

University of Montana

## ScholarWorks at University of Montana

---

Undergraduate Theses and Professional Papers

---

2015

# Wolf-Cougar Co-occurrence in the Central Canadian Rocky Mountains

Ellen Brandell

ellen.brandell@umontana.edu

Follow this and additional works at: <https://scholarworks.umt.edu/utpp>



Part of the [Biology Commons](#), and the [Population Biology Commons](#)

**Let us know how access to this document benefits you.**

---

### Recommended Citation

Brandell, Ellen, "Wolf-Cougar Co-occurrence in the Central Canadian Rocky Mountains" (2015).

*Undergraduate Theses and Professional Papers*. 58.

<https://scholarworks.umt.edu/utpp/58>

This Thesis is brought to you for free and open access by ScholarWorks at University of Montana. It has been accepted for inclusion in Undergraduate Theses and Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).

**CO-OCCURRENCE OF WOLVES (*CANIS LUPIS*) AND COUGARS (*PUMA  
CONCOLOR*) IN THE CENTRAL CANADIAN ROCKY MOUNTAINS**

ELLEN ELIZABETH BRANDELL

Spring Semester, 2015

Thesis submitted in fulfillment of the requirements of a Senior Honors Thesis  
WILD499/HONR499  
Wildlife Biology Program  
The University of Montana  
Missoula, Montana

Graduating May 16, 2015 with a Bachelors of Science in Wildlife Biology

Approved by:

Committee Chair: Dr. Mark Hebblewhite,  
Wildlife Biology Department,  
University of Montana

Committee Members:  
Dr. Mike Mitchell,  
Montana Cooperative Wildlife Research Unit,  
University of Montana

Dr. Hugh Robinson,  
Wildlife Biology Faculty Affiliate &  
Panthera, Landscape Ecologist

## **Abstract**

Cougars and wolves are top carnivores that influence the dynamics of an ecosystem, including prey behavior and dynamics, and interspecific competition. Studies about the interactions between wolves and cougars typically find wolves are dominant competitors to cougars. We examined single-species, single-season occupancy models and co-occurrence models of wolves and cougars in the Central Canadian Rocky Mountains to understand interactions between these two species on a grand landscape. Data was collected from 2012-2013 using remote wildlife cameras and separated into seasons. Naïve occupancy estimates were larger for wolves in both seasons, but both species had smaller ranges in winter. There were only slight differences in environmental covariates for the single-species, single-season occupancy models, yet wolf occupancy estimates were still higher than cougars in both seasons. When wolves were species A in the co-occurrence models, results showed cougar occurrence and detection to be independent of wolf presence. However, when cougars were species A in the co-occurrence models, top models showed wolf occurrence and detection to be conditional on cougar presence. Overall, the top competing models in both seasons for either species A had some conditionality, yet no environmental covariates were significant in any co-occurrence model. These results are difficult to interpret; we suspect slight spatial separation between wolves and cougars in this study area, but further studies about smaller-scale competition could uncover more significant interactions between the two carnivores.

## **Acknowledgements & Funding**

This project was only possible with the help of numerous Parks Canada employees from Waterton Lakes, Yoho, Kootenay, Banff, and Jasper National Parks. These individuals created the camera grid system, set up cameras, serviced cameras, and created a data-sharing program. This work allowed for not only this study to come out of this effort, but also numerous other studies and information for the Parks. Further, those at the Ya Ha Tinda Ranch serviced cameras, provided housing and horses, and overall helpfulness throughout many Parks camera-based projects. We also thank many data-collection volunteers for their time and effort.

We would like to thank Robin Steenweg (PhD. candidate University of Montana, Waterton Lakes wildlife biologist) for his extensive help in data analysis and great insight into the project. Similarly, Jesse Whittington (PhD, Parks Canada) has provided help with data analysis, data sharing, and servicing of cameras. Without this aid, this project would not have even gotten started.

Funding was provided by: Parks Canada, University of Montana, University of Calgary, Panthera Inc., and Alberta Tourism, Parks and Recreation.

## Table of Contents

<b>Abstract</b> .....	2
<b>Acknowledgements &amp; Funding</b> .....	2
<b>Table of Contents</b> .....	3
<b>Introduction</b> .....	3
<b>Table 1</b> .....	6
<b>Table 2</b> .....	7
<b>Methods</b> .....	7
<b>Figure 1</b> .....	7
<i>Study Area</i> .....	7
<i>Remote Camera Trapping Design</i> .....	8
<i>Occupancy Modeling</i> .....	9
<b>Equation 1</b> .....	9
<i>Co-occurrence Modeling</i> .....	10
<b>Equation 2</b> .....	10
<b>Table 3</b> .....	10
<i>Environmental Covariates</i> .....	11
<b>Results</b> .....	11
<i>Remote Camera Trapping</i> .....	11
<i>Single-species Occupancy Models</i> .....	12
<b>Table 4</b> .....	12
<b>Table 5</b> .....	12
<b>Table 6</b> .....	12
<b>Table 7</b> .....	13
<b>Table 8</b> .....	13
<b>Table 9</b> .....	14
<i>Co-occurrence models</i> .....	14
<b>Table 10</b> .....	15
<b>Table 11</b> .....	15
<b>Table 12</b> .....	15
<b>Table 13</b> .....	16
<b>Table 14</b> .....	16
<b>Table 15</b> .....	16
<b>Discussion</b> .....	17
<b>Literature Cited</b> .....	22

## Introduction

Cougars (*Puma concolor*) and gray wolves (*Canis lupus*) are two of the top carnivores in North America. Top carnivores can influence the dynamics of an ecosystem, including prey behavior, abundance, and distribution, and management practices (Ripple et al. 2014). In recent decades, wolves have been reintroduced into regions of their historical North American range, as well as recolonized regions that

they were formally extirpated (USFWS et al. 2008). This reestablishment of wolves has widespread effects on these ecosystems, in which cougars are often already established. The effects of wolves on ecosystems include trophic cascades where wolves directly affect large herbivore prey and vegetation (Hebblewhite et al. 2005; Ripple et al. 2014). Perhaps more underappreciated, however, is the possibility that interactions between wolves and their competitors will change the dynamics of these ecosystems (Hebblewhite and Smith 2011).

Wolf reestablishment will impact competitors, such as cougars, in many of the same ways as they impact their prey species (Ruth et al. 2011, Kortello et al. 2007, Bartnick et al. 2013, Husseman et al. 2013, Alexander 2006). There are two types of competition that could change with wolf recovery; interference competition where competitors directly kill one another, and exploitative competition where predators compete via effects on a shared prey species (MacArthur and Levins 1967, Elbroch et al. 2014). Together, these types of competition help explain wolf-cougar interactions and can be used to predict ecosystem dynamics. Both being top carnivores, many studies have focused on understanding the types and magnitude of competition between wolves and cougars (Ruth et al. 2011, Kortello et al. 2007, Bartnick et al. 2013, Husseman et al. 2013, Kunkel et al. 1999). While some studies have been able to conduct before-wolf and after-wolf comparisons (Ruth et al. 2011, Bartnick et al. 2013), most studies are forced to draw conclusions based on observational data because manipulative experiments are nearly impossible and potentially unethical to perform.

In the majority of studies, wolves were the dominant species in an ecosystem and cougars were subordinate in interactions with wolves (Ruth et al. 2011, Kortello et al. 2007, Bartnick et al. 2013, Husseman et al. 2013). Evidence for both interference and exploitative competition between wolves and cougars support the general result from previous studies that wolves may be better competitors. For example, Ruth et al. (2011) examined cougar survival in Greater Yellowstone following wolf recovery and found that about 20.025% of mortalities were due to wolf killings. Conversely, there are no studies we found to date that provide evidence of cougars killing wolves (Smith et al. 2010, Callaghan 2002, Webb et al. 2011). This may be due to asymmetric competition in that wolves are not as impacted by cougars, yet cougars heavily impact the dominant competitor, wolves. There may also be a reporting bias as people assume cougars do not kill wolves, they could be less likely to look for such a situation. As a consequence of this asymmetric interference competition, it is not unusual for wolves to displace cougars from their kills and scavenge the kill (Kortello et al. 2007). Cougars also temporally separate themselves from wolves on a small-scale (Kortello et al. 2007).

