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Wildlife mortality on roads and railways following highway mitigation

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Abstract. Wildlife mortality caused by collisions with vehicles on roads is increasingly and effectively mitigated with exclusion fencing and crossing structures, but this solution potentially changes wildlife habitat use and distribution to increase the risk of mortality on adjacent, unmitigated railways. We investigated this potential side-effect of mitigating the TransCanada Highway, which was completed in sections between 1983 and 2013, on the rate of wildlife mortality on the nearby transcontinental mainline of the Canadian Pacific Railway in Banff National Park. For each transportation class (highway and railway), we calculated collision rate as the number of collisions per year and km for two guilds (carnivores and ungulates) before and after mitigation occurred between 1981 and 2014. We constructed additional models for each transportation class and each of four species groups with adequate sample sizes: elk (*Cervus canadensis*), other ungulates (family Cervidae), bears (*Ursus* spp.), and coyotes (*Canis latrans*). Across guilds, mortality rates declined after mitigation, particularly on the highway (as expected) and most strongly for ungulates. For individual species groups, mortality on the railway for elk was best predicted by year and population size, without the inclusion of mitigation status on the adjacent highway. However, collision rates on the railway increased after mitigation for other ungulates (mostly deer, *Odocoileus* spp.) while also increasing over time. Collision rates on the railway increased over time for bears, but not in relation to highway mitigation. We found no evidence that the spatial distribution of collisions on the railway changed after highway mitigation, as might be expected from a funneling effect of crossing structures. Our results support and extend previous work demonstrating that exclusion fencing and wildlife crossing structures reduce wildlife mortalities on the highway at this location, and provide limited evidence, for other ungulates alone, that such mitigation may increase mortality on the adjacent railway. Similar analyses are warranted in other locations, particularly mountainous regions, where major transportation features often occur in close proximity.

Key words: grizzly bear; large mammals; population; road mitigation; wildlife-train collisions; wildlife-vehicle collisions.

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Introduction

Transportation networks benefit people by connecting societies and economies, but they have many negative consequences for terrestrial ecosystems and wildlife populations (reviewed by Trombulak and Frissell 2000, Coffin 2007, Benítez-López et al. 2010), including mortality from collisions with vehicles (reviewed by Glista et al. 2009, Taylor and Goldingay 2010).

Although road mortality usually has minimal effects on population viability (Forman 1998, Forman and Alexander 1998), particularly for abundant species with high reproductive rates (Glista et al. 2007), it can be detrimental for wide-ranging species with low population densities and reproductive rates (reviewed by Fahrig and Rytwinski 2009). Road mortality can be especially limiting for large carnivores, with demonstrated detrimental effects on tigers (*Panthera tigris*), and leopards (*Panthera pardus*; Baskaran and Boominathan 2010, Joshi 2010), African hunting dogs (*Lycaon pictus*; Drews 1995), Florida panthers (*Felis concolor coryi*; Foster and Humphrey 1995), and grizzly bears (*Ursus arctos*; Waller and Servheen 2005). The sensitivity of some wildlife populations and the concomitant danger to people posed by wildlife-vehicle collisions have supported the rapid development of the field of road ecology and associated mitigation actions (reviewed by Forman and Alexander 1998, Beckmann et al. 2010, van der Ree et al. 2015).

Overall, road mitigation has unambiguous net benefits for people and wildlife (Glista et al. 2009, Barrueto et al. 2014, Sawaya et al. 2014), particularly for mitigation that consists of exclusion fencing (to prevent animals from accessing the road) coupled with crossing structures (to facilitate their movement; Huijser et al. 2016, Rytwinski et al. 2016). This combination of mitigation works well if crossing structures are permeable and frequent enough in landscapes to support wildlife movement (Van Riper et al. 2001, Jaeger and Fahrig 2004) and it has gained widespread use around the world (Beckmann et al. 2010, van der Ree et al. 2015). Nonetheless, there is some potential for unintended negative consequences of road mitigation that have not been much studied. For example, when fencing occurs only in the vicinity of crossing structures, it must avoid funneling movement across roads at fence ends (Cain et al. 2003), which can usually be achieved if the sections of partial fencing are long enough (Ford et al. 2011, Huijser et al. 2016). Additionally, both partial and continuous fencing have some potential for exploitation by predators that might use them to trap prey (Gibeau and Heuer 1996, Gloyne and Clevenger 2001) and similar exploitation potentially occurs at crossing structures (Ford and Clevenger 2010, Mata et al. 2015). Detecting such subtle effects of road mitigation will benefit from information on changing population abundance and distribution (Mysterud 2004, Seiler 2004, Grilo et al. 2014) and long-term studies of landscape-level effects before and after road mitigation occurs (Rytwinski et al. 2016).

Among the understudied effects of road mitigation is its potential influence on wildlife use and mortality on adjacent transportation corridors, such as railways. In general, the study of railway effects on wildlife has lagged far behind that of roads (Borda-de-Água et al. 2017, Popp and Boyle 2017). Particularly in areas with complex topography, railways are often co-aligned with roads and can impose similar negative effects on wildlife, such as mortality from train strikes (Kušta et al. 2011, Dorsey et al. 2015). Railways also convey similar edge effects as roads, which typically increase the abundance, diversity, and growth rates of adjacent vegetation via greater light availability, warmth, and the spread of invasive species (Hansen and Clevenger 2005, Roever et al. 2008, Pollock et al. 2017). In addition to vegetative attractants, train collisions with wildlife produce carcasses that can attract and increase mortality risk for scavenging species (Wells et al. 1999, Heske 2015), which may be further attracted to railways as a travel route (Whittington et al. 2005). Finally, trains themselves can provide an additional food attractant via spilled agricultural products from the bottoms of hopper cars if their gates are not completely closed (Dorsey et al. 2015, Gangadharan et al. 2017). In combination, these features attract wide-ranging, omnivorous species, like bears (*Ursus* spp.; Murray et al. 2017) and are assumed to contribute to train-caused mortality of brown bears (*U. arctos*) in Europe (Huber et al. 1998) and grizzly bears (*Ursus arctos horribilis*) in the United States (Waller and Servheen 2005) and Canada (Bertch and Gibeau 2009, Dorsey et al. 2017). The negative effects of railways on wildlife might be worsened by road mitigation if it also increases the relative value of vegetation associated with transportation rights-of-way or carcasses stemming from collisions while displacing animals from previously occupied similar habitat on road verges, or funnels animals from crossing structures onto an adjacent railway.

