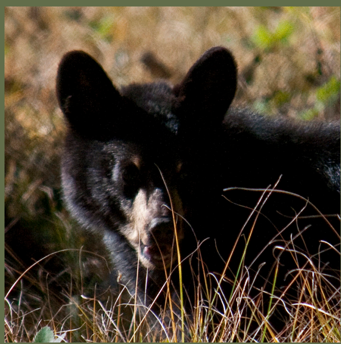
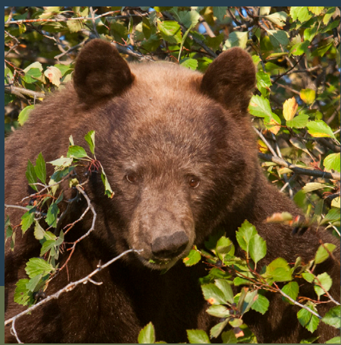
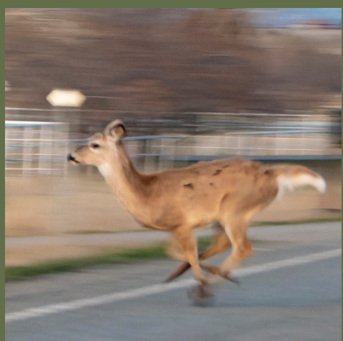


Long-term responses of an ecological community to highway mitigation measures

NDOT Research Report No. 701-18-803 TO 7





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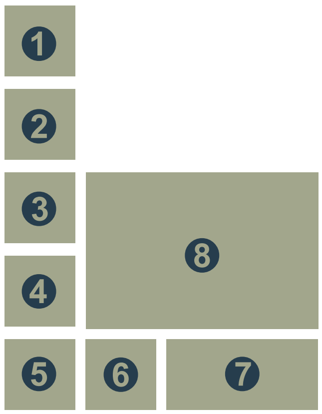

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NDOT Research Report

Report No. 701-18-803 TO 7

TPF-5(358)
LONG-TERM RESPONSES OF AN ECOLOGICAL COMMUNITY TO HIGHWAY MITIGATION MEASURES

June 2022

Nevada Department of Transportation
1263 South Stewart Street
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16. Abstract

In road mitigation systems characterized by multiple wildlife crossing structures (CS) and multiple-focal species, these species-specific design criteria are important to meeting management goals. CS types and locations are fixed in place and cannot be manipulated experimentally; long term studies may offer the best chance to inform evidence-based designs for new CS projects in the future. Long-term data from Banff National Park are uniquely posed to answer these critical questions. More recently, highway mitigation along US93 in Montana provides an additional case study with which to understand the responses of large animals to different CS designs. The purpose of this study is to identify factors affecting movement of large mammals through CS using data sets from both mitigation projects. Year-round monitoring of CS use was used in an analytical framework to address questions regarding species-specific and community level use of CS; design and habitat factors that best explain species-specific variation; and whether importance of design parameters changes over time. Over the 17 years of the Banff study, and the six years of the Montana study, CS facilitated over 200,000 crossing events at 55 locations. There were significant changes in annual crossing events over time. Variables associated with CS passage rates were species specific, but aligned with a few clusters of preference. With the exception of coyotes, all large carnivore species preferred open span bridges or overpasses to other CS types. In Montana, fencing was positively associated with passage rates for black bears and cougars. We found that wider CS tend to be preferred by most species, irrespective of their location. We also found that wider CS tend to have shorter 'adaptation' curves than narrower ones for grizzly bears, coyotes, cougars, and moose. Depending on the heterogeneity of the landscape near the highway, more CS may not create more crossing opportunities if local habitat conditions do not favor animals' access to the road. At the scale of ecological communities, the flows of mass and energy are likely enough to alter the distribution of ecological processes in the Banff and Montana ecosystems. Our results highlight the value of long-term monitoring for assessing the effectiveness of mitigation measures. Our work confirms the species-specific nature of measure CS performance, leading to our primary recommendation that a diversity of CS designs be considered an essential part of a well-designed mitigation system for the large mammals of western North America. Short-term monitoring efforts may fail to accurately portray the ecological benefits of mitigation for populations and ecological communities. Our results will help to inform design and aid in the establishment of robust, long-term performance measures.

17. Key Words	18. Distribution Statement
Banff National Park, design criteria, mammals, monitoring, Montana, mitigation, performance assessment, wildlife crossing structure	

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Long-term responses of an ecological community to highway mitigation measures

Final Report

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A report prepared for the:

Nevada Department of Transportation (NDOT)

Carson City, Nevada

POOLED FUND STUDY

TPF-5(358) TASK 1
Cost Effective Solutions
Research Projects

June 30, 2022

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1 Introduction

Linear infrastructure – such as roads, seismic lines, powerlines, and pipelines - generally has a negative effect on wildlife and biodiversity (Forman and Alexander 1998). Specifically, roads may form a barrier to movement due to behavioral responses of animals to changes in substrate, lack of cover, or an aversion to traffic noise, motion, and light (Mazerolle et al. 2005, Ford and Fahrig 2008, Bouchard et al. 2009, Jacobson et al. 2016). Roads also contribute to barrier effects at the population scale via wildlife vehicle collisions (Fahrig and Rytwinski 2009). Such collisions not only influence the connectivity of populations, they can also be dangerous to human health and property (Huijser et al. 2009). In the United States, for example, there were over 2.1 million wildlife-vehicle collisions in 2020-21 (Ortega, Jordi 2022).

While road closures and access management can improve connectivity in some limited cases such as protected areas (Whittington et al. 2019), the societal demand to keep roads accessible for the movement of goods and people means that mitigation is one of the only options to reduce the effects of roads on biodiversity. In the context of environmental assessment, mitigation refers to minimizing or avoiding impacts caused by human activity. Specific to roads, mitigation includes technologies, regulations, and policies that change driver behaviour (Huijser et al. 2015); separate animals from the road way (Ford et al in review); and create opportunity for safe passage for wildlife across the road. Wildlife detection systems, signs, cattleguards, speed limits, and established at-grade crossing areas are all mitigation methods that have been used with the aim to mitigate the direct mortality effect of roads on wildlife (Van der Ree et al. 2015). However, few technologies are as widely recognized for their effectiveness as the combined efforts of wildlife exclusion fencing and wildlife crossing structures.

Wildlife crossing structures (CS) and exclusion fencing have become synonymous with efforts to reduce wildlife vehicle collisions and maintain or improve connectivity across roads. In North America, the first recognized CS were built in Florida for black bears, and as of 2005, over 460 dedicated CS have been recorded in the USA and Canada (Cramer and Bissonette 2005). These CS include underpasses of various designs, overpasses, and target a range of species including aquatic species, herpetofauna, and large mammals. While there was a relative hiatus of efforts to monitor CS use through the 1980s, by the late 1990s investments in monitoring CS were renewed (Cramer and Bissonette 2005). The early results of these efforts, shared via landmark studies (e.g., Clevenger and Waltho 2000), indicated that there may be species-specific responses to CS design. In mitigation systems characterized by multiple CS and multiple-focal species, these species-specific design criteria are of particular importance to meeting management goals (Denneboom et al. 2021). For example, Ford et al (2017) found that grizzly bear family groups preferred overpasses while single bears used smaller underpasses. These authors concluded that a high density and diversity of CS designs may help reduce intraspecific interactions that could negatively affect the population.

With some longer-term monitoring of CS (>10 years) and associated databases available for analyses and an expanding demand for the 'greening' of new transportation infrastructure (Laurance et al. 2014), it is only now possible to answer questions about factors affecting CS use with unprecedented precision. Given that CS types and locations are fixed in place and cannot be manipulated experimentally, long term studies may offer the best chance to inform evidence-based designs for new CS projects in the future (Rytwinski et al. 2016). With enough effort, such studies can have the degrees of freedom to statistically account for confounding variation in key parameters of management interest (Rytwinski et al. 2016). Some of the more pressing questions about CS performance relate to ways in which agencies can achieve mitigation goals in a financially viable manner. Questions over location, density, and design of CS require answers from both an ecology and engineering perspective (McGuire and Morrall 2000, Clevenger et al. 2002). Some key ecological questions related to cost and performance trade-offs include: As CS designs vary significantly in cost (Ford et al 2017), what CS design is preferred by the focal species? How do local habitat conditions and CS design interact to affect use by focal species? Among different CS types, costs usually increase with width - which is suspected to increase use - but how big/wide do CS need to be? As CS numbers increase, so do total costs - how many CS are needed to maintain or restore connectivity? Does the importance of CS design change over time as species potentially adapt to the presence of CS in the landscape?

Data from Banff National Park in Alberta, Canada are uniquely poised to answer these critical questions. Banff National Park has the world's longest running program monitoring and evaluating wildlife crossing (WC) for large mammals. For over 17 years, more than 40 CS built along a 90 km section of highway (Figure 1) have been monitored for wildlife use on a year-round basis (Clevenger and Barrueto 2014). This 17-year dataset has been used to help answer pressing management questions related to species' patterns of WC use, species interactions, and anthropogenic effects on wildlife use (Clevenger and Waltho 2000, Ford et al. 2009a, Ford and Clevenger 2010, Barrueto et al. 2014). The dataset is uniquely poised to examine questions of species response to CS that short-term datasets are unable to examine.

