Anthropogenic effects on activity patterns of wildlife at crossing structures

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Abstract. Despite the popular perception of protected areas as vestiges of remnant wilderness, the behavior and activity patterns of wildlife in these areas are still subject to many forms of anthropogenic disturbances, such as roads, recreation and resource extraction. In Banff National Park, Alberta, efforts to mitigate the effects of roads on wildlife using wildlife crossing structures (WC) have been successful for a number of large mammal species, when measured as a reduction in mortality from vehicle collisions or the restoration of population connectivity; however, a comprehensive view of mitigation success should also account for the restoration of animal behavior and activity patterns. We evaluated the general hypothesis that existing WC have mitigated the effects of anthropogenic disturbance on wildlife activity, and predicted that the activity patterns of wildlife at WC should be similar to those in areas characterized by little or no human disturbance. We collected data from a long-term monitoring program of activity patterns, in an assemblage of large mammal species, using a network of camera traps throughout Banff National Park. We quantified the inter- and intra-specific overlap of diel activity patterns at 39 engineered wildlife crossings, varying in design (e.g., over and underpasses) and age. We compared activity at WC to baseline conditions at 126 backcountry sites (BC). In general, activity patterns at WC were found to closely match those at BC. Of the eight species we examined, only elk and coyotes showed significantly different peaks in activity. Activity between WC depended on the time of day, the amount of human use and age of the crossing structure; however, the impact of these factors varied among carnivores and ungulates. Our work demonstrates that the impact of people on wildlife activity at WC is highly context dependent and that the restoration of native patterns of activity within protected areas will require management of human activity, even in relatively remote areas.

Key words: activity patterns; anthropogenic disturbance; Banff National Park; camera traps; large mammals; traffic; Trans-Canada Highway; wildlife crossing structures.

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INTRODUCTION

National parks and other protected areas were typically created and managed for the preservation of natural heritage and conservation of biodiversity. However, recreation, tourism and human infrastructure within these refuges areas can have negative consequences on wildlife populations (Taylor and Knight 2003, Hebblewhite et al. 2005, Brown et al. 2012; Hansen et al., *in press*). Across southern Canada and the conterminous USA, most of the land designated

as a protected area occurs in mountainous landscapes. The complex topography of these ecosystems is characterized by a natural pattern of fragmentation entailing productive and speciose habitats at lower elevations, that are interspersed with largely low quality habitats of steep rocks, snow and ice at higher elevations. It is in these biologically-rich valley bottoms where anthropogenic activity is also concentrated, including disturbances from recreational activity, residential developments, resource extraction and transportation corridors (Theobald et al. 1997, Hansen et al. 2002). Despite the popular perception of these protected areas as vestiges of remnant wilderness, the behavior and activity patterns of wildlife moving through mountainous protected areas can be affected by a number of anthropogenic disturbances. These sub-lethal changes in wildlife activity can emerge as changes in animal physiology (Wasser et al. 1997, Millspaugh et al. 2001), the probability of human-wildlife conflict (Woodroffe et al. 2005), and inter-specific interactions (Hebblewhite et al. 2005, Berger and Gese 2007, Ford and Clevenger 2010, Muhley et al. 2013). To ensure the safe and sustainable co-existence of people and wildlife in mountainous areas, there is a pressing need to better understand how wildlife activity changes in response to human activity.

Previous studies have shown that both vehicle and foot traffic can alter wildlife behavior up to several kilometers away from the disturbance site for a number of large mammal species, including wolves (*Canis lupus*; Karlsson et al. 2007, Rogala et al. 2011), elk (*Cervus elaphus*; Cassirer et al. 1992, Naylor et al. 2009, Rogala et al. 2011), bears (*Ursus* sp.; McLellan and Shackleton 1988, Gibeau et al. 2002, Moen et al. 2012) and bighorn sheep (*Ovis* sp.; Longshore et al. 2013). At the same time, wildlife can become habituated to such disturbances and adjust their behavior to minimize encounters with people (Schultz and Bailey 1978, Burson et al. 2000, Brown et al. 2012); perhaps with little consequence to the demographic vital rates of wildlife populations. For example, wildlife typically cross highways at night when traffic volumes are low (Tigas et al. 2002, Chruszcz et al. 2003, Waller and Servheen 2005, Graves et al. 2006, Meisingset et al. 2013), suggesting that these labile responses are an important component of wildlife survival in human-occupied landscapes.

One of the most expensive and well-documented efforts to mitigate anthropogenic disturbances to wildlife occurs in Canada's national parks, where a series of fences and crossing structures have been built to facilitate the movement of large mammals across a major highway (Ford et al. 2010). In spite of this major highway, over 150,000 wildlife crossings have been recorded at these structures (Clevenger et al. 2009), rates of wildlife-vehicle collisions have dropped off (Clevenger et al. 2001), and demographic and genetic connectivity continues (Sawaya et al. 2013, 2014). However, a clear picture of how these mitigation measures have restored wildlife activity has not yet emerged. Understanding the extent to which vehicle traffic and human activity alters wildlife movement near highways will increase our ability to design more effective wildlife crossing structures (WC) and reduce the negative effects of habitat fragmentation in mountain ecosystems (Barber et al. 2011, Leblond et al. 2013).

To address this knowledge gap, we evaluated the general hypothesis that WC buffer the effects of anthropogenic disturbance on wildlife activity, and predict that the activity patterns of large mammals at WC should be similar to activity patterns in areas characterized by little or no human disturbance. We employed a long-term monitoring program (>4 years) to measure activity patterns for an assemblage of large mammal species, using a network of motion-activated cameras (camera traps) in Banff National Park, Alberta. We quantified the overlap of wildlife activity at 39 WC, with 126 sites that were undisturbed by transportation and human activity, located >2 km from transportation infrastructure (hereafter referred to as backcountry [BC]). Specifically, we first established species-specific patterns of diel activity and then analyzed (1) if the differences in diel activity between WC and BC sites are greater for some species groups (i.e., carnivores) than others (i.e., ungulates) (Hebblewhite et al. 2005, Ford and Clevenger 2010), and (2) if human use of WC and their novelty change the diel activity of wildlife (Clevenger and Waltho 2000). We examined the role of factors that can further explain these relationships, such as the design of the WC (e.g., over or underpass), fluxes in daily traffic volume
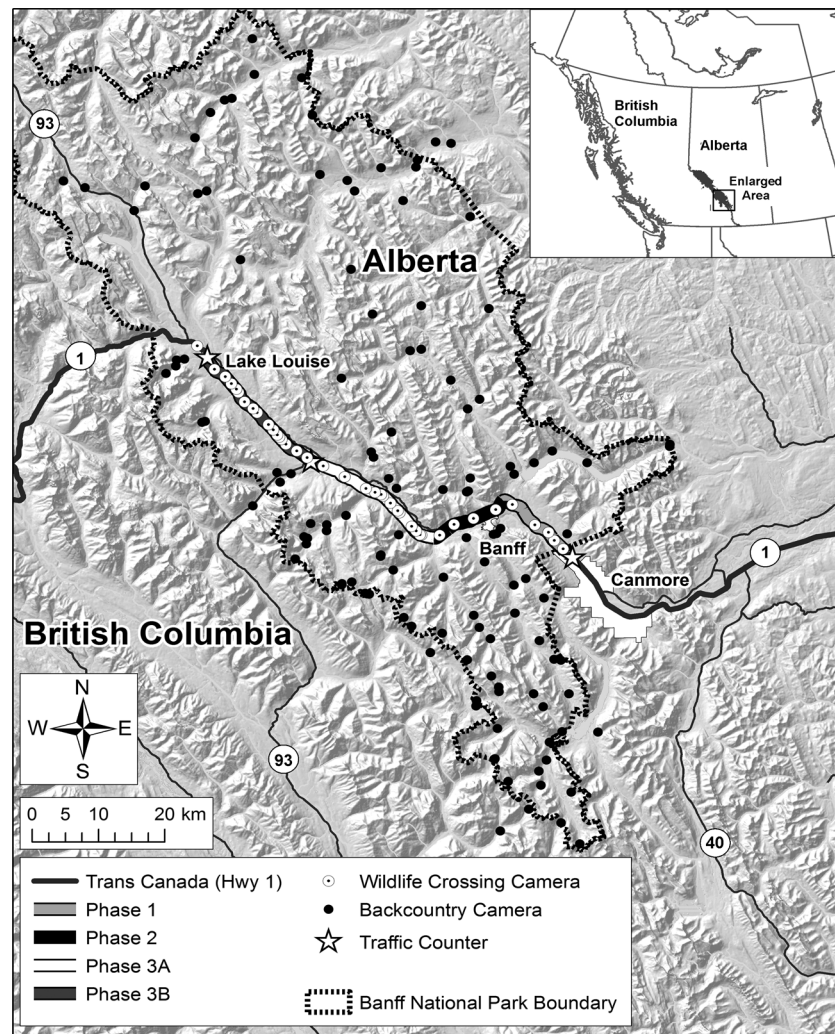
Fig. 1. Study area in Banff National Park, Alberta. White circles with black dots in center are the location of camera sites at wildlife crossings (WC) along the Trans-Canada Highway (TCH). Solid black dots are locations of backcountry cameras (BC). Stars represent the location of traffic counters along the TCH. The different phases of highway mitigation (1, 2, 3A, 3B) are shown spanning from east to west.

