



Validity of the Prey-Trap Hypothesis for Carnivore-Ungulate Interactions at Wildlife-Crossing Structures

ADAM T. FORD* AND ANTHONY P. CLEVENGER

Western Transportation Institute, Montana State University, P.O. Box 174250, Bozeman, MT 59717-4250, U.S.A.

Abstract: *Wildlife-exclusion fencing and wildlife-crossing structures (e.g., underpasses and overpasses) are becoming increasingly common features of highway projects around the world. The prey-trap hypothesis posits that predators exploit crossing structures to detect and capture prey. The hypothesis predicts that predation events occur closer to a highway after the construction of fences and crossing structures and that prey species' use of crossings increases the probability that predators will attack prey. We examined interactions between ungulates and large carnivores at 28 wildlife crossing structures along 45 km of the Trans-Canada Highway in Banff National Park, Alberta. We obtained long-term records of locations where ungulates were killed (kill sites) before and after crossing structures were built. We also placed remote, motion-triggered cameras at two crossing structures to monitor predator behavior following ungulate passage through the structure. The proximity of ungulate kill sites to the highway was similar before and after construction of fencing and crossing structures. We found only five kill sites near crossing structures after more than 32,000 visits over 13 years. We found no evidence that predator behavior at crossing structures is affected by prey movement. Our results suggest that interactions between large mammals and their prey at wildlife-crossing structures in Banff National Park are not explained by the prey-trap hypothesis.*

Keywords: carnivore, highway, kill sites, mitigation, road, ungulate

Validez de la Hipótesis de la Trampa del Depredador para Interacciones Carnívoro-Ungulado en Estructuras para Cruce de Vida Silvestre

Resumen: *Las estructuras para cercar y para cruce de vida silvestre (e. g., pasos subterráneos y cruces elevados) cada vez son aspectos más comunes en los proyectos de carreteras en todo el mundo. La hipótesis de la trampa del depredador postula que los depredadores explotan las estructuras para cruce para detectar y capturar presas. La hipótesis predice que los eventos de depredación ocurren más cerca de una carretera después de la construcción de cercos y cruces y que la utilización de cruces por especies de presas incrementa la probabilidad de que los depredadores los ataquen. Examinamos las interacciones entre ungulados y carnívoros mayores en 28 estructuras para cruce de vida silvestres a lo largo de 45 km de la Carretera Trans-Canadá en el Parque Nacional Banff, Alberta. Obtuvimos registros de localidades donde ungulados fueron muertos (sitios de depredación) antes y después de la construcción de las estructuras para cruce. También colocamos cámaras sensibles al movimiento en 2 estructuras para cruce para monitorear el comportamiento de depredadores después del paso de ungulados por la estructura. La proximidad de los sitios de depredación a la carretera fue similar antes y después de la construcción de estructuras de cercado y cruce. Solo encontramos 5 sitios de depredación cerca de estructuras para cruce en más de 32,000 visitas a lo largo de 13 años. No encontramos evidencia de que el comportamiento de los depredadores sea afectado por el movimiento de presas en las estructuras para cruce. Nuestros*

*Current address: Department of Zoology, University of British Columbia, 2370-6270 University Building, Vancouver, B.C. V6T 1Z4, Canada, email atford@gmail.com

resultados sugieren que las interacciones entre mamíferos mayores y sus presas en las estructuras para cruce de vida silvestre en el Parque Nacional Banff no se explican con la hipótesis de la trampa del depredador.

Palabras Clave: camino, carnívoro, carretera, mitigación, sitios de depredación, ungulado

Introduction

Mitigating the negative effects of roads on vertebrate animals, particularly large mammals, has become increasingly common in transportation projects around the world (Forman et al. 2003). One of the most effective highway mitigation systems designed for large mammals includes the use of ungulate-exclusion fencing and wildlife-crossing structures (WCS) (Huijser et al. 2009). Fencing prevents large mammals from accessing the highway right-of-way and WCS allow animals to safely cross the highway. Crossing structures are typically culvert or bridge underpasses, but they also include vegetated overpasses (Huijser et al. 2009). Results of previous studies show that WCS facilitate animal movement across roads and fencing reduces the number of wildlife-vehicle collisions (Clevenger & Waltho 2005; Gagnon et al. 2007); however, these mitigation measures also constrain animal movement to small and predictable areas along the highway (i.e., the width and location of WCS). Predators exploit high densities of prey near anthropogenic structures (e.g., Valeix et al. 2009; Jung & Kalko 2010); thus, the bottleneck effect of WCS could potentially increase prey densities near the highway and alter rates of prey mortality. If mortality in prey populations increases near WCS, then the conservation goals of the WCS may be compromised.

