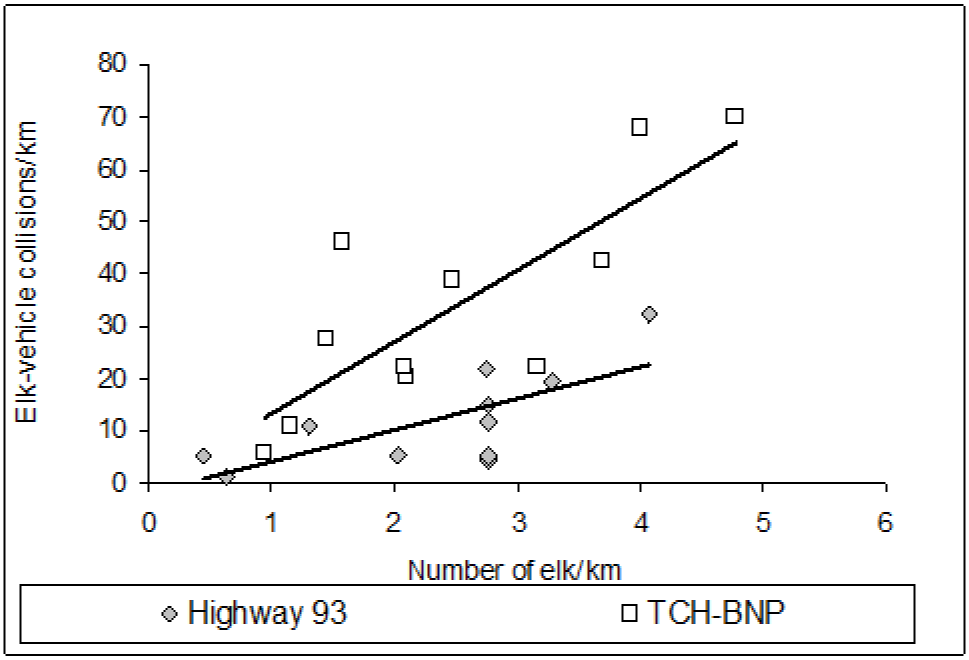

Figure 4: The interaction between elk population abundance (elk/km) and road type for Highway 93 and Trans-Canada Highway in BNP. As abundance increases, EVCs increase and this relationship is not significantly different between roads.

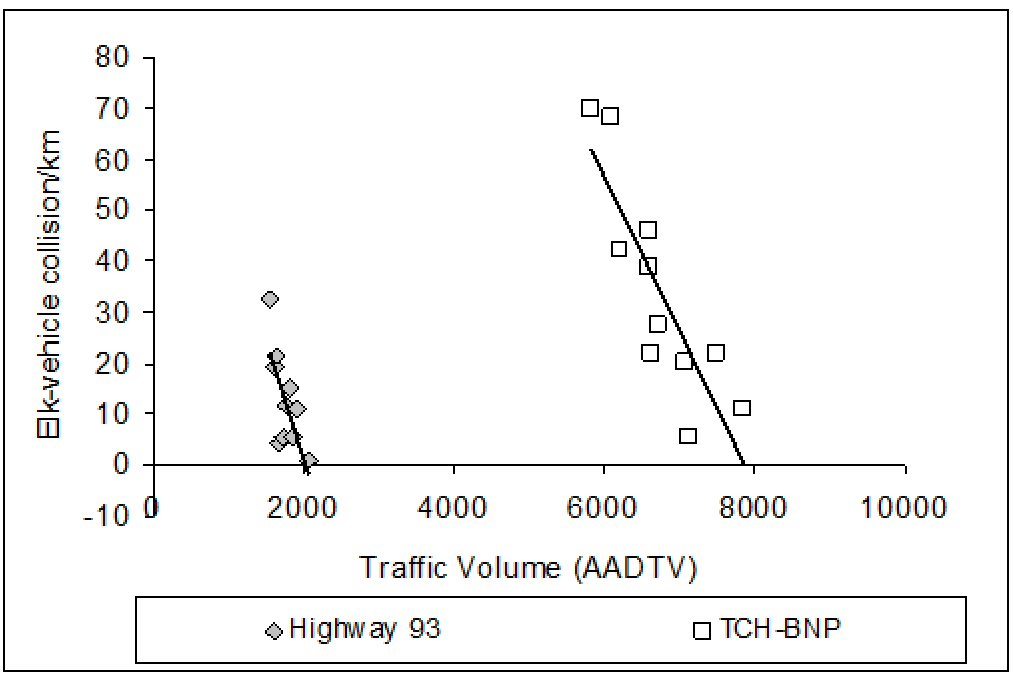

Figure 5: The interaction between annual average traffic volume (AADTV) and elk-vehicle collision rate on two roads: Highway 93 and Trans-Canada Highway in BNP. As traffic volumes increase, EVC rate decreases and this is more apparent on Highway 93.