and the age of the WC. Our results will assist transportation and wildlife managers in devising appropriate strategies for human use of WC and in designing WC structures to minimize changes in wildlife behavior.

METHODS

Study area

The study area, located in Banff National Park, is situated approximately 150 km west of Calgary, Alberta, in the Bow River Valley, along the Trans-Canada Highway (TCH; Fig. 1). The study area is characterized by mountainous landscapes, with a continental climate consisting of long winters and short summers (Holland and Coen 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.

With the exception of bison (*Bison bison*) and caribou (*Rangifer tarandus*), Banff National Park

retains the full complement of native large mammal species. We focused on camera images of wolves, coyotes (*C. latrans*), cougars (*Puma concolor*), black bears (*U. americanus*), grizzly bears (*U. arctos*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk, and moose (*Alces alces*). The two *Odocoileus* species (hereafter referred to as "deer spp.") were pooled due to similarities in habitat use, life-history, and the occasional difficulties in distinguishing the two species, particularly in some of the low-quality nighttime photos.

The TCH is the major transportation corridor through Banff National Park, covering roughly 80 km between the park's eastern and western boundaries. Traffic volume along the TCH is relatively high for the region, with an average of 17,970 vehicles per day in 2008 and increasing at a rate of 2.5% per year (Highway Service Centre, Parks Canada, Banff, Alberta).

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 (Fig. 1). Fencing and WC on the next 18 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 final 30 km of four-lane highway to the western park boundary (Phase 3B) includes 21 crossing structures, including four, 60-m wide wildlife overpasses and was completed in 2013.

Animal activity

To quantify animal activity, we employed motion-activated cameras to record the movement of large mammals: (1) at 39 WC along the TCH between 2007 and 2012; (2) throughout the BC of Banff National Park between 2008 and 2012 (Fig. 1). We define activity as an independent camera trap event at both WC and BC sites, which consists of passage by an individual, or group of the same species. We distinguished sequential events by a lapse in activity at the

camera lasting longer than 2 minutes. Prolonged feeding or resting behavior was not recorded as activity because cameras would typically record multiple images of the same individuals under 2 minutes. Thus, at both WC and BC sites, our activity data represent the travelling behavior of large mammals. At WC sites we also estimated the direction of travel and whether animals moved through the WC or turned back without crossing. We only used images captured between 1 May to 31 October to minimize seasonal bias caused by migration patterns (e.g., elk; Hebblewhite et al. 2002) or torpor (e.g., black and grizzly bears). This period also coincides with the highest levels of human use and traffic volumes in Banff National Park.

Since 2005, cameras were used to monitor wildlife use of the WC (Clevenger and Waltho 2000, 2005, Ford et al. 2009). WC cameras were located within or adjacent to (<10 m away) wildlife underpasses and centered on top of wildlife overpasses. Every 2–3 weeks, we inspected camera operation and downloaded images.

Since 2008, Parks Canada has used camera traps to monitor wildlife activity in BC areas of Banff National Park. At the local scale, BC cameras were set up to maximize detection of wildlife, given presence, but at the scale of the study area these sites were randomized across high- and low-use hiking trails, elevation and habitat types. BC cameras were checked 2–3 times during the calendar year.

Compared to direct observation, camera traps provide a relatively low-impact means of monitoring behavior and facilitate data collection on a continuous basis across diel periods (O'Brien 2010, McCallum 2012). All cameras used in this study were made by the same manufacturer (Reconyx, Holmen, Wisconsin, USA) and provided information on date, time and ambient temperature during each camera trap event. Cameras were operable 24 h/day, year-round, with occasional periods of malfunction or premature battery failure. We determined camera-sampling effort (camera-days) at WC and BC sites by calculating the number of days that cameras were operational.

We compared the number of camera trap events between WC and BC sites, by taxa, over a 24-hr cycle (0 to 2300 h MST). We monitored

WC using cameras and other methods almost continuously since 2008, and found in a previous analysis that cameras reliably detect crossing events (Ford et al. 2009).

Traffic volume data

Traffic volume data were obtained from three counters that measured the mean hourly traffic along the TCH (Highway Service Centre, *unpublished data*) from 2007 to 2012 (Fig. 1). We associated each WC with the data from the nearest traffic counter. Weekend traffic is typically higher than weekday traffic because of recreational use in this area (Rogala et al. 2011), creating a weekly periodicity of vehicle traffic (see Appendix: Fig. A1). We partitioned these data into high (weekend, Friday to Sunday) and low (weekday, Monday to Thursday) categories. We did not expect these two categories to impact wildlife beyond a potential effect of the higher traffic volumes on weekends.

Statistical analysis

To quantify overlap in inter-specific activity patterns, we compared the diel pattern of camera trap events for all species-pair combinations using two-sample Kolmogorov-Smirnov (KS) tests, separately for the WC and for the BC data. We defined a non-significant result from the KS test as a matching activity pattern, and a significant (at the 0.05 level) result as a non-matching activity pattern. The KS test has the advantage of making no assumption about the distribution of data, i.e., is non-parametric and distribution free, and can be used when sample sizes are unequal (Justel et al. 1997, Zar 1999). We then measured the overlap of intra-specific activity patterns between WC and BC sites, again using two-sample KS tests.

To quantify the potential effects of human (i.e., foot traffic) activity on wildlife at WC, we used KS tests to compare overlap of intra-specific activity patterns between WC with high and low human use. High human use WC were defined as those with >50 human events per year (reference years were 2010 to 2012), while WC with low human use had <50 human events per year. This cut-off was chosen because approximately 75% of WC had <50 human crossing events each year and there was a clear separation of WC with high use (mean = 255, min = 53, max

= 1046) and the rest receiving relatively low use (mean = 14.2, min = 0, max = 47). Because human use was confounded by WC design and age (e.g., overpasses and newer WC were virtually off-limits to people), we also performed this analysis on a subset of WC that had the same design and were built >15 years before this study began (i.e., Phase 1, Fig.1).

If wildlife habituation to roads increases their use of WC, we would expect to see changes in the activity patterns and frequency of use at WC varying in age, assuming that wildlife populations in the adjacent areas are the same. We used KS tests to determine if the novelty of WC played a role in wildlife activity patterns by pooling data from older WC built >15 years ago (Phases 1, 2, 3A) and comparing these activity patterns with novel (1–3 years old) WC along Phase 3B.