The prey-trap hypothesis posits that predators use WCS and highway fences to facilitate the detection and capture of prey (Little et al. 2002; Dickson et al. 2005). We tested three predictions derived from the prey-trap hypothesis (Little et al. 2002). (1) Wildlife crossing structures increase predator foraging efficiency; thus, sites where predators kill prey (kill sites) are closer to the highway after construction of WCS. (2) Predators systematically forage near or within WCS; thus, the density of kill sites at WCS is relatively higher than the density of kill sites in the surrounding landscape. (3) Prey activity at WCS increases the probability of an attack by predators; thus, prey use of WCS may be used to predict the probability of predator passage (MacNulty et al. 2007). We focused on interactions between five ungulate species (hereafter prey)—white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), and elk (*Cervus elaphus*)—and two species of large carnivore (hereafter predators)—wolves (*Canis lupus*) and cougars (*Puma concolor*).

Methods

Study Area

Our study site was in the Bow River Valley along the Trans-Canada Highway (hereafter the highway) in Banff National Park (hereafter Banff). Annual average traffic volume was approximately 17,630 vehicles/day in 2007 (Highway Service Centre, Parks Canada, unpublished data). From the late 1970s until 1987 wildlife exclusion fencing and 10 WCS had been built along 27 km of the highway (phases 1 and 2; Fig. 1). By 1996 another 21 km of highway had been fenced and an additional 13 WCS built, including two overpasses (phase 3A; Fig. 1) (Clevenger & Waltho 2000). Construction of additional fencing and WCS is scheduled to be completed by 2012 (phase 3B; Fig. 2).

Wolves recolonized the Bow River Valley in 1986, and since this time their annual abundance has ranged from 2 to 24 individuals among 1 to 3 packs (Hebblewhite et al. 2002). Elk abundance varies from 100 to 500 individuals annually (T. Hurd, personal communication). Direct estimates of cougar and deer abundance were unavailable, although deer abundance is thought to have increased since the 1980s (T. Hurd, personal communication), whereas annual cougar abundance has varied from 8 to 12 individuals (Kortello et al. 2007).

Field Data

We used data collected at kill sites in Banff since 1981 (Huggard 1993; Duke et al. 2001; Hebblewhite et al. 2003; Kortello et al. 2007). Researchers who collected the data primarily used snow-track transects and radiotelemetry to find kill sites of wolves and cougars. Transects began at the valley bottom and extended upslope until the first substantial obstacle to human movement was encountered (e.g., slopes $>30^\circ$). Transects were sampled within 3 days after snowfall. When predator tracks were found along a transect, researchers backtracked along the animal's pathway looking for a kill site. Snow tracking occurred continuously throughout the winter (November to April) as conditions allowed. Locations of cougars and wolves were monitored with radiotelemetry on a daily basis and subsequently tracked when radio signals indicated a possible kill site in the area (i.e., a signal was detected at the same location for at least 2 consecutive days). The search effort for kill sites varied in intensity