Exploitative competition is an indirect ecological interaction and involves a common limiting resource, such as the same prey (Hebblewhite and Smith 2011). Cougars and wolves eat very similar large ungulate prey when sympatric, with differences only in size, location of prey, or age. For example, Alexander (2006) found that cougars in south-central Alberta changed their habitat selection over

time with the reestablishment of wolves, and therefore their prey selection also changed. Kortello et al. (2007) had similar results from a wolf-cougar interaction study in Banff National Park, Alberta; diet overlap between the species diverged with an increase in wolf population and expansion of range. Similarly, cougars may switch their prey source as they spatially separate themselves from wolves (Bartnick et al. 2013). In Yellowstone National Park, wolves and cougars have differing kill rates throughout the year; wolves acquire the least biomass during summer, whereas cougar biomass acquisition is high during the summer (Metz et al. 2012). Wolves and cougars may also consume the same proportions of prey species, with similar ages condition, but in different habitat types as a spatial mechanism to decrease exploitative competition (Husseman et al. 2013).

However, there is also potential for wolves and cougars to have limited competition on a landscape. Because these types of studies are observational, there may be numerous confounding factors that are left unaccounted for. Some studies' results show that wolves and cougars can live sympatrically, without changing their behavior substantially. Kunkel et al. (1999) found that in Glacier National Park, Montana, cougars did not change their prey selection in the presence of recovering wolves and the two species had almost identical prey composition. Rates of biomass acquisition were similar year-round in Alberta, Canada (Knopff 2010). These results are often forgotten because of the large amount of recent publications on the effects of recolonizing wolves. The differences between wolves and cougars on a spatial scale may be overemphasized by this current interest. Further, many of these study areas have not been reevaluated years after wolf recolonization; therefore, we do not know if the initial changes in cougar behavior with wolves remain, or if cougars are able to acclimate to the presence of wolves and occupy similar areas with time.

Studying large carnivores to test for competition is financially and logistically challenging. Most previous studies have relied on intensive analyses of radiocollared individuals over small areas relative to population ranges of these carnivores. To overcome these limitations, remote wildlife cameras have recently grown in popularity (Burton et al. 2015, O'Brien et al. 2008). Cameras are an indirect method of observing species' distribution patterns, and provide presence/absence data for a species at a given site. The application of occupancy modeling to camera trapping data explicitly accounts for imperfect detection to estimate the true occupancy in single species applications (MacKenzie 2004). In two species models, the presence/absence data for a site can be used to infer competition between species if there are temporal and spatial differences (MacKenzie et al. 2006). MacKenzie developed the first co-occurrence framework for occupancy models, inferring competition between two species of salamanders in Great Smoky Mountain National Park (Reed 2011, Monterroso 2014). In another study done by Monterroso (2014), wildlife cameras were used to explore circadian patterns of mesocarnivores and their prey on the Iberian Peninsula. Because occupancy modeling estimates both probability of detection and probability of occupancy, this data can be used to understand how the presence of a species impacts the detection of another species. For example, Bailey et al. (2009) discuss the finding that northern spotted owls

vocalize less in the presence of barred owls (Crozier et al. 2006); this may create a detection bias and skew results. Nonetheless, occupancy and co-occurrence modeling can account for this. These studies were able to assess overlap between species and infer why these patterns might exist based on the presence/absence data.

Here, we will test for evidence of competition between wolves and cougars using co-occurrence occupancy modeling in the Rocky Mountains of Canada. My hypotheses and predictions are based on MacKenzie (2006) and refined recently by Robinson et al. (2014) (Table 1.). Table 1. is from Robinson (2014), defining parameters used in the co-occurrence model. Specifically, we have formulated five hypotheses based on current literature and knowledge of dominance interactions on detection and occupancy; 1) In the presence of wolves, cougars will occupy different habitat types – i.e. high elevations, more intense slopes, and more forested areas; 2) In the absence of wolves, cougars will occupy similar habitats to wolves; 3) In the presence of wolves, cougars will decrease their probability of detection while occupancy stays approximately constant; 4) During winter, when both species have a confined range, potential for competition will be greater because of more overlap in distribution; 5) Due to other factors, wolves and cougars will not compete on a level detectable by occupancy modeling, or will have very little competition. Evidence for the third hypothesis comes from a grizzly bear, bear-black bear study (Steenweg et al. Progress Report 2012) where, in the presence of grizzly bears, black bears avoided the main trails that grizzlies were using. Black bear occupancy remained approximately constant at those sites, yet the black bears decreased their detection by using lesser trails in the cell to avoid grizzly bears. Crozier et al. (2006) also supports the third hypothesis in that northern spotted owls vocalize less in the presence of a competitor, the barred owl. This decreases the detection of northern spotted owls while occupancy is relatively unchanged. The fifth hypothesis could result from many factors, including: decreased exploitative competition because of large prey populations, smaller-scale competition such as temporal separation between wolves and cougars, tolerance of each other because of evolutionary history, and other mechanisms.

**Table 1.**

Parameters used to estimate competition in co-occurrence models of wolves and cougars in the Central Canadian Rocky Mountains.

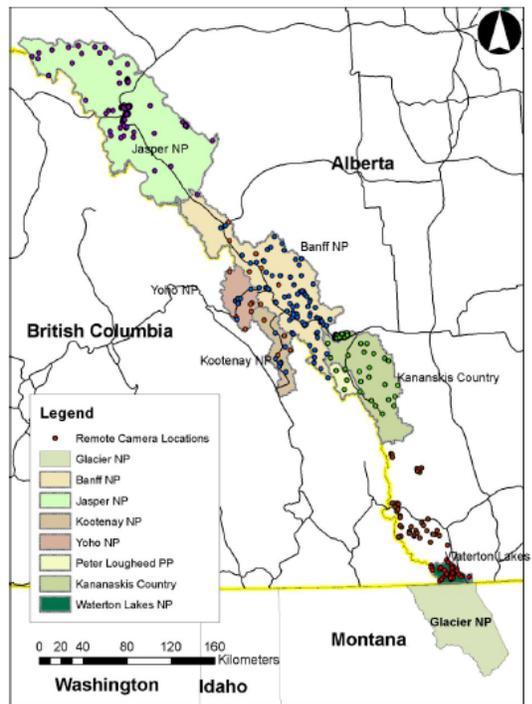
Parameter	Definition
$\psi_A$	Species A, probability of occupancy
$\psi_{Ba}$	Species B, probability of occupancy with species A absent
$\psi_{BA}$	Species B, probability of occupancy with species A present
$p_A$	Species A, probability of detection with species B absent
$p_B$	Species B, probability of detection with species A absent
$r_A$	Species A, probability of detection with species B present
$r_{BA}$	Species B, probability of detection with both species present and species A detected during sampling period
$r_{Ba}$	Species B, probability of detection with both species present and species A not detected during sampling period

**Table 2.**

Hypotheses in terms of ecology and occupancy and co-occurrence models.

