Grizzly bear response to linear features and human recreational activity

by

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Abstract

A major side-effect of industrial activity is the associated linear-feature footprint and increase in recreational access. Alberta's threatened grizzly bear (*Ursus arctos*) populations overlap with a multitude of different potential forms of human disturbance, including human recreational activity. Identifying the effects of recreation on grizzly bear behaviour and population recovery is challenging; both in terms of quantifying spatio-temporal variation in multiple types of human recreation at scales relevant to grizzly bears, and in documenting population-level responses by such a behaviourally variable species as grizzly bears. My first objective was to develop a method to quantify motorised and non-motorised recreational activity across a linear-feature network using trail cameras. Using a generalized linear mixed-effects model to estimate temporal variation in sampling, and Ordinary Kriging to interpolate spatial variation across a linear-feature network, I was able to create spatio-temporally varying maps of recreation that can be incorporated into habitat selection studies. I incorporated grizzly bear radiocollar data within an integrated step selection analysis (*i*SSA) to predict the importance, significance and directional effect of motorised and non-motorised recreation on grizzly bear habitat selection and movement. I concluded that grizzly bears select for trails when recreation is absent, however they display no response when recreational activity is high. Male grizzly bears also altered their movement behaviour in proximity of trails with high recreational activity; reducing movement speed when activity was absent and increasing speed when recreational activity was high. In general, males showed greater responses to recreation than females, and both male and female bears showed a stronger response to motorised versus non-motorised recreation. Using trail camera data on grizzly bears and black bears (*U. americanus*), I investigated the influence of recreational activity on bear habitat use within a multi-species framework. Grizzly bears and black bears displayed spatial segregation, rarely co-occurring on the landscape. Species' occurrence was not influenced significantly by the presence or absence of recreational activity, however, both species used sites where motorised activity was present less intensively, and this response was strongest in grizzly bears. As with the results from the *i*SSA, negative responses to motorised recreation were greater relative to non-motorised. Finally, I used the opportunity of having concurrent DNA capture-recapture, radiotelemetry and trail camera data to directly compare two methods of grizzly bear density estimation; 1) spatial capture-recapture and 2) spatial mark-resight. Results for both methods were similar, in terms of both accuracy and precision, highlighting options for density estimation of large mammals without relying on complete individual identification for the entire sampled population. Overall, my results demonstrate the need to incorporate intensity and type of recreational activity within habitat selection studies of grizzly bears and interactions with sympatric species such as black bears. Access management is a challenge that needs to be addressing in large mammal conservation, and will require methods for monitoring human activity and changes in wildlife behaviour and population demography.

Preface

This thesis is an original work by Andrew Ladle. Field methods were approved by the University of Alberta Animal Care and Use Committee (Protocol # AUP00000436) and University of Saskatchewan Animal Care Committee (#20010016).

A version of Chapter 2 is published in *Methods in Ecology and Evolution* with Tal Avgar, Matthew Wheatley and Mark S. Boyce as co-authors. Andrew Ladle collected and analysed all data and wrote the manuscript. Tal Avgar provided recommendations with data analysis and writing. Matthew Wheatley and Mark S. Boyce aided in securing funding as well as providing feedback on the manuscript itself.

A version of Chapter 3 will be submitted to *Behavioural Ecology*, and includes Tal Avgar, Matthew Wheatley, Scott E. Nielsen, Gordon B. Stenhouse and Mark S. Boyce as co-authors. Andrew Ladle collected and analysed all trail camera data and wrote the manuscript. Gordon B. Stenhouse supervised the collection of all grizzly bear radiotelemetry data, as well as contributing feedback on the manuscript. Tal Avgar provided recommendations with data analysis and writing. Scott E. Nielsen supplied food occurrence data and feedback on the manuscript. Matthew Wheatley and Mark S. Boyce aided in securing funding as well as providing feedback on the manuscript itself.

A version of Chapter 4 will be submitted to *Journal of Applied Ecology* and includes Robin Steenweg, Brenda Shepherd and Mark S. Boyce as co-authors. Andrew Ladle and Brenda Shepherd supervised all trail camera data collection. Robin Steenweg, Brenda Shepherd and Mark S. Boyce provided advice and feedback on analysis and writing.

A version of Chapter 5 will be submitted to *PLoS One* and includes Jesse Whittington, Gordon B. Stenhouse and Mark S. Boyce as co-authors. Andrew Ladle collected all trail camera data, analysed all data and wrote the manuscript. Gordon B. Stenhouse supervised the collection of all hair trap and radiotelemetry data collection. Jesse Whittington and Mark. S. Boyce provided guidance on the analysis and feedback on the manuscript.

In dedication to Mijbil, who was with me from the beginning, almost to the end (2009-2017).

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1 General Introduction

The inability of US and Canadian governments to take climate change seriously and implement restrictions on resource extraction activities, has led to continued encroachment into wilderness areas by oil, gas and timber industries across North America (Naugle 2012). Environmental groups devote large amounts of time focusing on challenging resource extraction lobbies regarding their activities (Mahoney 2007), but little attention is placed on the negative consequences associated with increased outdoor recreation afforded by access created by industry that persists long after the oil and gas companies move out (Floyd and Johnson 2002). Resource extraction requires new roads (McLellan and Shackleton 1988), creation of cutlines (Latham et al. 2011) and deforestation (Nielsen et al. 2004a), all of which increase the ability of the general public to access previously untouched wilderness (Havlick 2002). Relative to the short-term effects of the extraction processes themselves, the effects of the long-term persistence of linear-features and the associated increases in recreational activity are less clear. Protected areas tend to exclude industrial activity, allowing them to control human access for recreation. Public lands in North America primarily have unregulated access, resulting in an abundance of motorised and non-motorised recreation, with little information on the intensity of use and potential consequences for wildlife.

The west-central Alberta Rocky Mountains and foothills, despite being home to the world-renowned Banff and Jasper National Parks, are also heavily exploited; extensive oil and gas exploration, timber harvest and open-pit mining for coal are prevalent across the landscape (Cristescu et al. 2015a, 2015b). Although the majority of resource extraction has long since taken place, it has left behind a matrix that now contains a dense and complex network of roads, trails and seismic lines. This region of the province is also host to grizzly bears (*Ursus arctos*), which were designated as a threatened species in Alberta in 2010 (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Human access management is a central theme in grizzly bear science and management (Mattson et al. 1996) and has been identified as a key constraint to the success of recovering bear populations both in Alberta (Alberta Grizzly Bear Recovery Team 2008) and across their range (Proctor et al. 2012). Grizzly bear research has historically focused on roads, and their influence on movement (Roever et al. 2010, Northrup et al. 2012a), habitat selection (Mace et al. 1996), activity patterns (Graham et al. 2010), stress (Bourbonnais et al. 2013) and direct mortality (Boulanger and Stenhouse 2014, Lamb et al. 2017). Knowledge of how bear behaviour is influenced by recreational activity is relatively poor (Gibeau et al. 2002, Fortin et al. 2016). The foothills region is primarily public lands and sees unregulated off-highway vehicle (OHV) access, taking advantage of the dense linear-feature network left behind primarily unreclaimed by industry. The intensity of use by recreationists varies spatially and temporally, resulting in a form of disturbance that can be highly unpredictable for wildlife, and therefore potentially detrimental (Knight and Gutzwiller 1995).

Obtaining baseline information that quantifies the magnitude of recreational activity in public lands is one of many challenges faced by wildlife managers. Recreational activity is a form of human disturbance commonly restricted to linear features, such as trail networks, that can be difficult to predict. Local knowledge, designated and advertised trails, and scenic routing add variation that can be difficult to quantify (Drake et al. 2015, Hammitt et al. 2015). Identifying variables to predict the magnitude of recreational activity can be challenging. For this reason, many studies ignore the magnitude of activity on linear features, instead solely relying on metrics such as distance to feature, or feature density. As with many ecological variables sampled across a landscape, variables can be characterised in terms of spatial autocorrelation; the pattern that variables at locations closer together are more similar than variables at distant locations (Tobler 1970). Temporal variation in visitation rates to public and park lands adds an additional layer of complexity, requiring year-long monitoring of recreation, rather than snapshots that may give biased estimates. Trail counters are commonly deployed at trail heads in protected areas to obtain information on visitor frequency, however these data are lacking in terms of spatial coverage and details such as the type of recreation taking place (e.g. motorised versus non-motorised); both important variables when the focus is to model wildlife responses to recreation. Trail cameras give researchers the ability to identify types of recreation and can be set up easily across a trail network. In Chapter 2, using trail camera data on recreational activity spread across the linear feature network within my study area, I develop a method that combines mixed-effects generalised linear models with Ordinary Kriging (Tobler 1970) to estimate variation in the probability of motorised and non-motorised recreation in both time and space, which then can be applied to questions relating to wildlife responses to such a disturbance. Using model validation techniques, and an application to grizzly bear habitat selection, I evaluate the efficacy of the model and show that incorporating activity on top of the linear features themselves outperforms models that solely rely on linear feature data.

