CANADIAN WILDLIFE BIOLOGY & MANAGEMENT

CWBM 2016: Volume 5, Number 1 *ISSN: 1929–3100*

Original Research

Landscape of Fear for Naïve Prey: Ungulates Flee Protected Area to Avoid a Re-established Predator

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Abstract

Populations of large carnivores are re-establishing in many areas, resulting in direct and indirect effects on prey that can influence community structure and create conflicts with humans. We documented the rapid return of cougars (*Puma concolor*) to an isolated, protected mountain range in southeast Alberta and southwest Saskatchewan, Canada, establishing the highest population density ever reported. Cougars changed both the abundance and the distribution of large ungulates, causing them to move out of forested habitats in the park and onto adjacent agricultural lands. Balancing tradeoffs for people, predators, and their prey will be a challenge for conservation biologists as large carnivores continue to expand to their former range, especially in small protected islands of habitat where there is potential for conflict with adjacent agricultural interests.

Key Words: Alberta, Cougar, Deer, Elk, Human-carnivore Conflicts, Landscape of Fear, *Puma concolor*, Saskatchewan.

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INTRODUCTION

Historically, large predators in North America were perceived as competition for food and a risk to the safety of settlers and their livestock (Kellert *et al.* 1996). Predators were heavily hunted, trapped and poisoned to the point where species such as the cougar (*Puma concolor*), wolf (*Canis lupus*), and grizzly bear (*Ursus arctos*) were extirpated from much of their original range (Berger 1998; Terborgh *et al.* 2000). In the absence of predators, ungulates and other wildlife minimize their risk of human encounters by avoiding areas used for agriculture and recreation (Cuiti *et al.* 2012). Our activities, however, also can alter hidden interactions that exist within an ecosystem, sometimes to the point of disassembling entire natural communities (Hebblewhite *et al.* 2005; Ripple *et al.* 2014).

Restoration of predators to natural systems is underway, justified by a range of ecological services that can return with their re-establishment (Schmitz *et al.* 2010; Estes *et al.* 2011). Wolves were re-introduced to Yellowstone National Park in 1995 where predation on elk (*Cervus elaphus*) has helped to restore lower trophic levels of the ecosystem (Ripple *et al.* 2001; Beyer *et al.* 2007). In other parts of western Canada and the USA, predators are reclaiming portions of their former range on their own. As we encourage policies that restore natural ecosystems back to health, we need to consider both the apparent and hidden interactions occurring within ecosystems (Sinclair and Byrom 2006). Indirect effects that predators have on other ecosystem components merit careful attention because they can have implications for the way that human-wildlife conflicts might re-ignite.

Of all predators in North America, cougars in particular are achieving an astounding natural re-establishment throughout the western and mid-western United States and Canada during the past decade (Anderson *et al.* 2010). The expansion of white-tailed deer (*Odocoileus virginianus*) populations affords cougar abundant prey throughout much of the continent (Côté *et al.* 2004). However, where livestock and agriculture predominate, as in much of the Midwestern states and provinces, only small fragments of forest provide habitats where cougar populations could re-establish without serious conflicts and persecution from humans (Thompson *et al.* 2009).

We chronicle the emergence of indirect effects across the landscape that arise when one large predator, the cougar, becomes re-established in a park that constitutes an island of protected forest habitat. Human-wildlife conflicts might be expected to rise as a growing cougar population is accompanied by risk of livestock depredation in the adjacent agricultural landscape. Instead, we show that the indirect effect of the returned predator derives from the "landscape of fear" for wild ungulates from cougar presence inside the park (Brown *et al.* 1999; Laundré *et al.* 2001). Although prey typically avoid localities with a high risk of predation – even when those areas contain food and cover (Lima 1998) – naïve prey may not possess knowledge about local predators (Berger *et al.* 2001). Successful hunting, and in turn, establishment of a population by a new predator, is dependent upon behavioural changes, or lack thereof, by naïve prey (Brown *et al.* 1999).