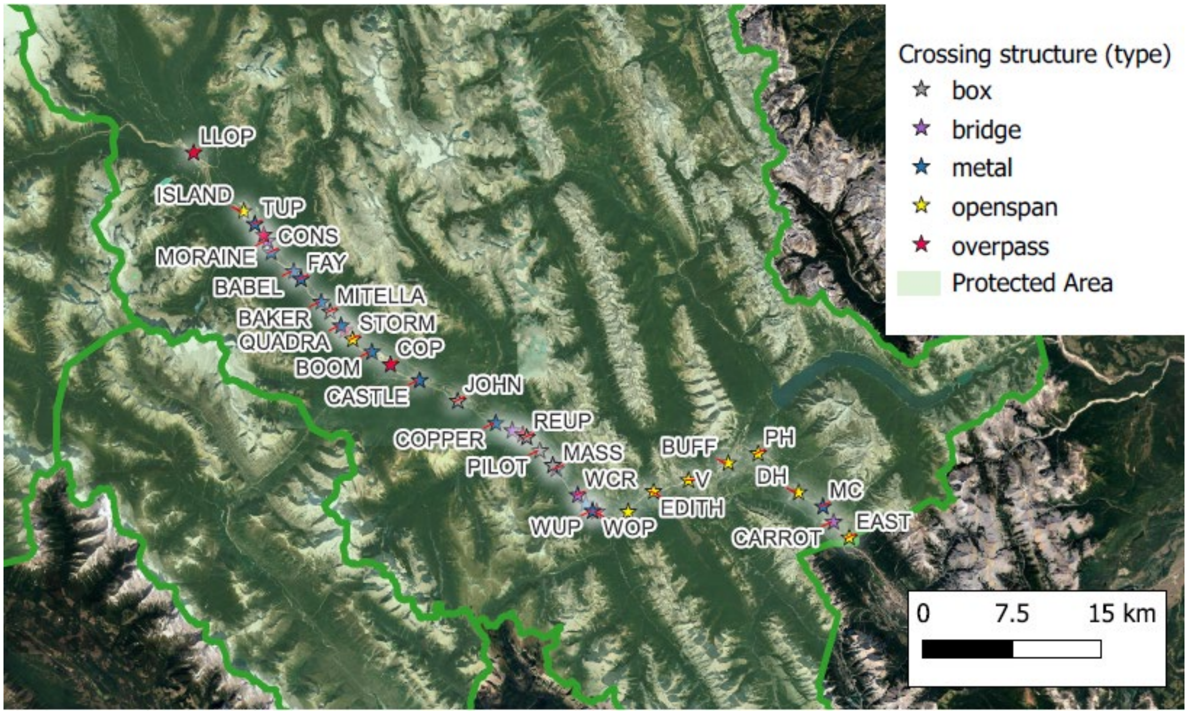

Figure 1. Study areas showing the mitigation phases and CS locations (top) along the Trans-Canada Highway, Banff National Park, AB. For the Montana study area, please see Huijser, M.P., W. Camel-Means, E.R. Fairbank, J.P. Purdum, T.D.H. Allen, A.R. Hardy, J. Graham, J.S. Begley, P. Basting & D. Becker. 2016. US 93 North post-construction wildlife-vehicle collision and wildlife crossing monitoring on the Flathead Indian Reservation between Evaro and Polson, Montana. FHWA/MT-16-009/8208. Western Transportation Institute – Montana State University, Bozeman, Montana, USA.

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More recently, highway mitigation along US93 in Montana provides an additional case study with which to understand the responses of large animals to different CS designs (Huijser et al. 2016). Here, CS have been monitored continuously with trail cameras from 2010 to 2015 for use by large mammals – including both rare carnivores like grizzly bear to more common ungulates like white-tailed deer. This combination of a relatively intact wildlife community in an area with substantive human disturbance creates a unique ‘reference’ condition to understand how highways and large mammals interact in a multi-functional landscape. As large carnivore populations expand across many parts of their former range, understanding how these species interact with road mitigation measures in such a reference area will provide critical information to planning mitigation measures in a cost effective and ecologically meaningful manner across North America.

The purpose of this study is to identify factors affecting movement of large mammals through CS using data sets from both well established and more recent highway mitigation projects. The key questions motivating this work address knowledge gaps in CS systems. These questions are targeted at 8 taxa as well as community-level responses.

1.1 Key Objectives and Research Questions

The following are the research questions addressed in this project:

1. Summarize species-specific and community level use of CS for Banff and Montana study areas.
2. What habitat, design, and temporal factors best explain species specific variation in CS use?
3. Does the type (design) of CS or location matter more?
4. How does the importance of CS design parameters [width] change with time since construction?
5. Does number of CS or design affect use - are more or wider CS better?

2 Methods

2.1 Study Area Banff National Park, Alberta, Canada

Banff National Park (hereafter referred to as Banff) is situated approximately 150 km west of Calgary, Alberta, in the Bow River Valley along the Trans-Canada Highway (TCH; see Ch. 1, Figure 1). The study area is characterized by mountainous landscapes with a continental climate consisting of long winters and short summers (Holland and Cohen 1983). Vegetation characteristic of the montane and subalpine ecoregions consists of open forests dominated by lodgepole pine *Pinus contorta*, Douglas-fir *Pseudotsuga menziesii*, white spruce *Picea glauca*, Englemann spruce *Picea englemannii*, trembling aspen *Populus tremuloides*, and natural grasslands.

The TCH is the major transportation corridor through Banff currently carrying an estimated annual average daily traffic volume of over 17,000 vehicles per day, with peaks of more than 30,000 vehicles per day during summer (Highway Engineering Services, Parks Canada, unpublished data). Traffic volumes in Banff are highest at the east gate and gradually decline westward through Banff and Yoho National Parks.

In the 1970s, safety issues compelled planners to upgrade the TCH within Banff from two to four lanes, beginning from the eastern boundary and working west (Ford et al. 2010). Large animals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway, and underpasses were built to allow wildlife safe passage across the road. The first 27 km of highway twinning (Phases 1 and 2) included 10 wildlife underpasses and was completed in 1988 (Figure 1). Fencing and WC on the next 20 km section (Phase 3A) was completed in late 1997 with 11 additional wildlife underpasses and two 50-m wide wildlife overpasses (Clevenger and Waltho 2000, 2005). The Castle wildlife underpass was constructed independent of Phase 3A and Phase 3B in 1990-91. For the purpose of this report, we included Castle as part of Phase 3A. The final 35 km of four-lane highway to the western park boundary (Phase 3B) includes 21 WC, including four, 60-m wide wildlife overpasses and was completed in late 2013.

2.1.1 Wildlife crossing structures – Banff National Park, Alberta, Canada

Our analyses involved 37 CS along the TCH, including 17 recently constructed within Phase 3B (Table 1). The WC constituted five different structural designs: 1) open span bridge underpass, 2) creek bridge underpass, 3) elliptical, metal culvert underpass 4) prefabricated concrete box underpass, and 5) wildlife overpass. The age of WC ranged from the oldest built on Phase 1 in the early 1980s to most recently constructed on Phase 3B between 2008 to 2013.

Table 1:Wildlife crossing structures (CS) monitored consistently along Trans-Canada Highway in Banff National Park, Alberta 1996-2014.

Location (km marker)	CS name	Type	Width (m)	Height (m)	Length (m)
0.1	EAST	openspan	9.8	2.8	63
2.5	CARROT	bridge	13.4	2.5	83
4	MC	metal	4.2	3.5	96
6.3	DH	openspan	9.8	2.9	40
11.4	PH	openspan	9.5	2.9	40
14.9	BUFF	openspan	10	3	27
19	V	openspan	9.8	2.7	27
22	EDITH	openspan	10.3	2.8	26
24.5	HEALY	openspan	9	2.9	4
27.3	WOP	overpass	50	7.8	72
27.5	WUP	metal	7.3	3.4	63
28.5	BOURG	metal	2	1.8	100
29.5	WCR	bridge	11.5	2.5	83
32.2	MASS	metal	7.2	3.6	51
32.7	SAW	box	3	2.4	58
34.3	PILOT	box	3	2.4	66
35.9	REUP	box	3	2.4	78
36.3	REOP	overpass	50	7.8	72
37.3	RECR	bridge	11.4	2.2	57
38.9	COPPER	metal	7.2	3.9	57
42.4	JOHN	box	3	2.4	58
47	CASTLE	metal	7.3	3.5	57
49	COP	overpass	56.3	14.2	105
51	BOOM	metal	7.1	3.5	44
53	STORM	openspan	19	5	46
54	POP	overpass	55.1	14.2	117
54.5	QUADRA	metal	7.1	3.3	55
56	MITELLA	box	3.6	2.1	57
57.1	BAKER	metal	7.8	2.9	59
59.7	FAY	metal	7.9	3.1	57
60.6	BABEL	metal	5.8	2.2	57
63	CONS	metal	8	3.3	51
64.1	MORAINE	bridge	23	1.6	42
64.7	TOP	overpass	56	14.2	123
65.9	TUP	metal	4.1	7.1	60
67.3	ISLAND	openspan	24	4	47
74.3	LLOP	overpass	58	14.2	93

2.1.2 Data Collection – Banff National Park, Alberta, Canada

Systematic year-round monitoring of CS began in November 1996 (Ford et al. 2009a). Monitoring consisted of checking the CS and recording animal movement across raked track pads. Track pads spanned the width of the wildlife underpasses, generally ≈2 m wide, and were set perpendicular to the direction of animal movement. At wildlife overpasses a single 3-m-wide track pad was set across the center and motion-sensitive cameras were used to supplement track pad data. Tracking material consisted of a dry, loamy mixture of sand, silt, and clay, 1–4 cm deep. Each CS was visited every two to four days throughout the year. Observers identified tracks to species, estimated the number of individuals, their direction of travel (northbound or southbound across the TCH), and whether they moved through the CS.

Since 2005, motion-sensitive digital cameras (Reconyx Inc., Holmen, Wisconsin) have been used, first to supplement and then replace track pads to monitor species use of the CS (Ford et al. 2009). WC cameras were located within or adjacent to (10-15 m away) wildlife underpasses and on top of and at the center of wildlife overpasses. All cameras used in this study provided metadata on date, time, and ambient temperature during each crossing/passage event (Barrueto et al. 2014). Once set up, all cameras were running 24 hrs/day, year-round, but with occasional periods of camera malfunctioning and/or premature battery failure. Cameras were checked for operation (battery life) and memory cards were switched out every 2-3 weeks year-round. Camera data collected at WC were stored in Microsoft™ Access and Excel databases on the Parks Canada server in Banff National Park, Alberta.

For this analysis we defined an event as a successful passage through a CS by an individual or groups of individuals of one species. An event had to be recorded by cameras greater than or equal to two minutes apart from other events, to account for large groups or lingering individuals. We determined camera-sampling effort at CS by calculating the number of days that cameras were operational (camera trap-days).

