Received: 24 January 2022 | Revised: 5 August 2022 | Accepted: 17 October 2022

DOI: 10.1111/csp2.12842

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

WILEY

A comparison of elk-vehicle collision patterns with demographic and abundance data in the Central Canadian Rocky Mountains

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Funding information
Public Works and Government Services Canada; Nevada Department of Transportation; Parks Canada; Woodcock Foundation

Abstract

Wildlife-vehicle collisions are a widespread phenomenon that are influenced by species behavior, abundance, and road and landscape interactions. The mortality rate of different age and sex classes can buffer or exacerbate how the population responds to vehicle collisions. We evaluated the demographic-specific patterns of elk-vehicle collisions in the Central Canadian Rocky Mountains. More females and adults were involved in collisions, but when compared to the sex and age of the population, males and subadults were more prone to collisions in the fall. The fat marrow content (condition) of elk was greater for road- and rail-kill than predator-killed elk indicating that vehicle collisions are an additive source of mortality. As traffic volumes increased elk collisions decreased because elk declined over the study period. Evaluation of long-term datasets can assist in designing mitigation that target the most vulnerable demographics of a population. For example, larger more open wildlife crossing structures have shown to be more suitable for vulnerable demographics such as female grizzly bears, male ungulates, and female ungulates traveling with young. When crossing structures are not practical, demographic-specific information can inform outreach and awareness programs that strive to elicit a favorable response from motorists ultimately avoiding collisions with animals on roads.

KEYWORDS

abundance, age, condition, demographic, elk-vehicle collisions, Rocky Mountains, sex

1 | INTRODUCTION

Roads are one of the most dominant forms of human-created transformations of the world's terrestrial ecosystems. There are an estimated 21 million kilometers (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 include 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 (Brady &

Richardson, 2017; Laurance et al., 2009). 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).

Many species of ungulates, for example, moose (*Alces alces*), elk (*Cervus canadensis*), and deer are fairly abundant in North America and Europe and their presence on roads pose a major safety hazard for motorists (Biggs et al., 2004; Bruinderink & Hazebroek, 1996; Conover et al., 1995). 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 $ 6617, respectively. These costs include damages to vehicle, injury or fatality to motorist, and other indirect costs such as towing, and loss of animal for hunting purposes.

The impacts of roads are notably more severe wherever suitable wildlife habitat, for example, protected areas occur adjacent to a major transportation corridor (Clevenger et al., 2001; Martinig & Bélanger-Smith, 2016). In the Canadian Rocky Mountains, highways bisect several protected areas, imposing a significant source of mortality and barrier effect on the wildlife community (Clevenger et al., 2015; Gunson et al., 2009). As a result, park managers began to recognize and document collisions between vehicles and wildlife, most notably ungulates in the mid-1970s (Banff Bow Valley Study, 1996; Damas & Smith, 1982; Holroyd, 1979).

Prior to installing exclusion fencing and wildlife crossing structures, elk comprised the second highest count of ungulate-vehicle collisions (27%) following mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) (58% collectively) in the mountain parks (Gunson et al., 2009). Given their important ecological role as a top predator for wolves (Hebblewhite et al., 2002), and potential for increased damage to vehicles, elk were prioritized for mitigation solutions to reduce wildlife-vehicle collisions. In the 1980s, Parks Canada initiated the construction of phased wildlife crossing structures and wildlife-exclusion fencing along the Trans-Canada Highway (TCH) in Banff National Park (Ford et al., 2011). These measures have proven most successful in reducing vehicle collisions for deer and elk whose collision rates were reduced by up to 80% (Clevenger et al., 2001; Woods, 1990). The success of these measures led to an expansion of exclusion fence with dedicated crossing structures along highways in both Kootenay and Yoho National Parks (YNPs), and a new wildlife overpass is being designed and planned for along the TCH adjacent to Banff National Park (BNP) in the province of Alberta.

The success of mitigation measures in reducing impacts of roads on wildlife is influenced, in part, on the spatial and temporal patterns of 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) and may be comprised of a disproportionately portion of the animal population—such as females undergoing overland turtle migrations or inexperienced migrants and dispersers moving to new habitat (Clark et al., 2010; Mumme et al., 2000; Steen et al., 2012). Finally, patterns of wildlife mortality from collisions may be further complicated in populations experiencing density-dependent constraints associated with poor nutrition and vulnerability to predators (Gervasi et al., 2012; Hebblewhite et al., 2002; Olson et al., 2014). Restoration of landscapes impacted by roads must consider these detailed patterns of mortality in order to more accurately emulate natural processes for those individuals most impacted by roads following mitigation.

To support more informed design and implementation of mitigation strategies that are effective for entire wildlife populations impacted by roads, we developed the following hypotheses, predictions and explanations related to the role of sex, age, season, condition, population size, and traffic volume in explaining patterns in elk-vehicle collisions (EVCs) (Table 1). We first looked at the demographic groups of elk that are most susceptible to EVCs by comparing these to the adjacent population structure. Next, we evaluated the condition of EVCs in relation to rail- and predator- killed elk. We then evaluated how abundance and traffic volume collectively and independently influence EVCs seasonally and annually. Our findings were then interpreted to support mitigation planning for wildlife in general including elk species evaluated in this study.

2 | 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 YNPs, 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 & Coen, 1983). The roads in the study traverse montane

TABLE 1 Hypothesis and predictions tested to explain elk-vehicle collisions in the Central Canadian Rocky Mountains

Hypothesis	Prediction	Explanation
H_{age}	The proportion of young animals killed in EVCs will be greater than expected than the age structure of the surrounding elk population in the landscape surrounding the road.	Younger elk are inexperienced with roads and traffic (no reference known).
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 (Olson et al., 2014).
$H_{body\ condition}$	Predator-killed elk have poorer health than transportation (i.e., road and railway)-killed elk.	Predators are more selective for body condition than vehicle mortalities (Huggard, 1993).
$H_{season\text{-}F}$	EVCs are more likely to occur in the fall than other seasons.	Rutting behavior increase the movement and activity of elk, making them more vulnerable to EVCs (Hubbard et al., 2000) and the addition of the spring calf cohort increases susceptibility of inexperienced individuals to EVCs.
$H_{season\text{-}S}$	EVCs are less likely to occur in the spring than other seasons	After harsh winter conditions, elk numbers are low (Romin & Bissonette, 1996).
$H_{season\text{-}W}$	EVCs are more likely to occur in the winter than other seasons.	Elk have larger home ranges in the winter, increasing liklihood of a road encounter (Anderson et al., 2005). Adverse driving conditions may also make elk more vulnerable in the EVCs in the winter.
$H_{traffic\text{-}neg}$	Traffic volume negatively affects EVC frequency.	Elk avoid roads because of traffic (Rost & Bailey, 1979).
$H_{traffic\text{-}pos}$	Traffic volume positively affects EVC frequency.	Elk do not avoid roads (Forrest & St. Clair, 2009) 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 (Joyce & Mahoney, 2001).