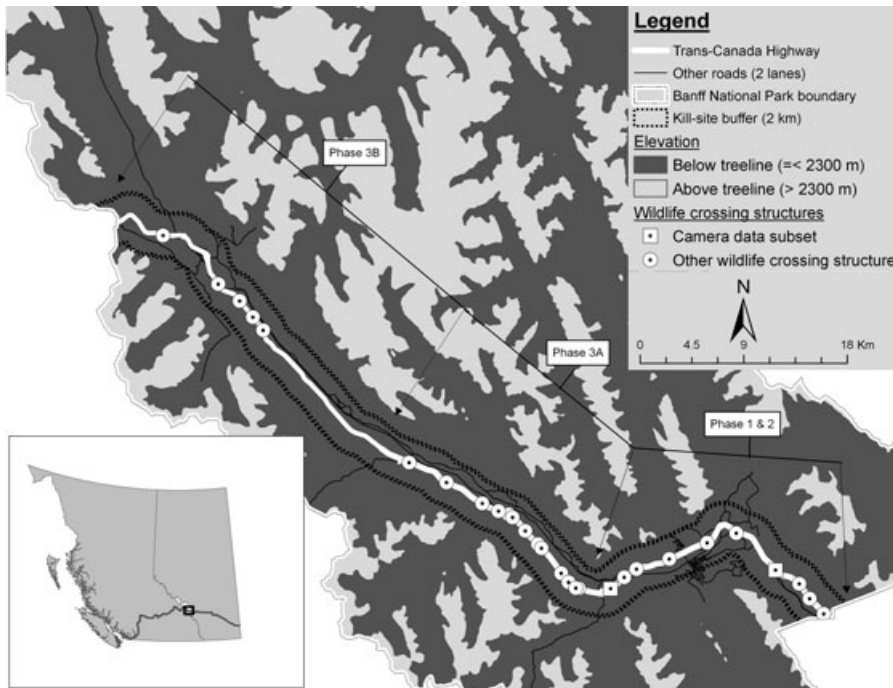


Figure 1. Study area and locations of wildlife crossing structures along the Trans-Canada Highway in Banff National Park, Alberta, Canada.

over the past 30 years, but was similar before and after migration (Fig. 2).

We also used records of incidental observations of kill sites made by trained Parks Canada staff conducting back-

country safety and enforcement patrols. We combined these sources of kill-site data to test whether predation events are closer to the highway after construction of highway fencing and WCS than before.

To address whether the number of kill sites near WCS is associated with higher foraging success for predators, we searched for kill sites in the vicinity of WCS entrances. We assumed that predators and prey use the WCS to cross the highway. To verify this assumption, we monitored 23 WCS within Banff by visiting each site every 2–4 days from November 1996 through April 2009 and used trackpads to estimate use of WCS by large mammals (Clevenger & Waltho 2000, 2005; Ford et al. 2009). Trackpads were areas 3–4 cm wide and 2–4 m long of sandy-loam substrate in the WCS. We raked trackpads smooth after each check to improve the clarity of tracks for researchers conducting subsequent checks. An additional five WCS were constructed in 2007 (Fig. 1), and we began monitoring these sites in winter 2008 (for a total of 28 WCS monitored). In addition to monitoring trackpads, we performed snowtracking surveys adjacent to the WCS during the winter (December–February) of 1997–2000. We created semicircular transects around both ends of each WCS. The radius of each transect was 100 m, and the center of the semicircle was at the WCS entrance. At least 48 h after a track-covering snowfall (i.e., >3 cm), we walked the transects looking for large mammal tracks and recorded any evidence of a predator-prey encounter (e.g., carcass, blood, fur piles).

To examine whether prey activity is associated with the timing of predator movement at WCS, we measured the interval between sequential predator and prey crossing events. The timing of crossing events was determined