We attempted to identify photographs at CS to species level. With the exception of bison and caribou *Rangifer tarandus*, Banff retains the full complement of native large mammal species: Wolves *Canis lupus*, coyotes *C. latrans*, cougars *Puma concolor*, lynx *Lynx canadensis*, black bears *U. americanus*, grizzly bears *U. arctos*, wolverine *Gulo gulo*, mule deer *Odocoileus hemionus*, white-tailed deer *O. virginianus*, elk, and moose *Alces alces*. Because of their similarity in habitat use and life-history, and occasional difficulties in distinguishing these two species from some of the low-quality nighttime photos, we pooled the two *Odocoileus* species (hereafter referred to as “deer spp.”). The analysis was conducted at a species level, pooling data from both sexes and all age classes.

2.1.3 Explanatory Variables– Banff National Park, Alberta, Canada

We identified a total of 37 field and geographic information system (GIS)-based variables that have been shown to influence passage by CS in previous research (Clevenger and Waltho 2000). Variables broadly encompassed three types: structural, environmental, and human-related (Table 2).

Table 2. The structures and structure types included in the analyses of monitoring data from US Hwy 93 North and the calendar years for which data were available based on trail cameras. The number in each cell represents the age of the structure in years for each calendar year.

CS name	Width (m)	Height (m)	Length (m)
Finley Creek 1	103.5	9.7	12
Finley Creek 2	7.95	5.55	32
Finley Creek 3	60	0	63
Finley Creek 4	7.75	5.1	24.7
Mission Creek	16.6	4.9	40
N Finley Creek	7.75	5.1	24.3
North Evaro	7.95	5.55	25.3
Overpass	7.95	5.55	21.9
Pistol Creek 1	7.3	5.2	40
Pistol Creek 2	7.3	5.2	40
Polson Hill	6.71	3.66	15.85
Post Creek 1	7.32	4.75	28.8
Post Creek 2	7.32	4.75	22
Post Creek 3	7.32	3.9	19.5
Railroad	7.75	5.1	25.8
Schley Creek	7.75	5.1	30
Spring Creek 1	8.5	3	44.4
Spring Creek 2	8.5	3	51.9

We included season as a temporal covariate, which we defined as: spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb). All species were active throughout the year except for grizzly and black bears. In addition, we used time varying covariates: time since construction of the CS (measured in months); absolute month (a measure of time). We tested all covariates for correlation and excluded predictors with a correlation >0.7.

2.2 Study Area - US Hwy 93 North

US Highway 93 North (hereafter referred to as "US Hwy 93 North") is located between Evaro and Polson on the Flathead Indian Reservation in northwest Montana, USA. The study area is a mixed-use landscape, including forested hills, upland natural grasslands, riparian zones along rivers, wetlands, pastures, cropland, and mixed housing densities. County and local roads cross through the landscape in the areas adjacent to US Hwy 93 North. Major mountain ranges include the Mission Mountains to the east and the Rattlesnake Mountains to the south-east. US Hwy 93 North is a major highway that connects Interstate-90 and Missoula to the Flathead Valley with Kalispell and Glacier National Park as major destinations. Average Annual Daily Traffic was 6,700-7,600 vehicles between 2010-2015 (Huijser et al., 2016).

The US Hwy 93 North reconstruction project (2004-2010) on the Flathead Indian Reservation in northwest Montana represents one of the most extensive wildlife-sensitive highway design efforts to date in North America. The reconstruction of the 90 km long road section included the installation of wildlife crossing structures at 39 locations and approximately 14 km) of road with wildlife exclusion fences (2.4 m tall) on both sides of the highway (Huijser et al. 2016).

The wildlife mitigation measures along US Hwy 93 North were an integral part of the reconstruction of this highway because the Confederated Salish and Kootenai Tribes required the reconstructed highway to be respectful of the land, the people and their culture, and wildlife (Becker & Basting, 2010). Without approval and collaboration of all three governments (i.e., Federal, State, and the Tribal government), the highway reconstruction project could not have been initiated (Becker and Basting 2010). After many years of negotiations, the three governments reached an agreement in 2000 (FHWA, MDT, & CSKT, 2000). This agreement is based on the idea that "the road is a visitor and that it should respond to and be respectful of the land and the "Spirit of the Place." The "Spirit of the Place" encompasses the entire Mission Valley, Mission and Salish Mountains, Jocko Valley, and Rattlesnake Divide. This broader environmental spectrum continuum has distinct landscapes like large outdoor rooms, which the existing road bisects. The design of the reconstructed highway needed to "be influenced by and respond to the land" so that it would "increase the perception that the road is integrated with the land rather than slicing through it" (US 93 Design Discussions Project Committee, 2000). "The guiding philosophy for modification of U.S. 93 is to protect cultural, aesthetic, recreational, and natural resources located along the highway corridor and to communicate the respect and value that is commonly held for these resources pursuant to traditional ways of the Tribes" (FHWA 2001). Values related to culture, landscape, and natural resources are not uniquely Native American. These values are present in almost any society. However, in the specific context of the reconstruction of a highway on a Native American reservation, these values were made an integral component of a context sensitive approach to redesigning a highway.

2.2.1 Wildlife crossing structures - US Hwy 93 North

Our analyses included 18 CS that were monitored for wildlife use with trail cameras between 2010 and 2015 (Table 3). Since the structures were built in different years, they had varying age during the research period.

Table 3. Description of data set including covariates used in analysis of long-term data to identify factors affecting movement of large mammals through wildlife crossing structures (CS). Covariates in red were not included in models.

Core model	Predictor (abbreviation)	Type
Habitat	Distance to forest (dist.for)	Continuous
	Percent forest cover in a 1km radius (tree.1km)	Continuous
	Percent herbaceous cover in a 1km radius (grass.1km)	Continuous
	Percent shrub cover in a 1km radius (shrub.1km)	Continuous
	Elevation (elevation)	Continuous
	Distance to closest built structure (dist_built)	Continuous
	Distance to closest secondary road (dist_road)	Continuous
	Solar radiation in a 1km radius (rad.1km)	Continuous
	Distance to water (dist.water)	Continuous
	Number of CS within 5km buffer (buff.5km)	Continuous
Design	Width (width)	Continuous
	Openness (open)	Continuous
	Length (length)	Continuous
	Type (type)	Factor
Location	Distance in KM from the East end of Banff National Park (location)	Continuous
Time varying	The number of months elapsed since the start of the study in November 1996 (absmonth)	Continuous
	The number of months elapsed since the CS was operationalconstructed and operational (TSC)	Continuous

2.2.2 Data Collection - US Hwy 93 North

Systematic year-round monitoring of CS with trail cameras (Reconyx Hyperfire PC900) included in this report began 1 January 2010 and ended 31 December 2015 (Table 1). CS cameras were located inside underpasses, or just outside underpasses, and on both approaches of the one overpass. All cameras used in this study provided metadata on date, time during each crossing/passage event. Once set up, all cameras were running 24 hrs/day, year-round, but with occasional periods of camera malfunctioning, full memory cards, and/or premature battery failure. SD cards were switched out every 4 weeks, and batteries were replaced every three months, year-round. Camera data collected at CS were stored in Microsoft™ Access and Excel databases.

For this analysis we defined an *event* as a successful passage through a CS by an individual or groups of individuals of one species. An event had to be recorded by cameras greater than or equal to five minutes apart from other events to account for large groups or lingering individuals. In addition, if we suspected the same animal, the same animal group or part thereof entered the crossing structure but returned within 5 minutes, it was considered an unsuccessful crossing by those individuals, and it was not included in these analyses.

We attempted to identify photographs at CS to species level. The areas immediately adjacent to US Hwy 93 North area includes the following free roaming native large mammal species: wolves, coyotes, cougars, black bears, grizzly bears, mule deer, white-tailed deer, elk, and moose.

2.2.3 Explanatory Variables - US Hwy 93 North

Design variables included CS dimensions: width, height, length (including central median), openness, and adjacent fence length. Fence length for each CS was measured on both sides of the structure, on both sides of the road, up to 1 km away from the structure. This resulted in a maximum fence length of 4 km for a structure. For a wildlife fence to be included, it had to be connected to structure concerned.

2.3 Data Analysis and Predictions

For all data analyses, we used the statistical program R (R Core Team 2022). We used question-specific methods for the main research questions:

2.3.1 Summarize species-specific and community level use of CS for Banff and Montana study areas.

We summarized annual crossing for the focal species, as well as crossing per CS. To calculate community-level metrics, we first aggregated the dataset to combinations of season and year for each CS. We then calculated the Shannon diversity index (D) and total biomass. We used average adult body masses from Wilman et al. (2014) multiplied by the number of crossings records for each species. We then compared D and log biomass by CS type using a Yuen t-Test For Trimmed Means. We calculated energetic flows by multiplying body mass by the formula: $E = 4.82*M^{0.73}$, where M is mass in grams (Nagy et al. 1999).

If connectivity is ‘CS-limited’ (i.e., there were ‘too few’ CS), we predict the following:

a) that the construction of new CS would lead to more crossing events across the system;
b) the number of crossing events *per* CS would be stable over time;
c) age of CS would have no effect on crossing events.

Furthermore, if connectivity is driven by behavioral adaptation, we predict the following outcomes:

a) there would be an increase in both total crossings and crossings per CS with time.

b) age of CS would have a positive effect on crossing events.

These predictions assume that wildlife population sizes are stable and related to CS use. It is likely that some species densities are changing through time in Banff, such as declines in elk (Hebblewhite et al. 2002).

2.3.2 What habitat, design, and temporal factors best explains species specific variation in CS use?

To quantify factors affecting CS use in Banff, we used a model selection framework to evaluate the top performing model. We bundled predictor variables into the following categories:

(1) *Habitat*, which included distance to forest, tree density in a 1 km radius, grass density in a 1 km radius, shrub density in a 1 km radius, elevation, distance to nearest buildings, distance to nearest secondary road solar radiation in 1km radius, distance to water, and number of neighboring CS within 5 km.