MATERIAL AND METHODS

Study Area

Our study focused on Cypress Hills Interprovincial Park, a 400 km² forested region that rises more than 500 m above the surrounding prairie ecosystem in southeast Alberta and southwest Saskatchewan, Canada (49°40´N, 110°15´W) (Figure 1). Cougars and wolves were eradicated from the Cypress Hills nearly 100 years ago and the area was given protected status as a Forest Reserve at about the same time in 1906, allowing wild ungulate populations to increase to high densities. Cypress Hills Interprovincial Park affords attractive habitats for wildlife; without large predators until the return of cougars wild ungulates had thrived in the park, evading human disturbances that prevailed on adjacent private lands.

Cougars had been occasionally sighted in the Park since the late 1990s, but not until 2006 was a resident breeding population of cougars confirmed. During a 3-year period from 2007 to 2009, we captured cougars on wildlife cameras 73 times, including several family groups (Figure 2). Based on individual characteristics (e.g., unique tails and/or ears, track size, body size) identified on photos taken from motion-activated remote cameras and observed while snow-tracking, and during capture efforts as well as from radiotelemetry of 6 cougars (Lotek, Newmarket Ontario), we estimated an interprovincial population of 15 - 20 resident adults, leading to an estimated density of 6.5 - 8.25 cougars/100 km^2, one of the highest ever reported (Sweanor and Logan 2010). Cougars' avoidance of open grasslands and agricultural lands has been well documented (Dickson and Beier 2002) and our telemetry data from 6 adult cougars revealed strong selection for the island of forest that is mostly contained within the park (Figure 1). Over 70% of their kills of ungulate prey occurred in forest cover; prey were identified by telemetry clusters and scat analysis (see Bacon *et al.* 2011 for capture, monitoring, and prey analysis). All field methods were approved under Animal Care Protocol #568802 authorized by the University of Alberta Animal Care Committee in compliance with guidelines approved by the Canadian Council on Animal Care.