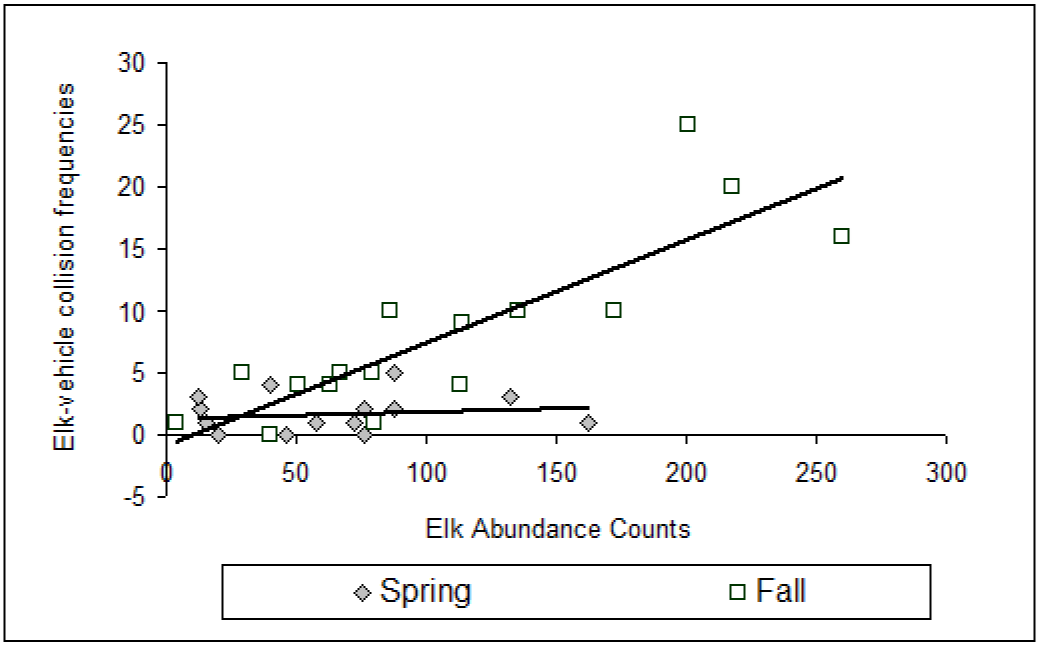

Figure 6: The interaction between elk abundance and elk-vehicle collision frequencies between spring and fall along the Trans-Canada Highway in BNP.

4. DISCUSSION

Our study provides novel and rare details on the links between the demographic structure of road mortalities and an adjacent large mammal population. While it is well established that roads can have negative impacts on biodiversity, it is less clear if road mortality is selective for particular individuals in a population. Some animals make greater contributions to population growth than others – for example – the survival of adult female ungulates is a critical parameter in wildlife management (Gaillard et al. 1998). Some animals may be vulnerable to mortality from multiple sources, i.e., compensatory mortality, such that road-kill has minimal impacts on populations (Hebblewhite et al. 2002). Finally, some animals may have higher value for people than others, such as harvestable-aged male ungulates (Mysterud et al. 2002; Arnett & Southwick 2015). If road mortality is selective for particular individuals, it may either exacerbate or buffer 1) the effect of roads on a population and 2) the perceived loss in ecosystem services to stakeholders (Knoche & Lupi 2007). Here, we tested hypotheses related to the role of sex, age, season, population size, and traffic volume in shaping spatial and temporal patterns in EVCs. Given the disproportionate role that some individuals make in the growth of wildlife populations – particularly adult females (Wilmers et al. 2020) – our study sheds important insights on mechanisms underlying the restoration and maintenance of biodiversity in human-occupied landscapes.