Finally, we assessed the impact of vehicle traffic on animal activity at WC. For the previous analyses we had pooled data across years and sites, and measured differences in resulting activity patterns with KS tests. To detect an effect of vehicle traffic volume on use of WC, while accounting for the time of day, required greater analytical resolution than the discrete- KS tests could provide. Exploratory analysis of the relationship between hour of day and activity was identified as non-linear, and based on earlier research, variation between behavior at the different sites was also expected. We used generalized additive mixed effects models (GAMMs) to take these non-linear and random effects into account (Wood 2006, Zuur et al. 2009). We used the number of successful crossing events per hour at each crossing structure as a function of vehicle traffic volume, time of day, human use of crossing structure, and age of crossing structure. Based on the expectation that changes in behavior occurred over the years, we also included interactions between hour of day and age of crossing structure, as well as an interaction of human use and age of crossing structure. Because wildlife response to hourly variation in traffic volume may depend on ambient or baseline traffic conditions, we partitioned our analysis into *high* (weekend) and *low* (week day) ambient vehicle traffic volumes. However, we did not expect the weekday factor to have an impact on animal behavior beyond the potential effect of increased traffic volumes seen

on weekends. Thus, we did not include the weekday factor itself as a covariate in the models. All species were analysed separately.

For all models, we used a Poisson distribution and log-link function (global model shown in Eq. 1).

$$\begin{aligned}
\text{Events}_{is} &\sim \text{Poisson}(\mu_{is}) \\
\eta_{is} &= \alpha + f_{\text{Phase}}(\text{Hour}) + f(\text{Mean traffic volume}) \\
&\quad + \beta_1 \times \text{Phase} + \beta_2 \times \text{Human} + \beta_3 \times \text{Phase} \\
&\quad \times \text{Human} + \text{LEffort} + a \\
a_i &\sim N(0, \sigma_a^2) \\
\log(\mu_{is}) &= \eta_{is}
\end{aligned}$$
(1)

We defined Events as the cumulative amount of activity (i.e., number of successful crossing events) at each WC(i) pooled across all years for each hour (s). Mean traffic volume was defined as the number of vehicles passing at each hour, averaged across all years. Human use (Human) was defined by a factor for 'high' (>50 crossings by humans) and 'low' (≤50 human crossing events). Age of crossing structures was defined by Phase with the four levels 1, 2, 3A and 3B, referring to the highway mitigation phases (Fig. 1). We treated WC as a random factor (a), and included the number of camera days (LEffort) at each WC as an offset, to account for unequal monitoring effort. Finally, the covariate Hour accounted for the strong diel activity patterns displayed by most species. To account for the circular nature of Hour, we used cyclic cubic regression splines for the smoothers. We created a Global model and performed step-wise variable removal until all covariates remaining were significant at the 0.05 level (Burnham and Anderson 2002). We returned variables to the resulting model to address heteroscedasticity in residuals. For a given species, we only included WC where at least one detection occurred. All modelling was performed with R (version 3.0.1; R Development Core Team 2008) using the mgcv package (Wood 2006) for the GAMMs.

RESULTS

Sampling effort

We captured >194,000 images at WC and >254,000 of images at the BC, resulting in a total of 33,732 and 6577 events for our eight focal species, respectively. Most of these images consisted of deer and elk (>75% of events at WC and >45% at BC). The total sampling effort was 31,750 camera-days at 39 WC sites and 19,097 at 126 BC sites.

Diel activity patterns

Most inter-specific pairs had non-matching activity distributions at WC and BC (Table 1). The only species pairs with matching activity patterns at both WC and BC sites were grizzly bear-black bear and elk-cougar, suggesting that WC buffers changes to probability of interspecific interactions. Four additional species pairs had matching activity patterns at BC sites only (Table 1) and no species had matching activity at WC sites only.

Intra-specific activity patterns at WC closely matched those at BC sites (Fig. 2), with the exception of elk and coyotes (Table 2). For elk, the activity peaks at the WC sites were one hour earlier in the morning and one hour later in the evening. Coyote activity peaked at 0900 h in the BC and at 0200 h at WC. Generally, at both WC and BC, deer, elk, moose, wolves and grizzly and black bears exhibited strong crepuscular activity patterns (Fig. 2). Cougar activity was primarily nocturnal at both WC and BC sites (Fig. 2).

The effect of human-activity on wildlife use of WC was significant for four species (Table 3). Black bears, deer sp., elk and wolves had significantly different activity at WC with high levels of human use compared to WC with low human use. Black bears were more active in the morning and less active in the afternoon and evening at high human use WC. Deer showed more nocturnal and less morning activity at high human use WC and elk were less nocturnal at high human use WC (Fig. 3). When we looked at just a subset of WC sites with identical designs, wolves and elk were still more nocturnal at high human use sites, but not black bears and deer (Table 4). This suggests that WC design may buffer human activity to shape when some species attempt to use WC.

Patterns of adaptation to WC varied among species. At novel WC, black bears concentrated activity during the crepuscular periods; while at established WC they were primarily active during the day (Fig. 4). Coyotes shifted their activity to mostly diurnal use at novel WC, while their activity was relatively constant during the night and day at old WC. Similar shifts towards

Table 1. Results of comparisons of inter-specific activity patterns at wildlife crossing structures and backcountry sites using two sample Kolmogorov-Smirnov tests. Activity (N) is defined as the number of independent camera events per species. Non-significant ($P > 0.05$) comparisons indicate matching activity patterns. D is the maximum vertical deviation between the two distribution curves.

Species 1 (N)	Species 2 (N)	D	P
Wildlife crossing structures			
Black bear (522)	Cougar (254)	0.2975	<0.001
	Coyote (719)	0.2246	<0.001
	Deer (16,225)	0.1826	<0.001
	Elk (6410)	0.3208	<0.001
	Grizzly (622)	0.0563	0.329
	Moose (245)	0.1570	0.005
	Wolf (1161)	0.2311	<0.001
Cougar (254)	Coyote	0.1383	0.001
	Deer	0.1923	<0.001
	Elk	0.0598	0.347
	Grizzly	0.2879	<0.001
	Moose	0.2065	<0.001
	Wolf	0.1066	0.017
Coyote (719)	Deer	0.1188	<0.001
	Elk	0.1317	<0.001
	Grizzly	0.2227	<0.001
	Moose	0.1363	0.002
	Wolf	0.0509	0.201
Deer (16,225)	Elk	0.2093	<0.001
	Grizzly	0.1325	<0.001
	Moose	0.1014	0.013
	Wolf	0.0966	<0.001
Elk (6410)	Grizzly	0.3125	<0.001
	Moose	0.2106	<0.001
	Wolf	0.1127	<0.001
Grizzly (622)	Moose	0.1199	0.012
	Wolf	0.2005	<0.001
Moose (245)	Wolf	0.0999	0.035
Backcountry			
Black bear (165)	Cougar (91)	0.2865	<0.001
	Coyote (354)	0.1626	0.005
	Deer (2025)	0.2070	<0.001
	Elk (853)	0.2074	<0.001
	Grizzly (715)	0.0830	0.314
	Moose (293)	0.1763	0.002
	Wolf (544)	0.2529	<0.001
Cougar (91)	Coyote (354)	0.1781	0.020
	Deer	0.1831	0.005
	Elk	0.1191	0.189
	Grizzly	0.2809	<0.001
	Moose	0.1430	0.116
	Wolf	0.1199	0.212
Coyote (354)	Deer	0.619	0.198
	Elk	0.1371	<0.001
	Grizzly	0.1306	<0.001
	Moose	0.1073	0.005
	Wolf	0.1505	<0.001
Deer (2025)	Elk	0.1830	<0.001
	Grizzly	0.1495	<0.001
	Moose	0.1469	<0.001
	Wolf	0.1199	<0.001
Elk (853)	Grizzly	0.1972	<0.001
	Moose	0.0593	0.427
	Wolf	0.1277	<0.001
Grizzly (715)	Moose	0.1643	<0.001
	Wolf	0.2332	<0.001
Moose (293)	Wolf	0.1375	0.0015

more diurnal activity patterns at novel WC were seen for wolves. Moose activity at novel WC peaked earlier in the morning and later at night, while deer were more active at night at novel WC.