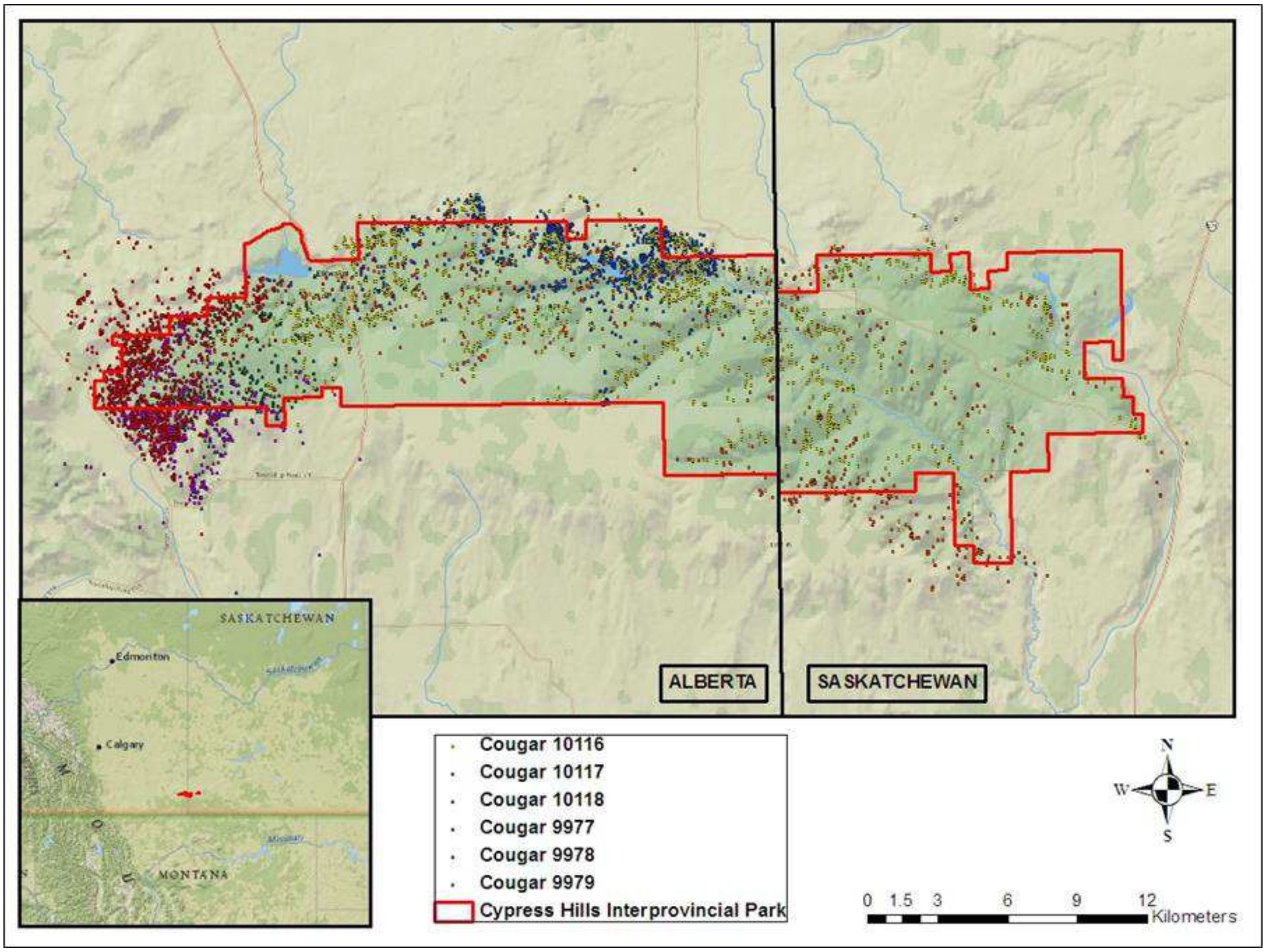

Figure 1. GPS telemetry relocations of 6 radiocollared cougars (colored dots) monitored March 2008 to December 2009 in Cypress Hills Interprovincial Park, Canada. The red line is the park boundary.

Field Survey

Aerial ungulate surveys were conducted annually in the Cypress Hills by Alberta Fish and Wildlife beginning in 1977 for managing elk harvests. Because the cougar population increased since the first detection in the mid-2000s, we analyzed aerial survey data collected each winter from 2000 to 2009. Each year, traditional elk wintering grounds were initially surveyed, followed by detailed aerial coverage of 4 identified survey units that include all forested areas of the park and adjacent lands. Although there are constraints of sightability in forest compared to open land cover types (Fleming and Tracey 2008), we assumed that bias was the same each year because the observers and survey methods were identical throughout the study period.

Data Analysis

Using a Geographical Information System (GIS) map of the study area in ArcMap 9.2 (ESRI 2006, Redlands, California, USA), we placed all ungulate locations on a 1-km^2 raster grid. We constrained our analysis to known cervid habitats during that decade, defined by the observation of any cervid during aerial surveys in any year between 2000 and 2009. We characterized each grid cell based on the dominant land-cover type, and denoted whether the cell was inside (1) or outside (0) the park boundary. We used zero-inflated negative binomial (ZINB) regression to characterize the distribution of counts of elk and white-tailed deer and the relative abundance of mule deer (*Odocoileus hemionus*) as

Figure 2. Family of 3 cougars travelling along a hiking trail in Cypress Hills Interprovincial Park, Alberta, December 23, 2009. Photo captured on a Reconyx RC55 RapidFire camera (Reconyx, Inc., Holman, Wisconsin, USA).

functions of the park boundary. In addition, the distribution of mule deer was modeled as a function of the amount of forest cover within each 1-km^2 pixel. Unlike Poisson regression, the negative binomial model does not assume equal variance and mean but rather that the variance is greater than the mean, which is appropriate for ecological studies because many animals, such as ungulates, aggregate into groups (Southwood and Henderson 2000). Zero-inflated methods simultaneously model the probability that the species occupies the grid cell (which gives relative distribution) and abundance (Wenger and Freeman 2008).