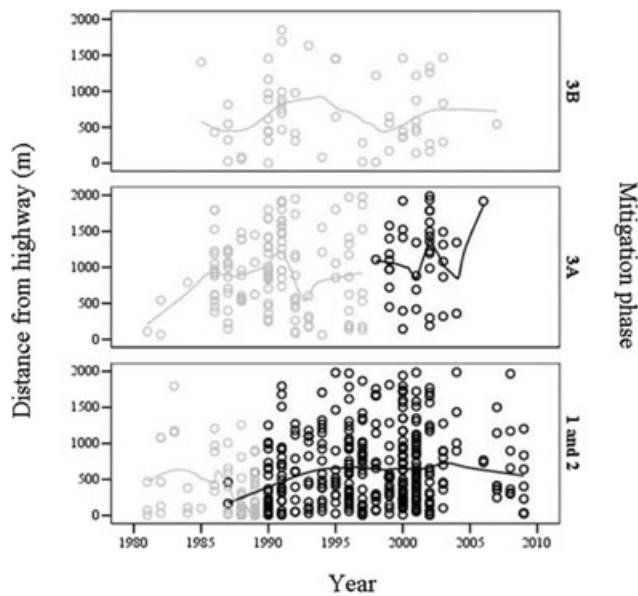


Figure 2. Distribution of kill sites adjacent to the Trans-Canada Highway in Banff National Park, Alberta, Canada, at three stages of development of wildlife crossing structures. Gray symbols are kill sites found before wildlife crossing structures were built and black symbols are kill sites found after structures were built. A locally weighted smoothing curve (LOESS) is fitted to the data.

by the time stamp recorded on digital photographs taken by motion-triggered cameras (Reconyx, Holmen, Wisconsin) (Ford et al. 2009). Cameras were installed at two WCS of the same design (open-span bridge; Clevenger & Waltho 2000), adjacent vegetation type, and construction dates (>20 years old). Cameras were in operation at both WCS for at least 2 years and the WCS were consistently used by cougars, wolves, elk, and deer. We used only records in which an individual of a prey species was followed by a predator or a predator was followed by a prey. To avoid counting individuals from the same herd or pack, we did not include records where prey followed other prey or predators followed other predators. Counting multiple individuals from the same group would have violated the assumption of independence in the analysis because group members influence the movement and behavior of each other. For the records we used, we calculated two time intervals: prey-predator interval (time elapsed between a prey crossing event and the next predator crossing event) and predator-prey interval (time elapsed between a predator crossing event and the next prey crossing event). We made the following predictions: the prey-predator interval will be less than the predator-prey interval if predators are actively pursuing prey at WCS; if prey are avoiding WCS because of recent predator activity, then the prey-predator interval will be greater than the predator-prey interval; and if species use of WCS is primarily independent of interspecific relations, then these two intervals will be roughly the same.

Data Analyses

We excluded all kill-site records >2 km from the highway in order to maximize our ability to detect a significant effect of mitigation measures on kill-site locations. A recent study in Banff documented 96 wolf-elk chase sequences, in which the maximum length of the chase was 1.7 km (Hebblewhite et al. 2005). Results of another study showed that the mean wolf-elk chase distance is 978 m (Kauffman et al. 2007). The chase distance of wolves, which are cursorial predators, is likely much greater than the typical chase distance of cougars, which are ambush predators. For example, there is anecdotal evidence of chase distances of <10 m for cougars (Beier et al. 1995). Thus, predation events resulting from a chase initiated at WCS are unlikely to occur >2 km from the highway (Hebblewhite et al. 2005), and by excluding records >2 km from the highway we increased the power of our analysis to detect increased predation near WCS and fences.

We classified kill sites by the nearest highway mitigation phase (1 and 2, 3A, or 3B; Fig. 1) and by whether the predation event occurred before or after construction of fencing and WCS. We then measured the distance from each kill site to the highway with the Hawth's Tools

extension (Beyer 2004) in ArcGIS 9.2 (ESRI, Redlands, California). We used distance to highway as the response variable and square-root transformed these values to normalize their distribution. We performed a generalized least-squares analysis with mitigation stage (before or after) as the categorical predictor variable. We controlled for season in which the kill occurred (winter, December to February; spring, March to May; summer, June to August; autumn, September to November), mitigation phase (1 and 2, 3A, 3B, prey species (white-tailed deer, mule deer, elk, moose, bighorn sheep), and year because these variables likely changed sampling effort and probability of finding a kill site (Hebblewhite et al. 2002, 2003). We assigned an identity variance structure to the year factor to address heterogeneous variances (Zuur et al. 2009).

We calculated the total number of predator and prey crossing events from trackpads, summed the number of visits to WCS by researchers, and then calculated the total number of kill sites or signs of predation that were detected. We also summed the number of snowtracking transects surveyed, the number of predator and prey tracks detected, and the number of kill sites or signs of predation that occurred within 100 m of WCS.