Effect of vehicle traffic, human use, age of structure and hour of day on wildlife crossing structure use

Wildlife demonstrated marked interspecific variation in diel patterns of WC use, but periodicity in activity was present for all species. Time of day was a strong factor in determining crossing events of elk in all Phases except 3A (Fig. 5; see Appendix: Table A1 for full results). Elk activity in Phases 1, 2 and 3B showed two activity peaks in the morning and evening hours (around 0600 and 2100 h) and low activity during the late morning and afternoon (1000 to 1600 h). At Phases 1 and 2, there was also a second period of low activity at night (0000 to 0300 h). WC along Phases 1 and 2 had higher numbers of elk crossings than those of Phases 3A and 3B.

Time of day was the most important covariate for deer, with all crossing events in all Phases exhibiting one peak in the morning (between 0600 and 1000 h), and a second, smaller peak around 2000 h (Fig. 5; see Appendix: Table A2 for full results). Deer activity was lowest at 1500 h and 0200 h. Age of structure also increased deer crossing events, with Phase 1 having more events per hour than Phases 3A and 3B.

For wolves, time of day interacted with age of WC and was a key driver of crossing events for wolves (Fig. 5; see Appendix: Table A3 for full results). While time of day was not significant in Phase 1, it was highly significant for Phase 2, with a distinct spike in crossing events at night (0500 h) and low activity during the day (1500 h); wolves moving along Phase 3A increased crossing events in the early morning hours (0500 h) and evening hours (2100 h). Traffic volume negatively affected crossing events across all phases. Human activity at WC also interacted with age of structure: crossing events were greater at low human use structures in Phase 1, but number of events declined at low human use structures WC along Phases 3A and 3B. In Phase 2, human use was not significant.

For coyotes, at high human use structures, hour was highly significant, with a peak at 0100 h
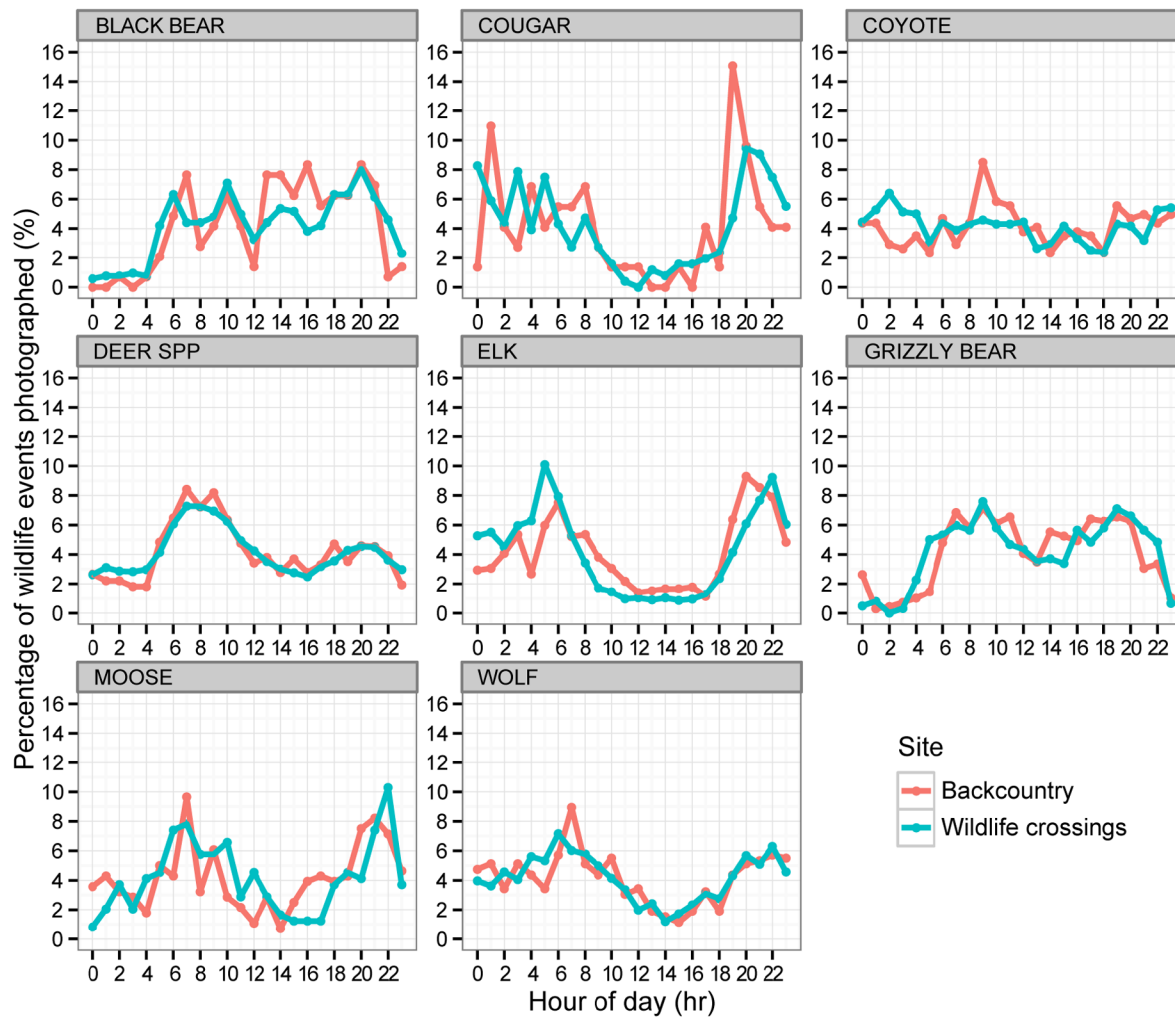
Fig. 2. Diel activity patterns of large mammals at wildlife crossings (WC) and backcountry (BC) sites in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at WC (turquoise solid line) and at BC sites (red solid line).

Table 2. Results of two sample Kolmogorov-Smirnov tests for intra-specific activity at wildlife crossing structure (WC) and backcountry (BC) camera sites. Listed are the number of camera events by species at WC and BC sites used in the analysis. Significant ($P < 0.05$) comparisons indicate different activity patterns. D is maximum vertical deviation between the two distribution curves.

	Camera location			
Species	BC	WC	D	P
Cougar	91	254	0.0622	0.957
Coyote	354	719	0.1057	0.010
Wolf	544	1161	0.0274	0.943
Grizzly bear	715	622	0.0420	0.600
Black bear	165	522	0.0532	0.870
Deer sp.	2026	16,255	0.0305	0.069
Elk	853	6410	0.1437	<0.001
Moose	293	245	0.0955	0.175

Table 3. Results of two sample Kolmogorov-Smirnov tests for activity patterns at wildlife crossing structures with high and low human use in Banff National Park, Alberta. Values for high and low refer to crossing events detected by motion-activated cameras at 39 sites. Significant ($P < 0.05$) comparisons indicate different activity patterns. D is the maximum vertical deviation between the two distribution curves.