Human disturbance can influence wildlife populations through a number of mechanisms. Roads have direct mortality consequences for grizzly bears (McLellan and Shackleton 1988, Boulanger and Stenhouse 2014, Lamb et al. 2017), however such demographic consequences are unlikely to be the same for off-road access. In fact, there have been zero fatalities associated with recreational trail use in my study area during the last 20 years (Stenhouse *pers. comm.)*. Many carnivores, despite being apex predators, respond to human disturbance as prey responds to a predator (Frid and Dill 2002a). Behavioural responses to anthropogenic disturbances are often initial indicators of stress to wildlife (Odden et al. 2014). Changes in habitat selection and movement are two such indicators that can inform managers of the potential impact recreation is having on grizzly bear populations. In Chapter 3, I employ the recreational activity model from Chapter 2, to radiotelemetry data collected from radiocollared grizzly bears within an iSSA (Avgar et al. 2016) to investigate how individual grizzly bears respond to trails and associated probability of motorised and non-motorised recreation in terms of habitat selection and movement behaviour. I assessed grizzly bear response to recreation by incorporating data on topographic features, food quality, linear features and probability of activity within a model selection framework (Burnham and Anderson 2002). Once I had identified the top model, I estimated selection and movement responses to trails and their associated probabilities of recreational activity for males, females and for the population.

Single- species responses to habitat disturbance are prevalent within the literature, yet there has long been a call for multi-species research and monitoring (Simberloff 1998). Multi-species analyses were historically rare due to logistical constraints on sampling; this has been changing in the past decade with advances in monitoring technology as well as multi-species models. A species' niche is defined not only by its interactions with its surrounding environment, but also by interactions with sympatric species (Rosenzweig 1991, Wiens 2011). Grizzly bears and black bears (*U. americanus*) are sympatric throughout most of the grizzly bears North American distribution and share similar niches (Schwartz et al. 2010) which can lead to competition. In turn, competition could alter the ability for grizzly bear recovery (Mattson et al. 2005). In Chapter 4, I assess the importance that recreational activity plays in influencing both grizzly bear and black bear spatial distribution and habitat use, as well as spatial and temporal interactions between the two species themselves. Using trail camera data collected between 2012 and 2014, I apply a multi-species occurrence analysis (Rota et al. 2016) that allows for the inclusion of habitat covariates as well as the occurrence of sympatric species, or in this case, forms of human recreation, to define species occurrence on the landscape and intensity of use.

Managers dealing with animals where the objective is population recovery require monitoring of demographic changes brought about by specific management actions. Many Recovery plans specifically require a long-term monitoring strategy to be in place before such actions as delisting can take place (Doremus & Pagel 2008; U.S. ESA of 1973*c* [as in U.S. Code 2000]). However, data on abundance and distribution of animals, especially large, elusive mammals, can be expensive and time consuming to collect (Kendall et al. 2009). The Alberta Grizzly Bear Recovery Plan (Alberta Grizzly Bear Recovery Team 2008) recommended a complete census of the provincial population of grizzly bears every five years. However due to the high costs associated with DNA capture-recapture methods, this commitment was not upheld. The need for more cost-effective methods for estimating grizzly bear populations and distribution is required. In Chapter 5, I estimate grizzly bear density for my study area using a spatial mark-resight technique that uses trail camera data and radiocollared bears as marked individuals (Sollmann et al. 2013a, 2013b, Royle et al. 2014). I compare the accuracy and precision of the estimates obtained from the method to estimates from spatial capture-recapture using hair DNA samples. Finally, in Chapter 6 I formulate conclusions based on my findings, and how they can be incorporated within future access management.

2 Predictive modeling of ecological patterns along linear-feature networks

2.1 Introduction

Linear-feature networks are prevalent within ecological landscapes and occur in numerous forms. Clearly defined examples of networks include rivers, streams, roads and trails, where ecological patterns and processes are restricted to the network by spatial barriers (Ganio et al. 2005). Semi-permeable examples of linear-feature networks might include conservation corridors (Hobbs 1992), or topographical constraints to movement (e.g. ruggedness), which are not an ultimate barrier, yet have important implications in the spatial configuration of species, and chemical and physical elements (e.g. spread of water pollutants or variation in water temperature). The spatial configuration of variables across a landscape is commonly characterized using spatial autocorrelation: a universal pattern found in ecological systems, whereby locations closer together are more similar than distant locations (Tobler 1970). Geostatistical analyses such as kriging exploit the correlation between covariance and Euclidean distance to estimate variables at unknown locations (Cressie 2015). When variables are constrained to a linear-feature network, Euclidean distance does not efficiently capture the pattern of autocorrelation, and prediction precision is likely compromised (Zou et al. 2012). For example, the occurrence or relative abundance of freshwater species varies spatially, however traditional geostatistical methods may not be the best tool for estimating this variance because the patterns across space are constrained by the stream network (Ganio et al. 2005).

Human movement through the landscape primarily takes place using roads and trails (Drake et al. 2015). Human activity along linear features is an ecological pattern that has many implications for wildlife ecology, and for this reason is a fundamental component of integrated land-use planning and policy development. Human activity and linear feature density have been linked with habitat degradation for many North American wildlife species, including golden eagles (*Aquila chrysaetos*; Steenhof et al. 2014), caribou (*Rangifer tarandus*; Seip et al. 2007), wolves (*Canis lupus*; Whittington et al. 2005), and grizzly bears (*Ursus arctos*; Boulanger and Stenhouse 2014). Access management aims to mitigate potential effects of linear features on habitat and wildlife; however identifying the directionality, let alone the magnitude, of these effects can be difficult due to challenges in the collection and application of access data (Hammitt et al. 2015), particularly when dealing with networks that are often complex and consist of multiple linear-feature types. Trail use, both motorised and non-motorised, has been less documented than road (paved, highways) effects (Fahrig and Rytwinski 2009), but is a form of disturbance that is growing (Knight and Gutzwiller 1995, Taylor and Knight 2003). For example, off-highway vehicle (OHV) registrations in North America have increased dramatically over the last few decades (Preisler et al. 2006).

Readily accessible GIS layers have improved measures of human disturbance, such as mapping of linear features, and are commonly applied within ecological studies. Effective methods for extending this information to estimate human activity within a network structure are lacking, however, leaving an information gap for cumulative effects assessments. The recent surge in deployment of remote sensor equipment, such as trail cameras and acoustic detectors (Burton et al. 2015, Lucas et al. 2015), provides ecologists with detailed data on human activity that can be pinpointed in time and space, significantly improving on temporally static linear feature layers. When studying wildlife, estimating the magnitude of human activity is a key, (Monz et al. 2013) and often challenging and therefore ignored, step in understanding its effects on animal distribution (Tigner et al. 2014), density (Thompson 2015), behaviour (Whittington et al. 2005, Beyer et al. 2013) and survival (Boulanger and Stenhouse 2014). Similarly, different forms of human activity (motorised versus non-motorised) are often overlooked, but can play an important role in wildlife responses. A more comprehensive method of estimating human activity, that incorporates network structure and spatio-temporal variation in human-use of the landscape, is required.

I evaluate an approach using a combination of mixed-effects generalised linear models (GLMMs) and Ordinary Kriging (OK) to estimate variation along an ecological linear-feature network, accounting for temporal variation in sampling intensity and timing. Specifically, this allowed me to estimate the probability of human activity in space and time across a landscape. I demonstrate that human activity is variable in both space and time, and argue this variability is adequately captured using the proposed method. I illustrate our approach using three years of trail camera data from the eastern slopes and foothills of Alberta's Rocky Mountains. This area is popular for many recreationists, and it sees large fluctuations in use between seasons, as well as variation in use across space. I predicted that activity would vary based on a number of covariates, including day of the year (a quadratic relationship with the peak at the height of summer), rainfall (decrease on rainy days), time of day (a decrease at night) and whether it was a weekday, weekend or long weekend (with activity increasing during the latter compared to the former). I also predicted that spatial variation is important and that consequently the inclusion of a random effect relating to sample location would substantially improve model fit and predictive capacity. I used our modelling procedure to estimate use for motorised and non-motorised activity separately, as I predicted that they would vary spatially due to access restrictions, and might be explained by different temporal covariates. Lastly, I assessed the accuracy of the model using cross-validation techniques.

2.2 Methods

Temporal model

When quantifying patterns in activity, or relative abundance for example, observed count data at a location traditionally is divided by the sampling effort, such as the number of days surveyed, giving an average daily measure (Carbone et al. 2001, Wang and Kockelman 2009). This approach is likely misleading, because count data are not only influenced by sampling effort, but also by various temporal attributes.

In general, detectors or observers are deployed and monitor activity at a number of sites (s) for a set period, which can be classified into discrete units, or observations (t). For example, any observation hour (one hour during which the detector was active) can be classified as 'present' (1) if recreational activity was detected, otherwise 'absent' (0). For a set of n predictor variables, $x_{k=1:n}$, a mixed-effects logistic regression (Zuur et al. 2009), in the following general form, is applied:

$$logit[p(present \text{ in } s \text{ at } t)] = [\beta_0 + \theta_{0,t,s}] + \sum_{k=1}^{n}[\beta_k + \theta_{k,t,s}] \cdot x_k(t,s) + \varepsilon_{t,s} \qquad (1)$$

where $\theta_{0,t,s}$, $\theta_{k,t,s}$, and $\varepsilon_{t,s}$ are normally distributed random variables with mean = 0 and independent standard deviations. Note that, depending on the required temporal resolution, as well as on the intensity of activity, count data can be used and a Poisson rather than a binomial formulation may be used. I focus here on the binomial case as I believe that it is more generally applicable.