Abbreviation: EVCs, elk-vehicle collisions.

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 (Holland & Coen, 1983).

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 highways within Banff, Yoho, and Kootenay National Park (KNP) and Alberta adjacent lands where reliable monitoring of EVCs and elk population sizes have occurred for decades (Table 2 and Figure 1). The Alberta adjacent lands and Banff and YNPs are bisected by a nationally significant transportation corridor consisting of the Canadian Pacific Railway and the 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 YNP. KNP is bisected by a north–south route called Highway 93 which connects Banff National Park southerly to Radium in the adjacent province of British Columbia. Annual Average Daily Traffic Volumes (AADTV) on all roads in the study area ranged from 2000 on Highway 93 to 16,960 east of BNP in the province in 2005 (Table 2; Parks Canada Highway Service Centre and Alberta Infrastructure, unpublished data).

2.2 | Data collection

We used elk mortality records collected year-round by Parks Canada (Banff, Yoho, KNPs) and Alberta Natural

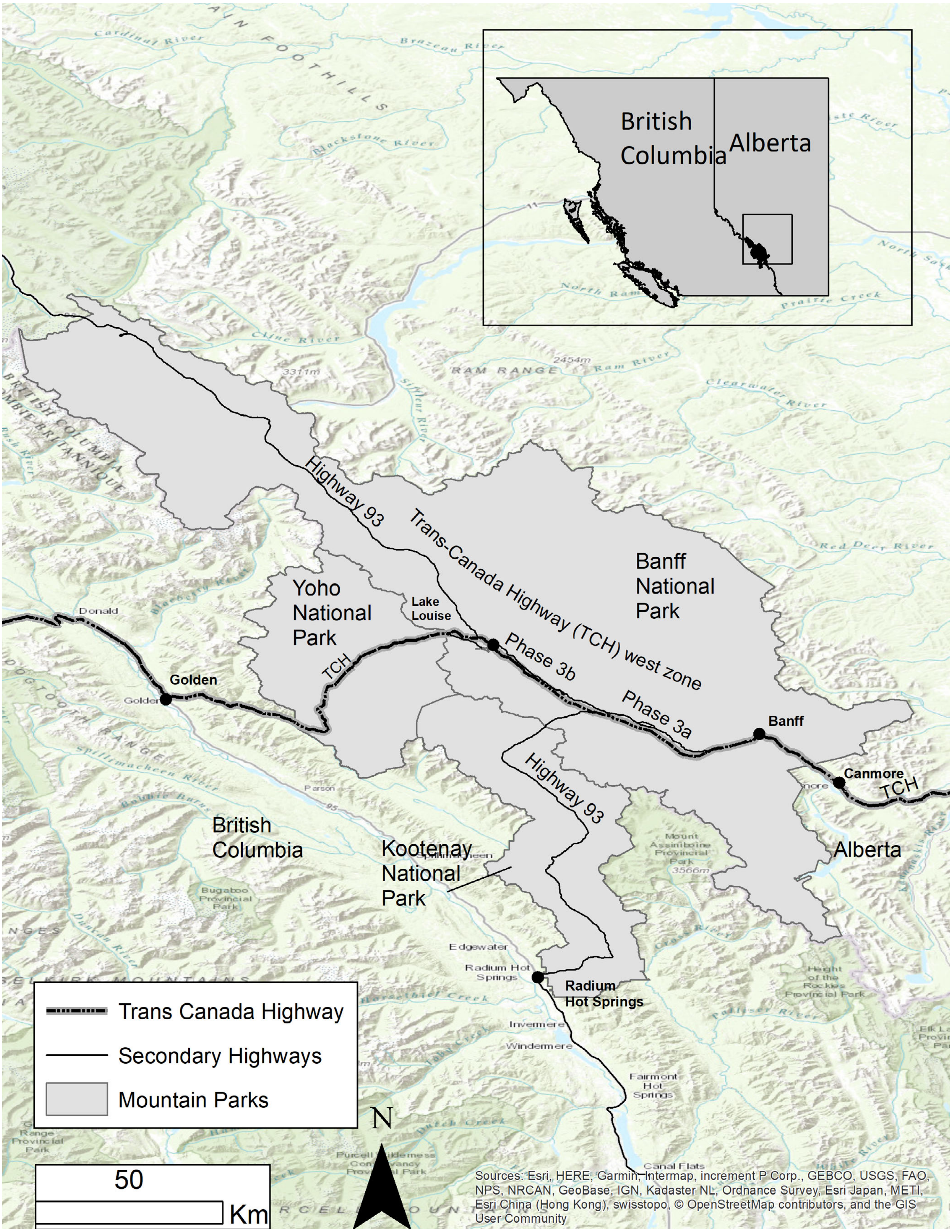

FIGURE 1 Location of study area and highways used to examine elk-vehicle collisions in the Central Canadian Rocky Mountains

TABLE 2 The location, general characteristics, and elk-vehicle collision rate from 1986 to 2000 on the four highways compared in the Central Canadian Rocky Mountains

Highway	Region	Road length (km)	Traffic volume (AADT V)[ab]	No. lanes	Posted vehicle speed (km/h)	Mean EVCs/km ± standard deviation
Trans-Canada Highway	Alberta, east of BNP	35.1	16,960	4	110	7.26 ± 7.86
Trans-Canada Highway (unfenced west zone)	BNP, Alberta	54.4	8000	2	90	3.73 ± 11.57
Trans-Canada Highway	Yoho National Park, British Columbia	45.6	4600	2	90	2.06 ± 4.20
Highway 93	Kootenay National Park, British Columbia and BNP (10 km)	102.6	2000	2	90	1.26 ± 9.21

Abbreviations: AADTV, annual average daily traffic volume; BNP, Banff National Park; EVCs, elk-vehicle collisions.
[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.

Resource Services from 1986 to 2000. The database is comprised of information that includes date, species, location, age, sex, and cause of death (railway, highway, predator), and condition of animal as obtained from Occurrence Reports and Mortality cards. Mortality cards are completed when an animal carcass is brought into the BNP abattoir and the carcass is evaluated for various conditions such as cause of death, age and condition. The age of elk was estimated by cementum analysis in conjunction with tooth eruption patterns for ungulates (Larson & Taber, 1980). Body condition was estimated by measuring percent marrow fat content in the femur as measured by Neiland (1970), however a dehydrator was used instead of an oven.