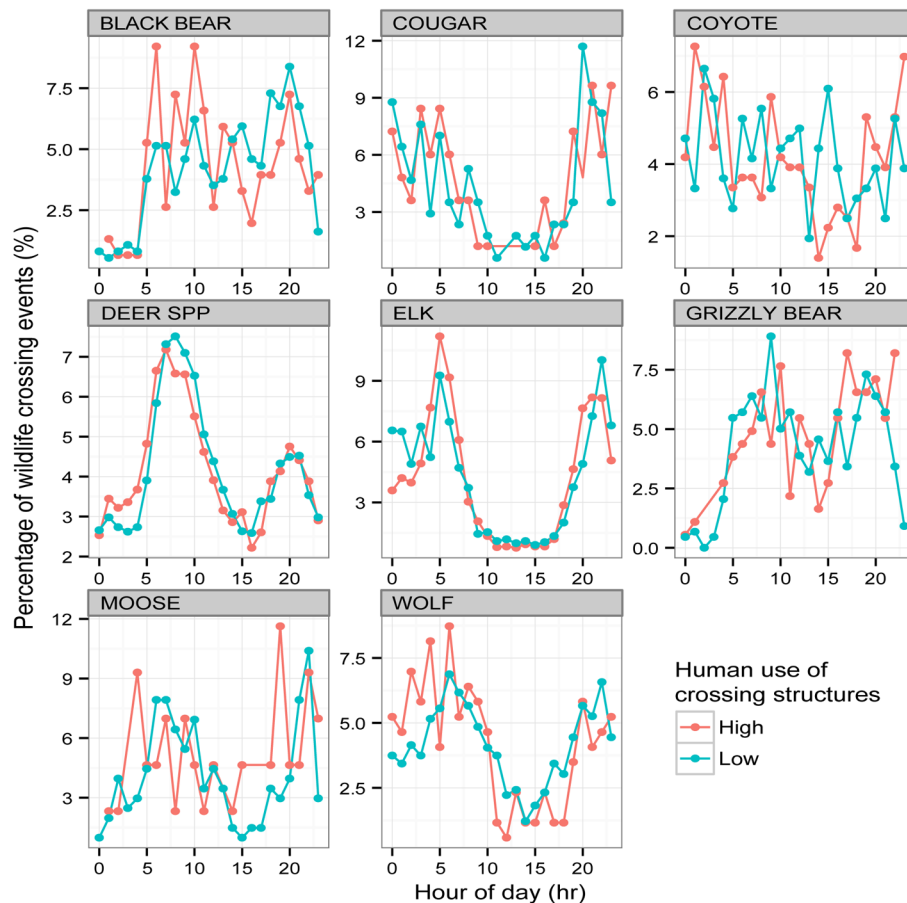| Species | Human use | | D | P |
	High	Low		
Cougar	83	171	0.0613	0.984
Coyote	358	361	0.0714	0.318
Wolf	172	989	0.1231	0.023
Grizzly bear	183	439	0.0950	0.193
Black bear	152	370	0.1345	0.041
Deer sp.	4374	11,850	0.0425	<0.001
Elk	2761	3649	0.0799	<0.001
Moose	43	202	0.1171	0.716

Fig. 3. Diel activity patterns of large mammals at high human-use and low human-use wildlife crossings in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at high human use WC (red solid line) and low human use WC (turquoise solid line).

Table 4. Results of two-sample Kolmogorov-Smirnov tests between activity patterns at wildlife crossing (WC) structures with high and low human use, standardized by open-span design type. Listed are the number (N) of camera events by species at high and low human use sites used in the analysis. Significant ($P < 0.05$) comparisons indicate different activity patterns. D is the maximum vertical deviation between the two distribution curves.

Species	Human activity		D	P
	High use (N)	Low use (N)		
Cougar	54	110	0.1350	0.523
Coyote	283	52	0.1309	0.438
Wolf	41	442	0.3290	<0.001
Grizzly bear	34	136	0.1029	0.935
Black bear	126	183	0.1556	0.053
Deer sp.	1336	4487	0.0330	0.213
Elk	2557	2735	0.1048	<0.001
Moose	6	14		. . .

Note: Insufficient data for moose to test.

and a low at 1500 h (Fig. 6; see Appendix: Table A4 for full results). At low human use WC coyotes showed no temporal variation in crossing events, as hour was not a significant predictor. Phases 1 and 2 had significantly more crossings than Phase 3B and Phase 1 also had more crossings than Phase 3A. The interaction of phase and human use on number of crossing events was highly significant, with high human use leading to fewer crossings in the newer Phases 3A and 3B, and to more crossing events in the older Phases 1 and 2.

For grizzly bears, we pooled weekend and weekday data due to low overall detections. Within these pooled data, both time of day and traffic volume were significant factors with activity peaking during the day (0600 to 1900 h), but otherwise decreasing with traffic volume (Fig. 6; see Appendix: Table A5 for full results).

As with grizzly bears, we pooled weekend and weekday data for cougars. Time of day was significant for both high and low human use WC, with more crossing events during the night and fewest around 1200 h (Fig. 6; see Appendix: Table A6 for full results). Phase 1 had more crossing events than Phase 2 or Phase 3A, while the newer Phase 3B had no crossings by cougars at all.

For black bears, as with grizzly bears and cougars, we pooled weekend and weekday. Time of day was an important explanatory variable, with decreasing number crossing events during the night (between 2100 and 0400 h) and a nearly uniform probability of crossing events during the remainder of the day (Fig. 6; see Appendix: Table

A7 for full results). At low human use structures, the number of events was highest in the evening (2000 h), while at high human use structures, there was a dip in crossing events in the afternoon (1500 to 1600 h) and there were more events at Phase 1 than at all other phases.

DISCUSSION

Our results demonstrated marked variation in the effect of anthropogenic disturbances on wildlife, including changes to the timing of interspecific interactions and the allocation of activity over daily cycles. The activity patterns of all species at WC showed some response to human activity. However, some species (deer, elk, coyotes, black bears) were sensitive to specific types of human activities, whereas large carnivores (wolves, grizzly bears, cougars) were sensitive to all forms of human disturbance that we measured.

While efforts to mitigate disturbance to wildlife arising from transportation infrastructure can be costly (McGuire and Morrall 2000, Huijser et al. 2009), this effort is leading to the restoration of animal movement (Gagnon et al. 2011, Van Manen et al. 2012, Sawaya et al. 2013, Sawyer et al. 2013) and genetic flows (Sawaya et al. 2014) across the landscape and a reduction in the risk of wildlife-vehicle collisions (Clevenger et al. 2001, McCollister and Van Manen 2010, Found and Boyce 2011). Indeed, the large number of wildlife using WC in our study area (Clevenger et al. 2009) may be interpreted by some observers
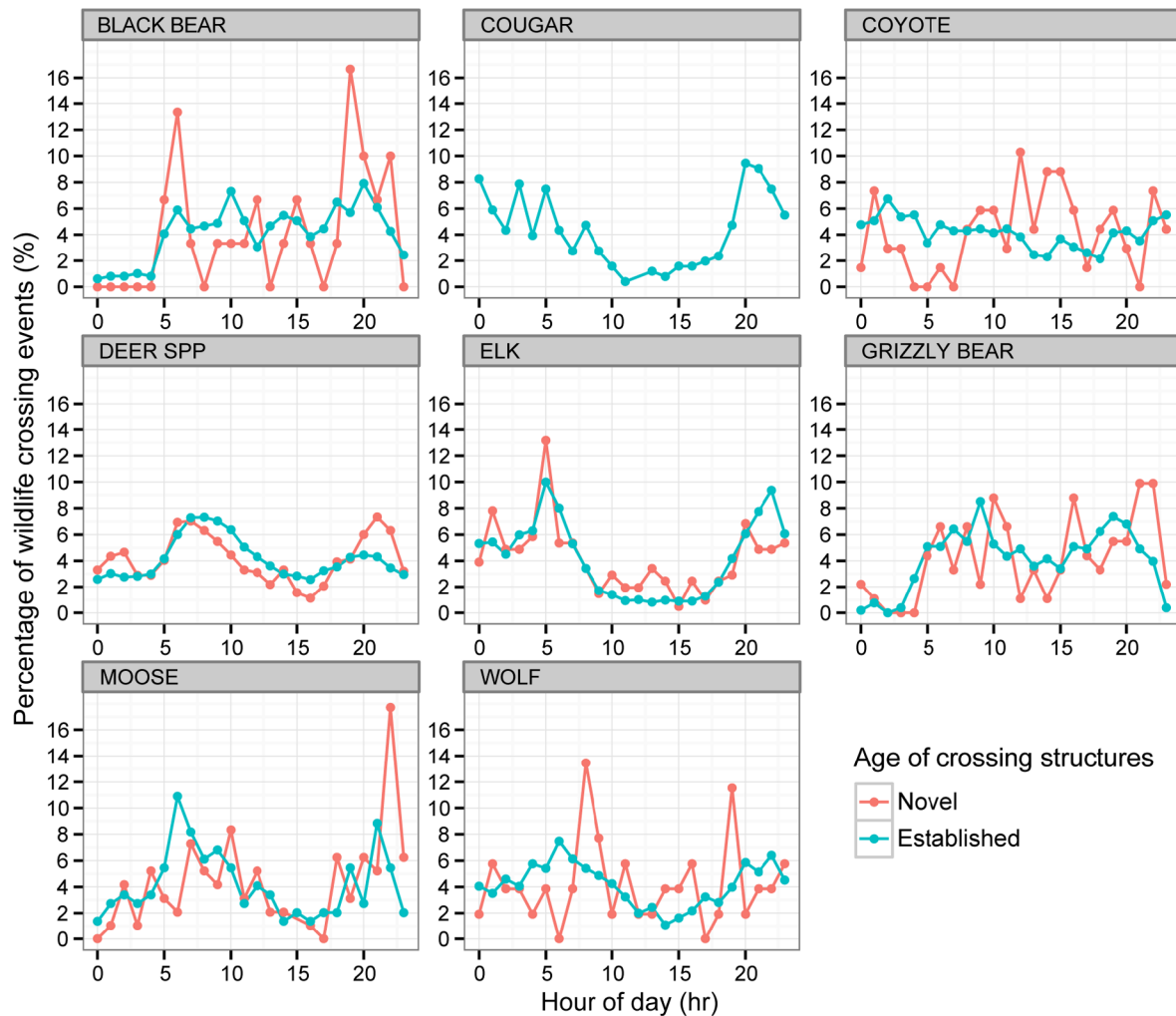
Fig. 4. Diel activity patterns of large mammals at novel vs. established wildlife crossings in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at novel WC (red solid line) and established WC (turquoise solid line). No data were obtained from cougars using novel wildlife crossings during the study period.