The response is the presence or absence of activity at site s at time t, and x_k are temporal or spatial predictor covariates (Table 2.1). $\theta_{k,t,s}$ are random effects, which can be applied to both the intercept ($\beta_0 + \theta_{0,t,s}$) and the slope of each covariate ($\beta_k + \theta_{k,t,s}$). Lastly, the Best Linear Unbiased Predictor (BLUP; Robinson 1991) method is used to calculate point estimates of a random effect (e.g., site for spatial random effects or year for temporal ones). The BLUPs are obtained post-hoc and represent the random deviation of this site/year from the fixed effect. BLUPs are conditional on the estimated random (i.e., standard deviations) and fixed (i.e., βs) effects within the model. It is important to note that BLUPs may be biased (underestimated) in relation to the true spatial or temporal variation (Hadfield et al. 2010) and should be taken as conservative estimates of site/year effects.

Network – Based Ordinary Kriging

In most imaginable scenarios (excluding surveys conducted over many years where year-level random effects should be considered), the random effects in equation 1 are spatial, resulting in site-level BLUPs. Predicting activity in unobserved sites requires spatial interpolation of such BLUPs. A common geostatistical method of predicting a variable at unobserved sites is ordinary kriging (OK: Cressie 2015). OK estimates values based on the spatial autocorrelation between sampled sites. This autocorrelation relationship is summarised in an experimental variogram where semi-variance is a function of the Euclidean distance between sampling points (Fortin et al. 2002). A recent extension to OK involves the use of network distance rather than ‘straight-line’ Euclidean distance to generate a variogram, and has been used with traffic data on road networks (Shiode and Shiode 2011, Selby and Kockelman 2013), fish data along stream networks (Ganio et al. 2005), and has many more applications that involve dealing with linear-feature networks.

Say we have an unobserved location (n_0) at which we wish to interpolate an unknown value to (z_0) using observed values at a set of sample location (z_1, z_2,.. z_n). This value is interpolated as the weighted mean of the observed values

$$Z_0 = \sum_{i=1}^{n} w_i \cdot z_i \text{ , where } \sum_{i=1}^{n} w_i = 1 \qquad (2)$$

Each weight (w_i) is calculated as a function of the shortest path along the network from the associated observed location (n_i) and the unobserved location (n_0), and the level of spatial correlation within the data. This spatial autocorrelation is represented in a variogram, which can take a number of different forms, based on the spatial pattern observed in the variable of interest (Cressie 2015). These are constructed and experimental variograms that best represent the spatial autocorrelation structure are fit to the data, parameters are estimated using nonlinear least squares (R Core Team 2014, Pinheiro et al. 2016) and AIC is used to select the appropriate model (Burnham and Anderson 2002).

Once an experimental variogram is identified this is then used to calculate the inverse Γ matrix, in the form:

$$\begin{pmatrix} \gamma_{1,1} & \cdots & \gamma_{1,j} & 1 \\ \vdots & \ddots & \vdots & \vdots \\ \gamma_{i,1} & \cdots & \gamma_{i,j} & 1 \\ 1 & \cdots & 1 & 0 \end{pmatrix}^{-1} \qquad (3)$$

Where γ_{ij} denotes the variogram values based on the network distances between sampled points i and j.

Weights are calculated as follows:

$$\begin{pmatrix} \gamma_{1,1} & \cdots & \gamma_{1,j} & 1 \\ \vdots & \ddots & \vdots & \vdots \\ \gamma_{i,1} & \cdots & \gamma_{i,j} & 1 \\ 1 & \cdots & 1 & 0 \end{pmatrix}^{-1} \cdot g, \text{ where } g = \begin{pmatrix} \gamma_{0,1} \\ \vdots \\ \gamma_{0,n} \\ 1 \end{pmatrix} \tag{4}$$

and n is the number of sample sites. Once the weights for n_0 are calculated for each sample location, these are multiplied by the BLUPs and summed to give the estimated intercept z_0. These would be calculated for each of the unobserved network segments to be interpolated.

Application to recreational activity data

Our data were obtained from a 2,824 km^2 region of the eastern slopes and foothills of central Alberta's Rocky Mountains (Fig. 1). Industrial activity in the area is prevalent and diverse, consisting of active open-pit coal mining, logging and oil and gas exploration, all of which have contributed to the high density of linear features (seismic lines, logging roads) on the landscape, with varying stages of regeneration. The area is predominantly Crown land (no recreational restrictions) and includes a portion of Jasper National Park (no motorised activity or hunting), Whitehorse Wildland Park (no motorised activity, hunting allowed) and private reclaimed mine land (designated access routes, no hunting).

Between May 2012 and November 2014, I deployed Reconyx HC500 motion-activated cameras (43 in 2012, 71 in 2013, 116 in 2014) on human-use trails (in this present context, defined as man-made linear features), collecting data at 238 different sample sites (Fig. 1) that were evenly distributed over the landscape. During 2012, I designated a single camera to each 50-km^2 hexagonal cell and rotated to one of three trail sites every 20 days. In 2013, I monitored three new sites using the same method as in 2012, with an additional stationary camera set up at a randomly selected 2012 location. In 2014, I deployed 116 stationary cameras at three of the six sites from 2012 and 2013. I monitored trail camera sites for a minimum of 20 days each. Cameras were deployed at a distance > one kilometer from the nearest current or previously sampled location. I set cameras to take pictures 24 hours a day at high sensitivity, and took a set of three pictures in rapid succession when triggered with no delay in between consecutive triggers. I deployed cameras to maximise the detection zone and to minimise the probability of missing fast-moving objects such as OHV's (angled and placed further from trail). Cameras were checked every 20-40 days to download images, replace depleted batteries, and rotate if required. I classified images by date, time, and direction of travel. Events were treated as independent if triggers were at least one minute apart. If human recreation was present, the type of recreation was identified (e.g. truck, OHV, hiker, horse rider) and categorised into motorised and non-motorised recreation. Images of project members were removed from the dataset. Total number of trap days varied among sites (128.6 days ± 118.9, *range* 21 – 535) due to equipment failure and different sampling protocols between 2012, 2013, and 2014.

I applied a specific form of equation 1 to the data (with t equal to one hour), where I assigned temporal covariates only, and the intercept was assumed to vary by spatial location;

$$logit[p(present \text{ in } s \text{ at } t)] = [\beta_0 + \theta_{0,s}] + \sum_{i=1}^{n} \beta_i \cdot x_i(t) + \varepsilon_{t,s} \tag{5}$$

This formation implies independence between spatial and temporal variation in the data. I estimated a set of 16 *a priori* candidate models for motorised and non-motorised activity (Table 2.1 and 2-2 respectively). I contrasted two model sets that varied based on the inclusion of average daily temperature versus day of the year, to test whether it was daily temperature or time of year that influenced the probability of detecting activity. I did not include both in the same models as they are highly correlated. Day of the year was included in the model as a quadratic term, as I predicted a maximum level of activity in the summer, with lower levels in the spring and fall. By including site as a random effect I was able to incorporate the BLUPs within a spatial prediction model, such as OK. All analyses were done in R (R Core Team 2014), using the lme4 package (Bates et al. 2015). I identified the top model(s) using AIC and extracted the BLUPs for each camera location which were then used in the second step of the modeling procedure. A recent method for obtaining R^2 from generalised linear mixed-effects models (Nakagawa and Schielzeth 2013) was used to estimate the variance explained by the fixed effects (marginal: $R^2_{GLMM(m)}$) and entire model which includes the random effects (conditional: $R^2_{GLMM(c)}$).

I assigned BLUPs to their corresponding camera location in space (Fig. 2.1), giving a value that represents relative probability of motorised and non-motorised activity, controlling for temporal variation in sampling intervals for different camera sites. The values correspond to a scaled flow of activity on a segment within the extensive linear-feature network. To predict probability of activity for the remaining unobserved linear features, I used network-based OK. This involved incorporating the network distance between sample sites and accounting for spatial autocorrelation in the data (Cressie 2015). I created evenly distributed points across the trail network, splitting it into 200m trail segments. I then calculated network distance for each of these points from each of the sample sites. All network-distance matrices were constructed using ArcGIS Network Analyst (ESRI 2015) and network-based OK was done in R (R Core Team 2014). For our example, I confined my variograms to two forms: 1) Spherical and 2) Exponential (see Appendix R code for formula) as these two models best represented the spatial autocorrelation structure of our data. Nugget effect (microscale variation or measurement error; Matheron 1963) was also assumed to be absent, as I treated sampling error as absent and had no reason to believe that a spatial structure was present with a range shorter than our sampling interval (i.e. minimum 1km between camera locations).

Each of the interpolated BLUPs was assigned to the corresponding 200m trail segment, resulting in a linear feature network where the probability of human activity varies in space. To estimate the probability of occurrence of motorised or non-motorised activity on a specific trail at a specific time, the BLUPs were incorporated into the predictions of the temporal GLMM described above.

Model validation

I validated the two stages of the model independently. First, the temporal data were split in half, stratified by sample site. One half was used as a training dataset, the other as a validation dataset. The top model was refitted using the training data. This model was then used to predict the probability of human activity in the validation set. I constructed a Receiver Operator Characteristic (ROC) curve, and calculated Area Under the Curve (AUC) for both motorised and non-motorised activity. Second, I tested network-based OK performance by removing a single camera BLUP, and then calculating the predicted value for that site. This was done for every camera site and the predicted values were compared to the observed values using a correlation test.

2.3 Results

Between May 2012 and November 2014, cameras were active for a total of 1,036,307 hours. During this period, I recorded a total of 18,542 human activity events. Of these, 11,055 were motorised activity (truck, ATV, dirt-bike, or snowmobile), and the remaining 7,487 were non-motorised recreation (hiking, horseback riding, biking, skiing, and snowshoeing).