Hypothesis	Occupancy predictions	Co-occurrence predictions
Null: no competition between wolves and cougars	No difference between covariates for $p$ and $\psi$	$\psi_A = \psi_{BA} = \psi_{Ba}$ $p_A = r_A$ $p_B = r_{BA} = r_{Ba}$
Wolves are dominant over cougars	Different and opposing covariates on $p$ and $\psi$	$\psi_A > \psi_{BA}/\psi_{Ba}$ $p_A > p_B$ $r_A > r_{BA}/r_{Ba}$
During winter, there will be stronger competition between wolves and cougars	Different and opposing covariates on $p$ and $\psi$ , with higher magnitude of difference	$\psi_A \gg \psi_{BA}/\psi_{Ba}$ $p_A \gg p_B$ $r_A \gg r_{BA}/r_{Ba}$

## Methods



**Figure 1.**  
Study area with 10x10 km grid cells and camera placements.

### Study Area

The study area is located in Alberta and British Columbia, Canada, including Waterton Lakes, Kootenay, Banff, Yoho, and Jasper National Parks and some adjacent provincial lands (Fig. 1). Wolves were extirpated from this Park system in the mid-1950s due to a Nation-wide poisoning campaign (Gunson 1992) and

recolonized the Canadian Rockies from north to south starting in the 1970's in Jasper (Carbyn 1974), late 1980's in Banff (Paquet 1993), and 1990s' in Waterton (Pletscher et al. 1991). In contrast, cougars have remained the Parks since earliest historical records (Holroyd & Van Tighem 1983). This ~21,000 km<sup>2</sup> landscape encompasses the Northern Rocky Mountains and is mainly comprised of montane and subalpine forests. The montane forests primarily have lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), willow (*Salix sp.*), and aspen (*Populus tremuloides*) tree species. The subalpine regions consist of Englemann spruce and subalpine fir (*Abies lasiocarpa*). The tree line is located at approximately 2,300 meters. Valley bottoms are wet throughout most spring and summer, resulting in wetland and muskeg regions. The study area also has a few thousand glaciers. Multiple large rivers intersect the area, such as the Bow River and Kootenay River.

The ecosystem has short, mild summers and long, cold winters. The warmest month is July, with an average high of 25<sup>o</sup> C in the southern region of the area. The coldest months are December and January, with an average low of -13<sup>o</sup> C in the northern region of the area. The summer has the most precipitation of the year, mostly in the form of rainfall (June with 55+ cm. per month), but winters bring heavy snowpack as well (40+ cm. per month). Prey species are abundant and include: elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), with rarer prey being moose (*Alces alces*) and mountain goats (*Oreamnos americanus*), and in Jasper, mountain caribou (*Rangifer tarandus*). Other large carnivores in the study area include: grizzly bear (*Ursus arctos*) and black bear (*Ursus americanus*).

### *Remote Camera Trapping Design*

Remote cameras were systematically placed in 10x10 km (e.g. 100 km<sup>2</sup>) cells across the study areas with large carnivores as the focal species for monitoring (Steenweg et al. Progress Report 2012). Camera types were Panthera (Panthera USA, New York, NY, USA) and Reconyx Hyperfire HC500 (Reconyx, Holmen, WI, USA); both are passive infrared cameras. Cameras were placed on trails because trails are used by many carnivores for easy travel, and this increases detection probability equivalent to baited camera traps for most species (Burton et al. 2015, Steenweg et al. Final Report 2015). Each camera was mounted on a tree angled towards the trail, about 1 meter off of the ground, and camouflaged. When the camera was triggered, it would take five sequential photographs. Cameras outside of the Parks had flashes during the night, and those within the Parks did not. Panthera cameras required six AA batteries and Reconyx Hyperfire cameras required twelve AA batteries. Due to differing battery life in the camera types, Pantheras were serviced more often (3-6 times a year) and Hyperfires were serviced less often (1-3 times a year). In this study, cameras were set up before November 2012 and remained in the same locations through October 2013.

Camera data was analyzed using Timelapse software (Greenberg and Goudin 2012). Data was classified by species, number of individuals, and event. Classifiers were Parks employees and volunteers. Groups of pictures of the same species were considered an event; there was a five-minute threshold between events, where if there were no pictures of the same species for five or more minutes, the next picture was considered a distinct event. Multiple events could occur simultaneously if different species were in the same picture. In this case, whichever species had a picture first was considered the first event. If the species appeared in the first picture together, event order was assigned arbitrarily. The specific event classification was assigned to the picture containing all or most of the individuals in the event. The length of the event was undefined; it occurred as long as there were pictures of a species, until there were no pictures of that species for five or more minutes.

### *Occupancy Modeling*

This indirect method of observing species' distribution patterns provides detection/non-detection data, which is appropriately addressed through occupancy modeling (MacKenzie et al. 2006). Occupancy models use the patterns of detection/non-detection, known as detection histories, at specific locations to estimate occupancy probability while accounting for imperfect detection of the species (MacKenzie et al. 2002, 2006; MacKenzie and Bailey 2004). Environmental covariates can then be added to the estimates to explain the distributional patterns of occurrence (MacKenzie et al. 2002, 2006). We describe environmental covariates we examined to explain cougar and wolf occupancy below.

$$L(\psi, p) = [\psi^n \prod_{t=1}^T p_t^{n_t} (1 - p_t)^{n - n_t}] \times [\psi \prod_{t=1}^T (1 - p_t) + (1 - \psi)]^{N-n}.$$

#### **Equation 1.**

The likelihood function from MacKenzie et al. (2002); describes the likelihood of getting our occupancy data, given the detection probabilities at each site. This equation describes how parameters are estimated for the single-species, single-season occupancy models through maximum likelihood in a logistic regression framework.

I will be using  $\hat{p}$  to denote the probability of detecting a given species at the camera site and  $\hat{\psi}$  to denote the probability of a given specie occupying a camera site. For example, a detection history of 101 means that the species had pictures taken on the first and third sampling occasions, but not the second. The naïve detection probability ( $\hat{p}$ ) for this history would therefore be  $2/3 = 0.6667$ . The site is considered occupied because there was a detection,  $\psi = 1$ . Through modeling, we can assign covariates that help describe the probability of detecting a species and the probability that a species occupies a site; this allows us to be able to predict detection and occupancy across a landscape. We also calculated the cumulative detection probability for each season; cumulative  $p$  is the probability of detecting a

wolf or cougar at least once over the entire season, if wolves/cougars truly occupy that site. Although  $p$  may be considered low for our one-week trapping sessions, over the course of the season, it accumulates to a high probability of detection.

Data collection occurred from 2012-2013. The data was split into 7-day trapping sessions for each site; this means that the detection history was a compilation of weekly data. This was done to increase  $p$  and allow for stronger estimates. The data was also divided into seasons based on current literature on wolves and cougars, and to reduce occupancy differences throughout the year that are not due to interspecific competition. We defined winter as November 2012-April 2013 and summer as May 2013-October 2013. Using the remote camera data, single-species, single-season occupancy models were created using the UNMARKED package in Program R (Fiske and Chandler 2011). Top models were selected using Akaike's Information Criterion (AIC) where the model with the lowest AIC score and no uninformative parameters (Arnold 2010) was chosen (Burnham & Anderson 2002). These top models were put into Program PRESENCE, where the co-occurrence model was built (Hines 2012).

### *Co-occurrence Modeling*

Co-occurrence modeling compares the natural, spatial variation in occupancy between species. This likelihood based method, developed by MacKenzie et al. (2004, 2006), estimates the species interaction factor (referred to as SIF), which is a ratio of how likely the two species are to co-occur compared to what would be expected under a hypothesis of independence (Richmond 2010). SIF can be calculated as:

$$\varphi = \frac{\psi^A \psi^{BA}}{\psi^A (\psi^A \psi^{BA} + (1 - \psi^A) \psi^{Ba})}$$

#### **Equation 2.**

Species Interaction Factor using co-occurrence modeling

An SIF value of one indicates the two species occur independently,  $SIF > 1$  suggests the two species are more likely to co-occur together than expected, and a  $SIF < 1$  suggests the species avoid each other – i.e. species B is less likely to occur with species A than expected (Robinson 2014).