Collisions with grizzly bears were among the motivations for mitigating the TransCanada

Highway through Banff National Park, Alberta, Canada (hereafter, "Banff"), which successfully reduced collisions with both ungulates and carnivores (Clevenger et al. 2001). Despite this reduction in highway mortality, no similar mitigation occurred on the railway and, since 2000, train collisions have become the leading source of mortality for grizzly bears in Banff (Bertch and Gibeau 2009, Dorsey et al. 2017). Grizzly bears in this area occur in relatively low densities and exhibit low reproductive rates (Weaver et al. 1996, Garshelis et al. 2005, Proctor et al. 2005). Transportation-related mortalities therefore have the potential to threaten local populations (Proctor et al. 2012, Hopkins et al. 2014). Likewise, wolves (*Canis lupus*) and many other species are vulnerable to train collisions (Gibeau and Heuer 1996, Paquet and Callahan 1996, Barrueto et al. 2014). The long-term efficacy of road mitigation will require that it be addressed holistically to accommodate multi-modal transportation corridors, as well as multiple species and ecological functions.

We sought to advance a more holistic understanding of road mitigation in Banff National Park, which occurred in several stages between 1983 and 2013, by addressing the following three objectives: (1) compare mortality rates from collisions on both the highway and the railway before and after road mitigation; (2) examine these temporal effects of mitigation more specifically for each transportation class and species or species groups; and (3) determine whether highway mitigation changes the spatial distribution of railway mortalities. We addressed these objectives by examining the temporal and spatial patterns of collisions on both the highway and the railway using a dataset collected by staff employed by Parks Canada Agency from 1981 to 2014. We tested the temporal hypothesis that road mitigation generally increases attraction by wildlife to the adjacent co-aligned railway by predicting that railway mortality would increase following highway mitigation, either generally or for particular species. We tested the spatial hypothesis that highway mitigation alters animal movement to increase railway mortality in specific locations by predicting that railway mortality would increase with proximity to what would become crossing structures on the highway.

Methods

Study site

Banff National Park is located in the southeastern portion of the Canadian Rocky Mountains, Alberta, Canada (51°15′ N, 115°54′ W), and is bisected west to east by the Bow River Valley (Fig. 1a; Benn and Herrero 2002). The Bow Valley contains approximately 80% of the park's productive but rare montane habitat (Fig. 1a; White 1985, Gibeau and Heuer 1996, Hebblewhite et al. 2003) making it highly attractive to wildlife (Holroyd and Van Tighem 1983*a*, *b*). This region also encompasses two high-volume transcontinental transportation corridors: the TransCanada highway (hereafter, "highway") and Canadian Pacific Railway (hereafter, "railway"; Fig. 1), and one low-volume road, the Bow Valley Parkway (Gibeau and Herrero 1998). Banff attracts almost 4 million visitors annually and is among the most human-dominated landscapes in North America with an extant grizzly bear population (Gibeau and Herrero 1998, Gibeau et al. 2002).

Wildlife transportation collisions

We examined the correlative association between road mitigation and vehicle collisions (on both highway and railway) using a mortality dataset collected by Parks Canada Agency over a 34-yr period (1981–2014) while accounting for different time periods of mitigation. To do so, we divided the transportation corridor into nine sections aligning with the staged installation of exclusion fencing and crossing structures (n = 44) along an 82 km span of the highway (Fig. 1a; Clevenger and Waltho 2005, Barrueto et al. 2014). We designated adjacent railway sections via perpendicular bisection from the highway. For each section, we determined the number of collisions per year and divided by the length of each section to derive a collision rate (collisions·km^{-1}·yr^{-1}; as recommended by Carvalho et al. 2017) reported on both the highway and the railway for the years before and after mitigation. We did not include in our rate estimate measures of traffic volume, which were only available on the highway (Fig. 3, Panel d). Mitigation sections (one to nine) proceeded approximately (but not always) from east to west to generate changing ratios in the associated