The location of the mortality was plotted as a Universal Transverse Mercator (UTM) coordinate to ±100 m on a 1:50,000 scale topographic map. All EVCs 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 in the 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).

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) from 1986 to 1996. 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). Counts were conducted along the road network, for example, TCH in the Bow Valley, which allowed the age and sex of elk to be observed. These counts captured 60% of the elk population (Woods, 1991), as evaluated by sightings of a known number of collared elk (Huggard, 1993). Spring counts occur after cows have calves, and fall counts occur when leaves have fallen to ensure optimal visibility.

Definitions of each variable used in the analysis, its source and range of years are given in Table 3. Season was defined as spring that occurred between March and May; summer between June and August, autumn between September and November and winter between December and February (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.

2.3 | Age (H_{age}) and sex (H_{sex}) patterns in elk-vehicle collision

We evaluated whether EVCs were biased by sex and age, and then 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 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, while adults were considered 2 years or older. We used records from the complete EVC dataset that had sex and age classes described from all regions between 1986 and 2000 (Table 2). In order to account

TABLE 3 Definition and description of variables used in the EVC analysis from 1986 to 2001

Variable name	Definition	Source	Year
Region	Geographical location of EVCs: BNP, YNP, KNP, and Alberta Province (province)	Geographic coordinate from EVC records	1986–2000
Road[a]	TCH-province = provincial highway with 4–6 lanes of high volume traffic and TCH in the 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 = ≥1 and ≤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	Obtained from North American Datum 83 maps and measured using ArcView 3.2 (ESRI 1999)	1986–2000
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

Abbreviations: AADTV, annual average daily traffic volume; BNP, Banff National Park; EVCs, elk-vehicle collisions; KNP, Kootenay National Park; TCH, Trans-Canada highway; YNP, Yoho National Park.

[a]All unmitigated highway sections, that is, no fence or wildlife crossing structures.

for population fluctuations, we grouped the EVC records into three 5-year periods from 1986 to 2000 and did a separate analysis for each period and again for all years. We performed three tests, one each for sex (2×2), age (2×2), and a combined analysis (4×4) and assumed a 1:1 ratio among classes.

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). Ground counts classified subadult elk as YoY and spike (yearling males), therefore only YoY and yearling males were included in the observed counts for EVCs.

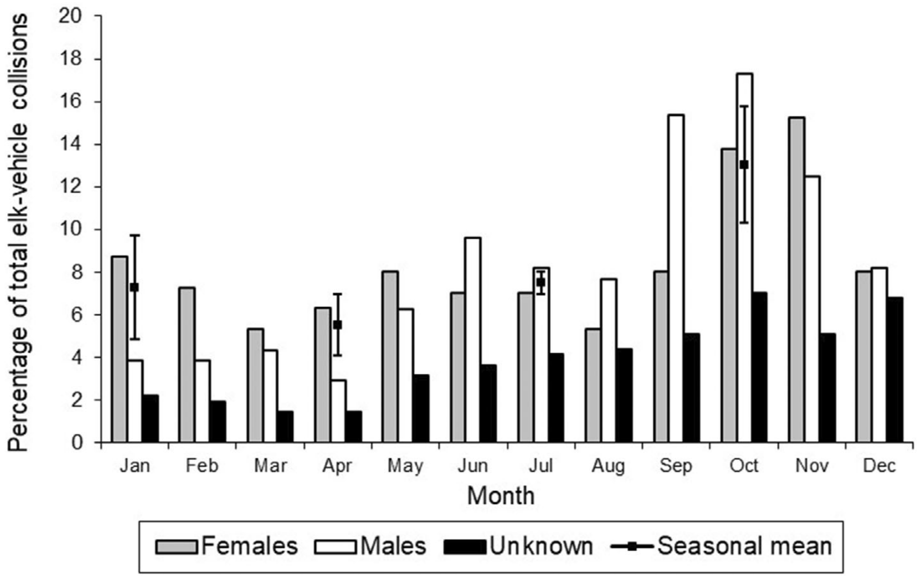

FIGURE 2 The percentage of monthly female, male, and unknown elk-vehicle collisions and the total seasonal mean with standard errors on the trans-Canada highway and highway 93 in the Canadian Rocky Mountains, from 1986 to 2000 ($n = 812$)

2.4 | Seasonality of elk-vehicle collisions (H_{fall}, H_{spring})

We evaluated when EVCs occurred by season and whether this was influenced by sex and age in the spring and fall. 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 by season, 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 zone.

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. We used a Kruskal–Wallis ANOVA test to determine if percent marrow fat content differed between the three mortality types.

2.6 | Traffic volume ($H_{traffic\text{-}neg}$, $H_{traffic\text{-}pos}$) and elk abundance ($H_{abundance}$)

We evaluated how traffic volume influenced EVC rates per km on each highway collectively from 1986 to 2000 (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 for each year 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 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 data was log transformed to obtain normal distribution (Zar, 1999).

Elk abundance and traffic volume were negatively correlated to each other on the two roads combined (Spearman's rank correlation, both $r > -0.80$, $p < .05$; 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. Traffic volumes are similar during the spring and fall periods (t test, $p > .05$, 1996–2000) therefore when using only these two seasons we have essentially controlled for the influence of traffic volume on EVC rates. This analysis was conducted for the TCH in the west zone only, where seasonal elk counts were available, therefore EVC frequencies, not rates were used.

3 | RESULTS

3.1 | Age (H_{age}) and sex (H_{sex}) patterns in elk-vehicle collisions

There were significantly more female EVCs ($n = 292$) than male adult EVCs ($n = 146$) on all four roads

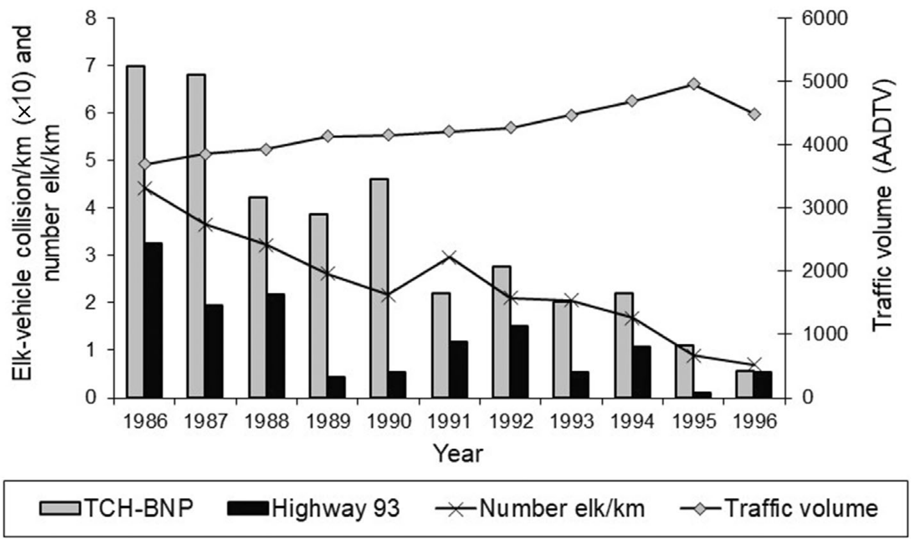

FIGURE 3 Standardized annual number of EVCs, with AADTV for both highways and estimated standardized elk abundance along highway 93 and the Trans-Canada highway in BNP, in the Central Canadian Rocky Mountains, 1986–1996. AADTV, annual average daily traffic volume; EVCs, elk-vehicle collisions