Using the top single-species, single-season occupancy model covariates, we chose covariates for univariate models for both  $\hat{p}$  and  $\hat{\psi}$  to test in the co-occurrence model. Few covariates are typically used in co-occurrence models; i.e. Reed (2011) – 3 on  $p$ , 0 on  $\psi$ ; Bailey et al. (2009) – 2 on  $p$  and  $\psi$ ; Robinson (2014) – 3 on  $p$ , 1/0 on  $\psi$ ; Apps (2006) – 1 on  $p$  and  $\psi$ . I tested the strength of slope and elevation on co-occurrence by creating four separately models:

#### **Table 3.**

Description of co-occurrence models, in words and in terms of parameters

Models	Parameters for detection	Parameters for occupancy
Independent $p$ , independent $\psi$	$p_A=r_A=1$ $p_B=r_{BA}=r_{Ba}=1$	$\psi_A=1$ $\psi_{BA}=\psi_{Ba}=1$
Independent $p$ , conditional $\psi$	$p_A=r_A=1$ $p_B=r_{BA}=r_{Ba}=1$	$\psi_A=1$ $\psi_{BA}=1$ $\psi_{Ba}=1$
Conditional $p$ , independent $\psi$	$p_A=r_A=1$ $p_B=1$ $r_{BA}=r_{Ba}=1$	$\psi_A=1$ $\psi_{BA}=\psi_{Ba}=1$
Conditional $p$ , conditional $\psi$	$p_A=r_A=1$ $p_B=1$ $r_{BA}=r_{Ba}=1$	$\psi_A=1$ $\psi_{BA}=1$ $\psi_{Ba}=1$

### *Environmental Covariates*

We developed a set of spatial environmental covariates that were the most widely used in wolf and cougar occupancy models, and that also represented environmental or spatial covariates which might help explain spatial avoidance based on previous studies (Ruth et al. 2011, Kortello et al. 2007, Bartnick et al. 2013, Husseman et al. 2013, Oakleaf et al. 2006, Hebblewhite and Merrel 2008). These included elevation, slope, landcover type (7 categories), distance to primary roads, distance to secondary roads, and NDVI; all models were screened for collinearity using a correlation coefficient of 0.5.

The chosen environmental covariates are important in describing wolf and cougar locations. Numerous studies have found cougars tend to occupy landscapes with steeper slopes, more rugged terrain, more forested areas, and higher elevations (Ruth et al. 2011, Bartnick et al. 2013, Husseman et al. 2013, Alexander 2006). On the other hand, wolves tend to occur at lower elevations, such as valley bottoms, more open landscapes, and less steep slopes (Husseman et al. 2013, Alexander 2006, Oakleaf et al. 2006, Hebblewhite and Merrel 2008, Bartnick et al. 2013). Habitat differences between wolves and cougars are important in understanding spatial separation, therefore these covariates were the most likely to demonstrate a distributional difference if it existed. In this study, NDVI refers to canopy-cover using a 250-meter resolution; a high NDVI is interpreted as higher canopy-cover, or more forested areas, and low NDVI is lower canopy cover, or open landscapes. The seven landcover types include: open-coniferous, closed-coniferous, mixed-deciduous, herbaceous, shrub, water, and rock/barren. Elevation, slope, and landcover are at a 30-meter resolution. The anthropogenic covariates were distance to primary and secondary roads. Due to the very low amount of human traffic in the study area, roads were the most appropriate human factor affecting these species' distributions. For this, we used a decay function where the impact of roads asymptotes at about 2 km. because past studies have demonstrated the negligible effect of roads after 2 km (Apps et al. 2004, Whittington et al. 2011). For further information, see Steenweg et al. (Progress Report 2012 – Appendix 6.0 A)

## **Results**

### *Remote Camera Trapping*

We used cameras with at least four weeks of data collection for each season in our data analysis so cameras with little data collection did not influence the results with a particular bias. This amounted to 201 cameras in the summer and 203 cameras in the winter. The naïve occupancy was: wolf-summer 0.5572, wolf-winter 0.4138, cougar-summer 0.2587, and cougar-winter 0.1330. Wolves had a wider distribution than cougars in both seasons, yet both decreased occupancy in winter. This is most likely due to confined ranges in winter because of high snow pack in the higher elevations of the study area.

### *Single-species Occupancy Models*

The top single-species, single-season occupancy models are shown in Tables 4-7 below. We displayed models with a  $\Delta AIC$  of 0-2 because these are the strongest competing models. Highlighted are the models we selected, based on which models contain all significant parameters ( $\alpha$ -level 0.05). For example, the selected cougar-summer model is third on the list based on AIC values, but it is the first model that has parameters with p-values < 0.05. The ‘p model’ denotes the significant covariates on probability of detection, while the ‘ $\psi$  model’ denotes the significant covariates on probability of occupancy for the given species and given season. A ‘1’ indicates the null model – no significant covariates.

**Table 4.**

AIC model selection table for wolves in summer 2013, displaying all models with  $\Delta AIC$  of 0-2

<b>p model</b>	<b><math>\psi</math> model</b>	<b>n</b>	<b><math>\Delta AIC</math></b>	<b>AIC weight</b>	<b>Cumulative weight</b>
elevation+barren+distance secondary roads	1	5	0	0.178	0.18
elevation+barren+distance primary roads	1	5	0.51	0.138	0.32
slope+barren	1	4	1.02	0.107	0.42
slope+barren+distance primary roads	1	5	1.08	0.104	0.53
slope+barren+distance secondary roads	1	5	1.74	0.074	0.6
elevation+barren+distance secondary roads	slope	6	1.86	0.07	0.67
elevation+barren+distance secondary roads	ndvi	6	1.94	0.068	0.74

**Table 5.**

AIC model selection table for wolves in winter 2012-2013, displaying all models with  $\Delta AIC$  of 0-2

<b>p model</b>	<b><math>\psi</math> model</b>	<b>n</b>	<b><math>\Delta AIC</math></b>	<b>AIC weight</b>	<b>Cumulative weight</b>
elevation+shrub+distance secondary roads	elevation+herbaceous+ndvi	8	0	0.91	0.91
elevation+shrub+distance secondary roads	elevation+ndvi	7	5.07	0.071	0.97
elevation+distance secondary roads	elevation+herbaceous+ndvi	7	8.69	0.012	0.98
elevation+shrub+ distance secondary roads		1	5	8.84	0.99

**Table 6.**

AIC model selection table for cougars in summer 2013, displaying all models with  $\Delta AIC$  of 0-2

<b>p model</b>	<b><math>\psi</math> model</b>	<b>n</b>	<b><math>\Delta AIC</math></b>	<b>AIC weight</b>	<b>Cumulative weight</b>
slope	barren+ distance secondary roads	5	0	0.22	0.22

slope+distance secondary roads	barren+ distance secondary roads	6	0.04	0.22	0.44
slope+distance secondary roads		1	4	0.83	0.15
slope+distance secondary roads	distance secondary roads	5	0.9	0.14	0.72
slope+distance secondary roads	barren	5	1.14	0.12	0.85
slope	distance secondary roads	4	1.18	0.12	0.97

**Table 7.**

AIC model selection table for cougars in winter 2012-2013, displaying all models with  $\Delta AIC$  of 0-2

p model	$\psi$ model	n	$\Delta AIC$	AIC weight	Cumulative weight
elevation+barren+distance primary roads		1	5	0	0.4353
elevation+barren+distance primary roads	ndvi	6	0.79	0.2934	0.73
elevation+barren+distance primary roads	slope	6	1.98	0.1619	0.89

In the summer and winter, wolf detection decreased at higher elevations and steeper slopes, although the top models suggested the effect of elevation was stronger than slope on detection (Tables 4,5). In both seasons, wolf detection increased closer to secondary roads, and in the summer, also increased in barren landscapes (Tables 4,5). Occupancy of wolves during summer was best explained by the null, no covariate model (Table 4). In contrast, for wolves during winter, there was only one top model within  $\Delta AIC$  of 0-2, which modeled detection increasing at lower elevations and closer to secondary roads, yet detection decreased in shrubby landcover (Table 5). Unlike summer, wolf occupancy during winter had three covariates; there was increased occupancy at lower elevations, lower NDVI, and with increasing herbaceous landcover (Table 5). However, we suspect that covariates on probability of occupancy inflate the occupancy estimate to larger than it truly is, thus we used the null occupancy model for wolves in winter for the naïve estimates (Table 10).