Temporal model

The top-ranked models for temporal variation in motorised and non-motorised activity included all temporal covariates, with day of the year performing better than average daily temperature (Table 2.1, 2-2). There was a higher probability of motorised activity on the weekend, during the day and during the summer months, as shown by the concave day of the year relationship. As expected, motorised and non-motorised activity was less probable during days with high rainfall (Table 2.3). The inclusion of sites as a random effect significantly improved AIC, indicating that the intensity of activity varied spatially. Inclusion of sample sites as a random effect increased R^2 values for both motorised ($R^2_{GLMM(m)}$ = 0.28 to $R^2_{GLMM(c)}$ = 0.75) and non-motorised ($R^2_{GLMM(m)}$ = 0.31 to $R^2_{GLMM(c)}$ = 0.78) models.

Experimental variogram

I estimated experimental variograms for both motorised and non-motorised BLUPs (Fig. 2.2). Distance bins were created so that equal sample sizes contributed to each value within the variograms. For both motorised and non-motorised, the best fitting variogram was the exponential model (equation 6):

$$\gamma(\boldsymbol{h}:\boldsymbol{\theta}) = \boldsymbol{c_e}\,(\boldsymbol{1} - \boldsymbol{e}^{-\frac{\boldsymbol{h}}{\boldsymbol{a_s}}}) \qquad (6)$$

Where h is the network distance (metres). The sill (c_e) and range (a_s), determine the shape of the variogram. c_e represents the asymptote at which variance ceases to increase with added distance and a_s represents the distance at which this sill is reached. Parameter estimates for motorised and non-motorised variograms were, c_e = 4.718 and 5.093, and a_s = 7620m and 14245m respectively.

Network-based Ordinary Kriging

In Fig. 3, I present kriged maps for motorised (left) and non-motorised (right) BLUPs. Variance maps can be viewed in Appendix S1 (Fig. S1). As expected, I estimated low motorised activity in the parks where motorised recreation is prohibited. Outside of the protected areas, motorised activity was estimated to be higher. The majority of non-motorised activity was localised on trails with motorised restrictions (Jasper National Park, Whitehorse Wildland Park, reclaimed mine areas), the only area showing high overlap between types of recreation being the trails around Hinton and the Cheviot mine lease, which allowed motorised access. Standard error estimates were far higher for motorised activity BLUPs relative to the non-motorised BLUPs, likely due to the small range within the variogram (motorised = 7620 meters, non-motorised = 14245 meters). Combining the spatial and the temporal predictions, shows that probability of activity depended heavily on both temporal variables and spatial location (Fig. 4).

Model performance

Our ROC results showed that both the motorised and non-motorised temporal activity models performed well ($AUC_{motorised}$ = 0.93, $AUC_{non\text{-}motorised}$ = 0.96). These values are classified as 'high accuracy' (Boyce et al. 2002). The second stage of the model: network-based OK, was less accurate, however, estimated values still showed substantial positive correlation with actual values. Accuracy was higher for non-motorised than motorised activity (r = 0.639 for non-motorised, r = 0.472 for motorised).

2.4 Discussion

Using the outlined method, I was able to predict the probability of motorised and non-motorised activity across a large trail network. By modeling variation in sampling intensity and timing, I created a probability surface across the linear feature network that was representative of the spatial variation in human activity. Ultimately, this approach yielded an evidence-based and accessible map of the area and can inform integrated-landscape management.

Temporal variation was accurately explained using a small number of covariates: time of day, day of the year, day of the week, holiday status, and average daily rainfall. The precision to which I was able to model the occurrence of both motorised and non-motorised activity indicates that temporal fluctuations in the occurrence of recreation are predictable. This temporal pattern is likely to be present outside of our study area, and in fact across much of North America (Taylor and Knight 2003). I clearly demonstrated that recreationists are more likely to be found on trails during the day, during the summer months, on weekends relative to weekdays, and to an even greater extent on long weekends. Day of the year was a better predictor than daily temperature, however weather did affect recreationists through rainfall reducing probability of occurrence. Although these results seem obvious, many ecological studies still continue to ignore temporal predictors of human activity, rather choosing to average across large timeframes, losing temporal resolution, making inferences without accurate human activity information.

Using a GLMM, and incorporating the sampling location as a random effect, I was able to extract BLUPs that represented the magnitude of activity independent of temporal variation in sampling. A relatively novel approach, modelling the BLUPs offers a convenient method of estimating site effects when they cannot be effectively modelled as a function of covariates, a useful tool in ecological research (Avgar et al. 2013). I acknowledge there are limitations with this method, specifically linked with the use of BLUPs to estimate unexplained variance partitioned using random effects (Hadfield et al. 2010). In this particular case, I believe that the estimation of spatial variation at camera sites using the BLUP method results in a more conservative estimation of this variation due to the tendency for the method to constrain values closer to the mean. In addition, the R^2 values show the importance of accounting for both temporal and spatial variation, as both contributed significantly to explained variance. Previous efforts to interpolate count data across a surface using kriging methods had problems with sampling effort and timing (Monestiez et al. 2006). By modeling the temporal variation in the camera data, rather than kriging the raw count data, our model not only controls for variation in survey length, but also identified temporal components of variation in human activity.

Despite improvement, Network-based OK results suggest that characterising spatial variation in human activity is more challenging. The fact that more deviance was explained for non-motorised activity stems from the pattern of spatial autocorrelation being better defined by our experimental variogram, therefore resulting in more accurate estimates. Motorised recreationists showed less-predictable movement, and the spatial correlation between sites was less defined. This is intuitive because distance is less of a cost for motorised vehicles than it is for people on foot or on horseback. Increasing sample sizes in general (i.e. more trail cameras), and specifically increased observations at smaller distances, may help better estimate the experimental variogram, improving interpolation results. The remaining unexplained variation is likely made up of a number of factors: type of trail, accessibility of trail routes, barriers to movement, scenic routing (Drake et al. 2015), advertised trails and human communication. All will all play a role in explaining spatial variation in the intensity of use, and are in many cases variables that are difficult to quantify. Consequently, mechanistic models attempting to capture spatial patterns of trail-use based on spatial predictors may often fail. As I demonstrated, the more phenomenological approach of krig-based interpolation using network distance offers an effective alternative. However, when potential spatial predictors are available, I recommend incorporating them in the GLMM, and identifying whether their inclusion improves model performance.

The relationship between wildlife and linear features is complex. Many animals show avoidance of roads and trails, whilst others use them to increase movement speed through their home ranges (Ehlers et al. 2014). Some animals are attracted to linear features due to increased vegetation growth (Roever et al. 2008). A number of ungulate species stay close to roads and trails, as there is a disproportionate response to human activity between prey and predators (Berger 2007, Muhly et al. 2011). Animal responses outlined above are not solely based on the presence of a linear feature, but also the intensity of use of that feature by humans. Changes in the amount of human activity on trails or vehicle traffic on roads is likely to influence how wildlife perceive and interact with linear features. Seasonal changes in animal behaviour and fluctuations in human activity further confound our understanding of how animals perceive linear features. These measures are key in understanding how wildlife alter not just their movement across the landscape, but also their activity patterns in response to encroaching human activity (Steenhof et al. 2014; Boyce et al. 2010; Martin et al. 2010). Estimating the probability of use of a linear feature can give a greater understanding of what wildlife are truly experiencing when it comes to human encroachment in wilderness areas (Monz et al. 2013). By ignoring measures of activity levels on linear features such as trails, researchers may be extracting incorrect inferences from our results, which could have strong implications for management. By using data collected with remote sensors, a form of data that is ever-increasing (Burton et al. 2015), and applying a combination of regression and geospatial statistics, this method creates a spatio-temporal map of human activity that can be applied to coordinate access management enforcement where most needed, as well as used in further ecological analyses of habitat suitability, degradation, mortality risk, and behavioural responses by wildlife. Future applications of this method will enhance our understanding of wildlife responses to recreation, and allow for more precise identification and resolution of conflicts through management, enhancing the efficacy of mitigative actions.

Our method has applications outside of modelling human activity across a landscape. Studies that attempt to estimate activity on road networks might benefit from using this method, especially if monitoring effort varied, as would studies using remote sensors to identify relative abundance, for example, in streams or on wildlife corridors

(Ganio et al. 2005, Peterson and Hoef 2010). Extensions could include additional network information such as barriers to movement (Beyer et al. 2014). As GIS techniques continue to improve, predictor variables relating to linear-feature mapping can be easily incorporated using our method, either with mixed-effects logistic regression, or as an intermediate step that further explains BLUP variability. In our example, I had no *a priori* reasoning to treat spatial and temporal variation as non-independent. If this is not the case, a random effect could be included to allow variation in the slope, in addition to the intercept, for a specific covariate. Lastly, my method is not constrained to occurrence data: by choosing an appropriate GLM family and link-function, our approach could be applied to modelling the abundance of animals within a corridor network, the concentration of toxins found in river and stream networks, and the spread of invasive species by hikers and motorists. Many of these are likely to require controlling variance created through sampling schedules before tackling the spatial component. I believe the application of a network based geostatistical approach in conjunction with controlling for sampling noise, will result in improved modelling efforts that will increase our understanding of how linear networks influence their surrounding ecosystems.

Table 2.1. Candidate models and associated AIC results for temporal activity in motorised recreational activity. Descriptions of each model variable can be found in Table 2.3.