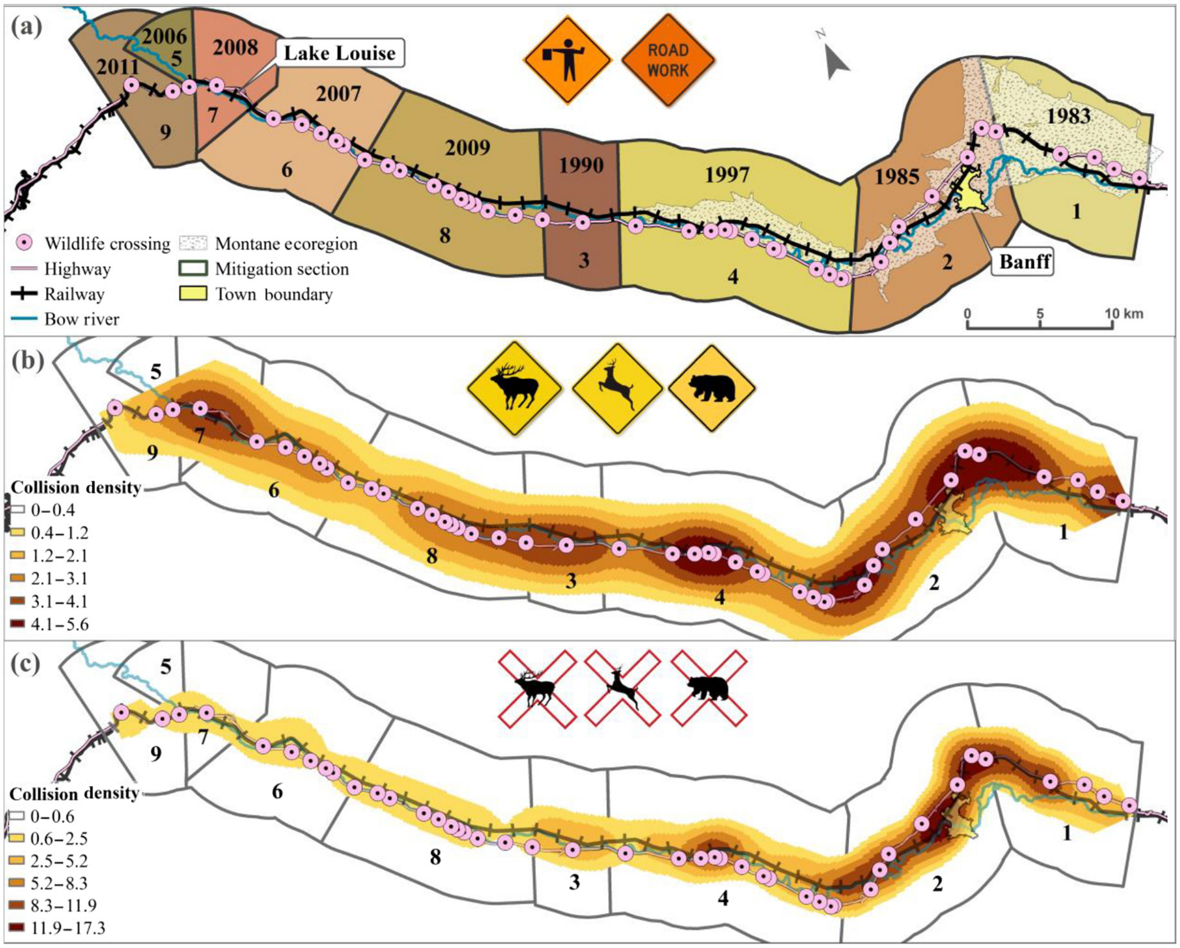

Fig. 1. (a) Nine areas in which highway mitigation occurred between 1983 and 2013 in Banff National Park, Canada, are denoted with a unique color and the year in which mitigation began to address wildlife-vehicle collisions that are depicted as quintiles of collision density for (b) the TransCanada Highway, and (c) the Canadian Pacific Railway for combined species groups or elk, other ungulates, and bears (Table 1) from 1981 to 2014. The areas denoting sections support visual identification but do not indicate the actual area of highway exclusion fencing. Colors in panels (b) and (c) reflect relative collision density for quintiles within (but not between) transportation classes, which had a larger range on the railway.

number of years before and after mitigation that are described in parentheses following the mitigation section, including section length: one (4:30; 11.2 km), two (7:27; 15.4 km), three (12:22; 5.3 km), four (18:16; 17.1 km), five (32:2; 0.4 km), six (30:4; 8.8 km), seven (30:4; 4.7 km), eight (30:4; 13.3 km), and nine (33:1; 5.6 km; Fig. 1a).

Records of animal-vehicle collision (n = 2775) between 1981 and 2014 included both confirmed mortalities (96%) and reported strikes (4%) with unknown animal fates (Table 1). These records stemmed from public and staff reports on the highway, train operator reports on the railway, and site investigations by parks staff on both transportation corridors. In general, collisions on the highway were more often reported with greater precision (100 m) than on the railway (800 m), but variability in precision occurred in both corridors. The consistency of reporting varied in time with an increase after 1998 when Parks Canada Agency introduced a standardized system for reporting incidents. We reviewed all collision records and attempted to increase their accuracy by cross-referencing information on their locations from descriptive notes in the original data source. When more than one mortality resulted from a single collision, we described it in our dataset as a single event. We omitted 31 records from further analyses that had no location data or were mislabeled.

Statistical analyses

We summarize our statistical approach in Table 2. To test the temporal hypothesis that highway mitigation increases railway mortality with maximum statistical power, we compared the rate of transportation moralities (log collisions·km^{-1}·yr^{-1}) with highway mitigation (before vs. after), transportation class (highway vs. railway), over time (year), and between broad groups of species (ungulates and carnivores; Table 2, global model). We used highway, ungulates, and before mitigation as the reference categories for their respective dichotomous variables. We examined collision rates with log-transformed linear models using a cross-sectional panel-data design (xtreg with maximum likelihood estimators) and included mitigation section (one–nine) as a random effect (i.e., panel ID variable). For the predictor variable year, we examined both linear and quadratic forms because this combination had the greatest explanatory power in a preliminary univariate model. We included all two-way interactions among variables, created models with all possible combinations of variables, and used Akaike information criterion (AIC) to identify the best-supported model with the lowest AIC value (Burnham and Anderson 2002).

To test the temporal hypothesis that highway mitigation increased mortality only for some combinations of transportation classes, species groups, or in relation to population trends, we constructed separate models for collision rate (as above) for each transportation class and species group, and used available data for elk to examine the effect of population size (Table 2, highway and railway model). For these models, we used the four species groups with sample sizes greater than 40 collision events: elk, other ungulates (bighorn sheep, *Ovis canadensis*; moose, *Alces alces*; mule deer, *Odocoileus hemionus*; unidentified deer, and white-tailed deer, *Odocoileus virginianus*), and bears (black bear, *Ursus americanus*; and grizzly bear, *U. arctos horribilis*; Table 1). We examined coyote collisions only on the highway

Table 1. Total number of collision events recorded over approximately 82 km of highway and adjacent railway between 1981 and 2014, in Banff National Park, Canada.