as a successful restoration of critical ecological flows across this human-occupied landscape. Less appreciated by these levels of wildlife use are the sub-lethal effects of highways on wildlife behavior and the extent to which mitigation buffers these effects.

Understanding the behavioral response of wildlife to people is an information gap with critical conservation and management implications (Buchholz 2007, Caro 2007, Blumstein and Fernandez-Juricic 2010). Previous studies have shown that large mammals can adjust their location and timing of certain behaviors to avoid interacting with people, including hikers (Rogala et al. 2011, Longshore et al. 2013), skiers (Ferguson and Keith 1982, Cassirer et al. 1992), aircraft (Weisenberger et al. 1996, Krausman et al. 1998) and vehicles (Burson et al. 2000, Brown et al. 2012). Some of these behaviors generate cascading effects on other human-wildlife interactions. For example, deer are more vulnerable to collisions with vehicles during hunting season, but only in areas where hunting is permitted (Sudharsan et al. 2006). Here we have shown that wildlife adjust their behavior in response to variation in human activity, and that this
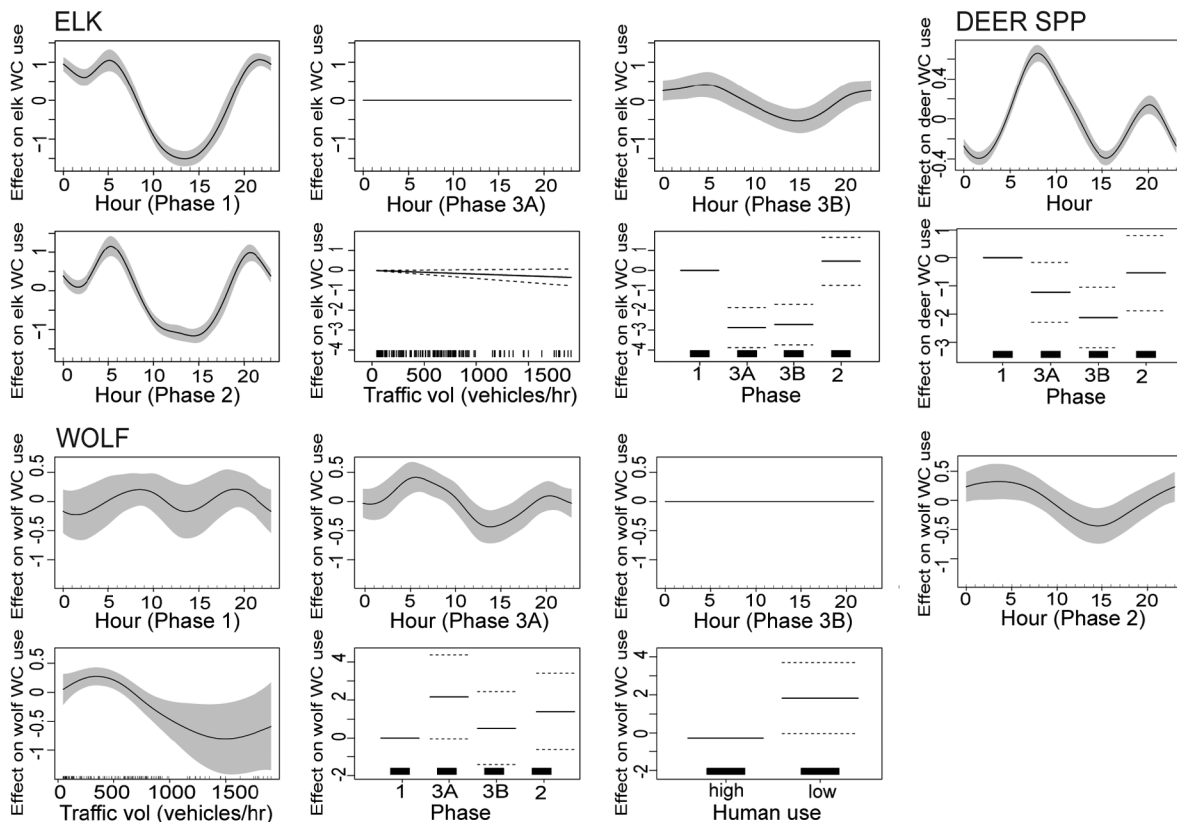
Fig. 5. Plots showing the smooth functions of continuous covariates and term plots of parametric terms of the best GAMM models for elk, deer and wolves in Banff National Park, Alberta. The x-axes of all smooth function plots show the covariate values, the x-axes of the term plots show the factor levels. In all plots, the y-axis is the covariate effect on the mean response, which is the number of animals per hour using an 'average' crossing structure. Values on the y-axis are on the linear predictor scale.

response depends on the baseline levels of human activity in the area. For instance, traffic volume negatively affected crossing count of wolves at all Phases, but the amount of wolf activity at WC depended on how many people also used the WC. Our results are consistent with others (e.g., Ng et al. 2004, Mata et al. 2005, Grilo et al. 2008) showing that the restoration of pre-disturbance activity patterns of wildlife living near highways will depend on the management of human use at WC.

Though our results showed that human use of WC affected wildlife activity, we found congruent overall activity patterns for most species among WC and BC sites. This result suggests that wildlife can habituate to some types of disturbances (e.g., vehicle traffic) but remain sensitive to others (e.g., foot traffic at WC), and