Cougars in the summer had higher detection at steeper slopes and further from secondary roads (Table 6). This is quite different from cougar detection in winter, which increased at lower elevations, more barren landscapes, and closer to primary roads (Table 7). In both seasons, there were no significant covariates on occupancy; therefore the null model described cougar occupancy the best (Tables 6,7).

**Table 8.**

Estimated coefficients from selected single-species, single-season occupancy models for wolves and cougars in the Canadian Rocky Mountains, developed from remote-camera trapping data, 2012-2013

Covariates on p	Wolf - summer		Wolf- Winter		Cougar - Summer		Cougar- Winter	
	$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
intercept ( $\beta_0$ )	-1.553	0.0595	-1.702	0.0693	-2.836	0.1480	-2.349	0.162
elevation	-0.127	0.0579	-0.202	0.0726	-	-	-0.284	0.141
slope	-	-	-	-	0.381	0.0727	-	-
landcover type	0.325	0.1602	-1.111	0.3863	-	-	1.889	0.589

ndvi	-	-	-	-	-	-	-	-
distance primary road	-	-	-	-	-	-	0.491	0.234
distance secondary road	0.149	0.0663	0.347	0.0873	-0.223	0.0962	-	-

Covariates on $\psi$	$\beta$	SE	$\beta$	SE	$\beta$	SE	$\beta$	SE
null - $\psi$ estimate	0.363	0.152	-	-	-0.419	0.227	-1.68	0.21
intercept ( $\beta_0$ )	-	-	-0.333	0.160	-	-	-	-
elevation	-	-	-0.469	0.216	-	-	-	-
landcover type	-	-	1.980	0.884	-	-	-	-
ndvi	-	-	-0.588	0.222	-	-	-	-

From these selected occupancy models,  $\hat{\psi}$  and  $\hat{p}$  are calculated (Table 9.).

**Table 9.**

Estimated probability of detection and probability of occupancy: naïve and from selected single-species, single-season occupancy models for wolves and cougars in the Canadian Rocky Mountains, developed from remote-camera trapping data, 2012-2013

	Wolf - summer	Cougar - Summer	Wolf- Winter	Cougar- Winter
<b>Naïve <math>\psi</math></b>	0.5572	0.2587	0.4138	0.1330
<b><math>\psi</math></b>	0.5900	0.3970	0.4460	0.1570
<b>p</b>	0.2270	0.0554	0.0550	0.3870
<b>Cumulative p of season</b>	0.9927	0.9860	0.9977	0.9953

After analyzing the single-species, single-season models, we decided upon using slope and elevation as the covariates in the co-occurrence models for both seasons on both parameters. These covariates are relevant in both seasons, for both species, on at least detection. Because of the differences in slope and elevation between the species, especially in summer, we suspected these covariates would describe the potential spatial separation between wolves and cougars.

### *Co-occurrence models*

Trapping sessions were expanded to four-weeks for the co-occurrence model because of the low detection of cougars (specifically  $\psi_{Ba}$ ). Low detection caused inflation of the parameter and standard error estimates in one-week and two-week trapping sessions; this issue was resolved in four-week trapping sessions in that the top models from this analysis were unaffected by inflation.

We ran null and univariate co-occurrence models on  $p$  and  $\psi$ , using the four types of co-occurrence for each (see Table 3.). Using AIC, the top model was selected. This is shown in Table 10. below with  $\Delta AIC$  0-~2.

**Table 10.**

AIC model selection table for co-occurrence between wolves and cougars in summer 2013, displaying all models with  $\Delta AIC$  of 0-2, with wolves as species A

$\psi$ model	p model	n	$\Delta AIC$	AIC weight
psi(indep)	p(indep)	4	0	0.5183
psi(cond)	p(cond)	5	1.8	0.2107
psi(cond)	p(indep)	5	2	0.1907

**Table 11.**

AIC model selection table for co-occurrence between wolves and cougars in winter 2012-2013, displaying all models with  $\Delta AIC$  of 0-2, with wolves as species A

$\psi$ model	p model	n	$\Delta AIC$	AIC weight
psi(indep)	psi(indep)	4	0	0.299
psi(indep)	p(cond)	5	0.02	0.296
psi(cond)	p(indep)	5	0.02	0.296
psi(cond)	p(cond)	6	2.02	0.1089

**Table 12.**

Estimates of parameters for the top models and 95% confidence intervals for the top co-occurrence model for wolves and cougars in summer and winter in the Canadian Rocky Mountains, developed from remote-camera trapping data, 2012-2013, with wolves as species A

	Summer $\psi$ (indep)p(indep)		Summer $\psi$ (indep)p(indep)	Summer $\psi$ (indep)p(cond)			
	Estimate	SE	95% Confidence Interval	Estimate	SE		
$\psi A$	0.1821	0.0648	0.0867-0.3431	0.1812	0.0645		
$\psi BA$	0.3892	0.0784	0.2503-0.5489	0.3907	0.0790		
$\psi Ba$	0.3892	0.0784	0.2503-0.5489	0.3907	0.0790		
pA	0.1792	0.0611	0.0882-0.3303	0.1793	0.0613		
pB	0.2159	0.0466	0.1384-0.3208	0.2258	0.0523		
rA	0.1792	0.0611	0.0882-0.3303	0.1793	0.0613		
rBA	0.2159	0.0466	0.1384-0.3208	0.1698	0.1014		
rBa	0.2159	0.0466	0.1384-0.3208	0.1698	0.1014		
	Winter $\psi$ (indep)p(indep)		Winter $\psi$ (indep)p(indep)	Winter $\psi$ (indep)p(cond)		Winter $\psi$ (cond)p(indep)	
	Estimate	SE	95% Confidence Interval	Estimate	SE	Estimate	SE
$\psi A$	0.1414	0.0818	0.0421-0.3816	0.1406	0.0812	0.1406	0.0812
$\psi BA$	0.1897	0.0591	0.0993-0.3321	0.2199	0.0703	-	-
$\psi Ba$	0.1897	0.0591	0.0993-0.3321	0.2199	0.0703	0.2199	0.0703
pA	0.1185	0.0732	0.0329-0.3469	0.1190	0.0734	0.1190	0.0734
pB	0.1949	0.0597	0.1031-0.3378	0.1954	0.0597	0.1954	0.0597
rA	0.1185	0.0732	0.0329-0.3469	0.1190	0.0734	0.1190	0.0734
rBA	0.1949	0.0597	0.1031-0.3378	-	-	0.1954	0.0597
rBa	0.1949	0.0597	0.1031-0.3378	-	-	0.1954	0.0597

Then, to compare and to explore the effects that cougars may have on wolves, we re-ran the co-occurrence models with cougars as species A. In the model framework, this means that wolf occupancy data was compared to cougar occupancy data, assuming that cougars occur and are detected irrespective to wolves.