TABLE 4 The number of elk-vehicle collisions by sex and age class in the Canadian Rocky Mountains from 1986 to 2000; assumed a 1:1 ratio among classes

Age	Males	Females	Total	Sex ratio EVCs (M:F)	χ^2_1 [a]
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***

[a]*$p < .05$, **$p < .01$, ***$p < .001$.

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) along the TCH in the west zone of Banff National Park from 1986 to 2000

	Males		Females		
Year sequence	Observed	Expected	Observed	Expected	X^2 [a]
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. *$p < .05$, **$p < .01$, ***$p < .001$.

TABLE 6 The number of elk-vehicle collisions involving subadults and adults compared to the expected frequencies from ground counts averaged for the spring and fall periods along the trans-Canada highway west zone in Banff National Park from 1986 to 2000

	Subadult		Adult		
Year sequence	Observed	Expected	Observed	Expected	X^2 [a]
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. *$p < .05$, **$p < .01$, ***$p < .001$.

($\chi^2_1 = 25.0$, $n = 438$, $p < .0001$) but sex did not influence EVCs for subadults (Table 4). Furthermore, there were significantly more adult elk ($n = 329$) involved in EVCs than subadults ($n = 109$) ($\chi^2_1 = 72.8$, $n = 438$, $p < .0001$, Table 4). The male: female ratio among adult EVCs was 0.45:1 and 0.68:1 among subadults (Table 4). When considering the sex ratio of the elk population adjacent to the TCH in the west zone, there was a greater proportion of male EVCs than females during each of the 5-year periods (all $\chi^2_1 \geq 10.8$, all $p < .05$; Table 5) and the overall 15-year period ($\chi^2_1 = 68.2$, $n = 374$, $p < .0001$; Table 5).

TABLE 7 Analysis of covariance of elk abundance and traffic volume (continuous variable), and season and road (categorical variables) on elk-vehicle collision rate on the Trans-Canada highway in the west zone and Highway 93

Source	d.f.	Type III SS	F	Pr. Type I error
Elk abundance model (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 (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 (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

The total number of adult and subadult EVC occurrences were similar along the TCH in the west zone (Table 6). However, when considering the distribution of age classes in the local population, there was a significantly greater frequency of subadult road mortality during both periods: 1986–1990 and 1991–1995 (both $\chi^2 \geq 12.5$, $p < .01$), whereas no significant difference was found in 1996–2000 ($p = .369$; Table 6). Over the entire duration of the study (1986–2000) significantly more subadult elk were killed than adults ($\chi^2_1 = 18.3$, $n = 291$, $p < .0001$; Table 6).

3.2 | Seasonality of elk-vehicle collisions (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, $F_{3,44} = 3.48$, $p = .025$; Figure 2). There were significantly more EVCs in fall compared to spring and winter (Tukey's HSD test, $p = .0030$ and $p = .0100$ 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 (${\chi^2}_3 = 6.77$, $n = 64$, $p = .079$). In the fall there were more male adult EVCs occurring than female adult EVCs as compared to the population (${\chi^2}_2 = 3.81$, $n = 47$, $p = .051$). 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 (${\chi^2}_3 = 29.28$, $n = 133$, $p < .0001$). 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 ($H_{\text{predation}}$)

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, $F_{2,397} = 9.45$, $p < .0001$). 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, $p < .05$).

3.4 | Traffic volume ($H_{\text{traffic-neg}}$, $H_{\text{traffic-pos}}$) and elk abundance ($H_{\text{abundance}}$)

EVC rates were significantly different between each road type (Kruskal–Wallis test, $H_{3,60} = 14.99$, $p = .001$; 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 four roads was along the TCH in the province (7.26 ± 7.86); TCH in the west zone BNP (3.73 ± 11.57); TCH in YNP (2.06 ± 4.20) and highway 93, 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 in the 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 ($p < .0001$, $R^2 = 0.75$) and traffic volume ($p < .0001$, $R^2 = 0.82$) independently on EVC rate on Highway

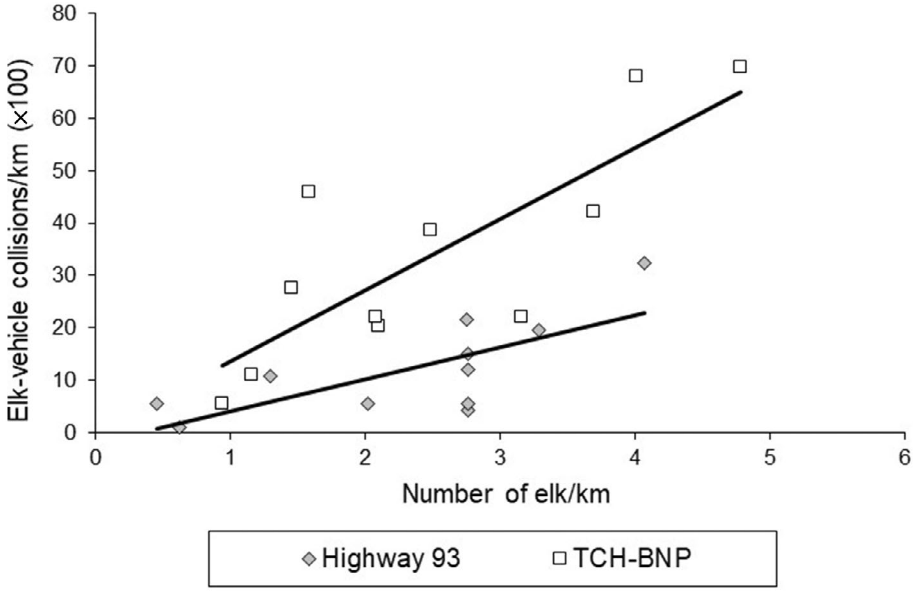

FIGURE 4 The interaction between elk population abundance (elk/km) and road type for Highway 93 and Trans-Canada Highway in BNP. As abundance increases, EVCs increase and this relationship is not significantly different between roads. EVCs, elk-vehicle collisions