We used a general linear model with interval type (i.e., prey-predator or predator-prey) as the response variable. We performed an analysis for intervals ≤ 8 h and for intervals ≤ 48 h. After 48 h it is unlikely that individual prey affect the timing of predator movement. For example, antipredator responses of elk (i.e., group size) strengthen within 48 h of exposure to wolves, peaking within 8 h of exposure (Proffitt et al. 2009). We included site as a random effect and square-root transformed the response variable to normalize their distribution. We examined the intraclass correlation for the site effect to determine whether it was appropriate to combine data from both locations in the same analysis (Zuur et al. 2009). Analyses were performed with R (version 2.9.2) statistical software and the nlme package (R Development Core Team 2009).

Results

We examined data collected from 1981 to 2009 from 729 kill sites. Most of the kills were of elk (63%), deer (25%), bighorn sheep (11%), and moose (2%). Fifty-nine percent of all predation events at kill sites occurred after WCS were constructed. After controlling for the effects of mitigation phase, year, prey species, and season, we found no significant decrease ($t = -0.03$; $p = 0.80$) in the distance from kill sites to the highway after WCS construction. Kill sites were almost exactly the same distance to the highway before mitigation (mean = 698 m [SD 561]; $n = 272$) and after (mean [SD] = 700 m [531], $n = 389$). In the immediate vicinity of the highway, 19% of kill sites recorded before construction were <100 m

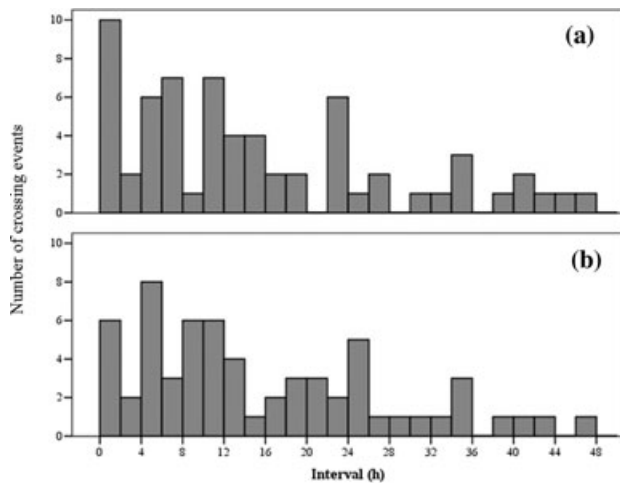


Figure 3. Frequency of (a) prey-predator time intervals (time between appearance of prey and appearance of the next predator) and (b) predator-prey time intervals (time between appearance of predators and appearance of the next prey) (intervals calculated with timestamp data on motion-triggered cameras).

from the highway, whereas 12% of kill sites recorded after construction were <100 m from the highway.

Between November 1996 and April 2009, we visited 28 WCS a total of 32,188 times, and recorded 6,571 predator crossings and 187,333 prey crossings. We surveyed 638 snowtracking transects and detected 87 and 451 sets of predator and prey tracks, respectively. These two data sets documented five kill sites (three elk, one deer, and one bighorn sheep). Three of the kill sites (all elk) were found in the winter of 2008 and 2009, when Parks Canada staff used rail fencing across the entrance of some of the WCS to control movement of elk, but not predators, across the highway (T. Hurd, personal communication).

Between August 2007 and April 2009, the number of prey-predators intervals ($n_{\leq 48\text{h}} = 65$, $n_{\leq 8\text{h}} = 25$) and predator-prey intervals ($n_{\leq 48\text{h}} = 62$, $n_{\leq 8\text{h}} = 19$) were nearly equal. The predator-prey and prey-predator intervals did not differ significantly within 48 h ($df = 124$; $t = -0.52$; $p = 0.60$) or within 8 h ($df = 41$; $t = -0.59$; $p = 0.56$). The prey-predator interval was almost identical (mean_{48h} [SD] = 15.4 h [13.0]; mean_{8h} = 3.5 h [2.6]) to the predator-prey interval (mean_{48h} = 15.8 h [12.0]; mean_{8h} = 3.7 h [2.6]) (Fig. 3). Site had a low intraclass correlation (<0.001) for the ≤ 48 h and the ≤ 8 h analyses, which indicates the treatment effects were not strongly influenced by location.