	Collisions					
Wildlife	Before	After	Total	Before	After	Total
Ungulates						
Bighorn sheep (*Ovis canadensis*)	67	3	70	2	7	9
Elk (*Cervus canadensis*)	559	96	655	216	545	761
Moose (*Alces alces*)	40	3	43	12	20	32
Mule deer (*Odocoileus hemionus*)	232	44	276	17	71	88
Unidentified (other)	10	7	17	5	15	20
White-tailed deer (*Odocoileus virginianus*)	158	48	206	20	112	132
Total	1066	201	1267	272	770	1042
Carnivores						
Black bear (*Ursus americanus*)	18	22	40	21	20	41
Coyotes (*Canis latrans*)	98	186	284	12	7	19
Cougar (*Puma concolor*)	1	3	4	0	3	3
Grizzly bear (*Ursus arctos horribilis*)	2	3	5	4	11	15
Wolves (*Canis lupus*)	17	17	34	6	15	21
Total	136	231	367	43	56	99
Grand total	1202	432	1634	315	826	1141

Notes: Events are summed for the site-specific periods before and after mitigation of the highway via wildlife crossing structures and fencing. Mitigation occurred in stages across nine highway sections between 1983 and 2013. Corresponding railway sections are identified by the nearest adjacent of highway sections (Fig. 1a). These totals have not been adjusted for number of years sampled, which varied among sites, or for changes in population sizes or distributions. Collisions that involved multiple individuals at the same location and time were tallied as single events.

Table 2. The purpose, variables (response and predictor), and the predicted effect of mitigation used in three sets of models examining a mortality dataset collected from 1981 to 2014 (Table 1).

Response	Species group	Predictor variables	Prediction
Global model†			
Collision rate	Ungulates vs. Carnivores (n = 2309; 466)	Mitigation; Class; Guild	–
Highway model‡			
Collision rate	Elk (n = 452)	Mitigation; Year; Population	–
Collision rate	Other ungulates (n = 612)	Mitigation; Year	–
Collision count	Bears (n = 45)	Mitigation; Year; Species	–
Collision rate	Coyotes (n = 284)	Mitigation; Year	–
Railway model§			
Collision rate	Elk (n = 687)	Mitigation; Year; Population	+
Collision rate	Other ungulates (n = 281)	Mitigation; Year	+
Collision count	Bears (n = 56)	Mitigation; Year; Species	+
Distance model¶			
Distance (m)	All species (n = 1141)	Mitigation, dist. to highway, dist. to wildlife crossing	–

Notes: Predictor variables for the global models included (1) transportation class (highway vs. railway), (2) guild (ungulates vs. carnivores), and (3) mitigation status (before vs. after mitigation). Associated statistical models for the global analysis set the first term in each set of parentheses as the reference category and examined two-way interactions. For the separate transportation class models (highway and railway), we added covariates for year, population size (only for the elk-specific models), and species (only for the bear models) and examined two-way interactions. For the distance model, we used the distance of railway collision to either the highway or associated wildlife crossing structures after highway mitigation. For all statistical models, we used mitigation section as the random effect (Fig. 1).

† To examine the combined effects of highway mitigation on the frequency of both road and railway collisions over space and time while maximizing statistical power.

‡ To determine the long-term effectiveness of highway mitigation from 1981 to 2014 separately for four species or species groups with adequate sample sizes.

§ To determine whether highway mitigation increased the rate of wildlife-train collisions for three species or species groups with adequate sample sizes.

¶ To determine whether highway mitigation increased the rate of wildlife-train collisions after highway mitigation in closer proximity to the highway or wildlife crossing structures.

because the sample size on the railway was too small (n = 19; Table 1). We excluded wolves from the second set of analyses on the highway (n = 34) and railway (n = 21; Table 1) due to low sample sizes and recent recolonization in the Bow Valley during the mid-1980s (Hebblewhite et al. 2002). We entered zero if there were no records for a given year-section-species combination.

As for the separate highway and railway models, we used log-transformed linear regressions (xtreg), included mitigation status as a fixed effect, and used mitigation section as a random effect. We added covariates for year, population size (only for the elk-specific models), and species (only for the bear models; Table 2). Elk population data were collected by Parks staff each spring and entered for our purposes in relation to the mitigation section that contained each set of census coordinates. The elk models used only those years in which collision data could be matched to available spring population censuses (1985–2013), therefore excluding mitigation sections one and nine from the analysis (Fig. 1). The bear models used black bears as the reference category and used logistic regressions (xtlogit) with an offset for the length of each section (km) because a preliminary analysis of residuals did not support a linear model. For each set of models, we retained the stronger of two correlated variables (r > 0.6), standardized continuous predictor variables (mean = 0, standard deviation = 1), and evaluated the fit of both linear and quadratic forms for continuous covariates.

Finally, to test the spatial hypothesis that highway mitigation changes the spatial distribution of railway mortalities, we calculated the distance from each railway mortality to the highway and to the nearest wildlife crossing structure (or, rather, what would become a crossing structure post-mitigation) for all railway collisions. We maximized the statistical power of this analysis by combining all species, except cougars (*Puma concolor*) for which there were too few records on the railway

(n = 3; Table 1). We used distance to the nearest wildlife crossing structure as our response variable and included covariates for mitigation (before and after), distance to the highway, and their two-way interaction (Table 2, Distance Model). We used log-transformed linear regressions (xtreg) and included mitigation section as a random effect. All analyses were conducted using the statistical software Stata (version 14.1, StataCorp, College Station, Texas, USA).

Results

We analyzed a total of 1634 highway and 1141 railway collision events over the 34-yr dataset to calculate the number of collisions per year per km (i.e., collision rate). Despite substantial temporal and spatial variation, collisions were concentrated in the higher-quality and human-dominated montane habitat (sections one, two, and four) in the eastern portion of the study area where they comprised 69% of the highway total (n = 858) and 89% of the railway total (n = 972; Figs. 1a–c, 2). Among the three species groups we examined (elk, other ungulates, and bears), mean collision rate was at least 10 times higher for elk (0.21 collisions$\cdot$yr$^{-1}\cdot$km^{-1} on the highway, n = 655; 0.20 collisions$\cdot$yr$^{-1}\cdot$km^{-1} on the railway, n = 761) and other ungulates (0.24 collisions$\cdot$yr$^{-1}\cdot$km^{-1} on the highway, n = 542; 0.076 collisions$\cdot$yr$^{-1}\cdot$km^{-1} on the railway), relative to bears (0.007 on the highway, n = 45; 0.014 collisions$\cdot$yr$^{-1}\cdot$km^{-1} on the railway, n = 56).