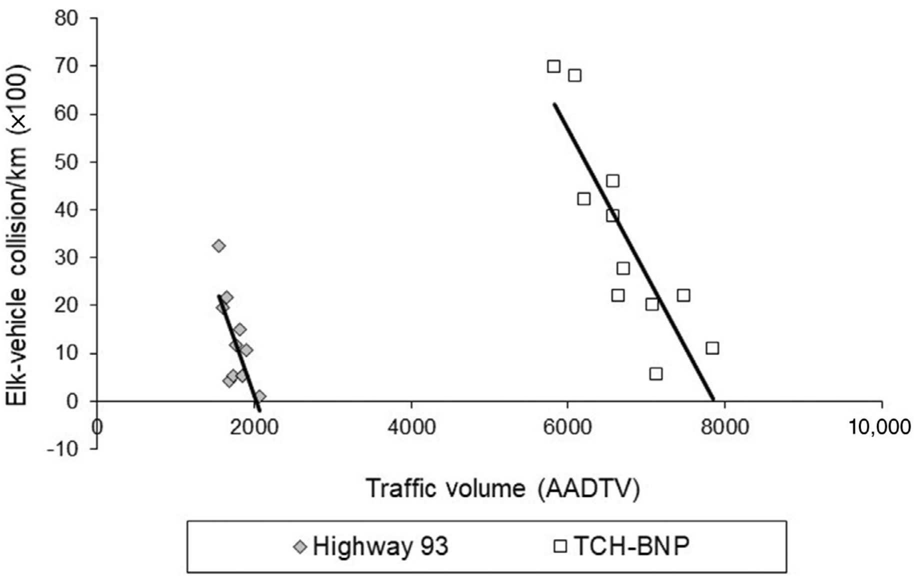

FIGURE 5 The interaction between annual average daily traffic volume (AADTV) and elk-vehicle collision rate on two roads: Highway 93 and Trans-Canada Highway in BNP. As traffic volumes increase EVC rate decreases and this is more apparent on Highway 93. AADTV, annual average daily traffic volume; EVCs,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

93 and TCH in the west zone were significant (Table 7). As elk abundance decreased, EVCs significantly decreased and this relationship was consistent between roads (Table 7 and Figure 4). As traffic volumes increased EVC rate significantly decreased and this relationship was more evident on highway 93 than on the TCH in the west zone (Figure 5).

We found a significant positive influence of elk abundance on EVC occurrence in the seasonal model (Table 7; $p < .0001$) when traffic volume remained constant along the TCH in the west zone. More specifically, EVCs increased at a greater rate during the fall season when elk abundance numbers were significantly higher ($t = -2.09$, $n = 16$, $p = .045$; Figure 6).

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, that is, compensatory mortality, such that road-kill has minimal impacts on

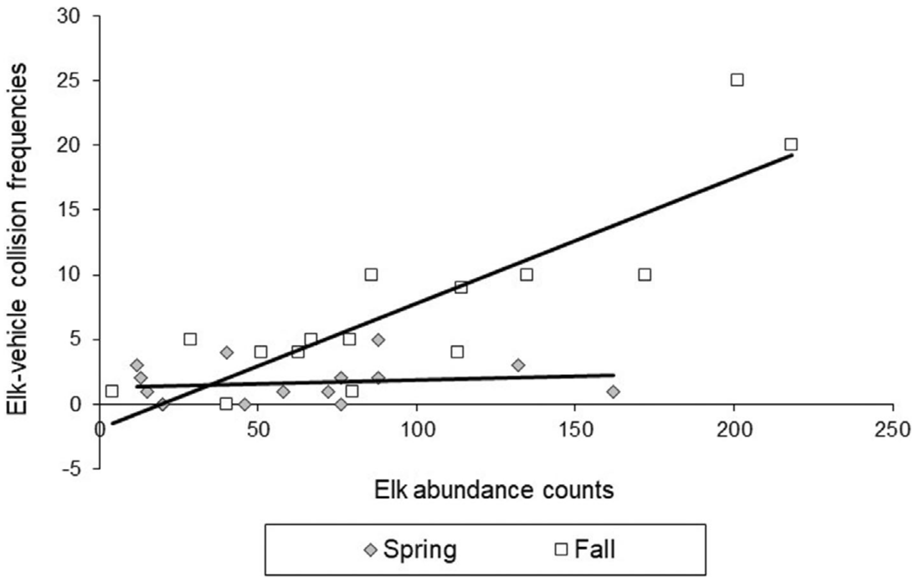

FIGURE 6 The interaction between elk abundance and elk-vehicle collision frequencies between spring and fall along the Trans-Canada Highway in BNP

populations (Hebblewhite et al., 2002). Finally, some animals may have higher value for people than others, such as harvestable-aged male ungulates (Arnett & Southwick, 2015; Mysterud et al., 2002). If road mortality is selective for particular individuals, it may either exacerbate or buffer the effect of roads on a population and 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 for studies that examined road-kill in mule deer and white-tailed deer in the United States (Allen & McCullough, 1976; Bellis & Graves, 1971; Olson et al., 2014). However, when we compared the proportion of female and male road-kill to the sex ratio in the population directly, there were more males being road-killed than expected by chance. Similar male-biased road mortalities have been found for moose in Newfoundland (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 (Hebblewhite et al., 2002; Woods, 1991).

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 more likely to be 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 (Allen & McCullough, 1976; Bellis & Graves, 1971; Joyce & Mahoney, 2001; Pennsylvania Game Commission, 1969). The collision frequencies tend to increase from early spring to fall, peaking in October and November during the rut and/or hunting season (Bruinderink & Hazebroek, 1996; Creech et al., 2019; Hubbard et al., 2000; Neumann et al., 2012).

This fall peak has been attributed to increased ungulate activity level associated with migration and breeding behavior, which brings ungulates in contact with the road network more frequently (Ager et al., 2003; Woods, 1991). More EVCs occurred in winter in the Jemez Mountains plateau region of New Mexico and was attributed to migration behavior 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 behavior and eastern counties where migratory behavior 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 (Gagnon et al., 2019; Hebblewhite et al., 2002). We found elk killed by vehicles and trains tended to be in better body condition than elk killed by natural predators similar to that found by Huggard (1993)—a pattern that is suggestive of additive mortality. When road mortalities occur for animals that would have otherwise been killed by natural predators or disease (i.e., because they have poor body condition), then the population is experiencing compensatory mortality (Boyce et al., 1999; Fowler, 1987). For example, O'Gara and Harris (1988), found that predators such as cougars and coyotes killed deer in good condition, while deer killed by vehicles were in poor condition in western Montana. They attributed this finding to sick and malnourished deer moving to and congregating in valley bottoms along roadsides clear of snow in winter months.