Discussion

We found three lines of evidence that suggest the prey-trap hypothesis does not explain predator-prey interac-

tions at WCS in Banff: kill sites were not closer to the highway after fencing and WCS were built; kill sites in or near WCS were extremely rare events, especially given the background rate of predation in the study area and the extent to which large mammals used WCS; and prey use of WCS was not soon followed by predator activity near WCS. Collectively, these results do not preclude the possibility that predation events occurred because of prey detection and capture at WCS. We documented some instances of predation in WCS. Nevertheless, our results strongly suggest that predators are not systematically exploiting prey movement at WCS, as others have found (reviewed in Little et al. 2002; Dickson et al. 2005).

The spatial distribution of kill sites was not indicative of systematic exploitation of prey at WCS. Estimated predation rates in Banff are 0.29–0.33 kills·day⁻¹·wolf⁻¹ pack (Hebblewhite et al. 2003) and 0.01–0.09 elk kills·day⁻¹·cougar⁻¹ (Kortello et al. 2007). With a low estimate of predator abundance of 1 wolf pack and 5 cougars and a high estimate of predator abundance of 3 wolf packs and 10 cougars (T. Hurd, personal communication), there were 1547–8600 predation events, respectively during the 13-year monitoring period in Banff, which is equivalent to 0.007–0.040 kills·ha⁻¹·year⁻¹. Because some topographic features of Banff (e.g., mountain tops, steep cliffs) do not serve as habitat for predators or prey, the actual density of kill sites within the 2-km buffer (16,600 ha) near the highway may have been even greater. Conversely, the density of kills per hectare per year within 100 m of the 28 WCS (0.004 kills·ha⁻¹·year⁻¹) was much lower than in the surrounding landscape. The five kill sites we observed near the WCS were <1% (0.06–0.32%, depending on the abundance of predators) of the estimated kills in Banff during the 13-year study period. Similarly, Dickson et al. (2005) did not find evidence of ungulate predation by 17 radiocollared cougars within 300 m of WCS.

There are a number of possible reasons why our findings do not support the prey-trap hypothesis. First, our methods for locating kill sites near WCS may have led us to underestimate the actual number of kill sites because we did not find evidence of predation in the field. For example, pursuit of prey by predators may have begun at WCS but the carcass was not found because the kill occurred beyond the area we searched. Data used in Hebblewhite et al. (2005) indicate that 39 of 96 (40%) wolf-elk chases in Banff were ≤ 100 m long and 15% were <30 m long (M. Hebblewhite, personal communication). These distances are within the observable area near WCS entrances, which suggests that if systematic predation occurs here, then we would have found >5 kill sites in 13 years.

Second, the hypothesis may simply not explain interactions among large mammals at WCS in Banff. Predator-prey interactions near highways are affected by species-specific responses to the road environment,

efficiency of predator foraging, and evolutionary responses to predation risk. Many species of large mammals avoid roads (Jaeger et al. 2005), including wolves (Hebblewhite et al. 2005) and cougars (Dickson et al. 2005), which, counter to the prey-trap hypothesis, may make roadside areas safer for prey (e.g., Hebblewhite et al. 2002; Berger 2009). Additionally, with a mean distance of 2.0 km between WCS, both prey and predators have access to several WCS within their home ranges. Consequently, prey species may be lowering the probability of predation by crossing the highway at a number of WCS (Lima 2002). Spacing crossing structures for ungulates no more than 2 km apart may reduce the probability of creating prey traps.

Empirical tests of the prey-trap hypothesis are important to furthering understanding of the design and management of mitigation systems for linear human-made structures (e.g., canal, railway, pipeline, road, or highway). For example, tunnels for herpetofauna, culverts for small mammals, arboreal crossing structures, and fish passages are being used to mitigate the effects of roads on animal populations (Clevenger & Huijser 2009). It is therefore important to understand which factors contribute to the occurrence of prey traps. Compared with Banff, the prey-trap hypothesis may have greater predictive power where there are higher ratios of predators to prey, more predictable prey movements, and species with less aversive responses to the road environment.