(2) *Design*, which included sub models for type (i.e., a factor representing open span, box, elliptical culvert, creek crossing, or overpass = with 'box culvert' set as the reference level), CS width, CS length, and CS openness. Since these variables are correlated, we evaluated each sub model using Akaike information criterion (AIC). We found that 'type' was the strongest predictor for most species and carried this model forward to represent 'design' in comparisons with other models.

(3) *Location*, which included the kilometers marker of the CS, starting at the eastern most end of the study area.

(4) *Time varying*, which included sub models for time since construction, month of the study, both in an additive model and both in an interactive model. We evaluated each sub model using AIC. The interactive time varying model had the highest support, and so we carried this model forward to represent 'time' in comparisons with other models.

In addition to these four 'core' models, we combined them in a factorial manner, such that we evaluated: (5) *Habitat* and *Design*; (6) *Location* and *Time*; (7) *Location*, *Design*, and *Time*; and (8) *Habitat*, *Location*, *Design*, and *Time*. We evaluated all eight models on a species-specific basis.

For the *Habitat* and *Design* models, we used a generalized linear mixed model with a fit models with a negative binomial distribution using the R function `glmmTMB`from the package glmmTMB. We used a random intercept for CS site. For the *Location* and *Time Varying* models and all models that included these variables, we used Generalized Additive Models (GAM) with a smoother for the predictors and random effect smoother for CS site. We used a negative binomial distribution for the GAMs. All continuous variables were centered (scaled) prior to analysis.

For the US Hwy 93 North study area, we focused on *Design* variables (width, openness) and presence of a fence. We used a Poisson distribution using the R function glmmTMB from the package glmmTMB.

2.3.3 Does the type of CS or location matter more?

We used bivariate GAM plots to visually assess how CS use changes across a parameter space of CS width and km marker. We needed to use CS width to represent design because: 1) it is often the most elastic dimension used in debates over the cost of CS construction; 2) statistically, we needed a continuous variable so could not use the factor 'type' in this analysis. If CS width drives use, we expect to see little variation in km location and persistent, high values for wider CS. If location matters more, then we expect to see persistent high values in specific locations, irrespective of the width of the CS in that location.

2.3.4 How do design parameter [width] change with time since construction?

We used bivariate GAM plots to visually assess how CS use changes across a parameter space of CS width and time since constriction of the CS. We needed to use CS width to represent design because: 1) it is often the most elastic dimension used in debates over the cost of CS construction; 2) statistically, we needed a continuous variable so could not use the factor 'type' in this analysis. If CS width drives use, we expect to see little variation in time and persistent, high values for wider CS. If time or adaptation matters more, then we expect to see greater use with time, irrespective of the width of the CS in that location. We may also expect an interaction, whereby wider CS have shorter adaptation times than narrower CS.

2.3.5 Does number of CS or design parameter affect use? are more or wider CS better?

We used bivariate GAM plots to visually assess how CS use changes across a parameter space of number of CS within 5 km (CS_buffer) and CS width. If CS width drives use, we expect to see stable or declining use as CS_buffer increases and increasing use for wider CS. If CS density drives use, and more CS increase connectivity, then we expect to see higher use with increasing CS_buffer and no change in values across CS widths. If CS density drives use, but the CS density exceeds the minimum amount needed to increase connectivity, then we expect to see declining or no change in use with increasing CS_buffer.

3 Results

Our Banff study is based on 162,434 site-days of monitoring. When accounting for the total width of all CS (0.6 km) and the sum total number of days that all CS were monitored (i.e., summing the total of the number of days of monitoring per CS x number of CS = 445 CS·monitoring· years), this data set captured 5.7 km·years' worth of continuous biodiversity sampling.

3.1 Species-specific and community level use of CS for Banff and Montana study areas.

In Banff, we recorded 141,953 crossing events from eight taxa and 25,937 crossing events by people. Over the duration of this project, we recorded 239 wildlife crossing events for every meter of CS constructed, and we recorded a new crossing event for every 20 hours of monitoring. At the community level, the Banff CS conveyed the movement of ~13,570 tons of mammalian biomass across the Trans-Canada Highway. Based on established relationships with body size and energy use (Nagy et al. 1999), the CS conveyed 2840 gigajoules of metabolic load across the Trans-Canada Highway over the course of this study.

The majority (85%) of crossing events were by deer (48%) and elk (37%), with wolves and coyotes each at ~5% of all crossing events recorded. Cougars, black bears, and grizzly bears each represented ~2% of all crossing events and moose were less than 0.5% (Figure 2.). Most crossing events occurred in summer (44%), followed by fall (27%), spring (19%) and winter (10%). Most CS had low crossing events, partly explained by lower sampling efforts at newer sites. Three CS, in Phase 1 (BUFF, DH, EAST) combined for ~ 34% of all crossing events, while the remaining sites have <10% each. Use of CS varied over time for all species, but there was a tendency to observe fewer overall crossing events after 2005 or 2010 even though more CS came online (Figure 2 and Figure 3).

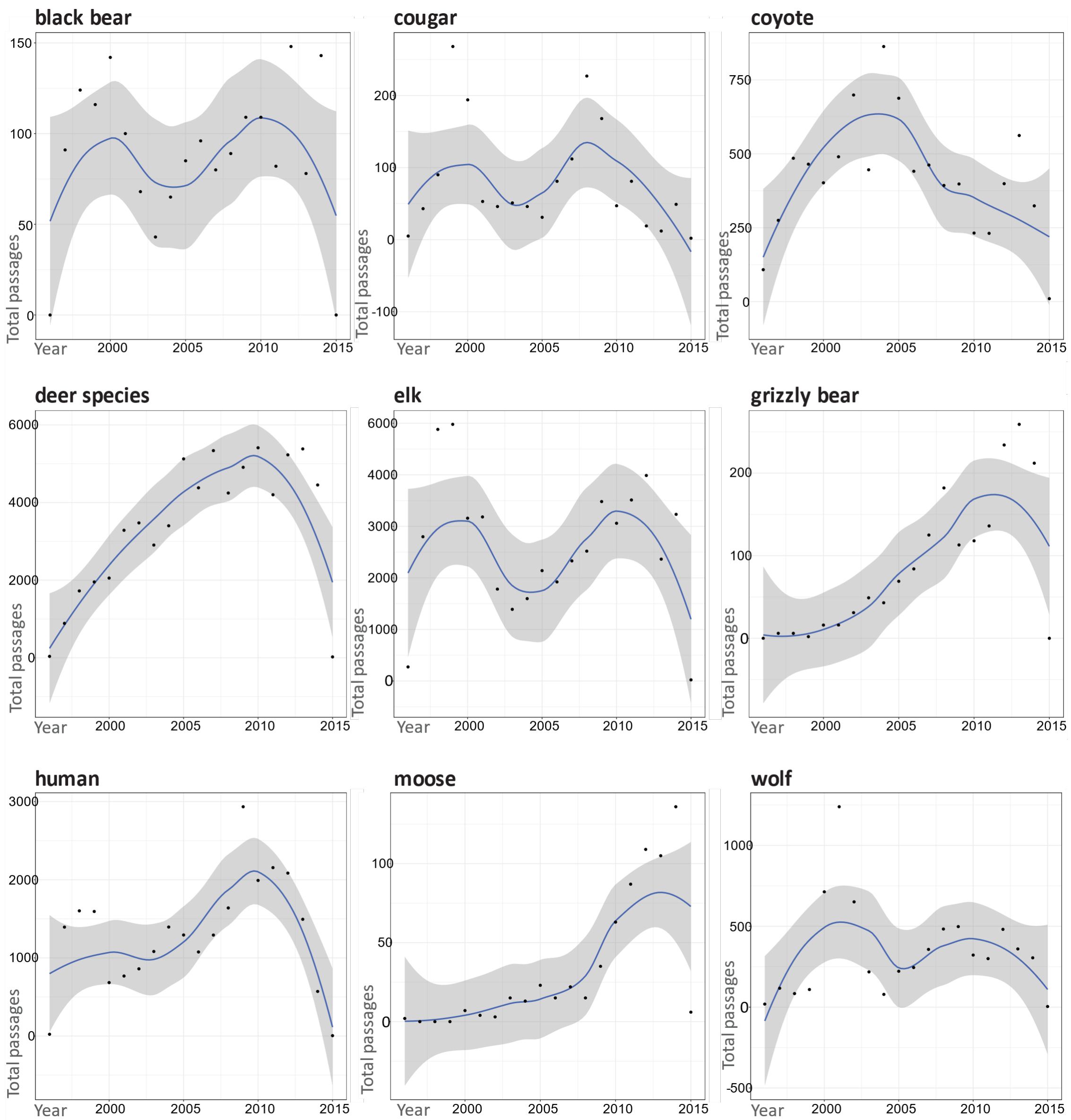

Figure 2. Total number of passages among all crossing structures in Banff National Park, AB, Canada, for black bears, cougars, coyotes, deer spp, elk, grizzly bears, people, and moose. Shading represents the 95% CI and the blue line is the mean value fit by a LOESS curve.