Additive mortality occurs when road-killed elk have a fairly high probability of survival and this may have been contributing to the decline of elk population size in Banff National Park seen in the early 2000s (Parks Canada, unpublished data). The recolonization of wolves to Banff and KNP in the 1980s is also a likely contributor to the decline in elk abundance and subsequently EVCs. Wolves reduced annual survival rates for elk from 0.89 to 0.61 from the central zone (no wolves) to the west zone in BNP (high wolf density), respectively (Hebblewhite et al., 2002; McKenzie, 2001). 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 declined to almost nothing (Clevenger & Barrueto, 2014).

4.4 | Effects of traffic volume and abundance on road mortality

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. Unexpectedly, traffic volume negatively influenced EVC rates on both highways and this relationship was more evident on Highway 93. As expected, abundance positively influenced the occurrence of EVCs, especially in the fall. These findings indicate parameters such as traffic volume need to be statistically analyzed 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; Philcox et al., 1999; Romin & Bissonette, 1996; Seiler, 2004; van Langevelde & Jaarsma, 2004). However, animals may avoid roads because of traffic (Gagnon et al., 2007) or because of the road surface (Ford & Fahrig, 2008; Shine et al., 2004) or other reasons. If road avoidance behavior 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-kill rarely occurred (Eberhardt et al., 2013; Zimmermann 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.

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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 (Olson et al., 2014; Ramp et al., 2005). These insights add to the growing body of evidence that demographic-specific variation in behavior and vulnerability to roads needs to be considered in order to maximize population-level benefits of mitigation (Ford et al., 2017) especially for rare and declining populations vulnerable to additive mortality e.g., freshwater turtles (Steen & Gibbs, 2004).

To address demographic-specific vulnerabilities, mitigation measures such as crossing structures that are designed for vulnerable animal groups, for example, females traveling with young and male elk may be more effective for the population. There is a growing body of research that has showed greater frequencies of passages by wildlife assemblages at overpasses (Clevenger & Barrueto, 2014; Simpson et al., 2016), and that Grizzly bear (*Ursus arctos*) females and offspring in Banff National Park selected for more open crossing structures such as open-span underpasses and overpasses (Ford et al., 2017). In addition, a study in Ontario, showed that male moose and deer used a wildlife overpass more than expected when compared to the surrounding population (Eco-Kare International, 2020).

When more permanent measures such as crossing structures and exclusion fencing are not practical for a specific site, motorist-focused campaigns are often employed. These campaigns can be greatly improved with informed messaging that target specific animal demographics in specific regions. Campaigns for ungulates may be timed to fall periods when male elk and new calf cohorts are vulnerable to collisions. Freshwater turtle populations are particularly vulnerable to adult female-biased road-kill because of delayed sexual maturity (Congdon et al., 1993) and because females move overland during nesting migrations (Steen et al., 2012). Therefore, campaigns in northeastern North America, need to remind motorists to watch for, avoid and help turtles move across roads safely in June when adult female turtles move overland to nest.

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. Collective evaluation of long-term datasets can help tease out mechanisms for population declines and assist with appropriate recovery efforts prior to a local population becoming depleted near roads.

AUTHOR CONTRIBUTIONS

Kari Elizabeth Gunson led the data acquisition from Parks Canada and other researchers, conceptual design, data analysis, and write-up of the manuscript; Anthony Paul Clevenger contributed to data analysis and write-up of the manuscript. Adam Thomas Ford provided clear direction for analytical methods and data interpretation, and contributed peer-review and critical references for later drafts of the manuscript.

ACKNOWLEDGMENTS

Funding for this research came from a variety of sources including Parks Canada and Public Works and Government Services Canada, Parks Canada's Ecological Integrity Innovation and Leadership Fund, the Parks Canada Ecosystem Science Office (National Office) and the Woodcock Foundation. We thank the Transportation Pooled Fund Study *TPF 5(358)* committee and the Nevada Department of Transportation for funding and valuable contributions to this paper. We thank the Parks Canada warden service, and Alberta Natural Resource Services for the accumulations of elk-vehicle collision and abundance data for analysis. We thank Bryan Chruszcz who helped conceive and design the initial study. Jon Jorgenson, Alan Dibb, Tom Hurd, and Cliff Nietvelt helped with data collection needs and logistics.

FUNDING INFORMATION

Funding for this research came from a variety of sources including Parks Canada and Public Works and Government Services Canada, Parks Canada's Ecological Integrity Innovation and Leadership Fund, the Parks Canada Ecosystem Science Office (National Office) and the Woodcock Foundation.

CONFLICT OF INTEREST

The authors declare no potential conflict of interests.

DATA AVAILABILITY STATEMENT

Data are available from Parks Canada, Banff and Kootenay Field Units.

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REFERENCES

Ager, A. A., Johnson, B. K., Kern, J. W., & Kie, J. G. (2003). Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy*, *84*, 1076–1088.

Allen, R. E., & McCullough, D. R. (1976). Deer-car accidents in southern Michigan. *The Journal of Wildlife Management*, *40*, 317–325.

Anderson, D. P., Forester, J. D., Turner, M. G., Frair, J. L., Merrill, E. H., Fortin, D., Mao, J. S., & Boyce, M. S. (2005). Factors influencing female home range sizes in elk (Cervus elaphus) in North American landscapes. *Landscape Ecology*, *20*, 257–271.

Arnett, E. B., & Southwick, R. (2015). Economic and social benefits of hunting in North America. *International Journal of Environmental Studies*, *72*, 734–745.

Banff Bow Valley Study. (1996). *Banff-Bow Valley: At the crossroads. Summary report for the Banff-Bow Valley task force*. Government of Canada, Department of Canadian Heritage.

Bellis, E. D., & Graves, H. B. (1971). Deer mortality on a Pennsylvania interstate highway. *Journal of Wildlife Management*, *35*, 232–237.

Biggs, J., Sherwood, S., Michalak, S., Hansen, L., Bare, C., & Jones, C. A. (2004). Animal-related vehicle accidents at the Los Alamos national laboratory, New Mexico. *The Southwestern Naturalist*, *49*, 384–394.

Bottini, M. (1987). *Elk roadkills on the Trans Canada Highway in Banff National Park* (Unpublished report to Parks Canada).

Boyce, M. S., Sinclair, A. R. E., & White, G. C. (1999). Seasonal compensation of predation and harvesting. *Oikos*, *87*, 419–426.

Brady, S. P., & Richardson, J. L. (2017). Road ecology: Shifting gears toward evolutionary perspectives. *Frontiers in Ecology and the Environment*, *15*, 91–98.