The best-supported global model of collision rates from both transportation classes (highway and railway) and two broad guilds of wildlife did not support the hypothesis that railway mortality increased following mitigation. In this analysis, the most-supported model showed that collision rates were generally lower on the railway, lower for carnivores, and lower after mitigation (Table 3), but with moderation of these effects via two, two-way interactions. The negative interaction between transportation class and guild (Table 3) revealed that the lower collision rate on the railway was more pronounced for carnivores than for ungulates. The positive interaction between transportation class and mitigation showed that the reduction in collision rate after mitigation occurred mainly on the highway when guilds were combined.

For the second set of analyses, the highway models confirmed the global model that collision rates declined after mitigation and over time for each of elk and other ungulates, while increasing over time for bears, especially black bears, and decreasing over time for coyotes (Table 3, Fig. 3). The most-supported Railway Model for elk did not include mitigation status and showed that collision rates declined over time for elk and increased with population size, especially earlier in the time series when population sizes were higher (Table 3, Fig. 3). Collision rates on the railway for other ungulates increased after mitigation, but also over time without a significant interaction between them, indicating that higher mortality occurred on the railway after mitigation, even after accounting for increases through time that might have been caused by (unmeasured) population increases (Table 3). Collision rates on the railway for bears decreased following mitigation, but increased over time, and were lower for grizzly bears than black bears (Table 3, Fig. 3). The most-supported railway model for bears did not contain the interaction between mitigation and species, as would be expected if road mitigation was associated with the rise in grizzly bear mortality on the railway.

We found no evidence that crossing structures on the highway funneled animals onto the railway to change the distribution of mortalities after mitigation. The average distance between railway collision locations and (what would become) the nearest highway crossing structure did not change after highway mitigation occurred (Z = 0.32; P = 0.75).

Discussion

This study examined whether highway mitigation, consisting of exclusion fencing and crossing structures, increased the rate or changed the spatial distribution of wildlife-train collisions on a nearby railway where no such mitigation occurred. The impetus for this research was the recent increase in rail-caused mortality of grizzly bears, for which continued high mortality could threaten local population persistence (Bertch and Gibeau 2009). We examined the potential for highway mitigation to influence railway mitigation with three main analyses: (1) a global model that emphasized temporal effects of mitigation

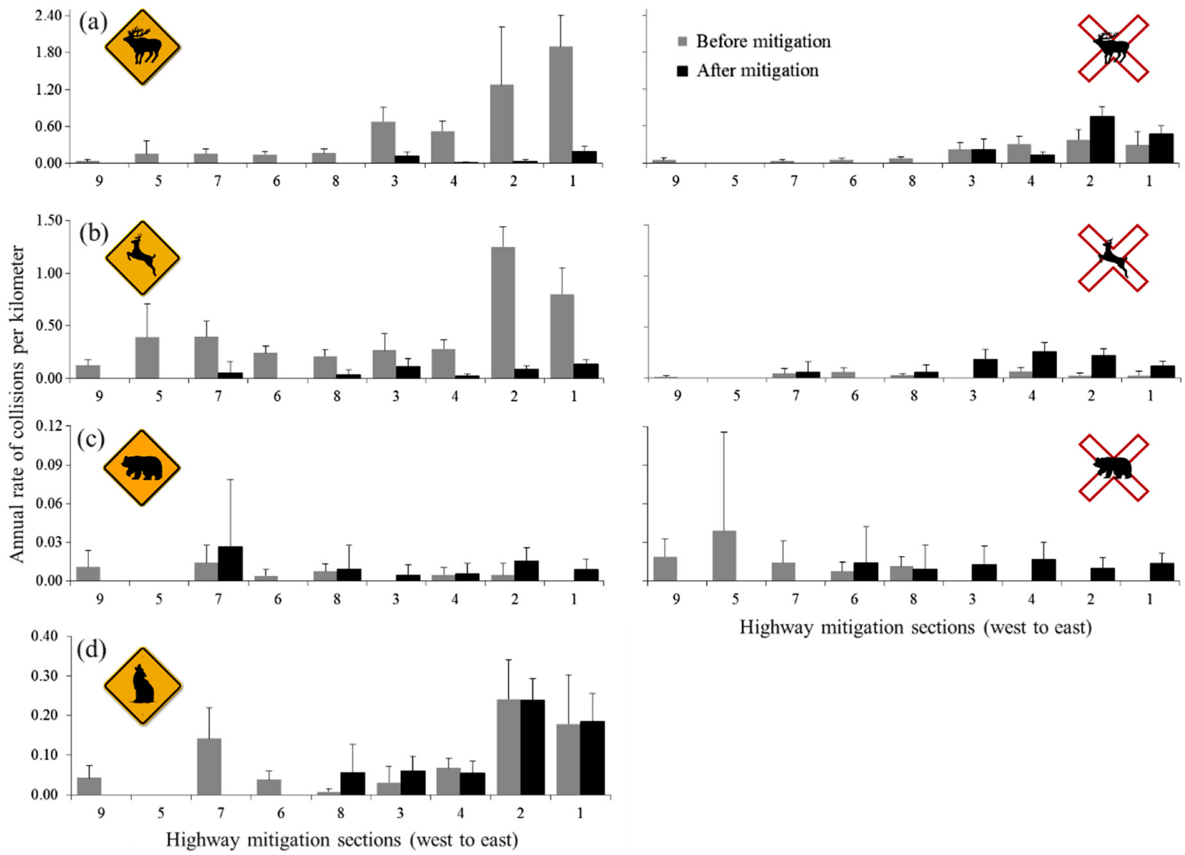

Fig. 2. Annual rate of wildlife collisions per km (±95 CI) on a highway (left panels) and railway (right panels) in Banff National Park, Canada, before and after mitigation occurred in nine sections, labeled from west to east with numbers that correspond to their order of installation (Fig. 1a). Collision rates were calculated by dividing the total number of collisions by the number of years before or after mitigation occurred and the total kilometers per section for four species groups that included (a) elk, (b) other ungulates, (c) bears, and (d) coyotes.