Acknowledgments

This project was supported by the Western Transportation Institute—Montana State University (WTI), the Woodcock Foundation, the Henry P. Kendall Foundation, the Wilburforce Foundation and Parks Canada. Support from Parks Canada came from the Ecological Integrity Innovation and Leadership Fund, the Parks Canada Ecosystem Science Office (national office), the Banff and Lake Louise, Yoho, Kootenay Field Units and contract KKP 2675. Partial funding came from the U.S. Department of Transportation's Research Innovation and Technology Administration funding to WTI and the Calgary Foundation and the Mountain Equipment Co-operative. The Yellowstone-to-Yukon Conservation Initiative and Canadian Parks and Wilderness Society generously helped with contracting services. We are grateful to M. Hebblewhite for access to data and Parks Canada staff logistical support, particularly C. White, T. Hurd, B. Fyten, T. Gui, and A. Dibb. We thank two anonymous reviewers, E. Main, E. Fleishman, and P. Beier for helpful comments on a previous draft of this paper.

Literature Cited

- Beier, P., D. Choate, and R.H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. *Journal of Mammalogy* **76**:1056–1070.
- Berger, J. 2009. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* **3**:620–623.
- Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. Available from <http://www.spatial ecology.com/htools> (accessed November 2009).
- Clevenger, A. P., and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology* **14**:47–56.
- Clevenger, A. P., and N. Waltho. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation* **121**:453–464.
- Clevenger, A. P., and M.P. Huijser. 2009. Handbook for design and evaluation of wildlife crossing structures in North America. Department of Transportation, Federal Highway Administration, Washington, D.C.
- Dickson, B.G., J.S. Jenness, and P. Beier. 2005. Influence of vegetation, topography and roads on cougar movement in southern California. *Journal of Wildlife Management* **69**:264–276.
- Duke, D.L., M. Hebblewhite, P.C. Paquet, C. Callaghan, and M. Percy. 2001. Restoring a large carnivore corridor in Banff National Park. Pages 261–275 in D. S. Maehr, R. F. Noss, and J. L. Larkin, editors. Large mammal restoration: ecological and sociological challenges to the 21st century. Island Press, Washington, D.C.
- Ford, A. T., A. P. Clevenger, and A. Bennett. 2009. Comparison of methods of monitoring wildlife crossing-structures on highways. *Journal of Wildlife Management* **73**:1213–1222.
- Forman, R. T. T., et al. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.
- Gagnon, J. W., T. C. Theimer, N. L. Dodd, A. L. Manzo, and R. E. Schweinsburg. 2007. Effects of traffic on elk use of wildlife underpasses in Arizona. *Journal of Wildlife Management* **71**:2324–2328.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos* **111**:101–111.
- Hebblewhite, M., P. C. Paquet, D. H. Pletscher, R. B. Lessard, and C. J. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. *Wildlife Society Bulletin* **31**:933–946.
- Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology* **80**:789–799.
- Huggard, D. J. 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition. *Canadian Journal of Zoology* **71**:140–147.
- Huijser, M. P., J. W. Duffield, A. P. Clevenger, R. J. Ament, and P. T. McGowen. 2009. Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada; a decision support tool. *Ecology and Society* **14**: <http://www.ecologyandsociety.org/vol14/iss2/art15/>.
- Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* **185**:329–348.
- Jung, K., and E. Kalko. 2010. Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *Journal of Mammalogy* **91**:144–153.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* **10**:690–700.
- Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Ecoscience* **14**:214–222.
- Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology & Evolution* **17**:70–75.
- Little, S. J., R. G. Harcourt, and A. P. Clevenger. 2002. Do wildlife passages act as prey-traps? *Biological Conservation* **107**:135–145.

- MacNulty, D. R., L. D. Mech, and D. W. Smith. 2007. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy* **88**:595-605.
- Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *Journal of Wildlife Management* **73**:345-356.
- Valeix, M., H. Fritz, A. Loveridge, Z. Davidson, J. Hunt, F. Murindagomo, and D. Macdonald. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology* **63**:1483-1494.
- Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York.