Bruinderink, G., & Hazebroek, E. (1996). Ungulate traffic collisions in Europe. *Conservation Biology*, *10*, 1059–1067.

Clark, R. W., Brown, W. S., Stechert, R., & Zamudio, K. R. (2010). Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. *Conservation Biology*, *24*, 1059–1069.

Clevenger, A. P., & Barrueto, M. (Eds.). (2014). *Trans-Canada highway wildlife and monitoring research. Part B: Research* (Final report prepared for Parks Canada Agency, Radium Hot Springs, BC). 314 pp.

Clevenger, A. P., Barrueto, M., Gunson, K. E., Caryl, F. M., & Ford, A. T. (2015). Context-dependent effects on spatial variation in deer-vehicle collisions. *Ecosphere*, *6*, 1–20.

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2001). Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*, *29*(2), 646–653.

Congdon, J. D., Dunham, A. E., & van Loben Sels, R. C. (1993). Delayed sexual maturity and demographics of Blanding's turtles (Emydoidea blandingii): Implications for conservation and management of long-lived organisms. *Conservation Biology*, *7*, 826–833.

Conover, M. R., Pitt, W. C., Kessler, K. K., DuBow, T. J., & Sanborn, W. A. (1995). Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin*, *23*, 407–414.

Creech, T. G., Fairbank, E. R., Clevenger, A. P., Callahan, A. R., & Ament, R. J. (2019). Differences in spatiotemporal patterns of vehicle collisions with wildlife and livestock. *Environmental Management*, *64*, 736–745.

Damas, & Smith. (1982). *Wildlife mortality in transportation corridors in Canada's national parks* (Report to the Canadian Parks Service, vol. 1, Main report, Ottawa, Ontario).

Dusek, G. L., MacKie, R. J., Herriges, J. D., Jr., & Compton, B. B. (1989). Population ecology of white-tailed deer along the lower Yellowstone River. *Wildlife Monographs*, *104*, 3–68.

Eberhardt, E., Mitchell, S., & Fahrig, L. (2013). Road kill hotspots do not effectively indicate mitigation locations when past road kill has depressed populations. *The Journal of Wildlife Management*, *77*, 1353–1359.

Eco-Kare International. (2020). *Effectiveness monitoring of wildlife mitigation measures for large-and mid-sized animals on highway 69 in Northeastern Ontario: September 2011 to September 2019* (Final report submitted to the Ministry of Transportation, North Bay, Ontario).

Fahrig, L., Neill, K. E., & Duquesnel, J. G. (2001). Interpretation of joint trends in traffic volume and traffic-related wildlife mortality: A case study from key largo, Florida. In G. Evink & K. P. McDermott (Eds.), *Proceedings of the international conference of ecology and transportation* (pp. 518–522). The Center for Transportation and Environment, North Carolina State University.

Fahrig, L., Pedlar, J. H., Pope, S. E., Taylor, P. D., & Wegner, J. F. (1995). Effect of road traffic on amphibian density. *Biological Conservation*, *73*, 177–182.

Flook, D. R. (1970). Causes and implications of an observed sex differential in the survival of wapiti. In *Canadian wildlife service bulletin report series, 11*. Canadian Wildlife Service.

Ford, A. T., Barrueto, M., & Clevenger, A. P. (2017). Road mitigation is a demographic filter for grizzly bears. *Wildlife Society Bulletin*, *41*, 712–719.

Ford, A. T., & Fahrig, L. (2008). Movement patterns of eastern chipmunks (Tamias striatus) near roads. *Journal of Mammalogy*, *89*, 895–903.

Forman, R. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R., Goldman, C. R., Heanue, K., Jones, J. A., Swanson, F. J., Turrentine, T., & Winter, T. C. (2003). *Road ecology: Science and solutions*. Island Press.

Forrest, A., & Clair, C. S. (2009). Impacts of vehicle traffic on the distribution and behaviour of rutting elk, Cervus elaphus. *Behaviour*, *146*, 393–413.

Fowler, C. W. (1987). A review of density dependence in populations of large mammals. In H. H. Genoways (Ed.), *Current mammalogy* (Vol. 1, pp. 401–441). Springer.

Gagnon, J. W., Dodd, N. L., Sprague, S. C., Ogren, K. S., Loberger, C. D., & Schweinsburg, R. E. (2019). Animal-activated highway crosswalk: Long-term impact on elk-vehicle collisions, vehicle speeds, and motorist braking response. *Human Dimensions of Wildlife*, *24*, 132–147.

Gagnon, J. W., Theimer, T. C., Dodd, N. L., Manzo, A. L., & Schweinsburg, R. E. (2007). Effects of traffic on elk use of wildlife underpasses in Arizona. *The Journal of Wildlife Management*, *71*, 2324–2328.

Gaillard, J.-M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, *13*, 58–63.

Gervasi, V., Nilsen, E. B., Sand, H., Panzacchi, M., Rauset, G. R., Pedersen, H. C., Kindberg, J., Wabakken, P., Zimmermann, B., & Odden, J. (2012). Predicting the potential demographic impact of predators on their prey: A comparative analysis of two carnivore–ungulate systems in Scandinavia. *Journal of Animal Ecology*, *81*, 443–454.

Gunson, K. E., Clevenger, A. P., Ford, A. T., Bissonette, J. A., & Hardy, A. (2009). A comparison of data sets varying in spatial accuracy used to predict the occurrence of wildlife-vehicle collisions. *Environmental Management*, *44*, 268–277.

Gunson, K. E., Mountrakis, G., & Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. *Journal of Environmental Management*, *92*, 1074–1082.

Hebblewhite, M., & Merrill, E. H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, *90*, 3445–3454.

Hebblewhite, M., Pletscher, D. H., & Paquet, P. C. (2002). Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, *80*, 789–799.

Holland, W. D., & Coen, G. M. (1983) *Ecological land classification of banff and jasper national parks. i. summary*. Publication M-83-2. Alberta Institute of Pedology, Alberta, Canada.

Holroyd, G. L. (1979). *The impact of highway and railroad mortality on the ungulate populations in the Bow Valley, Banff National Park*. Canadian Wildlife Service.

Hubbard, M. W., Danielson, B. J., & Schmitz, R. A. (2000). Factors influencing the location of deer-vehicle accidents in Iowa. *The Journal of Wildlife Management*, *67*, 707–713.

Huggard, D. J. (1993). Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology*, *71*, 130–139.

Huijser, M. P., Duffield, J. W., Clevenger, A. P., Ament, R. J., & McGowen, P. T. (2009). Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: A decision support Ttool. *Ecology and Society*, *14*, 1–26.

Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D. A., Vale, M. M., Hobson, P. R., & Selva, N. (2016). A global map of roadless areas and their conservation status. *Science*, *354*, 1423–1427.