(before vs. after) for both transportation classes and all species (carnivores vs. ungulates), (2) separate highway and railway models to identify variation in temporal responses among species or species groups, and (3) a spatial distance model that explored whether highway mitigation funneled animals onto specific railway locations even without a numerical change in frequency. Together, these analyses indicated that highway mitigation reduced collision rates overall, but mainly for ungulates on the highway. The elk-specific model showed that highway collision rates declined with both mitigation and over time, whereas the railway model suggested that reduced collision rates were driven by correlated changes in population size (84% reduction), not mitigation per se. In fact, other ungulate mortality increased on the railway both after mitigation and over time. For bears, especially black bears, mitigation was associated with lower collision rates on the railway, which increased over time on both the highway and the railway. The spatial distance model showed that collision rates on the railway were not associated with the locations of what would become crossing structures on the railway, which might have occurred if animal movement was funneled by highway crossing structures onto the railway.

Our global model confirmed and extended the analyses of Clevenger et al. (2001) showing that highway mitigation reduced wildlife mortality for each of elk, other ungulates, and coyotes. However, the models specific to transportation class and species groups showed that population size for elk was more important than the effect of mitigation for explaining elk collision rates on the railway. The railway-specific models showed that collision rates increased over time for both other ungulates and bears, potentially revealing that these groups had increasing population sizes. However, the best model for other ungulates also included an effect of highway mitigation, providing some evidence that highway mitigation may increase mortality rates on an adjacent railway for some species. Overall, our results support the continued use of exclusion fencing and crossing structures as the primary form of road mitigation worldwide (Glista et al. 2009, Borda-de-Água et al. 2017).

We anticipated that the positive effect of highway mitigation could be limited in some taxonomic groups, particularly those that can climb over or dig under exclusion fences (Clevenger et al. 2001). Coyotes readily dig under fences

Table 3. Predicted effects of highway mitigation on the frequency of wildlife collisions on the highway and railway through Banff National Park, Canada.

Species group	Variables	β	SE	Z	P
Highway and Railway					
All species	Class	−1.91	0.29	−6.48	<0.001***
	Guild	−2.35	0.29	−7.97	<0.001***
	Mitigation	−2.14	0.37	−5.71	<0.001***
	Class × Guild	−0.71	0.37	−1.92	0.055
	Class × Mitigation	1.98	0.38	5.19	<0.001***
	Intercept	−2.61	0.67	−3.73	<0.001***
Highway					
Elk†	Mitigation	−2.35	0.80	−2.96	0.003
	Year	−1.36	0.28	−4.84	<0.001***
	Intercept	−4.85	0.70	−6.95	<0.001***
Other ungulates	Mitigation	−2.66	0.65	−4.08	<0.001***
	Year	−0.69	0.23	−2.96	0.003
	Intercept	−3.48	0.71	−4.89	<0.001***
Bears‡	Year	0.43	0.18	2.34	0.019
	Species	−2.14	0.50	−4.31	<0.001***
	Intercept	−12.64	1.36	−9.24	<0.001***
Coyotes	Year	−0.13	0.16	−0.78	0.437
	Year^2	−0.76	0.18	−4.14	<0.001***
	Intercept	−5.49	0.76	−7.23	<0.001***
Railway					
Elk†	Population	0.14	0.07	2.21	0.027
	Year	−0.86	0.21	−4.05	<0.001***
	Population × Year	0.09	0.04	2.35	0.019
	Intercept	−5.80	0.95	−6.09	<0.001***
Other ungulates	Mitigation	1.21	0.58	2.10	0.036
	Year	0.78	0.20	3.83	<0.001***
	Intercept	−7.10	0.58	−12.18	<0.001***
Bears‡	Mitigation	−1.04	0.60	−1.74	0.082
	Year	1.40	0.26	5.38	<0.001***
	Species	−1.26	0.35	−3.53	<0.001***
	Intercept	−11.59	1.47	−7.88	<0.001***

Notes: SE, standard error. Most-supported models were identified by Akaike information criterion (AIC) and ranked based on changes in AIC scores. The first model shown used the entire dataset from 1981 to 2014 (Table 1) and included the predictor variables of (1) transportation class (railway vs. highway), (2) guild (carnivores vs. ungulates), and (3) mitigation (after vs. before mitigation), and their two-way interactions; we set the first term in each set of parentheses as the reference category. Subsequent models are divided by transportation class and species groups with high local management relevance (elk, other ungulates, and bears). Italics in the Variables column represents interaction terms in the models.

† Elk collision data matched with available elk population estimates from 1985 to 2013, removing sections one and nine from analysis.

‡ Species: Grizzly (reference Black).