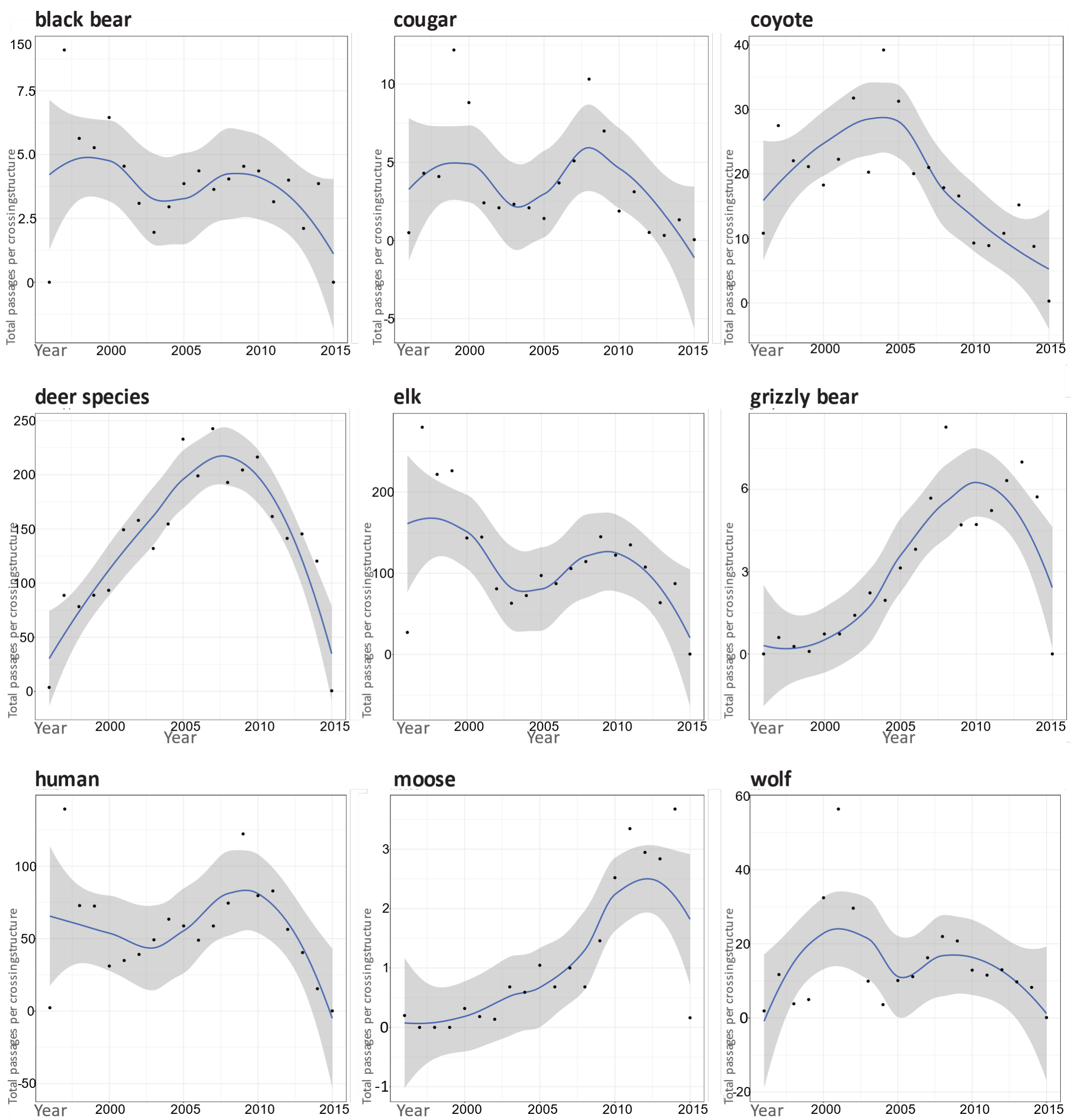

Figure 3. Total number of passages per available crossing structure among all crossing structures in Banff National Park, AB, Canada, for black bears, cougars, coyotes, deer spp, elk, grizzly bears, people, and moose. Shading represents the 95% CI and the blue line is the mean value fit by a LOESS curve.

In the US Hwy 93 North study, we recorded 58,084 crossing events by 6 taxa; 98% of which were by deer. No wolves were recorded. Information on seasonal use were unavailable. Three CS (railroad, Post Creek 2, and Post Creek 3, and overpass) accounted for 68% of all crossing events. The remaining 14 CS had 5% or fewer crossing events each.

3.2 What habitat, design, and temporal factors best explains species specific variation in CS use?

The top performing Banff model for black bear, cougar, deer, and elk was *Habitat*, *Location*, *Design*, and *Time* (Table 4). The top performing model for grizzly bear, moose, and wolf was *Time*. For ease of comparison among species, we present the coefficients for the *Habitat*, *Location*, *Design*, and *Time* model for all species (Table 2). There was a tendency for open span bridges and overpasses to be used significantly more than box culverts for black bears, cougars, and wolves. CS type did not have a significant effect on other species, but we note for coyote and deer, the mean effect was negative (i.e., overpasses preferred less than box culverts). Other species did not show a significant effect of CS type. Distance to forest, grass coverages, and solar radiation did not significant affect CS use by any species. Tree cover near the CS tended to increase use by black bears and cougars, whereas shrub cover tended to reduce use by these two species. Greater distance from built structures had a positive effect on grizzly bear use, but not for other species. The number of nearby CS had a significantly negative effect on crossing rate for cougar, coyote, deer, and elk. For black bears, grizzly bears, moose and wolves, the effects of nearby CS were negative but not significant. Smooth terms for location, time since contraction, and absolute time were significant in almost all cases (Table 2).

In the US Hwy 93 North study, fencing had a positive effect on the number of crossing events for cougars and deer (Table 5). Black bears tended to use more open CS types. However, width, openness, and fencing had no statistically significant effect on other species.

Table 4. Model output for factors affecting long-term use of wildlife crossing structures in Banff National Park, AB. Bolded values indicate p<0.10 and gray shaded cells indicate negative coefficients. The variables in this model are the top-ranked model for each species, except for To illustrate between species differences, we showed the global model here, which was the top ranked model for black bear, cougar, coyote, deer, and elk. The top models for grizzly bear, moose, and wolf as the 'time only' model. Box culvert was set as the reference category for the 'Type' factor.

	black bear		cougar		coyote		deer spp		elk		grizzly bear		human		moose		wolf	
Predictor variable	*B*	p	*B*	p	*B*	p	*B*	p	*B*	p	*B*	p	*B*	p	*B*	p	*B*	p
Type																		
box	—		—		—		—		—		—		—		—		—	
bridge	0.75	0.4	**3.9**	**<0.001**	0.79	0.6	2.5	0.7	0.22	>0.9	1.0	0.3	0.05	>0.9	-0.88	0.6	1.5	0.012
metal	0.45	0.5	**1.6**	**0.019**	-0.16	0.9	-1.2	0.8	-1.0	0.7	0.04	>0.9	-1.7	0.5	-0.84	0.5	0.60	0.2
openspan	**1.8**	**0.004**	**2.8**	**0.002**	1.2	0.4	1.0	0.9	3.4	0.2	**1.7**	**0.033**	0.92	0.8	1.7	0.3	**1.7**	**<0.001**
overpass	**1.8**	**0.002**	**2.0**	**0.013**	-0.10	>0.9	-2.6	0.6	0.24	>0.9	**2.5**	**<0.001**	-2.1	0.4	0.39	0.8	**1.7**	**<0.001**
dist.for.s	-0.09	0.5	-0.16	0.4	-0.08	0.8	-0.27	0.8	0.08	>0.9	0.05	0.8	0.44	0.6	0.49	0.2	-0.01	0.9
tree.1km.s	**0.60**	**0.056**	0.15	0.7	-0.33	0.6	-3.1	0.3	-1.0	0.5	0.05	0.9	-1.9	0.3	-1.3	0.13	0.12	0.6
grass.1km.s	-0.07	0.7	**0.43**	**0.056**	0.79	0.056	3.2	0.060	1.3	0.11	0.31	0.2	1.3	0.2	0.45	0.4	**0.35**	**0.021**
shrub.1km.s	**-0.49**	**0.030**	**-0.38**	**0.087**	-0.16	0.8	-1.4	0.6	-0.32	0.8	-0.21	0.5	-0.68	0.6	-1.2	0.086	-0.19	0.3
elevation.s	**1.2**	**0.060**	1.1	0.3	1.7	0.4	3.8	0.5	2.8	0.5	-0.32	0.7	1.6	0.8	-0.50	0.8	**-1.2**	**0.080**
dist.built.s	-0.18	0.5	0.47	0.2	0.46	0.4	1.6	0.5	0.46	0.7	**0.68**	**0.039**	-0.23	0.9	0.34	0.6	0.02	>0.9
dist.road.s	**0.45**	**0.025**	0.27	0.3	-0.23	0.7	-4.0	0.039	-0.06	>0.9	0.20	0.5	-0.43	0.7	-0.58	0.4	**0.66**	**<0.001**
rad_1000m.s	-0.07	0.8	0.14	0.5	-0.14	0.8	-2.8	0.2	-0.14	0.9	0.07	0.8	-0.21	0.9	-0.72	0.2	-0.05	0.7
dist.water.s	0.24	0.3	**0.72**	**0.009**	-0.24	0.6	-0.62	0.8	-1.0	0.3	0.23	0.4	-1.4	0.2	-0.08	0.9	0.21	0.3
buff.5km.s	-0.13	0.6	**-0.65**	**0.062**	**-2.0**	**<0.001**	**-5.5**	**0.005**	**-3.4**	**<0.001**	-0.32	0.3	**-4.5**	**<0.001**	-0.21	0.7	-0.34	0.12
s(km)		0.2		0.2		**0.022**		**0.026**		**0.013**				**<0.001**				
s(absmonth,TSC)		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**
s(CS)		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**		**<0.001**

Table 5. Model output for factors affecting long-term use of wildlife crossing structures for the US Hwy 93 North study area. Bolded values indicate p<0.10 and gray shaded cells indicate negative coefficients.

Predictor variable	black bear		cougar		deer		elk		grizzly bear		moose	
	B	p	*B*	p	*B*	p	*B*	p	*B*	p	*B*	p
open.s	**0.86**	**0.055**	0.61	0.2	0.53	0.3	-1.2	0.4	-0.04	>0.9	-0.53	0.8
width.s	0.72	0.10	0.47	0.3	0.24	0.6	-0.95	0.3	-46	0.7	-2.8	0.9
fence.s	**1.1**	0.002	**1.3**	<0.001	0.36	0.4	4.6	0.4	-2.1	0.8	77	>0.9

3.3 Does CS type or location matter more

While the parameter space of width and location is incomplete (i.e., there are no very wide CS <20 km), and no CS in the 24-45 m wide range), the bivariate gam plots reveal some species-specific insights about the role of these two parameters (Figure 4). For ease of communicating these results, we refer to km marker locations 0-30 as ‘eastern’ and >30 km as the western side of the Banff study area. Black bears, coyotes, deer, and elk tended to prefer wider CS in the west and use narrower CS in the east. Cougars tended to be concentrated in the eastern part of the study area, and as use dropped off further west (>30 km) there was no noticed effect of width. Grizzly bears showed demonstrable preference for wider CS, irrespective of location. Moose showed strong preference for the western end of the study area across a range of CS widths.