Model (motorised)	**Number of parameters (*k*)**	**AIC**	**Δ AIC**	**AIC weight**
Average daily rainfall (mm) + Day of the year + Day of the year^2 + Week day + Time of Day + (1|location)	6	65886	0	1
Day of the year + Day of the year^2 + Week day + Time of Day + (1|location)	5	66026	140	0
Average daily rainfall (mm) + Average daily temperature (*C) + Week day + Time of Day + (1|location)	5	66425	539	0
Average daily temperature (*C) + Week day + Time of Day + (1|location)	4	66535	649	0
Day of the year + Day of the year^2 + Time of Day + (1|location)	4	67779	1893	0
Average daily rainfall (mm) + Time of Day + (1|location)	3	68604	2718	0
Time of Day + (1|location)	2	68786	2900	0
Average daily rainfall (mm) + Day of the year + Day of the year^2 + Week day + (1|location)	5	71481	5595	0
Day of the year + Day of the year^2 + Week day + (1|location)	4	71614	5728	0
Average daily rainfall (mm) + Average daily temperature (*C) + Week day + (1|location)	4	71840	5954	0
Average daily temperature (*C) + Week day + (1|location)	3	71895	6009	0
Week day + (1|location)	2	72810	6924	0
Average daily rainfall (mm) + Average daily temperature (*C) + (1|location)	3	73550	7664	0
Average daily temperature (*C) + (1|location)	2	73603	7717	0
(1|location)	1	74549	8663	0
Day of the year + Day of the year^2 + Week day + Time of Day	4	82022	16136	0

Table 2.2. Candidate models and associated AIC results for temporal activity in non-motorised recreational activity. Descriptions of each model variable can be found in Table 2.3.

Model (non motorised)	**Number of parameters (*k*)**	**AIC**	**Δ AIC**	**AIC weight**
Average daily rainfall (mm) + Day of the year + Day of the year^2 + Week day + Time of day + (1|loc	6	44915	0	1
Day of the year + Day of the year^2 + Week day + Time of day + (1|location)	5	45009	94	0
Average daily rainfall (mm) + Average daily temperature (*C) + Week day + Time of day + (1|locatio	5	46006	1091	0
Day of the year + Day of the year^2 + Time of day + (1|location)	4	46053	1138	0
Average daily temperature (*C) + Week day + Time of day + (1|location)	4	46115	1200	0
Average daily rainfall (mm) + Time of day + (1|location)	3	47349	2434	0
Time of day + (1|location)	2	47504	2589	0
Average daily rainfall (mm) + Day of the year + Day of the year^2 + Week day + (1|location)	5	49753	4838	0
Day of the year + Day of the year^2 + Week day + (1|location)	4	49842	4927	0
Average daily rainfall (mm) + Average daily temperature (*C) + Week day + (1|location)	4	50611	5696	0
Average daily temperature (*C) + Week day + (1|location)	3	50668	5753	0
Week day + (1|location)	2	51388	6473	0
Average daily rainfall (mm) + Average daily temperature (*C) + (1|location)	3	51608	6693	0
Average daily temperature (*C) + (1|location)	2	51664	6749	0
(1|location)	1	52411	7496	0
Day of the year + Day of the year^2 + Week day + Time of day	4	63556	18641	0

Table 2.3. Estimated β coefficients and standard errors from a generalized linear mixed-effects model for both the motorised activity top model and the non-motorised activity top model, including a description of each model variable.

Model variable	**Description**	**Motorised**	**SE**	**Non-motorised**	**SE**
Intercept	-	-7.6130	0.1978	-11.0377	0.2640
Rainfall	Daily rainfall (mm)	-0.0310	0.0028	-0.0300	0.0033
Day_of_year	Scaled day of the year	9.5310	0.3707	14.7900	0.4394
Day_of_year^2	-	-8.2970	0.3364	-12.3500	0.3821
Time of day (Reference = Day)	-				
Dawn	+/- 1 hour civil dawn	-2.7370	0.1339	-3.1130	0.1807
Dusk	+/- 1 hour civil dusk	-1.0820	0.0605	-1.7421	0.0940
Night	-	-3.9460	0.1220	-4.1950	0.1501
Day of week (Reference = Long Weekend)	Includes Sat-Mon on holidays				
Weekday	Mon-Fri	-1.3080	0.0313	-1.0560	0.0401
Weekend	Sat, Sun	-0.6120	0.0339	-0.2340	0.0424

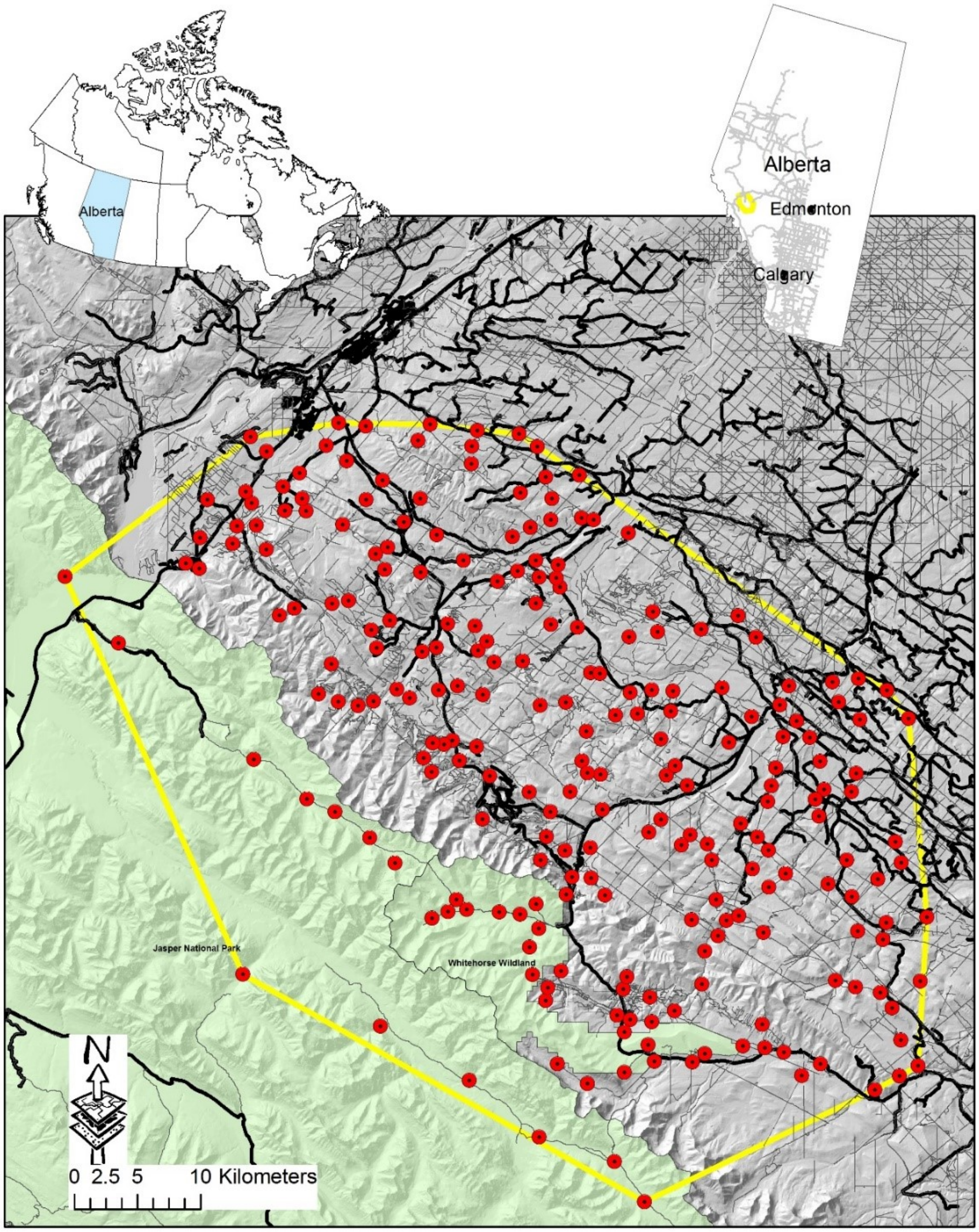


Fig. 2.1. Map of study area, located in west-central Alberta in the eastern slopes and foothills of the Rocky Mountains. Roads (black), trails (grey) and trail camera sites (red). Are included on the map. Protected areas are also shown in green shade. Trails are defined as any man-made linear feature excluding designated roads (e.g. seismic lines, designating hiking and ATV trails, discontinued logging roads).