***$P < 0.001$.

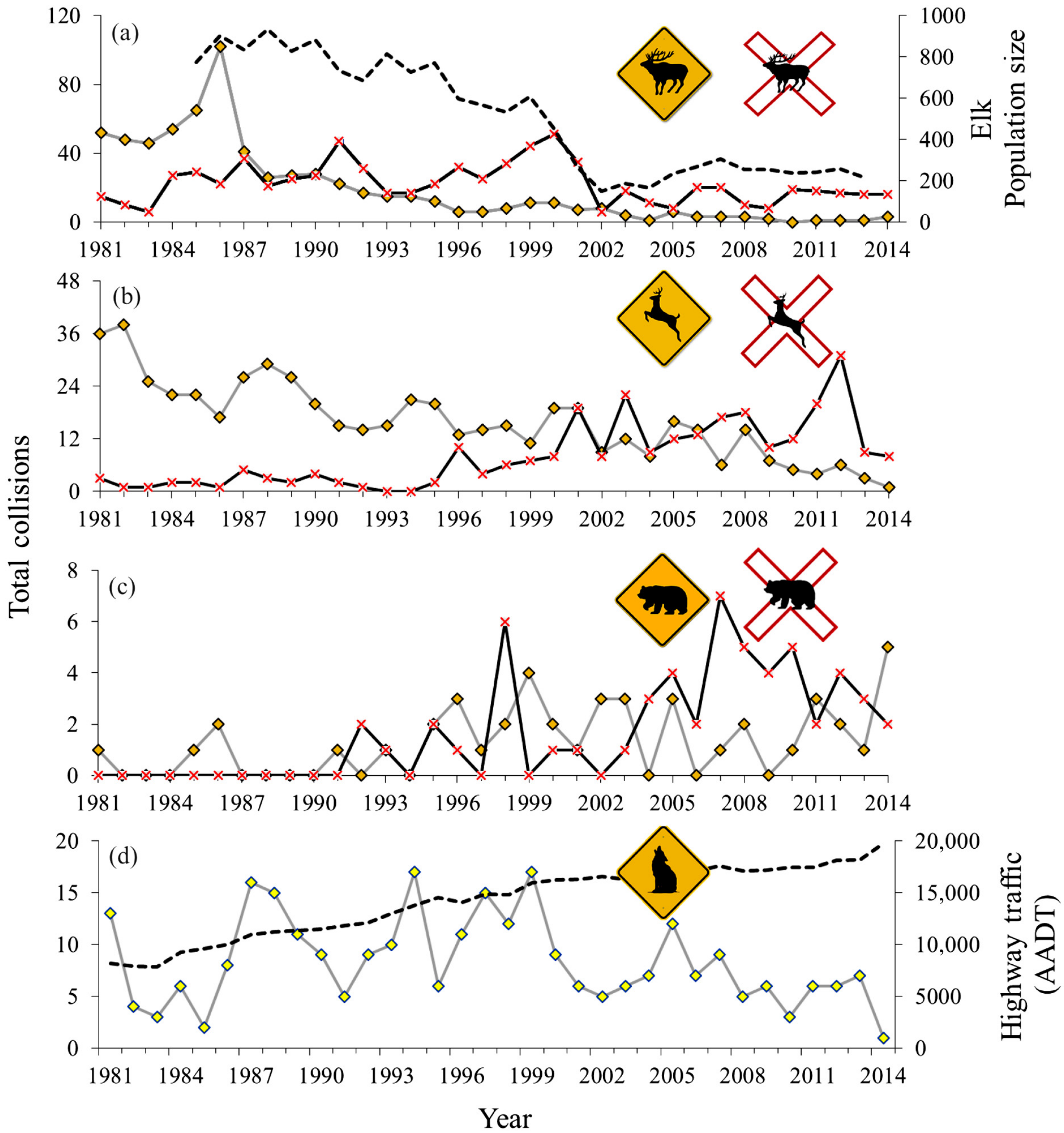

Fig. 3. Total wildlife-vehicle collisions per year in Banff National Park, Canada, between 1981 and 2014 on the highway (yellow diamonds) and railway (red x) for species including (a) elk, (b) other ungulates, (c) bears, and (d) coyotes. Annual population estimates are provided for elk between 1985 and 2013 (dashed line, panel a), and annual average daily traffic (AADT) volume (dashed line panel d) is provided for the highway between 1981 and 2014 for an area just west of Banff National Park gates (Alberta Transportation 2017).

and exploit maintenance-caused breaches (Foster and Humphrey 1995, Clevenger et al. 2001) or enter highway verges from the nearby townsite of Banff (Gibeau 1998). Similarly, black bears readily climb over the highway fence (Clevenger et al. 2001), and grizzly bears may breach it by tearing wire fencing from the posts to which is it stapled (C.C. St. Clair, *personal observations*). These issues are being addressed by ongoing efforts in Banff and elsewhere via installation of aprons to the base of fences (Beckmann et al. 2010), floppy edges or outriggers to the top (Foster and Humphrey 1995, Dodd et al. 2004, Klar et al. 2009), and electric mats at fence ends (A. Forshner, *personal communications*). Nonetheless, our results did not suggest these breaches are common. Indeed, the rate of coyote collisions has declined over time, perhaps in association with recolonization of the study area by wolves (Hebblewhite et al. 2002), which typically displaces coyotes. Although collision rates for bears increased over time on both the highway and the railway, rates within corridor sections generally declined after mitigation. Increased mortality on the railway over time may have resulted from changing management practices for bears (Benn and Herrero 2002) with compensatory mortality of grizzly bears on the railway (C. C. St. Clair et al., *unpublished manuscript*).

The strong effect of population size on the rate of elk collisions on the railway demonstrates the importance of examining population change as part of any study investigating the long-term and landscape-level effects of transportation mitigation (Mysterud 2004, Seiler 2004, Grilo et al. 2014). Despite the lack of census data, it is likely that the increase in collisions that we detected over time for other ungulates (on the railway) and bears (on both the highway and railway) was also associated with population increases. Populations of white-tailed deer appear to have increased in abundance over the past two decades in Banff National Park (J. Whittington, *personal observations*) as they have done in several nearby ecosystems (Robinson et al. 2002, Latham et al. 2011). Such an increase would necessarily cause this species to comprise a larger proportion of the class of animals we called other ungulates after mitigation, separate from the effect of year. White-tailed deer are attracted to several agricultural products that are spilled from trains (Wells et al. 1999). This tendency may combine with their attraction to linear features (Popp and Hamr 2018) to contribute to increased railway mortality for other ungulates after mitigation.