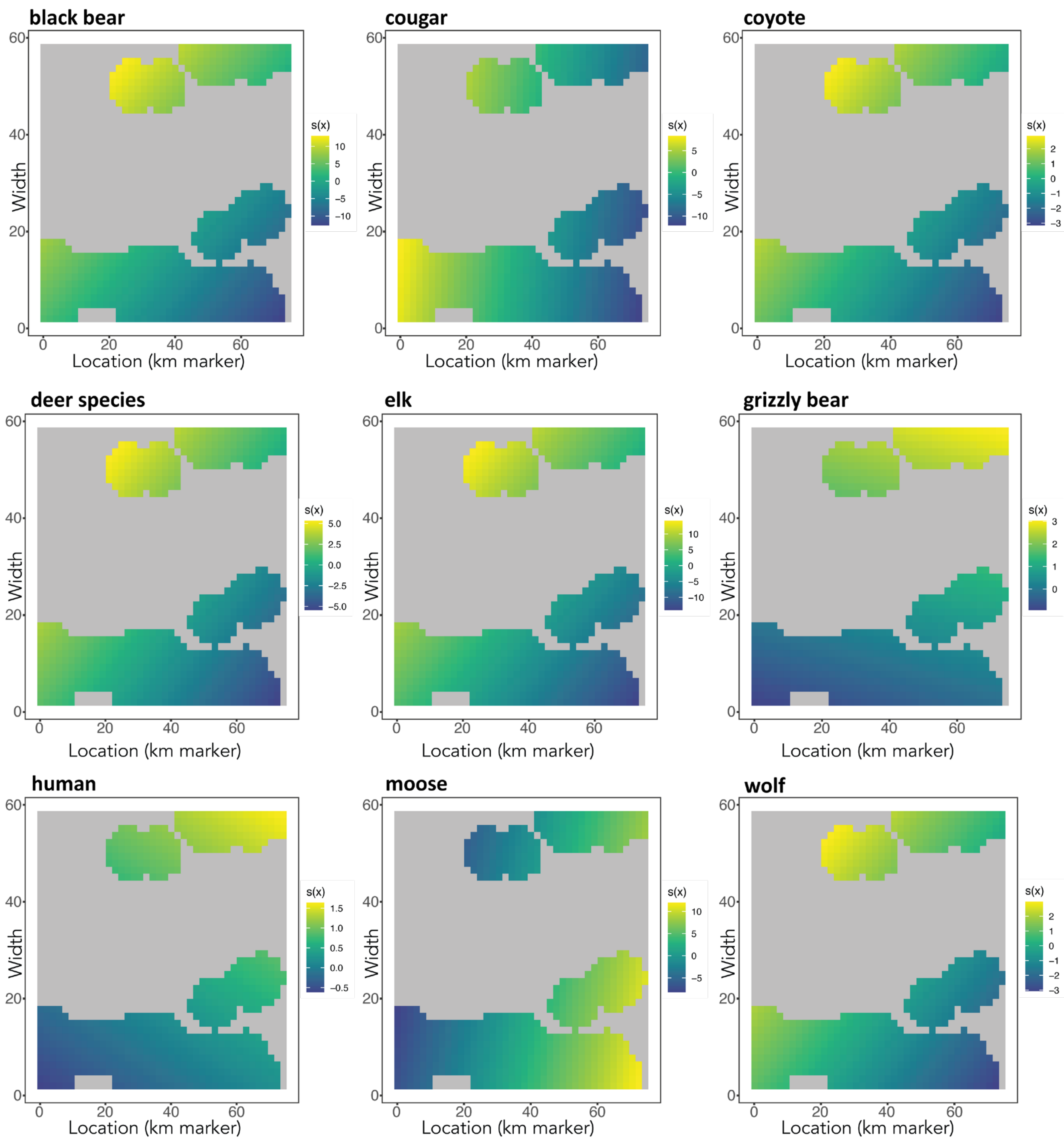

Figure 4. Bivariate generalized additive model plot showing the relative effects of location (kilometer marker) and width of crossing structure on the number of crossing events in Banff National Park, AB, Canada, for black bears, cougars, coyotes, deer spp, elk, grizzly bears, people, and moose. Brighter colours indicate the model predicted greater passages. Gray areas indicate a lack of data in that parameter space.

3.4 How do design parameter [width] change with time since construction?

While the parameter space of width and time is incomplete (i.e., there are no very wide CS that are older than 20 years), the bivariate *gam* plots reveal some species-specific insights about the role of these two parameters (Figure 5). Relative to width, age of CS did not strongly affect black bear or coyote crossing rates, which tended to be greater at wider CS. Cougar and wolf use of narrower (<30 m) crossing was unstable over time, but their use of wider CS seemed to increase with age of the CS. Deer showed a similar response to coyotes and black bears but had a slight increase in use of wider CS with time. Likewise, elk showed a similar response to coyotes and black bears but had a slightly decreasing use of wider CS with time. Grizzly bears increased their use of CS with time across and range of CS widths, but the rate of increase was ~3x faster for wider CS. Moose tended to use older CS, irrespective of width.

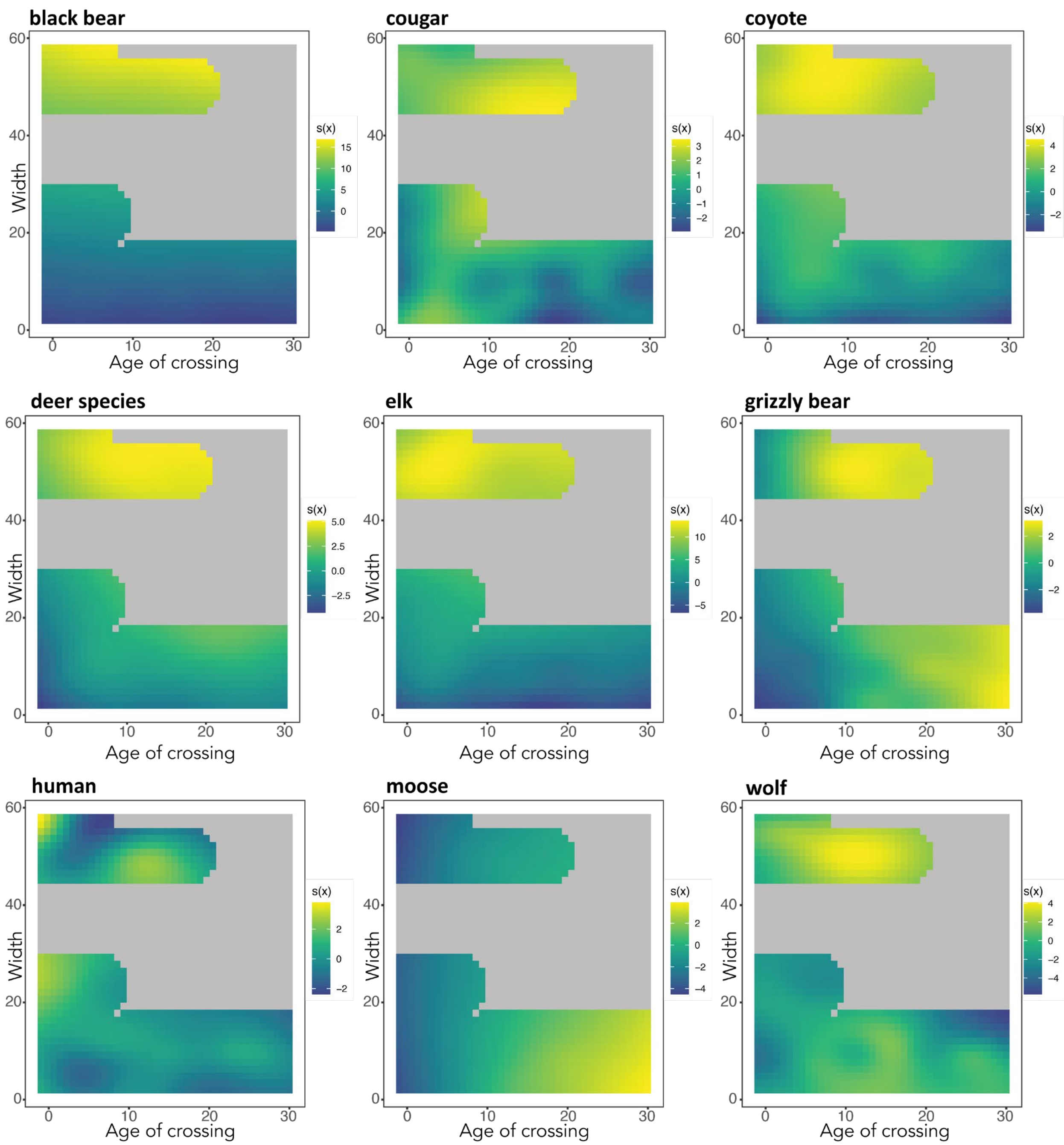

Figure 5. Bivariate generalized additive model plot showing the relative effects of width of crossing structure and age of crossing structure on the number of crossing events in Banff National Park, AB, Canada for black bears, cougars, coyotes, deer spp, elk,

grizzly bears, people, and moose. Brighter coulours indicate the model predicted greater passages. Gray areas indicate a lack of data in that parameter space.

3.5 Does number of CS or design parameter affect use? are more or wider CS better?

While the parameter space of width and time is incomplete (i.e., there are no CS in the 24-45m wide range), the bivariate gam plots reveal some species-specific insights about the role of these two parameters (Figure 6). Black bears and grizzly bears, tended to use wider CS, irrespective of the number of nearby CS. In contrast, cougars and moose tended to use narrower CS irrespective of the number of nearby CS. Coyotes, deer, elk, and wolves showed declining use as CS density increased across a range of widths. In all cases, the number of nearby CS did not have a strong effect on CS use relative to CS width.