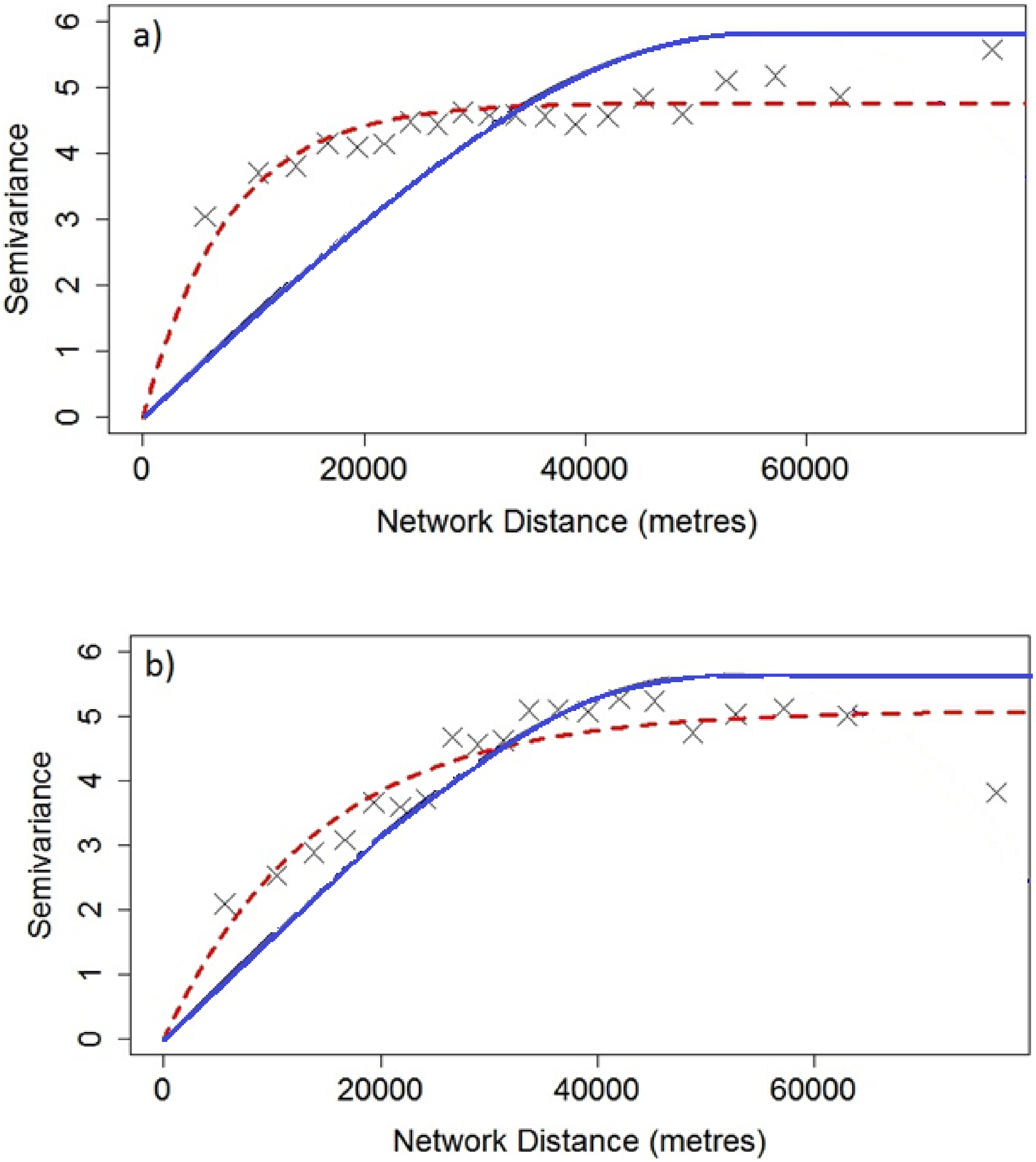


Fig. 2.2. Experimental variograms on BLUPs (exponential model = red/jagged, spherical model = blue/full) for a) motorised and b) non-motorised activity. AIC values for the motorised models were: spherical = 68.19, exponential = 13.86 and for non-motorised were: spherical = 37.68, exponential = 27.71. Model parameters were estimated using least-squares.

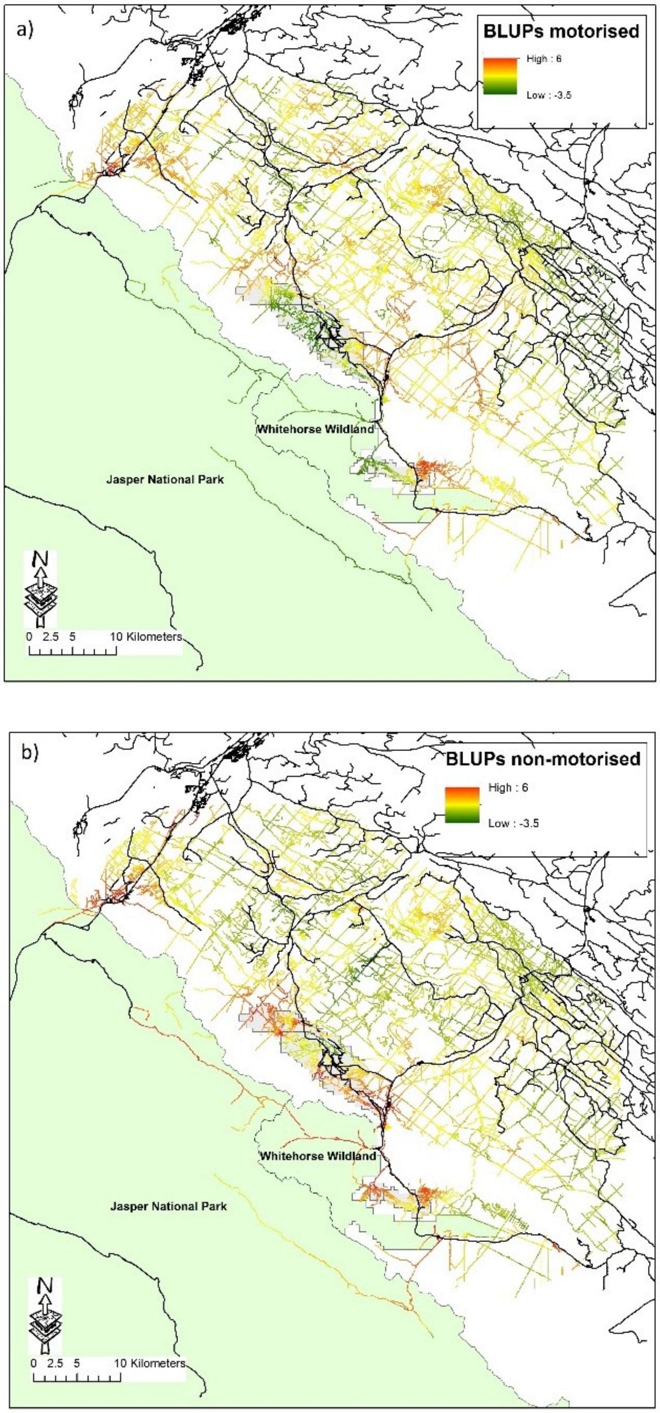


Fig. 2.3. Map of interpolated BLUPs using network-based Ordinary Kriging for a) motorised and b) non-motorised activity. High BLUP values (red) represents a high spatial probability of motorised and non-motorised activity relative to low BLUP values (green). Roads (black) and protected areas (green) are included in the map.

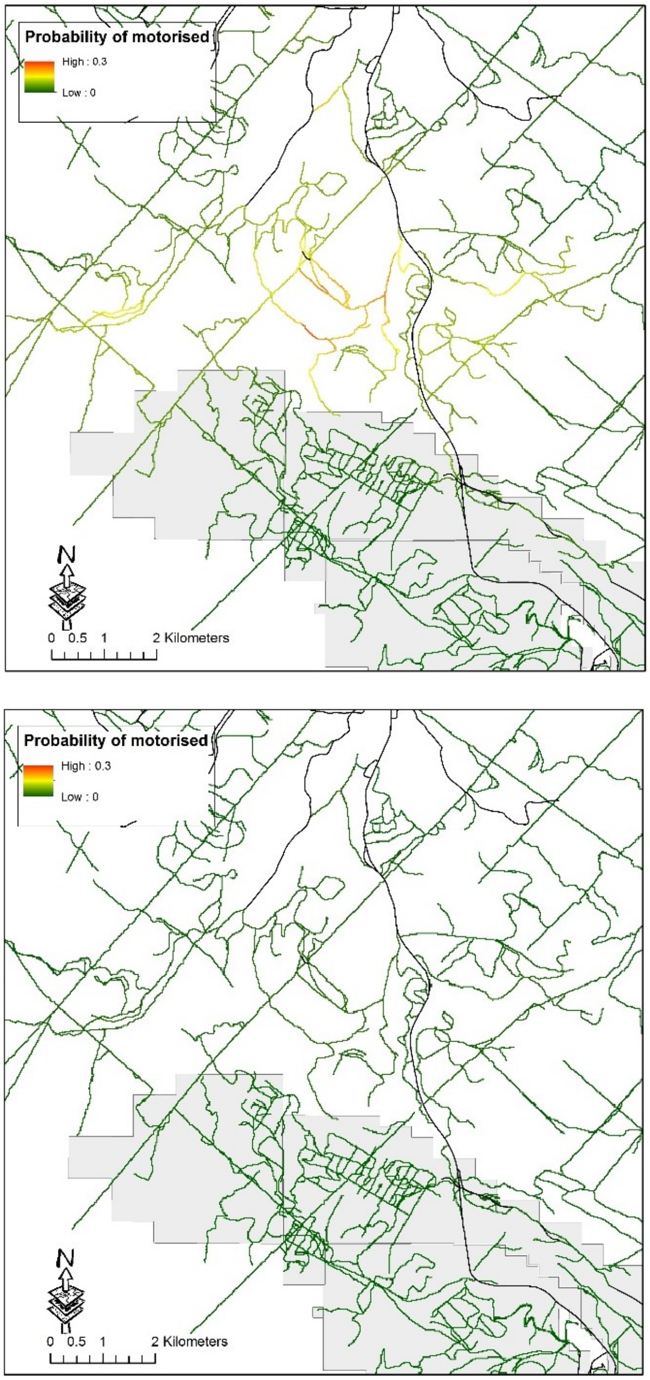


Fig. 2.4. Maps of a subset of the study area showing a combination of spatial and temporal results: a) summer long weekend, and b) spring weekday. Values represent the probability of motorised activity for each 200m segment of the trail network. Roads (black) and mine sites (grey) are included in the map.