Future analyses may demonstrate that the increase in mortality over time we observed for bears may generalize for other carnivores if their populations are increasing in the region. Following their recolonization of the area in the mid-1980s, wolves have exhibited gradual increases in population size and distribution (Hebblewhite et al. 2002). A stable or increasing black bear population may result from high immigration rates from other areas, which would likely be needed to support ongoing, high rates of mortality in the Bow Valley (Hebblewhite et al. 2003). Camera traps placed over the last several years suggest a stable population size of grizzly bears in Banff National Park since 2006 (Whittington et al. 2018). All of these patterns support the recommendation by others to plan transportation mitigation with multiple sources of data, including information on trends in abundance, rather than just collision hotspots (Teixeira et al. 2017).

It is intriguing to consider whether declines in population size and distribution of elk, which occurred rapidly between 1999 and 2002, are associated with the spike in bear mortality that occurred in 1998 and the greater prevalence of grizzly bear mortality that began in 2000 (Fig. 3). The absence of wolves throughout the 1970s and 1980s led to an increase in elk abundance and the suppression of elk forage, such as willows and aspen (White et al. 1998, Hebblewhite et al. 2005). These elk were likely predated on by grizzly bears (Hilderbrand et al. 1999, Felicetti et al. 2005). As wolves recolonized in the late 1980s and early 1990s (Hebblewhite et al. 2002), an increasing proportion of the elk population resided year-round near the townsite of Banff, which attracted predators and compromised human safety (Kloppers et al. 2005). The combination of predation and elk translocations or removal succeeded in reducing the population by 84% from its high in 1988 (n = 934) to its lowest level in 2002 (n = 151), with an average annual population of 238 elk near the townsite of Banff between 2003 and 2013 (Fig. 3). The increase in grizzly bear railway mortality that has occurred since 2000, also concentrated near the townsite of Banff, may thus relate to the combined effects of lower absolute abundance of elk, increased concentration near the townsite, and associated increases in scavenging opportunities caused by train strikes on elk and other ungulates (St. Clair et al., *unpublished manuscript*). Bears have frequently been observed scavenging on train-struck carcasses (Wells et al. 1999), and similar increases in transportation-related mortality have been associated with changes in resource distribution for other species (Grilo et al. 2014).

Despite the coincidental timing of lower elk abundance and increased frequency of grizzly bear railway collisions, our study found no support for the hypothesis that highway mitigation caused an increase in the frequency of train collisions with grizzly bears, but there is some evidence that it increased collision rates for ungulates other than elk. Separate from the effect of highway mitigation, grizzly bears may be attracted to the railway for several food-related benefits, such as the attraction to wildlife associated with spilled grain (Gangadharan et al. 2017), increased plant growth (Pollock et al. 2017), and predation and ungulate scavenging opportunities (Murray et al. 2017), and even inter-specific food conditioning (Put et al. 2017). Small changes in any foraging opportunity are likely to be important to grizzly bears, which are generally limited by access to protein (Hilderbrand et al. 1999, López-Alfaro et al. 2015) especially in this landscape (Garshelis et al. 2005). Food availability on the railway may determine the vulnerability trains cause to bears, potentially explaining why brown bear mortalities in Croatia were over twice as common on a railway than a co-aligned highway (Huber et al. 1998).

For shy, wide-ranging species, including bears, railways may attract wildlife if they occur on leased land that prohibits access by the public. In our study area, high human use of an adjacent secondary road (Gibeau et al. 2002) may have diverted animals to the railway where trespassing is prohibited. Despite the quickness with which grizzly bears adapt to new food sources (Hamer and Herrero 1987*a*, Gibeau and Herrero 1998), they generally avoid people and initially appeared to avoid new crossing structures in Banff (Clevenger and Waltho 2005, Barrueto et al. 2014, Sawaya et al. 2014). Avoidance of people or vehicles might also be the reason that grizzly bears crossed highways at night when traffic volume was lowest in Montana (Waller and Servheen 2005), Alaska (Graves et al. 2006), and Alberta (Northrup et al. 2012), when railway traffic was sometimes higher. Black bears also appear initially to shy away from highway construction and mitigation, and to initiate use of the new structures when traffic volume (and human activity) is low (Van Manen et al. 2012). These observations suggest that bears need long periods of time to adapt to changing landscapes, including those associated with mitigation. Similar periods of adjustment were needed to accommodate railway mitigation by long-lived Tibetan ungulates (Baofa et al. 2006) and Herman's tortoises (*Testudo hermanni boettgeri*; Iosif 2012).

Despite the long duration of our database (34 yr) and high number of collisions on a parallel highway (n = 1634) and railway (n = 1141), we may have lacked sufficient statistical power to thoroughly explore changes caused by highway mitigation alone, owing to simultaneous changes in several other factors that may have affected population sizes and distributions. In addition to changing sizes of several populations (above), there were changes to garbage management (Benn and Herrero 2002), fire suppression (Hamer and Herrero 1987*b*, White et al. 1998), predator abundance (Hebblewhite et al. 2002), management of human-bear conflict (Bertch and Gibeau 2010), and railway practices (Wells et al. 1999). Such factors logically influence wildlife use of transportation corridors to determine the effects of mitigation, particularly for parallel transportation classes (van der Ree et al. 2007, van der Grift et al. 2013, Dorsey et al. 2015).

If wildlife managers are to meet the challenges of expanding global transportation networks, which are projected to be 60% higher by 2050 (Dulac 2013), they will need more studies that address the multi-faceted complexity of transportation mitigation. These studies must pair accurate reporting of collisions (Child et al. 1991) with powerful BACI (before-after-control-impact) designs (van der Grift et al. 2013, Rytwinski et al. 2015, 2016) that simultaneously examine multiple species and demographic classes of predators and prey (Ford et al. 2017), for which changes in abundance are also assessed (Teixeira et al. 2017). Railways must reach the level of study, understanding, and mitigation that has long been applied to roads (Dorsey et al. 2015, Popp and Boyle 2017). Together, this information could offer managers the opportunity for holistic, long-term, and landscape-level approaches to understanding and mitigating wildlife-vehicle collisions with the explicit integration of parallel transportation routes.

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