**Table 13.**

AIC model selection table for co-occurrence between wolves and cougars in summer 2013, displaying all models with  $\Delta AIC$  of 0-2, with cougars as species A

$\psi$ model	p model	n	$\Delta AIC$	AIC weight
psi(cond)	p(cond)	6	0	0.6114
psi(indep)	p(cond)	5	1.29	0.3208

**Table 14.**

AIC model selection table for co-occurrence between wolves and cougars in winter 2012-2013, displaying all models with  $\Delta AIC$  of 0-2, with cougars as species A

$\psi$ model	p model	n	$\Delta AIC$	AIC weight
psi(cond)	p(indep)	5	0	0.5274
psi(cond)	p(cond)	6	1.71	0.2243

**Table 15.**

Estimates of parameters for the top models and 95% confidence intervals for the top co-occurrence model for wolves and cougars in summer and winter in the Canadian Rocky Mountains, developed from remote-camera trapping data, 2012-2013, with cougars as species A

	Summer $\psi(\text{cond})p(\text{cond})$		Summer $\psi(\text{cond})p(\text{cond})$	Summer $\psi(\text{indep})p(\text{cond})$	
	Estimate	SE	95% Confidence Interval	Estimate	SE
$\psi A$	0.5945	0.0586	0.4766-0.7025	0.5862	0.0584
$\psi BA$	0.5220	0.0724	0.3820-0.6586	0.5867	0.0597
$\psi Ba$	0.8458	0.2086	0.1928-0.9921	0.5867	0.0597
pA	0.4111	0.0328	0.3487-0.4765	0.4168	0.0331
pB	0.1921	0.0680	0.0915-0.3594	0.2507	0.0603
rA	0.4111	0.0328	0.3487-0.4765	0.4168	0.0331
rBA	0.4686	0.0458	0.3808-0.5584	0.4538	0.0493
rBa	0.4686	0.0458	0.3808-0.5584	0.4538	0.0493
	Winter $\psi(\text{cond})p(\text{indep})$		Winter $\psi(\text{cond})p(\text{indep})$	Winter $\psi(\text{cond})p(\text{cond})$	
	Estimate	SE	95% Confidence Interval	Estimate	SE
$\psi A$	0.4032	0.0533	0.3044-0.5105	0.4031	0.0533
$\psi BA$	0.3359	0.0855	0.1926-0.5174	0.3485	0.0932
$\psi Ba$	0.5992	0.0781	0.4415-0.7388	0.5926	0.0777
pA	0.3925	0.0374	0.3222-0.4676	0.3925	0.0374
pB	0.3304	0.0347	0.2663-0.4015	0.3426	0.0415
rA	0.3925	0.0374	0.3222-0.4676	0.3925	0.0374
rBA	0.3304	0.0347	0.2663-0.4015	0.2964	0.0703
rBa	0.3304	0.0347	0.2663-0.4015	0.2964	0.0703

Finally, the SIF value was calculated for each season, for each species being “dominant” in the model. Wolf species A summer SIF = 0.9001, wolf species A winter SIF = 0.7765, cougar species A summer SIF = 0.7990, and cougar species A winter SIF = 0.6813.

## Discussion

Spatial separation between species is a way to decrease competition directly or indirectly, such as resource partitioning. Using remote wildlife cameras, we tested hypotheses regarding wolf dominance over cougars in the central Canadian Rocky Mountains. Our study was robust in that we had a very large sample size ( $n > 200$ ) and very high cumulative probability of detection. These strengths allowed us to thoroughly assess our hypotheses, which stated: 1) In the presence of wolves, cougars will occupy different habitat types – i.e. high elevations, more intense slopes, and more forested areas; 2) In the absence of wolves, cougars will occupy similar habitats to wolves; 3) In the presence of wolves, cougars will decrease their probability of detection while occupancy stays approximately constant; 4) During winter, when both species have a confined range, potential for competition will be greater because of more overlap in distribution; 5) Due to other factors, wolves and cougars will not compete on a level detectable by occupancy modeling, or will have very little competition. Interestingly, the results of the occupancy and co-occurrence models did not support any of our hypotheses fully. Slope and elevation were insignificant for detection and occupancy in all co-occurrence models; all top co-occurrence models contain no covariates. This means that spatial differences between wolves and cougars are irrelevant of slope and elevation, or that there are no differences in slope and elevation on probability of occupancy and probability of detection between the two species.

The summer occupancy models differ on  $p$  and are the same for  $\psi$ : wolves =  $\psi(1)p(\text{elevation} + \text{barren} + \text{distance secondary roads})$ ; cougars =  $\psi(1)p(\text{slope} + \text{distance secondary roads})$ . The lack of significant covariates on occupancy is interpreted as both species being habitat generalists in summer. However, the detection models are quite different. Wolves had higher detection at lower elevations while cougars had higher detection at more intense slopes. Since slope and elevation tend to be positively correlated, this difference in models is suggestive of spatial separation. Further, the  $\beta$  estimates on distance to secondary roads are opposite, indicating opposing responses to roads.

There was slight competition for the top summer co-occurrence model, with wolves as species A, with three models within  $\sim 2 \Delta\text{AIC}$ . The selected model was:  $\psi(\text{independent})p(\text{independent})$ . The second ranked model was:  $\psi(\text{conditional})p(\text{conditional})$ . This model means that cougar occupancy depends on wolf occupancy, and cougar detection depends on wolf detection, at a given site. It is interesting that two opposite models are the top two models, which makes understanding spatial differences between the wolves and cougars difficult.

Independence in probability of occupancy is interpreted as wolves and cougars are present on the landscape regardless of the other species. It is expected that wolves would occur independently of cougars because they were selected as the dominant species in the model, and this result was found in numerous studies mentioned previously. However, it was surprising that cougars were independent of wolves; technically, cougars had the same occupancy patterns whether or not wolves were also present at a site. The parameters for probability of occupancy had overlapping 95% confidence intervals, therefore wolves and cougars had approximately equal occupancy on the landscape. This was also surprising because, based on naïve  $\hat{\psi}$  and  $\hat{\psi}$  from the occupancy models, wolves had higher occupancy than cougars in both seasons.

Independence in  $p$  is interpreted as the probability of detecting a wolf or cougar does not depend on the detection of the other species. This is expected for wolves, the dominant species in the model, in that detection of wolves with or without the detection of cougars is equivalent. Independent detection of cougars refutes our hypotheses because it means that cougar detection is the same whether or not wolves are detected at the same site. Essentially, the results of the summer co-occurrence model demonstrate that cougars are not changing their behavior in the presence of wolves, with respect to both  $\psi$  and  $p$ .

In winter, the occupancy models differed slightly in  $p$  and drastically on  $\psi$ : wolves =  $\psi(\text{elevation} + \text{shrub} + \text{ndvi})$   
 $p(\text{elevation} + \text{herbaceous} + \text{distance secondary roads})$ ; Cougars =  $\psi(1)p(\text{elevation} + \text{barren} + \text{distance primary roads})$ . Because the models are different, there is suggestive evidence of spatial separation between the species. However, the sign on the estimate of the parameter ( $\beta$ ) is the same for elevation (negative) and distance to roads (positive), indicating the same response to these covariates. We suspect the top winter wolf models with covariates on  $\psi$  were inflating the estimate because occupancy estimates were around double naïve occupancy; this did not happen for any other occupancy models and seemed incorrect. Therefore, we used the model:  $\psi(1)p(\text{elevation} + \text{herbaceous} + \text{distance secondary roads})$ . All covariates on  $p$  had nearly identical estimates and p-values, and using the null occupancy model this allowed for uniform  $\psi$  models for all species in all seasons.