3 Movement ecology of a large carnivore responding to human recreational activity

3.1 Introduction

Advancement in GPS radiotelemetry technology has led to increasingly finer scales of animal relocation data (Cagnacci et al. 2010). This has subsequently improved our ability to approximate the true path taken by animals through the landscape (Thurfjell et al. 2014). Finer-scale relocation information has implications for movement ecology research, linking mechanisms that drive movement behaviour to the observed movement pattern (Kays et al. 2015), and in turn, animal distribution (Turchin 1998). Specifically, greater temporal resolution in animal relocations results in better understanding of the interplay between fundamental characteristics of movement: (i) external factors that motivate and affect movement, (ii) constraints on how the animal can move, and (iii) the internal state of the animal that drives its reasons to move (Nathan et al. 2008).

Animal movement is the mechanism that links space-use with habitat selection and avoidance of external factors (Avgar et al. 2015). Traditional uses of telemetry data to document animal distributions include modeling space-use with environmental variables to infer resource selection (Manly et al. 2002). Resource selection functions (RSFs) compare a set of used points (relocation data) to a set of available points randomly distributed across a landscape (Manly et al. 2002, Johnson et al. 2006). Applications of this method often ignore animal movement, due in part to low temporal resolution of telemetry relocation data. Advances in data collection have been mirrored by advances in analytical techniques, especially relating to incorporating animal movement in habitat selection studies (Fortin et al. 2005, Forester et al. 2009, Potts et al. 2014). Initial analysis extensions involved constraining availability of selection for a single step (straight line connecting two sequential relocations) by the movement constraints of the animal (part ii; Nathan et al. 2008). Step selection functions (SSFs; Fortin et al. 2005), have the advantage of relocations being temporally defined, thus allowing inclusion of fine-scale, temporally dynamic variables. These methods are especially useful for monitoring large, free-roaming mammals, that allow the application of radiocollars with enough power to obtain frequent relocations over a long period (Cagnacci et al. 2010). However, this method still lacks the ability to explicitly test hypotheses relating to differences in movement as a function of internal state and external factors (part i and iii; Nathan et al. 2008), because movement and selection are treated as independent processes.

Grizzly bears (*Ursus arctos*) are large mammals for which movement and habitat selection is defined by both an internal state (e.g. sex, reproductive status, genotype) and external factors, such as topography (Mace et al. 1996), food distribution (Nielsen et al. 2010) and human disturbance (Mace et al. 1996, Gibeau et al. 2002, Boulanger and Stenhouse 2014, McKay et al. 2014). There are significant knowledge gaps related to our understanding of grizzly bear movements. However, a common theme is that bears have high individual variability, making population-level inference challenging (Boyce et al. 2010, Northrup et al. 2012a, Cristescu et al. 2016). Despite this, bears do respond consistently to certain landscape variables. For example, areas of high terrain ruggedness tend to be avoided, likely due to its constraints on animal movement (Roever et al. 2010), while areas of high food quality are selected (Nielsen et al. 2004a) which results in slower foraging-based movements in other species (e.g. in elk, *Cervus canadensis,* Frair et al. 2005). Roads, and associated human activities negatively influence grizzly bear persistence by reducing survival (Boulanger and Stenhouse 2014, Lamb et al. 2017), and indirectly by altering habitat availability and movement (Roever et al. 2010, Northrup et al. 2012a). Analysis of autocorrelation patterns in grizzly bear step lengths concluded that bears in areas of high road-density displayed higher movement rates at night and disrupted daily movement patterns (Boyce et al. 2010). Conversely, positive associations with linear features have also been found, such as increased foraging opportunities adjacent to roadsides (Roever et al. 2010, Kite et al. 2016) and areas associated with roads (Nielsen et al. 2004a). Linear disturbances, such as seismic lines that are a product of industrial exploration, can lead to increases in carnivore movement rates, thus improving their search efficiency for prey (Latham et al. 2011, Dickie et al. 2016).

Moreover, selection and movement responses to external factors such as linear disturbances may not be constant across time, because the magnitude of human activity on such features can be dynamic (Ladle et al. 2017). This may result in spatio-temporally varying 'landscape of fear' (Laundré et al. 2001, Ciuti et al. 2012a), whereby grizzly bears might perceive human activity as a form of risk (Frid and Dill 2002). Risk avoidance can have implications for habitat selection (L. Thomson et al. 2006, McGreer et al. 2015), and the implementation of risk avoidance behaviours reduce fitness through diminished survival and reproduction (Creel et al. 2007, Creel and Christianson 2008). Such changes in habitat selection have been documented in grizzly bears (Brown and Kotler 2004, Nielsen et al. 2006), and risky habitats also can lead to increased grizzly bear movement (Graham et al. 2010).

To document how grizzly bears alter their movement and selection in relation to linear disturbance, I investigated grizzly bear response to human recreational activity, and extend previous methods in modelling habitat selection using an integrated step selection analysis (*i*SSA; Avgar et al. 2016, Prokopenko et al. 2017). Outdoor recreation on trails can negatively impact wildlife (Seip et al. 2007, Reed and Merenlender 2008, Rogala et al. 2011, Hammitt et al. 2015, Thompson 2015, Fortin et al. 2016, Larson et al. 2016), and may influence the perception of linear disturbances by grizzly bears, altering their movement and habitat selection in response to changes in perceived risk. To address this, I formulated the following set of questions; A) Do bears select trails and how does selection vary with different probabilities and forms of recreational activity? B) Do I observe changes in movement rates in relation to trail proximity? C) Is movement independent of recreational activity, or does it vary based on recreational activity (displacement as a response to recreation)?

3.2 Methods

Study area

I conducted the study in a 2,824 km^2 region of the eastern slopes and foothills of central Alberta's Rocky Mountains (Fig. 3.1). The landscape consists of rugged, mountainous terrain to the west, with transition to the east into rolling, lower-elevation foothills. Coniferous forest dominates, consisting of spruce (*Picea* spp.), fir (*Abies* spp.) and lodgepole pine (*Pinus contorta*), with an increase in mixed forest, including aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) farther east and at lower elevations. The study region contains multiple land-use types, with a variety of restrictions in recreational-use. The area is predominantly public land (few recreational restrictions), including portions of Jasper National Park (JNP; no motorised activity or hunting), Whitehorse Wildland Park (WWP; no motorised activity, hunting allowed) and leased reclaimed mine land (designated access routes, no hunting). Natural resource extraction is prevalent and diverse on public lands in the region, consisting of active open-pit coal mining, forest harvesting and oil and gas exploration, all of which have contributed to a high density of linear disturbance (cutlines, resource access roads, powerlines, pipelines) on the landscape, with varying stages of regeneration.

Grizzly bear movements

Between April 2011 and November 2015, Foothills Research Institute's Grizzly Bear Program (FRIGBP; Hinton, Alberta, Canada) collected location data for 16 grizzly bears (6 males, 10 females; Table 1) residing in and around the study area using Global Positioning System (GPS) radio-telemetry collars (Followit, Lindesberg, Sweden). Capture and handling complied with the Canada Council of Animal Care handling guidelines and were approved annually by the University of Saskatchewan Animal Care Committee (#20010016), and University of Alberta Animal Care (AUP00000436). All captures were either using culvert trap or aerial helicopter methods (Cattet et al. 2003). Duration of monitoring varied across bears, with some individuals only collared for a single season, whilst others were collared for multiple years. All collars were programmed to record locations every hour. For this study, I included all locations between April 14 – September 30 (when information on bear foods was available) and inside the camera trap array. I identified consecutive locations (separated by 55-65 minutes) for each bear and created a total of 74,925 individual steps (range: 624 – 8493 steps per individual bear, median: 3090 steps; Table 1). I split data by bear and year and removed partitioned datasets with < one week of data (168 steps). I further categorized steps as either night or day, based on sunrise/sunset data (http://www.nrc-cnrc.gc.ca/eng/services/sunrise/). This resulted in 54 individual datasets (27 day, 27 night), each analyzed independently.

Recreational activity

I recorded hourly presence of motorised and non-motorised recreational activity between May 2012 and November 2014, at 240 locations. I placed infrared remotely triggered trail cameras (Reconyx LLP, Holmen, Wisconsin, USA) on human-use trails (in this present context, defined as any man-made linear features). I selected trail locations using a stratified random sampling design based on land cover type, and I monitored each for >= 20 days. If human recreation was present, I identified the type of recreation (truck, OHV, hiker, horse rider) and categorized it into motorised and non-motorised recreation. I created models of motorised and non-motorised activity using the trail camera data (see Ladle et al. 2017 for full description). First, I fit a generalized linear mixed effects model with a binomial link function (Zuur et al. 2009) with hourly presence/absence information of recreational activity as the response variable, various temporal covariates as fixed effects and trail camera sampling location as a random effect. I extracted the best linear unbiased predictors (BLUPs) at each sampling location and spatially interpolated across the trail network using Network-based Ordinary Kriging (Shiode and Shiode 2011). Network distance between each sampled camera location was calculated using ArcGIS Network Analyst (ESRI, Redland, CA). The final product consisted of spatiotemporal probability of motorised and non-motorised recreational activity across the entire trail network. I ran the model for each year of data independently, and applied a cross-validation method by evaluating the yearly performance of each model in predicting the presence/absence of activity in alternate years. I identified no clear directional trend in recreational activity across years, and single-year models were successful at predicting the probability of motorised and non-motorised occurrence in the other years monitored, I was thus confident in using the temporal model to extrapolate the probability of motorised and non-motorised occurrence for all bear-year combinations. Lastly, I logit-transformed all probability of recreational activity variables (see Table 3.2).