Land cover of the 270 used cells was comprised of 42% forest, 32% grasslands, 14% agricultural lands, 11% shrub, and 1% water. The zero-inflated model accounts for an excess of zeros, or "unused", cells in each year of the analysis, verified by a Vuong (V) test. Predictor covariates for each species were selected a priori based on previously published habitat-selection models (Williamson and Hirth 1985; Lingle and Wilson 2001; Vucetich *et al.* 2005; Naylor *et al.* 2009). All statistical analyses were conducted using STATA 11.0 (STATA 2009).

RESULTS

Winter aerial ungulate surveys revealed that cougars have indirect effects on the distribution of prey populations. The presence of cougars during the past decade apparently caused deer and elk to leave the security of forest cover that now harbors a highly effective predator (Figure 3). Mule deer responded most strongly to the presence of cougars, increasing 6% per year outside the Park relative to inside even though total counts decreased throughout the study period (β = - 0.037, P = 0.03), and specifically showing a 7% rise in their occurrence on grasslands and agricultural land cover types relative to forests (β = 0.133, P = 0.001).

Figure 3. Elk feeding at hay bales intended for cattle in Alberta. Photo credit Alberta Fish and Wildlife.

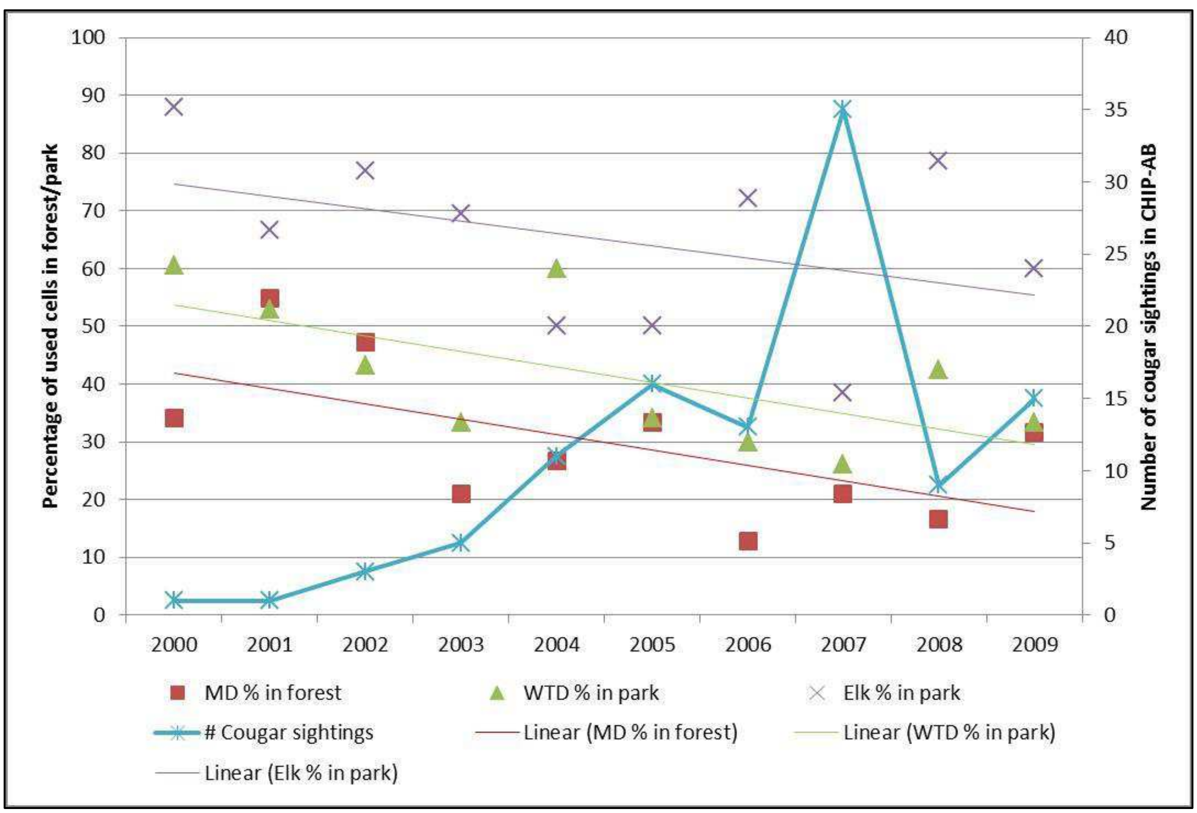

Figure 4. Probability of mule deer occurring outside of forest, and white-tailed deer and elk occurring outside the protected park, from 2000 to 2009. Cougar sightings reported to Cypress Hills Interprovincial Park-Alberta during the same time period is included on the secondary y-axis.