There were tightly competing models for the winter co-occurrence model; the second and third models were within 0.02  $\Delta$ AIC of the top model. The selected model,  $\psi(\text{independent})p(\text{independent})$ , was the only model with interpretable and logical  $\beta$  estimates. This model contradicts our hypotheses in the same ways as the summer model. However, the second and third models (2 =  $\psi(\text{independent})p(\text{conditional})$  and 3 =  $\psi(\text{conditional})p(\text{independent})$ ) were extremely close to the top model and have very different interpretations that should be considered. Conditional probability of occupancy describes cougars

occupying different sites when wolves are present and absent. Conditional probability of detection describes a difference in cougar detection when wolves are present and absent from a site. Both of these imply spatial separation between wolves and cougars. It is more difficult to draw conclusions based on the winter co-occurrence models, yet the selected model indicates that cougars do not change their behavior with respect to wolves in winter.

The models using cougars as species A, or the dominant species for which wolves are compared to, are opposite to the wolf species A co-occurrence models. Summer had the model:  $\psi(\text{conditional})p(\text{conditional})$ ; and winter has the model:  $\psi(\text{conditional})p(\text{independent})$ . This would mean that wolves are changing their behavior in the presence of cougars by occupying different locations and decreasing their detection (Tables 13, 14). This can be seen in Table 15, where  $\psi_{BA} < \psi_{Ba}$  and  $p_B > r_{BA}/r_{Ba}$ . Although different from most literature, the results of models with cougars as the dominant species claim a difference in distributions.

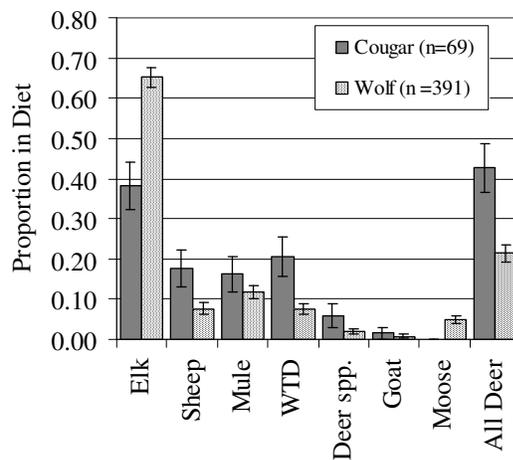
Because all top models for all analyses do not contain covariates, we cannot claim a reason for these differences. The conflicting co-occurrence models between species may not be meaningful; if wolves truly are the dominant species, the results from the cougar co-occurrence models could be by chance or due to numerous other factors, such as habitat selection. However, because conditionality was in top models with wolves as species A and the cougar co-occurrence models all resulted in conditionality, we are led to believe there is an element of spatial separation occurring.

SIF values are less than 1 for both seasons with either species as dominant in the co-occurrence model. This indicates that wolves and cougars are less likely to occur together than by chance, and there is some element of spatial separation. Wolves as species A in the summer had a value very close to 1 (0.9001), meaning that wolf and cougar occurrence was almost independent; this agrees with the independent co-occurrence model selected. The lowest SIF was cougars as species A in winter (0.6813), indicating the most avoidance in winter. This agrees with our fourth hypothesis that there is more competition between the species in the winter because of their restricted range. Although all SIF values were below 1, they were not drastically low; this means that there is slight avoidance by the subordinate species in the respective co-occurrence, but it is not overwhelming evidence of spatial separation.

Models with wolves as species A (our original hypotheses), demonstrate a lack of spatial separation, and therefore assumed lack of intense competition (hypothesis 5), which could result from numerous other mechanisms. Firstly, aside from the recent extirpation and recovery of wolves, wolves and cougars have co-existed in the study area for centuries (Paquet 1993). Although wolves were extirpated for multiple decades, the recolonization of wolves may not have strongly impacted cougars. The Canadian Rocky Mountains also have a very abundant prey source. The study area has numerous prey species, generally with large populations.

This may reduce competition between these two top carnivores, both directly and indirectly.

Another probable explanation for the lack of spatial differences is prey specialization between wolves and cougars. Kortello et al. (2007) found that diet overlap between the two species diverged with an increase in the wolf population and expansion of wolf range. Similarly, wolves and cougars both tend to be present in the presence of main prey species, meaning they overlap in distribution and diet (Alexander 2006). In our study area and based on our original hypotheses, we would predict that although wolves and cougars are not spatially distinct, they consume different prey species or the same species but differing age and condition. Below is a figure of diet data, determined through scat collection in the study area (Hebblewhite 2000 unpublished).



**Figure 2.** Proportion (+/-1 S.E.) of prey species killed by wolves and cougars during the winter in the Bow River Valley and tributaries from 1987-2000. Prey species composition differs by species ( $\chi^2_{(d.f.=5)} = 467.1, p < 0.00001$ ).

The figure above demonstrates prey specialization between wolves and cougars in the study area. Cougar diet was comprised of more deer than wolves', both white-tailed and mule, far more bighorn sheep, and slightly more mountain goat although this prey species was trace for both carnivores. Wolf diet was comprised more of elk and moose than cougars'. This leads us to believe that although our results demonstrate lack of spatial separation between wolves and cougars, there are other mechanisms for competition and avoidance between the two species because diet specialization decreases interference and exploitative competition.

Our study also has a few prominent caveats. For example, Waterton Lakes National Park has more suitable cougar habitat and a high abundance of cougars while Jasper National Park has poor cougar habitat with low cougar abundance (Steenweg et al. Final Report 2015). There is potential for unaddressed heterogeneity in occupancy of both species across the study area. Further, current

occupancy status may not fully disclose competition. For example, gathering occupancy data before and after wolf recolonization would provide information with greater depth and inference potential. Direct competition was also left unaddressed, and this type of study design does not allow for the investigation of direct competition. Our study is purely observational; observational studies do not hold as much power as genuine experiments.

Another competition characteristic we did not analyze is temporal separation between wolves and cougars. Based on our original hypotheses, I would predict that cougars would separate themselves more temporally from wolves than wolves would separate themselves from cougars (i.e. there would be more time in between pictures of wolves then cougars, than cougars then wolves), or there would not be temporal separation if there was no competition (hypothesis 5). This type of separation to reduce competition is common with carnivores and affects behavior and distribution (Broekhuis et al. 2013; Lovari et al. 2014). Exploring this aspect of competition with our data may provide us with differing results from the co-occurrence model because this examines a different feature of the presence/absence data.

One issue with occupancy modeling is comparing species with differing home ranges; this could cause incorrect interpretations of occupancy for wolves and cougars in our study. In this study area, a pack of wolves has a home range of ~1000 km.<sup>2</sup> (Hebblewhite and Merrill 2008, Webb et al. 2011), whereas cougars have a home range of ~100 km.<sup>2</sup> or less (Kortello et al. 2007, Russell et al. 2012). Our camera trapping design is set up for one camera per cougar home range, yet this means there are about 10 cameras in a wolf-pack range. At this scale, cougars may not be able to change their behavior enough to change occupancy estimates depending on the surrounding landscape. For example, a cougar and multiple wolves may occupy a valley bottom camera site, surrounded by uninhabitable rocky slopes, and the cougar cannot shift its range to the mountains and cliffs around the cell so it remains in the same cell as wolves. This scale is not conducive to analyzing cougar behavioral changes because it is too large. With this knowledge, we may better understand why the cougar species A models were conditional – the large scale used allowed us to see wolf distributions and behavioral changes easier than we can see cougar distributions within their respective home ranges. In this case, our measurement of wolf occupancy is similar to wolf *use* of a site because we can detect these smaller changes and differences.