4.1. Sex and Age Effects

Compared to males, we found significantly more female elk were killed on roads in the Rocky Mountains. We anticipate that this result is largely based on a female-biased sex ratio in the local population that has been observed since at least the 1970s (Flook 1970; Holroyd 1979). Similar sex ratios have been found in studies on the road-kill in mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) (Olson et al. 2014; Bellis & Graves 1971; Allen & McCullough 1976). However, when we compared the proportion of female road-kill to the sex ratio in the population directly, there were more males than expected by chance. In other words, males are being killed on roads at rates greater than expected from the structure of the local population. Similar male-biased road mortalities have been found in moose in other study areas (Joyce & Mahoney 2001). Male elk – like other ungulates – may be more vulnerable to road mortalities because of their larger home range sizes and greater vagility during particular seasons. Specific to the Bow Valley, male elk migrate more than females to access rutting grounds, mates, and foraging areas (Woods 1991; Hebblewhite 2002).

We found that more adult elk are killed on the highways than young animals. We anticipate that this result is largely based on an adult-biased age ratio in the local population (Parks Canada, unpublished data). However, when taking into account the age structure of the local population, subadults were significant more likely to killed by vehicles. This pattern of age-selectivity is similar to earlier results found in the study area (Bottini 1987) and for yearling male white-tailed deer in the lower Yellowstone River in Montana (Dusek et al. 1989). It is likely that subadults are more vulnerable to collisions than adults because they lack the necessary experience to navigate vehicular traffic. In addition, calves may be more prone to collisions during the mating season when cow movements are disrupted by males.

4.2. Seasonal Effects

Seasonal variations in ungulate-vehicle collisions have been noted since some of the earliest published records of road-related mortality of wildlife (Pennsylvania Game Commission 1969; Bellis & Graves 1971; Allen & McCullough 1976; Joyce & Mahoney 2001). The collisions frequencies tend to increase from early spring to fall, peaking in October and November during the rut and/or hunting season (Bruinderink & Hazebroek 1996; Hubbard et al. 2000; Neumann et al. 2012; Creech et al. 2019; Ignatavicius et al. 2020).

This fall peak has been attributed to increased ungulate activity level associated with migration and breeding behaviour, which brings ungulates in contact with the road network more frequently (Woods 1991; Ager et al. 2003). More EVCs occurred in winter in the Jemez Mountains plateau region of New Mexico and was attributed to migration behaviour of elk during heavy snowfall in the adjacent higher terrain (Biggs et al. 2004). However, migration may not be an important factor in other areas. Creech et al. (2019) found little difference in seasonal WVC patterns between western Montana counties where ungulates tend to exhibit migratory behaviour and eastern counties where migratory behaviour is less common.

Notably, we found that subadults were killed more often in the fall than in the spring. This age-related pattern is likely attributed to changes in seasonal population demographics more than other factors such as traffic volume, because the spring and fall traffic volumes are similar on the TCH in the Bow Valley. There is a doubling of the elk population in the fall due to the addition of a relatively inexperienced spring calf cohort into the population. This coupled with possible reduced population numbers after harsh winter conditions in the spring would further explain seasonal changes in sub-adult EVCs (Romin & Bissonette 1996).

4.3. Condition of Elk

Elk populations have several sources of mortality, with predators and collisions with vehicles having significant effects in some populations (Hebblewhite et al. 2002; Gagnon et al. 2019). We found elk killed by vehicles and trains tended to be in better body condition than elk killed by natural predators – a pattern that is suggestive of additive mortality. If road mortalities occur for animals that would have otherwise been killed by natural predators (i.e., because they have poor body condition), then the population is experiencing compensatory mortality (Fowler 1987; Boyce et al. 1999). In contrast, additive mortality occurs when road-killed elk have a fairly high probability of survival and this could contribute to the regulation of elk population size.

Our results contrast with O'Gara & Harris (1988), who found that predators such as cougars and coyotes killed deer in good condition, while deer killed by vehicles were in poor condition. They attributed this finding to sick and malnourished deer moving to and congregating in valley bottoms in winter months where traveling on roadsides clear of snow is easier. In order to better understand how road-related mortality may impact ungulate populations, a more detailed understanding is needed of age- and sex-biased collision rates and timing of these kills.