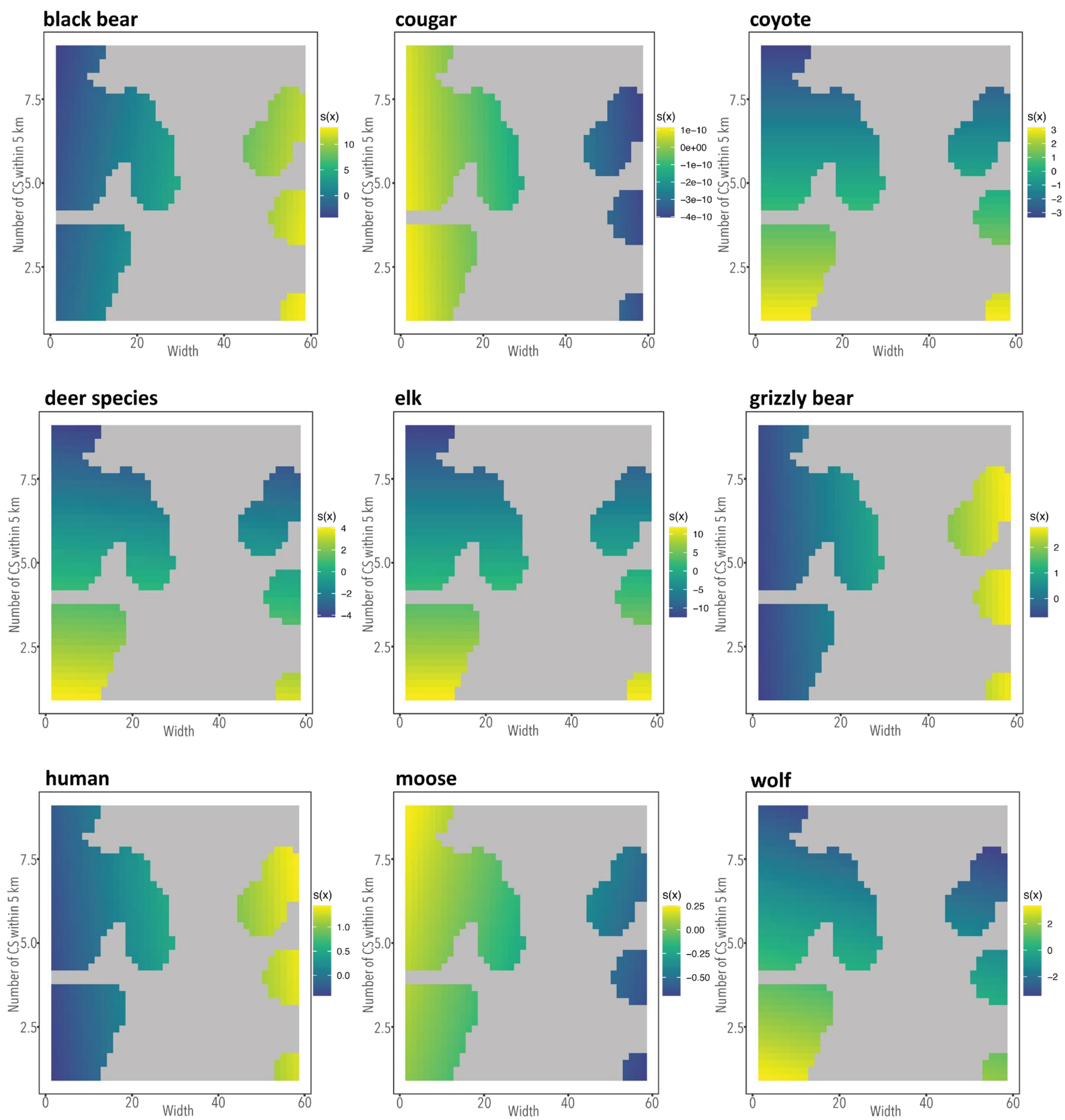

Figure 6. Bivariate generalized additive model plot showing the relative effects of width of crossing structure and number of crossing structures within 5km on the number of crossing events in Banff National Park, AB, Canada for black bears, cougars, coyotes, deer spp, elk, grizzly bears , people, and moose. Brighter colours indicate the model predicted greater passages. Gray areas indicate a lack of data in that parameter space.

Shannon diversity varied significantly among the CS types, with open span bridges having the greatest and box culverts and metal culverts having the lowest diversity (Figure 7).

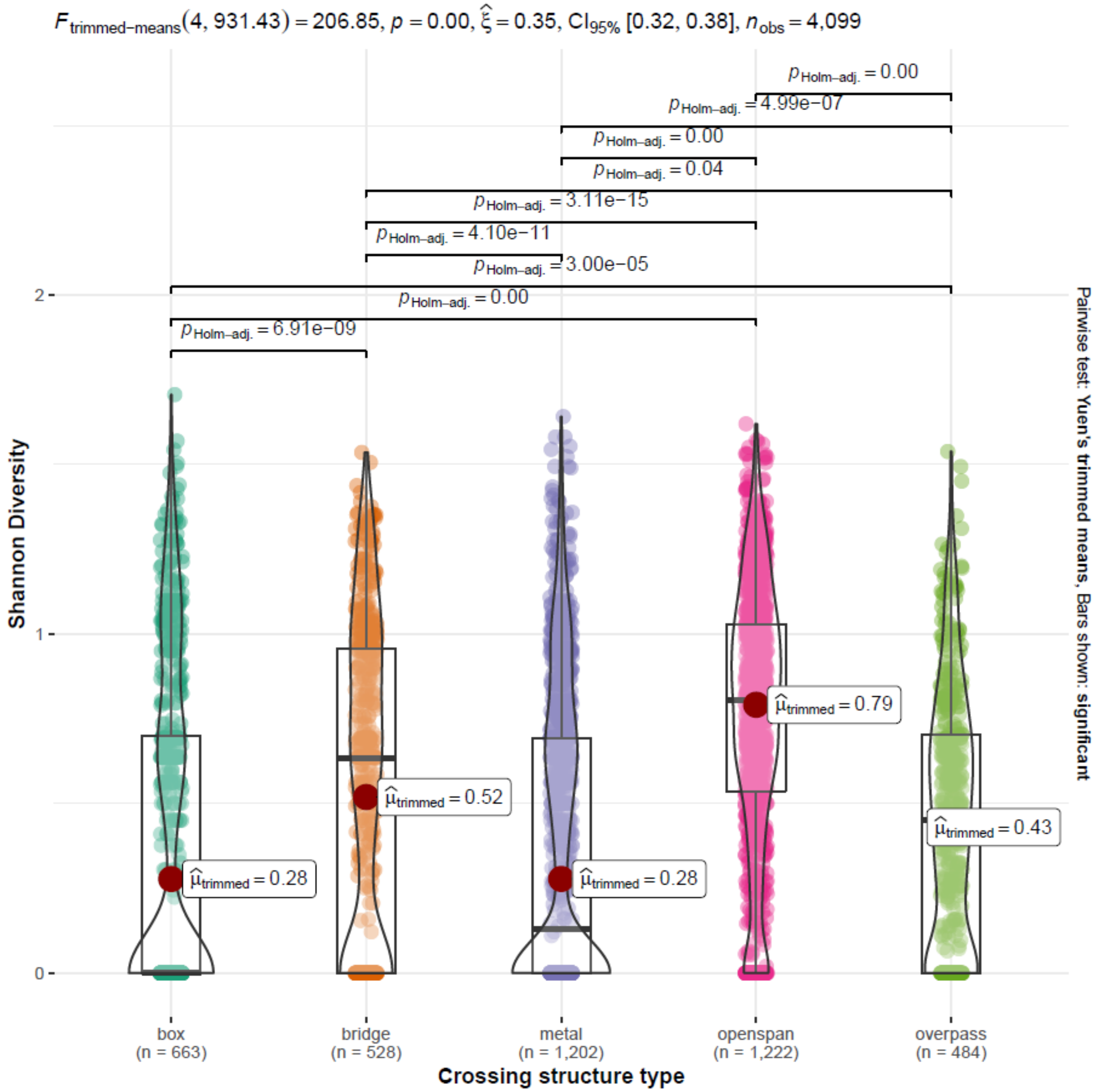

Figure 7.The Shannon diversity of crossing events for 7 wildlife species by crossing structure type in Banff National Park, AB, Canada.

The log transformed biomass passing through the CS was also highest at open span bridges, followed by overpasses (Figure 8).