that the WC designs used at our study site are capable of buffering at least some of the potentially aversive stimulus (e.g., noise, chemo-sensory emissions, light) produced by roads and traffic (Barber et al. 2009, Brown et al. 2012, McClure et al. 2013). If wildlife habituation to roads increases use of WC, we predicted the frequency of crossing events would increase with age of WC, which was the case for all species but wolves and grizzly bears. Gagnon et al. (2011) also found an adaptive response of elk and deer to WC in Arizona over a 4-year period and Ford et al. (2010) present data suggesting adaptive responses by grizzly bears to use of WC. These adaptive responses by wildlife support the use of long-term monitoring (e.g., ≥4years) to fully understand the effectiveness of mitigation (Cle-venger et al. 2009), at least for long-lived, wide-
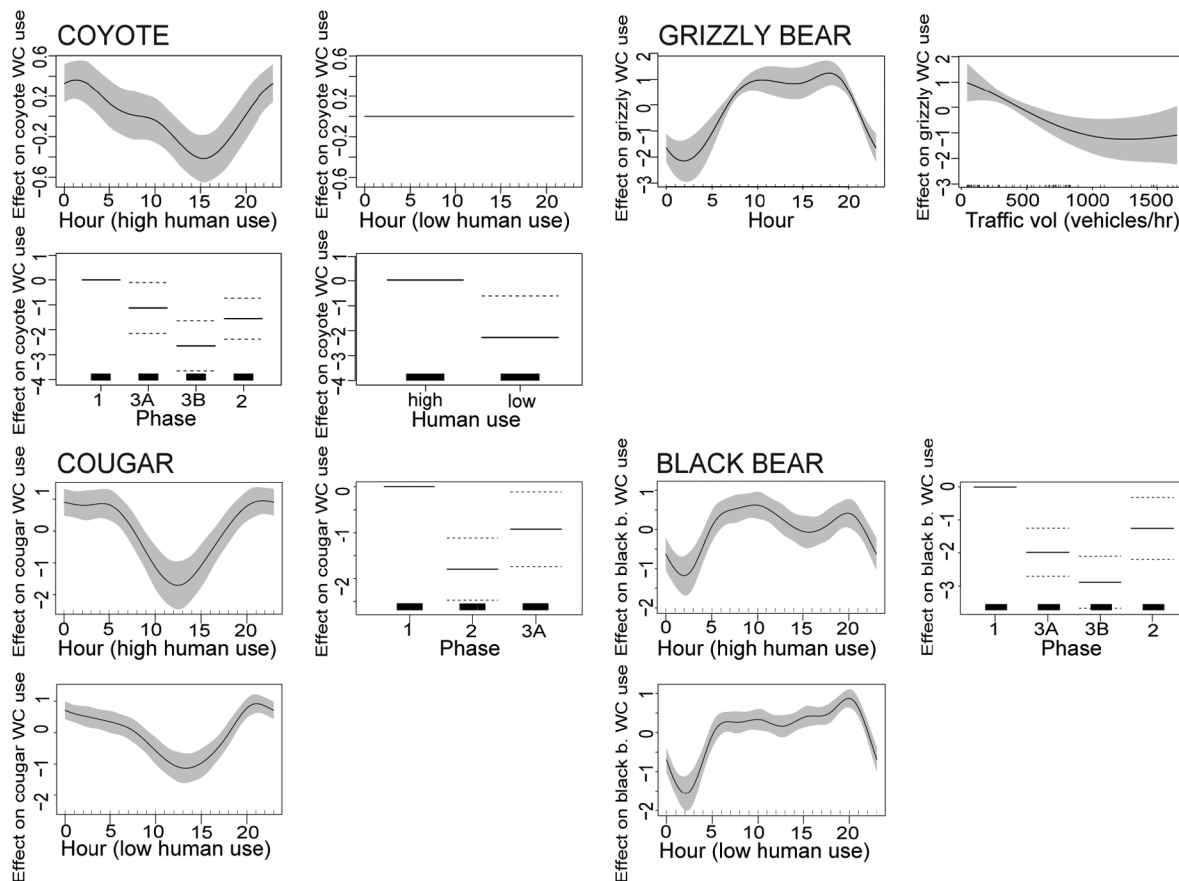
Fig. 6. Plots showing the smooth functions of continuous covariates and term plots of parametric terms of the best GAMM models for coyotes, grizzly bears, cougars and black bears in Banff National Park, Alberta. The x-axes of all smooth function plots show the covariate values, the x-axes of the term plots show the factor levels. In all plots, the y-axis is the covariate effect on the mean response, which is the number of animals per hour using an 'average' crossing structure. Values on the y-axis are on the linear predictor scale.

ranging species like large terrestrial mammals.

Protected areas are one of the most widely used approaches to conserving wildlife; however, conservation goals can be compromised when people reside and continue to use protected areas for resource extraction, transportation and recreation (Woodroffe and Ginsberg 1998, Ament et al. 2008). In an effort to restore ecosystem processes and structures, a central focus for the management of protected areas has been to mitigate the effects of people on wildlife movement and mortality (McNeely et al. 1990, Cooperrider and Noss 1994). Transportation and land managers should be cognizant of the potential negative effects of anthropogenic disturbances compromising the ecological and conservation

value of WC. Rigorous long-term monitoring of WC and anthropogenic disturbances associated with them will provide sound information for managers responsible for ensuring the efficacy of WC. Furthermore, information on the relationship between wildlife and anthropogenic disturbance will aid in assessing the performance of mitigation efforts aimed at increasing landscape connectivity, reducing the risk of human-wildlife conflict and conserving wildlife populations.

ACKNOWLEDGMENTS

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SUPPLEMENTAL MATERIAL
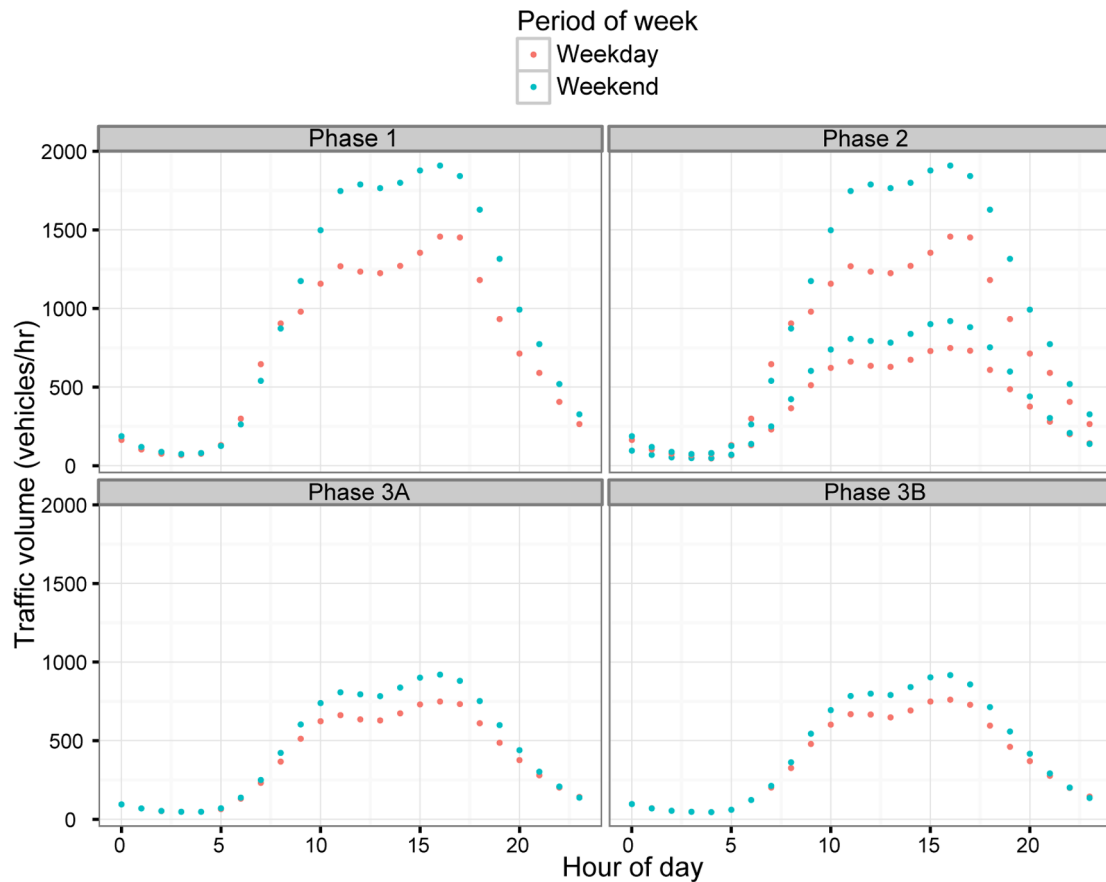
APPENDIX

Period of week
• Weekday
• Weekend

Fig. A1. Plots of traffic volume in average number of vehicles/hour obtained from three traffic counters on the Trans-Canada Highway (TCH) in Banff National Park, Alberta. Traffic volume data are shown for the four phases of the TCH from 2007–2013. Red solid dots are weekday (Monday–Thursday) traffic, while turquoise solid dots are weekend (Friday–Sunday) traffic volumes.