Joyce, T. L., & Mahoney, S. P. (2001). Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. *Wildlife Society Bulletin*, *29*, 281–291.

Knoche, S., & Lupi, F. (2007). Valuing deer hunting ecosystem services from farm landscapes. *Ecological Economics*, *64*, 313–320.

Larson, J. S., & Taber, R. D. (1980). Criteria of sex and age. In *Wildlife Management Techniques Manual* (Vol. 686, pp. 190–197). The Wildlife Society.

Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, *24*, 659–669.

Martinig, A. R., & Bélanger-Smith, K. (2016). Factors influencing the discovery and use of wildlife passages for small fauna. *Journal of Applied Ecology*, *53*, 825–836.

McKenzie, J. (2001). *The selective advantage of urban habitat use by elk in Banff National Park. A thesis submitted in partial fulfillment of the requirement for the degree of Masters of Science*. University of Guelph.

Meijer, J. R., Huijbregts, M. A., Schotten, K. C., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, *13*, 064006.

Mountrakis, G., & Gunson, K. E. (2009). Multi-scale spatiotemporal analyses of moose–vehicle collisions: A case study in northern Vermont. *International Journal of Geographical Information Science*, *23*, 1389–1412.

Mumme, R. L., Schoech, S. J., Woolfenden, G. E., & Fitzpatrick, J. W. (2000). Life and death in the fast lane: Demographic consequences of road mortality in the Florida scrub-jay. *Conservation Biology*, *14*, 501–512.

Munro, K. G., Bowman, J., & Fahrig, L. (2012). Effect of paved road density on abundance of white-tailed deer. *Wildlife Research*, *39*, 478–487.

Mysterud, A., Coulson, T., & Stenseth, N. C. (2002). The role of males in the dynamics of ungulate populations. *Journal of Animal Ecology*, *71*, 907–915.

Neumann, W., Ericsson, G., Dettki, H., Bunnefeld, N., Keuler, N. S., Helmers, D. P., & Radeloff, V. C. (2012). Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. *Biological Conservation*, *145*, 70–78.

O'Gara, B. W., & Harris, R. B. (1988). Age and condition of deer killed by predators and automobiles. *The Journal of Wildlife Management*, *52*, 316–320.

Olson, D. D., Bissonette, J. A., Cramer, P. C., Bunnell, K. D., Coster, D. C., & Jackson, P. J. (2014). Vehicle collisions cause differential age and sex-specific mortality in mule deer. *Advances in Ecology*, *2014*, 1–10.

Pennsylvania Game Commission. (1969). Over 21,000 deer on state roads in 1968. *Pennsylvania Game News*, *40*, 40.

Philcox, C. K., Grogan, A. L., & Macdonald, D. W. (1999). Patterns of otter Lutra lutra road mortality in Britain. *Journal of Applied Ecology*, *36*, 748–762.

Ramp, D., Caldwell, J., Edwards, K. A., Warton, D., & Croft, D. B. (2005). Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. *Biological Conservation*, *126*, 474–490.

Reijnen, R., Foppen, R., & Meeuwsen, H. (1996). The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation*, *75*, 255–260.

Romin, L. A., & Bissonette, J. A. (1996). Deer-vehicle collisions: Status of state monitoring activities and mitigation efforts. *Wildlife Society Bulletin*, *24*, 276–283.

Rost, G. R., & Bailey, J. A. (1979). Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management*, *43*, 634–641.

Seiler, A. (2004). Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology*, *10*, 301–313.

Seiler, A. (2005). Predicting locations of moose–vehicle collisions in Sweden. *Journal of Applied Ecology*, *42*(2), 371–382.

Shanley, C. S., & Pyare, S. (2011). Evaluating the road-effect zone on wildlife distribution in a rural landscape. *Ecosphere*, *2*, 1–16.

Shine, R., Lemaster, M., Wall, M., Langkilde, T., & Mason, R. (2004). Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (Thamnophis sirtalis parietalis). *Ecology and Society*, *9*, 9.

Simpson, N. O., Stewart, K. M., Schroeder, C., Cox, M., Huebner, K., & Wasley, T. (2016). Overpasses and underpasses: Effectiveness of crossing structures for migratory ungulates. *The Journal of Wildlife Management*, *80*, 1370–1378.

Steen, D. A., & Gibbs, J. P. (2004). Effects of roads on the structure of freshwater turtle populations. *Conservation Biology*, *18*, 1143–1148.

Steen, D. A., Gibbs, J. P., Buhlmann, K. A., Carr, J. L., Compton, B. W., Congdon, J. D., Doody, J. S., Godwin, J. C., Holcomb, K. L., Jackson, D. R., Janzen, F. J., Johnson, G., Jones, M. T., Lamer, J. T., Langen, T., Plummer, M. V., Rowe, J. W., Saumure, R. A., Tucker, J. K., & Wilson, D. S. (2012). Terrestrial habitat requirements of nesting freshwater turtles. *Biological Conservation*, *150*, 121–128.

Thurfjell, H., Spong, G., Olsson, M., & Ericsson, G. (2015). Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. *Landscape and Urban Planning*, *133*, 98–104.

van Langevelde, F., & Jaarsma, C. F. (2004). Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, *19*(8), 895–907.

Wilmers, C. C., Metz, M. C., Stahler, D. R., Kohl, M. T., Geremia, C., & Smith, D. W. (2020). How climate impacts the composition of wolf-killed elk in northern Yellowstone National Park. *Journal of Animal Ecology*, *89*, 1511–1519.

Woods, J. G. (1990). *Effectiveness of fences and underpasses on the trans-Canada highway and their impact on ungulate populations* (Report to Banff National Park Warden Service, Banff, Alberta).

Woods, J. G. (1991). Ecology of a partially migratory elk population. In *A thesis submitted in partial fulfillment of the requirement for the degree of Doctor of Philosophy*. University of British Columbia.

Woods, J. G., Cornwell, L., Hurd, T., Kunelius, R., Paquet, P., & Wierzchowski, J. (1996). Elk and other ungulates. In J. Green, C. Pacas, L. Cornwell, & S. Bayley (Eds.), *Ecological outlooks project. A cumulative effects assessment and future outlook of the Banff Bow Valley*. Government of Canada, Department of Canadian Heritage.

Zar, J. H. (1999). *Biostatistical analysis* (4th ed.). Prentice Hall.

Zimmermann, T. F., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, *54*, 1544–1551.

How to cite this article: Gunson, K. E., Clevenger, A. P., & Ford, A. T. (2022). A comparison of elk-vehicle collision patterns with demographic and abundance data in the Central Canadian Rocky Mountains. *Conservation Science and Practice*, e12842. https://doi.org/10.1111/csp2.12842