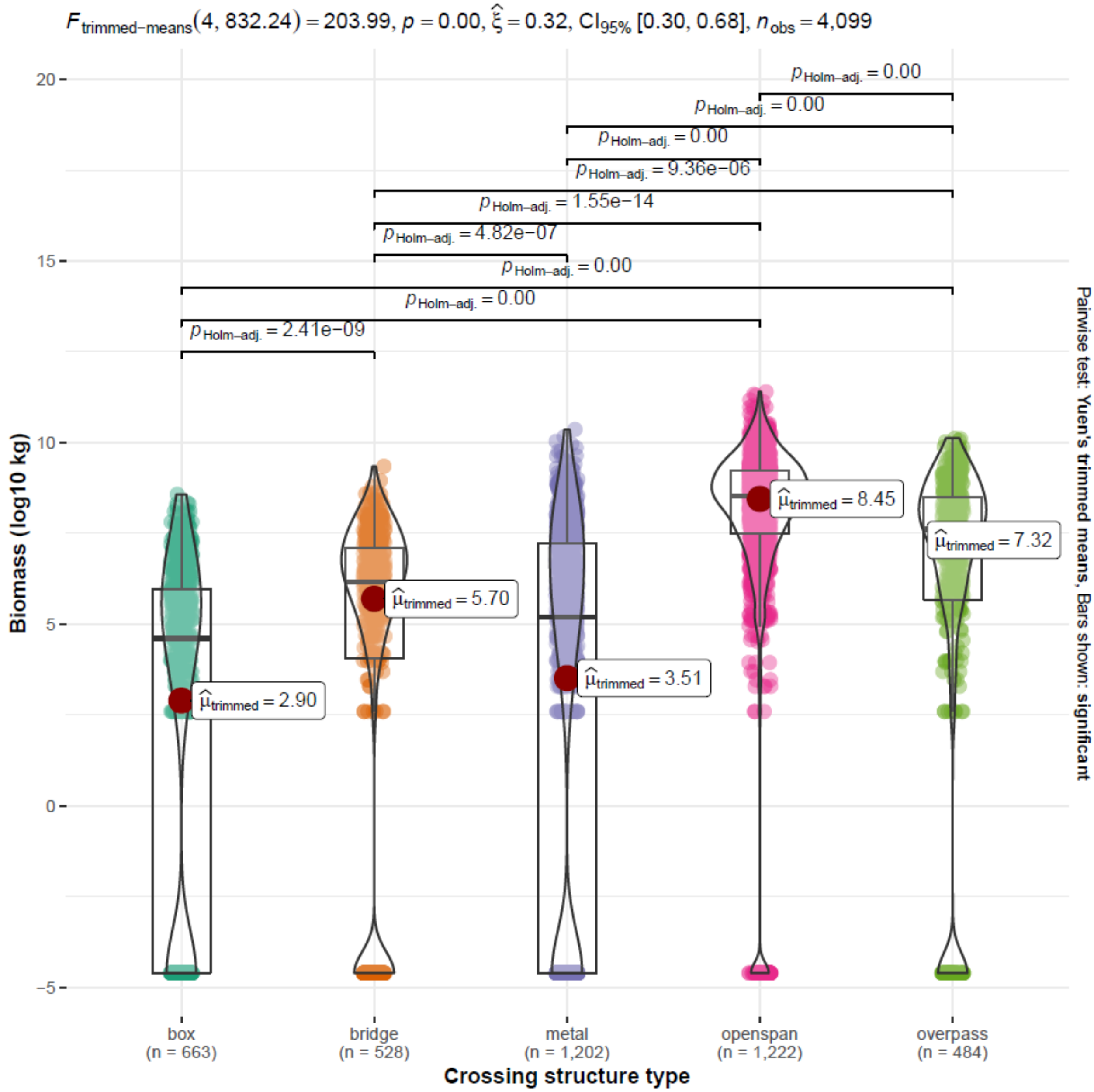

Figure 8. The biomass of all crossing events for 7 wildlife species by crossing structure type in Banff National Park, AB, Canada.

4 Discussion

Over the 17 years of the Banff study, and the six years of the Montana study, CS facilitated over 200,000 crossing events at 55 locations. This flow of animals is equivalent to 16,804 tonnes (18,524 US tons) of mammalian biomass. In both study areas, deer and elk were dominant in terms of crossing events. Although these ungulates are a lower conservation priority than some rarer species (e.g., carnivores), the results of our study indicate that CS likely improve connectivity, human safety, and the viability of wildlife populations for species most likely to be involved in wildlife-vehicle collisions (Clevenger et al. 2015).

In Banff, we documented significant changes in annual crossing events over time. With the exception of moose, all species crossing rates have been declining since 2010. These declines may be associated with broader scale changes in population size (e.g. elk have been declining since the 1990s (Hebblewhite et al. 2002). On a per CS basis, crossing events were also declining, suggesting that the number of CS is not limiting connectivity rates for most species in Banff. Over 20% of Banff's CS included at least one CS within 1km. It is unknown if densities below this amount would hinder passage rates. Moreover, crossing events alone may not be the most wholistic measure of ecological conditions. For example, a high density and diversity of CS may prevent intraguild predation and unwanted species interactions at CS (Ford and Clevenger 2010, Barrueto et al. 2014, Ford et al. 2017).

Variables associated with CS passage rates were species specific but aligned with a few clusters of preference. Habitat heterogeneity appeared to be associated with CS passages. For example, black bears, cougars, and wolves crossing rates were associated with proximity to forests and the amount of grassland near the CS. With the exception of coyotes, all large carnivore species preferred open span bridges or overpasses to other CS types. The effects of habitat and CS design on coyotes, deer, and elk were not significant, but the number of CS within 5 km was negatively associated with crossing events. This suggests that at current population sizes, additional CS will not enhance connectivity for these taxa. In Montana, fencing was positively associated with passage rates for black bears and cougars. All CS were fenced in Banff, so we cannot compare the effects of fencing among study areas. Our results are roughly consistent with Clevenger and Waltho, 2005 who found that structure attributes of CS are a key driver of passage rates in the central part of the study area. Our work is also consistent with Clevenger and Waltho, 2000, who concluded that habitat conditions in the eastern part of the study area are important predictors of passage rates. As the current study included both the eastern, central, and the newly analyzed western regions of Banff, it is not surprising that our system-wide analyses have common findings as these earlier landmark studies.

Building on previous studies in Banff (Clevenger and Waltho 2000, 2005), we examined data relative to key decision points and trade-offs in CS system design: 1) does CS design or location matter more? 2) How do species adapt to different CS designs? 3) What is the relative effect of CS density vs CS design in affecting passage rates by wildlife? We found that wider CS tend to be preferred by most species, irrespective of their location. We also found that wider CS tend to have shorter 'adaptation' curves than narrower ones for grizzly bears, coyotes, cougars, and moose. Assuming a population is stable over time, the notion of CS adaptation reflects the idea that it may take multiple generations of animals using and adapting to the presence of new CS before passage rates increase and reach an asymptote (Ford et al. 2009b). Thus, for populations facing more immediate threats of decline, or with longer generation times, wider CS can assist in ‘fast tracking’ the effectiveness of mitigation.

Another key question in CS system design related to the width or density of CS, brings to light a long-standing debate in conservation science: assuming a finite budget, should investment be made in several smaller interventions or fewer large ones? Specific to road mitigation, the Single Larger or Several Small [SLOSS] debate arises when costs of CS types are juxtaposed with the number of CS built (Karlson et al. 2017, Ford et al. 2017, Helldin 2022). Typically, wider CS are more expensive and may have additional engineering constraints with respect to site selection (McGuire and Morrall 2000). In some cases, less expensive, but abundant CS (e.g., box culverts) can facilitate segregation of individuals that may have negative interactions if they co-occurred at the same CS (Ford et al. 2017). Relative to local density of CS, black bear and grizzly bears used wider CS, while cougars and moose used narrower CS. In contrast, passage rates by coyotes, deer, and elk did not vary with CS width, but did increase with fewer CS. This finding suggests that ‘several small’ is a better strategy for coyotes, deer, and elk; “fewer small” is a better strategy for per-CS crossing rates by cougars; and “fewer large” CS is better for bears. In addition to species-specific preference, the generality of SLOSS to other regions may further depend on the focal species preferred CS type. If the mitigation objective is connectivity for bears, *fewer large* should guide planning and design, whereas *several small* would benefit focal species such as coyote and elk. Last, depending on the heterogeneity of the landscape near the highway, more CS may not create more crossing opportunities if local habitat conditions do not favor animals’ access to the road.

At the scale of ecological communities, the flows of mass (>16,000 t of biomass) and energy (>2840 gigajoules of metabolic load) are likely enough to alter the distribution of ecological processes in the Banff and Montana ecosystems. Seed dispersal (Tucker et al. 2021), nutrient flows (McDowell et al. 2004), and trophic cascades/predation (Hebblewhite et al. 2005, Ford and Clevenger 2010) are likely altered by the location and design of CS. Indeed, overpasses and open span bridges both conveyed higher diversity than other CS types. In both Banff and Montana, the dominance of a few CS locations on ungulate passage rates likely means an inordinate density of browsing and fecal nutrient depositions in a small area. This concertation may be affecting local ecological communities, such as shrub regeneration and songbird abundance (Hebblewhite et al. 2005). Further, the concentration of animals at a few CS – particularly cervids - may contribute to the spread of diseases such as Chronic Wasting Disease (Habib et al. 2011), meningeal worm, and tuberculosis (Maskey Jr et al. 2015). Although Banff has a high density of CS, finding ways to dilute use among more CS locations could reduce these risks posed by diseases. Finally, modifications to select CS to facilitate selective permeability of some species (e.g., carnivores) and not others (e.g., elk) may reduce risk of disease spread and human wildlife conflict (Ford 2021).

5 Limitations

While this study provides an unprecedented look at the long-term response of a large mammal community to highway mitigation, we note a few important caveats. First, our methods did not distinguish between individual animals, so it is difficult to quantify population-level benefits of the CS system for multiple species. Studies in the Banff area concluded that a few individuals may comprise the majority of CS passages, and that many more individuals may use the CS less frequently. It is important to note, however, that the Banff CS allowed demographic connectivity and sufficient gene flow to prevent genetic isolation of black and grizzly bears (Sawaya, Clevenger, & Kalinowski, 2013) (Sawaya, Kalinowski, & Clevenger, 2014). Second, we were unable to match the long-term trends in passage rates to estimates of population sizes. This means we cannot distinguish if variation in passage rates is caused by changes in animal behaviour or changes in population size. It is likely that both of these factors are influencing variation in passage rates.

6 Conclusions and recommendations

Our results highlight the value of long-term monitoring for assessing the effectiveness of mitigation measures to reduce wildlife-vehicle collisions and enhance connectivity across major roads. Our work confirms the species-specific nature of measure CS performance – leading to our primary recommendation that a diversity of CS designs be considered an essential part of a well-designed mitigation system for the large mammal fauna of western North America. We found no evidence of a general finding to resolve the debate of few large or many small CS – different species preferred different designs and CS densities. We found non-linear effects of time on passage rates, suggesting that short-term monitoring efforts may fail to accurately portray the ecological benefits of mitigation for populations and ecological communities. As park and transportation managers rely on CS to offset the impacts of road expansion projects and other disturbances, our work will help inform design and aid in the establishment of robust, long-term performance measures.

7 References

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