Table A1. Best generalized additive mixed models (GAMMs) for elk. $N = 1632$, $R^2(\text{adj}) = 0.514$. ICC = Intra-class correlation. Smooth terms are denoted with s(). σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−4.210	0.419	−10.046			<0.001			
Fixed	Traffic†	0.000	0.000	−1.678			0.094			
Fixed	Phase 3A	−2.873	0.507	−5.667			<0.001			
Fixed	Phase 3B	−2.721	0.510	−5.338			<0.001			
Fixed	Phase 2	0.467	0.612	0.762			0.446			
Fixed	s(hr): Phase 1				7.129	43.799	<0.001			
Fixed	s(hr): Phase 3A				0.000	0.000	0.436			
Fixed	s(hr): Phase 3B				3.024	1.885	<0.001			
Fixed	s(hr): Phase 2				7.417	37.275	<0.001			
Random	Crossing structure							0.815	1.535	0.347

Notes: Traffic (indicated with †) was modeled as a smooth term first, but was found to be equal to a linear effect. Estimated df = 1. An ANOVA for the parametric coefficient Phase resulted in a P value of <0.001, with df = 3 and $F = 22.069$.

Table A2. Best generalized additive mixed models (GAMMs) for deer spp. $N = 1680$, $R^2(adj) = 0.293$. ICC = Intra-class correlation. Smooth terms are denoted with s(). σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−3.482	0.447	−7.791			<0.001			
Fixed	Phase 3A	−1.229	0.528	−2.327			0.020			
Fixed	Phase 3B	−2.123	0.537	−3.953			<0.001			
Fixed	Phase 2	−0.541	0.671	−0.806			0.420			
Fixed	s(hr): Phase 1				3.540	0.939	0.045			
Fixed	s(hr): Phase 3A				4.504	2.932	<0.001			
Fixed	s(hr): Phase 3B				0.000	0.000	0.953			
Fixed	s(hr): Phase 2				2.439	1.086	0.006			
Fixed	s(Traffic)				3.960	4.391	0.002			
Random	Crossing structure							0.987	1.881	0.344

Note: An ANOVA for the parametric coefficient *Phase* resulted in a *P* value of <0.001, with df = 3 and *F* = 22.069.

Table A3. Best generalized additive mixed models (GAMMs) for wolf. $N = 1440$, $R^2(adj) = 0.351$. ICC = Intra-class correlation. Smooth terms are denoted with s(). σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−8.454	0.870	−9.717			<0.001			
Fixed	Phase 3A	2.163	1.103	1.961			0.050			
Fixed	Phase 3B	0.510	0.966	0.528			0.598			
Fixed	Phase 2	1.387	1.009	1.375			0.170			
Fixed	HumanL	2.100	0.934	2.249			0.025			
Fixed	Phase 3A: HumanL	−2.616	1.170	−2.236			0.026			
Fixed	Phase 3B: HumanL	−2.468	1.086	−2.273			0.023			
Fixed	Phase 2: HumanL	−0.016	1.255	−0.013			0.990			
Fixed	s(hr): Phase 1				3.540	0.939	0.045			
Fixed	s(hr): Phase 3A				4.504	2.932	<0.001			
Fixed	s(hr): Phase 3B				0.000	0.000	0.953			
Fixed	s(hr): Phase 2				2.439	1.086	0.006			
Fixed	s(Traffic)				3.960	4.391	0.002			
Random	Crossing structure							0.440	0.994	0.307

Notes: An ANOVA for the parametric coefficient Phase resulted in a *P* value of 0.099, with df = 3 and *F* = 2.096. An ANOVA for the parametric coefficient Human resulted in a *P* value of 0.025, with df = 1 and *F* = 5.059. An ANOVA for the interaction of Phase and Human resulted in a *P* value of 0.012, with df = 3 and *F* = 3.649.

Table A4. Best generalized additive mixed models (GAMMs) for coyote. $N = 1536$, $R^2(adj) = 0.277$. ICC = Intra-class correlation. Smooth terms are denoted with s(). σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use. HumanH = High human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−5.684	0.354	−16.044			<0.001			
Fixed	Phase 3A	−1.128	0.509	−2.217			0.027			
Fixed	Phase 3B	−2.647	0.501	−5.281			<0.001			
Fixed	Phase 2	0.022	0.411	0.053			0.958			
Fixed	HumanL	−1.472	0.417	−3.534			0.000			
Fixed	Phase 3A: HumanL	1.054	0.570	1.850			0.064			
Fixed	Phase 3B: HumanL	2.184	0.590	3.701			0.000			
Fixed	Phase 2: HumanL	−0.078	0.639	−0.123			0.902			
Fixed	s(hr): HumanH				3.277	2.617	<0.001			
Fixed	s(hr): HumanL				0.000	0.000	0.463			
Random	Crossing structure							0.106	1.040	0.092

Notes: An ANOVA for the parametric coefficient Phase resulted in a *P* value of <0.001, with df = 3 and *F* = 15.692. An ANOVA for the parametric coefficient Human resulted in a *P* value of <0.001, with df = 1 and *F* = 12.489. An ANOVA for the interaction of Phase and Human resulted in a *P* value of <0.001, with df = 3 and *F* = 6.094.

Table A5. Best generalized additive mixed models (GAMMs) for grizzly bear. $N = 768$, R^2(adj) $= 0.188$. ICC $=$ Intra-class correlation. Smooth terms are denoted with s(). $\sigma_i^2 =$ variance of the random intercept; $\sigma_r^2 =$ variance of the (working) residuals. HumanL $=$ Low human use. HumanH $=$ High human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−7.690	0.159	−48.470			<0.001			
Fixed	s(hr)				4.704	13.553	<0.001			
Fixed	s(Traffic)				2.573	5.551	0.002			
Random	Crossing structure							0.649	1.008	0.391

Table A6. Best generalized additive mixed models (GAMMs) for cougar. $N = 360$, R^2(adj) $= 0.325$. ICC $=$ Intra-class correlation. Smooth terms are denoted with s(). $\sigma_i^2 =$ variance of the random intercept; $\sigma_r^2 =$ variance of the (working) residuals. HumanL $=$ Low human use. HumanH $=$ High human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−6.929	0.239	−29.004			<0.001			
Fixed	Phase 3A	−1.796	0.339	−5.302			<0.001			
Fixed	Phase 2	−0.925	0.407	−2.273			0.024			
Fixed	s(hr): HumanH				4.039	4.269	<0.001			
Fixed	s(hr): HumanL				4.536	7.090	0.732			
Random	Crossing structure							0.238	0.923	0.205

Note: An ANOVA for the parametric coefficient Phase resulted in a P value of <0.001, with df $= 2$ and $F = 14.070$.

Table A7. Best generalized additive mixed models (GAMMs) for black bear. $N = 696$, R^2(adj) $= 0.395$. ICC $=$ Intra-class correlation. Smooth terms are denoted with s(). $\sigma_i^2 =$ variance of the random intercept; $\sigma_r^2 =$ variance of the (working) residuals. HumanL $=$ Low human use. HumanH $=$ High human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−6.264	0.247	−25.366			<0.001			
Fixed	Phase 3A	−1.960	0.306	−6.405			<0.001			
Fixed	Phase 3B	−2.168	0.366	−5.927			<0.001			
Fixed	Phase 2	−1.210	0.392	−3.088			0.002			
Fixed	s(hr): HumanH				5.039	3.280	<0.001			
Fixed	s(hr): HumanL				6.657	9.208	<0.001			
Random	Crossing structure							0.276	0.945	0.226

Note: An ANOVA for the parametric coefficient *Phase* resulted in a P value of <0.001, with df $= 3$ and $F = 16.770$.