Table 1. Estimated coefficients, standard error (SE), P-value and 95% confidence intervals (CI) for zero-inflated negative binomial (ZINB) models used to estimate change in distribution over time for elk, mule deer and white-tailed deer populations in Cypress Hills Interprovincial Park, 2000-2009. Inflate coefficients represent the strength of those covariates that account for "excess" zeros beyond those predicted by the negative binomial model.

Species	Variable	Coeff.	SE	P value	95% CI	Z-stat for zero-inflation
Elk	park	0.86	0.268	0.019	(0.139, 1.58)	2.29
	year	0.021	0.064	0.739	(-0.104, 0.147)	
	-cons	-40.76	128.37	0.751	(-292.36, 210.84)	
Inflate	park X year	0.144	0.073	0.047	(0.002, 0.287)	
	park	-290.6	145.8	0.046	(-576.37, -4.804)	
	year	0.007	0.054	0.896	(-0.098, 0.113)	
	-cons	-12.42	108.3	0.909	(-224.7, 199.9)	
Mule deer	park X year	-0.074	0.031	0.018	(-0.135, -0.012)	8.12
	year	-0.037	0.017	0.03	(-0.071, -0.0035)	
	park	148.05	62.59	0.018	(25.36, 270.74)	
	-cons	77.46	24.801	0.026	(9.25, 145.67)	
Inflate	forest X year	0.133	0.04	0.001	(0.052, 0.214)	
	forest	-265.6	83.2	0.001	(-428.72, -102.6)	
	year	-0.035	0.021	0.104	(-0.077, 0.007)	
	-cons	71.35	43.2	0.099	(-13.32, 156.03)	
White-tailed deer	grass	0.355	0.166	0.03	(0.027, 0.68)	4.36
	ag	0.44	0.165	0.008	(0.115, 0.764)	
	shrub	0.251	0.189	0.184	(-0.119, 0.621)	
	year	0.026	0.021	0.22	(-0.015, 0.067)	
	-cons	-51.36	42.62	0.228	(-134.9, 32.19)	
Inflate	park X year	0.153	0.046	0.001	(0.062, 0.244)	
	park	-307.15	93.1	0.001	(-489.63, -124.67)	
	year	-0.119	0.03	0.00	(-0.178, -0.06)	
	-cons	241.18	60.85	0.00	(121.9, 360.4)	

Likewise, white-tailed deer relative abundance increased on both grassland ($\beta = 0.355$, $P = 0.033$) and agricultural land ($\beta = 0.44$, $P = 0.008$) relative to forest cover, and their proportional distribution shifted from inside the protected area to more outside park boundaries ($\beta = 0.153$, $P = 0.001$). Also, the proportion of the park landscape that was unoccupied by elk increased during the period of cougar re-establishment ($\beta = 0.144$, $P = 0.047$), although their abundance still remained higher inside the park ($\beta = 0.86$, $P = 0.019$) (Table 1, Figure 4).

DISCUSSION

The shift in distribution of cervids, particularly mule deer, during the decade of cougar re-establishment demonstrates that cougars have restored a landscape of fear in the Cypress Hills, causing prey to leave the security of the protected park and forest cover that now harbors a highly effective predator. During the period of our study, radiotelemetry data for cougars showed that the predator remained primarily within the confines of the protected forest (Figure 1). Analysis of aerial ungulate surveys showed that deer and elk shifted their distribution outside the Park during the same time period, when cougar presence was the only significant change in the region. These results are corroborated by local ranchers, who observed an increase in deer on their agricultural lands subsequent to the return of cougars to the Cypress Hills.