4.4. Effects of Traffic Volume and Abundance on Road Mortality

In our study, EVCs were positively related to traffic volumes on a broad geographic scale in the Rocky Mountains, however when dissecting this further over time, the collision rate (mean number of EVCs per km of road) decreased as traffic volume increased. Unexpectantly, traffic volume negatively influenced EVC rates on both highways and this relationship was more evident on Highway 93. As expected, abundance was positively correlated to EVCs and was a major driving factor in the fall. These results indicate correlates such as traffic volume need to be statistically analysed at different resolutions, and additional tests should evaluate how abundance and traffic volume interact and influence road-kill by road-type and region (Clevenger et al. 2015).

Wildlife-vehicle collisions could be assumed to increase with the abundance of animals and vehicles since these two forces, animal presence and vehicles on a road simultaneously, create a collision (Fahrig et al. 1995; Romin & Bissonette 1996; Philcox et al. 1999; Seiler 2004; van Langevelde & Jaarsma 2004). However, animals may avoid roads because of traffic (Gagnon et al. 2007) or because of the road surface (Shine et al. 2004; Ford & Fahrig 2008) or other reasons. If road avoidance behaviour co-varies with traffic (Seiler 2005; Thurfjell et al. 2015), then increasing traffic volume may have minimal effects on road-kill rates (Fahrig et al. 2001).

Another explanation for the negative effect of traffic volume on EVCs is that mortalities may eventually contribute to population declines (but see Munro et al. 2012). Other studies have shown that road-related mortality depressed populations to the point that road-kills rarely occurred (Eberhardt et al. 2013; Zimmermann Teixeira et al. 2017) in areas of high traffic volumes. Given the corroborating evidence that EVCs are comprised of a high proportion of adult female elk in good body condition, the additive mortality hypothesis warrants further investigation as a partial explanation for the decline of elk. The recolonization of wolves to Banff and Kootenay National Parks in the 1980s is also a likely contributor to the decline in elk abundance. Wolves reduced annual survival rates for elk from 0.89 to 0.61 from the central zone (no wolves) to the BNP-west zone (high wolf density) respectively (McKenzie 2001; Hebblewhite et al. 2002).

Following the installation of road mitigation measures in 1997 (Phase 3A) and further west in 2009 (Phase 3B), elk populations have stabilized and EVCs have dropped to almost nothing (Clevenger & Barrueto 2014) in spite of an ongoing presence of wolves. Without information on elk abundance and road-kill rates prior to wolf recolonization, the effects of changing traffic patterns on additive mortality will be impossible to determine. As such, the recent trends of elk abundance in the post-mitigation phases of the TCH suggests that EVCs are unlikely to be limiting the elk population as long as wolves are in the system.

5. CONCLUSIONS AND RECOMMENDATIONS

We found that by incorporating population structure into the analysis of vehicle collisions with elk, new perspectives on the relative vulnerability of animals to mortality were revealed. These perspectives emerged from information on local (i.e., near the road) wildlife populations that are typically unavailable for most road mortality studies (Ramp et al. 2005; Olson et al. 2014). These insights add to the growing body of evidence that demographic-specific road mitigation efforts are needed to restore animal movements at the landscape scale (Ford et al. 2017).

Patterns of traffic volume and population abundance on WVCs can help managers predict long-term viability of wildlife populations and assess when and where wildlife mitigation is most effective for targeted species. In the past road agencies have often installed mitigation where road-kill is the highest and this may ignore locations where road-kill has already depressed populations and recovery efforts are required prior to a population crash.

Mitigation measures that are more effective when targeted for specific periods and discrete locations, such as seasonal warning signage or awareness campaigns, can be implemented during peak collision times, i.e. in the fall months for most ungulates in North America. To address the demographic specific vulnerabilities that we observed in our study, road safety awareness campaigns can account for sex and age bias with messages like ‘Watch for cow elk with calves crossing roads’ to inform motorists travelling through an area.

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7. ABBREVIATIONS AND ACRONYMS

AADTV	Annual Average Daily Traffic Volumes
ANCOVA	Analysis of Covariance test
ANOVA	Analysis of Variance test
BNP	Banff National Park
EVC	Elk-Vehicle Collision
KNP	Kootenay National Park
TCH	Trans-Canada Highway
UTM	Universal Transverse Mercator
WVC	Wildlife-Vehicle Collision
YNP	Yoho National Park
YoY	Young-of-the-year

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