Overall, wolves and cougars did not have strong indications of spatial disparities, and therefore landscape-scale competition, based on single-species, single-season occupancy models and co-occurrence models. Occupancy models did not contain many differing covariates, and the selected covariates proved insignificant in the co-occurrence model with wolves and cougars as the dominant species. However, when cougars are the modeled dominant specie, occupancy and detection of wolves is conditional on the presence of cougars. Interpreting these results is difficult, yet there is evidence of some spatial separation of these two

species. In this Canadian National Park chain, the interactions between wolves and cougars are not extreme enough to draw strong conclusions. Presence/absence data does not fully describe all aspects of competition, and further analysis is encouraged to deduce smaller-scale competition between wolves and cougars, where the majority of the competition most likely lies.

## Literature Cited

- Alexander, S.M., Logan, T.B., and P.C. Paquet. 2006. Spatio-temporal co-occurrence of cougars (*Felis concolor*), wolves (*Canis lupus*) and their prey during winter: a comparison of two analytical methods. *Journal of Biogeography* 33: 2001-2012.
- Apps, C.D., McLellan, B.N., Woods, J.G., and M.F. Proctor. 2004. Estimating grizzly bear abundance relative to habitat and human influence. *Journal of Wildlife Management* 74: 1175-1178.
- Apps, C.D., McLellan, B.N., and J.G. Woods. 2006. Landscape partitioning and spatial interferences of competition between black and grizzly bears. *Ecography* 29: 561-572.
- Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175-1178.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2009. Spatial Partitioning of Predation Risk in a Multiple Predator-Multiple Prey System. *Journal of Wildlife Management* 73:876-884.
- Bartnick, T.D., T.R. Van Deelen, H.B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology* 91: 82-93.
- Broekhuis, F., Cozzi, G., Valeiz, M., McNutt, J.W., and D.W. Macdonald. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology* 82: 1098-1105.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 10: 1365-2664.
- Callaghan, C. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the Central Rocky Mountains, Canada. Department of Zoology, University of Guelph, Guelph, ON.
- Carbyn, L. N. 1974. Wolf population fluctuations in Jasper National Park, Alberta, Canada. *Biological Conservation* 6:94-101.
- Crozier, M.L., Seamans, M.E., Gutiérrez, R.J., Loschl, P.J., Horn, R.B., Sovern, S.G., and E.D. Forsman. 2006. Does the presence of barred owls suppress the calling behavior of spotted owls? *Condor* 108: 760-769.
- Elbroch, M.L., Lendrum, P.E., Maximilian, L.A., and H.U. Wittmer. 2014. Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology* 00: 1-8.
- Fiske, I., and R. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife

- occurrence and abundance. *Journal of Statistical Software* 43:1–23.
- Greenberg, S., and T. Godin. 2012. *Timelapse Image Analysis Manual*. Research report 2012-1028-11, Department of Computer Science, University of Calgary. Calgary, Alberta, Canada.
- Gunson, J. R. 1992. Historical and present management of wolves in Alberta. *Wildlife Society Bulletin* 20:330-339.
- Hebblewhite, M. 2000. Diet analysis using scat for wolves and cougars in Canadian Rocky Mountain National Parks. Unpublished.
- Hebblewhite, M., and E. Merrill. 2008. Modeling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45:834-844.
- Hebblewhite, M., and D. W. Smith. 2011. Wolf community ecology: ecosystem effects of recovering wolves in Banff and Yellowstone National Parks. *in* M. Musiani, L. Boitaini, and P. C. Paquet, editors. *The world of wolves: new perspectives on ecology, behavior, and policy*. University of Calgary Press, Calgary, AB.
- Hebblewhite, M., C. A. White, C. Nietvelt, J. M. McKenzie, T. E. Hurd, J. M. Fryxell, S. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86:2135-2144.
- Hines, J. E. 2012. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC. <<http://www.mbrpwrc.usgs.gov/software/presence.html>>. Accessed 28 Nov 2012.
- Holroyd, G. L. & K. J. Van Tighem (eds.), 1983. *Ecological (Biophysical) Land classification of Banff and Jasper National Parks. Volume I. The wildlife inventory. Part A.* Canadian Wildlife Service, Edmonton, Alberta.
- Husseman, J.S., D.L. Murray, G. Power, C. Mack, C.R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *OIKOS* 101: 591-601.
- Knopff, K.H., Knopff, A.A., Kortello, A. and M.S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. *The Journal of Wildlife Management*, 74, 1435–1447.
- Kortello, A.D., Hurd, T.E., and D.L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupis*) in Banff National Park, Alberta. *Ecoscience* 14: 214-222.
- Kunkel, K.E., T.R. Ruth, D.H. Pletscher, and M.G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. *The Journal of Wildlife Management* 63: 901-910.
- Lovari, S, Pokheral, C.P., Jnawali, S.R., Fusani, L., and F. Ferretti. 2014. Coexistence of the tiger and the common leopard in a prey-rich area: the role of prey partitioning. *Journal of Zoology* 295: 122-131.
- MacArthur, R.H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101:377–385.
- MacKenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management* 70:367-374.
- MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. *Journal of*

- Agricultural, Biological, and Environmental Statistics 9: 300-318.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. Pollock, L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling - inferring patterns and dynamics of species occurrence. Elsevier Publishing, London, United Kingdom.
- Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R., and R.O. Peterson. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* 81: 553-563.
- Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat Selection by Recolonizing Wolves in the Northern Rocky Mountains of the United States. *Journal of Wildlife Management* 70:554-563.
- O'Brien, T.G., and F.M. Kinnard. 2008. A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conservation International* 18: S144-S162.
- Paquet, P. C., 1993. Summary reference document: Ecological studies of recolonizing wolves in the central Canadian Rocky Mountains. Final Report. Parks Canada, Banff National Park, Banff, Alberta.
- Pletscher, D. H., R. R. Ream, R. Demarchi, W. G. Brewster, and E. E. Bangs. 1991. Managing wolf and ungulate populations in an international ecosystem. *Transactions of the 56th North American Wildlife and Natural Resources Conference* 56:539-549.
- Richmond, O.M.W., J.E. Hines, and S.R. Beissinger. 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications* 20: 2036-2046.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnik, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological effects of the world's largest carnivores. *Science* 343:123148.
- Robinson, Q.H., D. Bustos, and G.W. Roemer. 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. *Ecology* 95: 3112-3123.
- Russell, R.E., Royle, J.A., Desimone, R., Schwartz, M.K., Edwards, V.L., Pilgrim, K.P, and K.S. Mckelvey. 2012. Estimating abundance of mountain lions from unstructured spatial sampling. *The Journal of Wildlife Management* 76: 1551-1561.
- Ruth, T.K., M. A. Haroldson, K.M. Murphy, P.C. Buotte, M.G. Hornocker, and H.B. Quigley. 2011. Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. *The Journal of Wildlife Management* 75: 1381-1398.
- Smith, D. W., E.E. Bangs, J.K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of Colonizing Wolves in the Northern Rocky Mountains of the United States, 1982-2004. *Journal of Wildlife Management* 74:620-634.
- Steenweg, R., Whittington, J., and M. Hebblewhite. 2012. Canadian Rockies carnivore monitoring project: examining trends in carnivore populations and their prey using remote cameras. Progress Report – Park Canada.
- Steenweg, R., Whittington, J., and M. Hebblewhite. 2015. Canadian Rockies remote camera multi-

species occupancy project: examining trends in carnivore populations and their prey using remote cameras in Banff, Jasper, Kootenay, Yoho and Waterton Lakes National Parks. Final Report – Parks Canada.

USFWS (US Fish and Wildlife Service), N.P.T., National Park Service, Montana Fish, Wildlife and Parks, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Idaho Fish and Game, and USDA Wildlife Services. 2008. Rocky Mountain wolf recovery 2007 annual report. USFWS, Ecological Services, Helena, Montana.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. *Canadian Journal of Zoology* **89**:744-752.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurt, J., and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-even approach. *Journal of Applied Ecology* **48**: 1535-1542.