When new predators establish and their population explodes within a decade, as has been the case for cougars in the Cypress Hills, we expect to see direct effects on prey population size resulting from predation; indeed, 76% of cougar kills in the Cypress Hills were deer, and 15% were elk (Bacon *et al.* 2011). Anticipating and planning for the indirect effects of a landscape of fear is more difficult. Isolated, island-like protected areas exist throughout the mid-western states and provinces that might serve as stepping stones to facilitate expansion of predator populations farther into their historic range (Sweanor *et al.* 2000). However, most of these protected areas are not sufficiently large to contain the natural interactions that exist within ecosystems, and human-wildlife conflicts inevitably arise as the dynamics between predator and prey spills over onto private land (Forbes and Theberge 1996; Sinclair 2012). Prey that had lived with little fear of large predators for ca. 40-50 generations must now trade-off between avoiding humans and avoiding predators. Indeed, in some instances, humans might act as a shield against cougar predation because they present less risk of mortality for prey (Berger 2007) and because cougars are deterred from human-dominated areas (Morrison *et al.* 2014).

Predation affects broad ecosystem processes and biodiversity, and has implications – both beneficial and detrimental – for all components of an ecosystem, including humans. As prey adapt to the presence of predators, so too must humans adopt new behaviours as predators reclaim portions of their former ranges (Shivik 2006). Our results demonstrate that conservation efforts aimed at protecting species on landscapes must consider the lines of dependence that are recreated with the entire system, rather than merely at a single-species perspective (Estes *et al.* 2011). Predators might aggravate human-wildlife conflicts, but this could be solved with larger and more abundant parks, or with buffered lands connecting parks. Balancing ecological tradeoffs between humans and wildlife is a challenging issue that resource managers throughout North America now face, and must be resolved if there is any hope for continued coexistence (Treves and Bruskotter 2014).

ACKNOWLEDGEMENTS

Funding was provided by the University of Alberta, Alberta Environment and Parks, Saskatchewan Environment, Alberta Conservation Association, Alberta Sport Recreation Parks and Wildlife Foundation, Medicine Hat Fish and Game Association, Canadian Wildlife Federation, TD Friends of Environment, Heritage Association of Cypress Hills, Safari Club International-Northern Alberta Chapter, and The Lions Club. Ungulate surveys were conducted by J. Taggart, D. Eslinger and O. Tarnasky. We are grateful to many volunteer field technicians, and for the assistance of L. Hindbo, K. and A. Knopff and N. Webb during captures. C. Nielsen, J. Northrup, and K. Dawe provided assistance with GIS and statistical analysis. We thank Cypress Hills Interprovincial Park-Alberta for in-kind and logistical support during field work. Thanks also to local landowners who provided access to their lands. Spatial data provided by Alberta Environment and Parks, Agriculture and Agri-Food Canada, and Natural Resources Canada. Thanks to O. Schmitz, K. Stewart, C. Cassady St. Clair, N. Krogman and anonymous reviewers for comments on the manuscript.

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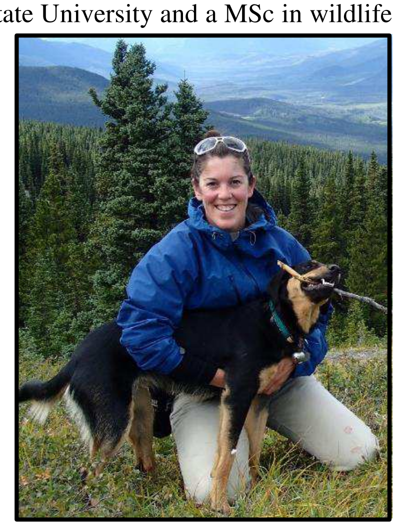

worked as a species-at-risk biologist for the Alberta provincial government's caribou program, assisted in cheetah (*Acinonyx jubatus*) reproductive research for the

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Received 9 January 2016 – Accepted 18 March 2016