Habitat covariates

In addition to recreational activity, I included a number of covariates known to influence grizzly bear habitat selection and movement (Nielsen et al. 2002, Northrup et al. 2012). I used a spatiotemporal food quality index following Nielsen et al. (2010). Briefly, I condensed nine grizzly bear food species distribution models (SDMs) into six categories representing the presence or absence of different grizzly bear food types. The ungulate model only contained moose. Next, I generated biweekly food quality maps by multiplying the species distribution maps by importance weight of that food for that biweekly period (Munro et al. 2006)and then summing these values. I attached seasonal importance weights to each SDM using previously collected data from within the study area on percent dry digestible matter from scats obtained during each biweekly period (Munro et al. 2006; Fig. S1). I also used landscape variables including distance to road, distance to trail, distance to forest edge (both inside edge and outside edge; Nielsen et al. 2009, Stewart et al. 2013), distance to stream and terrain ruggedness with natural logarithm transformations used for distance to road and streams. All variables were calculated using ArcMap (ESRI 2015).

*Integrated Step-Selection Analysis (i*SSA)

An *i*SSA assumes that animal space use consists of two main components: a discrete-time movement kernel, and the habitat-selection function (Avgar et al. 2016). The movement kernel is the spatial probability density function of relocating from spatial location x_{t-1} to x_t at time t and in the absence of habitat selection. The movement kernel thus includes explicit probability functions for the step length (the Euclidean distances between x_t and x_{t-1}, and possibly x_{t-1} and x_{t-2}), the directional bias and the turning angle (the angular deviation between consecutive steps), each of which could include the effects of spatial and temporal covariates. The habitat-selection function takes the exponential form and yields the conditional probability of observing the animal at a specific location, given a set of location attributes and in the absence of movement constraints. See Avgar et al. (2016) for further background and Prokopenko et al. (2017) for a similar application.

I first characterized a tentative population-level probability distribution of step lengths. This was done using a gamma probability density function where maximum likelihood estimates of the shape (b_1) and scale (b_2) parameters were obtained using non-linear least squares from the MASS package in R (Venables and Ripley 2002), with all observed step lengths (across all bear years) as the input ($b_1 = 0.492$, $b_2 = 588$). Next, I sampled a set of 10 random steps and associated end points and coupled them with each animal use location. Random steps were generated by sampling a step length and turning angle: distance relative to the start location was sampled from the parameterized gamma distribution, turning angles were sampled from a uniform angular distribution, because mean cosine $\theta \approx 0$, which infers a random walk with no directional persistence (Benhamou 2006). I extracted covariates (Table 3.2) for both the start and end points for each step (both used and random), based on their spatial and temporal positions. I modeled habitat selection and movement using conditional logistic regression in R (*clogit;* Therneau 2015), with cluster ID (a group of one use step and its ten associated random steps) ID as strata.

I included variables predicted to influence grizzly bear habitat selection and movement within a set of *a priori* candidate models for each individual bear. I included the natural logarithm of step length (hereafter *lnSlength*) as a covariate to estimate the basal movement kernel when habitat selection is accounted for; the associated statistical coefficient is a modifier of the tentative gamma shape parameter (b_1; Avgar et al. 2016). The inclusion of *lnSlength* as a covariate also controls for individual variation in movement behaviour relative to the population level, and it can be used to evaluate alternative hypotheses relating changes in movement to habitat covariates, which I do here. I analyzed steps taken during night and day separately based on my expectation that I will see responses to recreational activity during the day, when both bears and recreationists are most active.

Model Selection

I constructed a set of candidate models representing a number of alternative hypotheses. The null model consisted of food quality and landscape covariates (Table 3.3, model 1) predicted to affect general patterns of grizzly bear habitat selection. Alternative models incorporated linear disturbances and human activity covariates, although these models did not consider interactions with movements (Table 3.3, models 2-5). Lastly, to model movement responses by grizzly bears, I also included interactions between *lnSlength*, natural logarithm of distance to trail (*lnDtrail*; see Table 3.2 for full description of transformations) at the start of the step and recreational activity (Table 3.3, models 6-

8). The global model included *lnDtrail*, motorised and non-motorised activity at the nearest trail segment, the interaction between these two covariates, and interactions with *lnSlength* (Table 3.3, model 9). I based model selection (Burnham and Anderson 2002) on individual grizzly bear-years. I calculated AIC weights for each of the competing models to identify the importance of incorporating estimates of recreational activity and movement interactions. Lastly, I calculated mean AIC weight across bear-years for each model, and compared both day and night models to determine the most supported model at the level of the population.

Population-level responses to recreation

I used individual-based modeling, rather than mixed-effects conditional logistic regression (Duchesne et al. 2010), and then obtained values for the population-level response post-hoc (Fieberg et al. 2010). To obtain coefficient estimates at the population level, I bootstrapped coefficients. I subsampled β coefficients for each bear, irrespective of the number of years sampled, x times, where x = number of individual bears in each subset, and a mean coefficient was calculated. This was repeated 2,000 times for each β coefficient, to obtain population level averages and confidence intervals (based on the 2.5th and 97.5th quantiles). I calculated bootstrapped βs at the population level, and also for males and females separately.

I assessed the log-Relative Strength of Selection (*ln*-RSS; Avgar et al. *in Review*) to investigate how bears respond to our covariates of interest, specifically the interaction between *lnDtrail* and motorised and non-motorised activity on the trail. The *ln*-RSS was calculated:

$$\left\{ln\left(\frac{h_i\,(x_1) - \Delta h_i}{h_i\,(x_1)}\right)\right\} * \;[\beta_i + \beta_{ij} * h_j\,(x_1)], \tag{1}$$

where $h_i\,(x_1)$ was *lnDtrail*, Δh_i was the *ln* average step length, which represents the difference in *lnDtrail* in one time-step, h_j was the logit-transformed probability of motorised or non-motorised activity and β_i and β_{ij} were the population-level β coefficients for *lnDtrail* and the interaction term with recreational activity respectively. In this context, *ln*-RSS can be defined as the relative selection strength of moving one mean step length away from the trail relative to one mean step length towards the trail as a function of absolute *lnDtrail* and whether recreational activity was absent or at high levels.

I corrected our original gamma distribution coefficients by adding the *lnSlength* estimate (change in shape parameter) and then multiplying this by our estimated scale to obtain an expected selection-free displacement rate (m/hr). I calculated population-level changes in movement rate as a function of *lnDtrail* and recreational activity by incorporating the bootstrapped β coefficients for the interactions between *lnDtrail* and *lnSlength*, and the further interactions with motorised and non-motorised activity.

3.3 Results

Model selection

Daytime models that incorporated interactions with *lnSlength* performed significantly better in terms of AIC weight, and inclusion of an interaction between distance to trail and probability of motorised and non-motorised activity further improved daytime model performance. The same result did not hold for night-time models (Fig. 3.2), where performance was not improved by adding recreational activity terms, however including *lnDtrail* did improve model selection for some bears. Although the daytime global model had the highest average AIC weight, this was highly variable across individual bear-years.

Habitat selection and recreational activity

Grizzly bears showed positive selection for food quality (mean β = 0.16, 0.025 : 0.975 quantiles = 0.054 : 0.27), less-rugged terrain (mean β = -0.00093, 0.025 : 0.975 quantiles = -0.0015 : -0.00032), areas close to streams (mean β =0.085, 0.025 : 0.975 quantiles = 0.064 : 0.11), areas closer to the inside edge of forest cover (mean β =-0.0020, 0.025 : 0.975 quantiles = -0.0027 : -0.0015), as well as areas close to outside edge (mean β =-0.00084, 0.025 : 0.975 quantiles = -0.00013 : -0.00048).

At the population level, bears showed no significant selection response to proximity to roads (mean β =0.015, 0.025: 0.975 quantiles = -0.025: 0.051; Fig. 3a), however, I found that there was a positive selection for areas closer to trails (mean β =0.12, 0.025: 0.975 quantiles = 0.039: 0.21; Fig. 3.3a). Selection for areas closer to trails disappeared when probability of motorised or non-motorised recreational activity was high (Fig. 3.3a, 3-3b). The strength of this selection can be seen using a *ln*-RSS plot (Fig. 3.3b). When close to trails, bears are less likely to move away from the trail than they are towards it, as shown by the negative log-RSS values. This diminishes farther from the trail, with indifference to trails at approximately 400 m from the trail (Fig. 3.3b). Selection was indistinguishable between males and females for variables associated with human recreational activity (Fig. 3.3a).

Movement and recreational activity

Coefficients affiliated with *lnSlength* represent deviations from the gamma shape value used to sample random steps. Grizzly bear selection-free movement rates (i.e. after accounting for habitat selection) were significantly larger than the observed step length. When estimating coefficients at the population level, bears did not significantly alter their step length relative to trail proximity (mean β=-0.032, 0.025: 0.975 quantiles =-0.065: 0.0048; Fig. 3.4), However, when split by sex, males moved significantly slower when close to trails (mean β =-0.081, 0.025: 0.975 quantiles =-0.10: -0.057; Fig. 3.4). Females did not display the same response (mean β =-0.032, 0.025: 0.975 quantiles =-0.065: 0.0048; Fig. 3.4), although there was a large amount of variation across individual females. When the probability of motorised recreation was high, male bears significantly altered their movement behaviour, increasing their movement rates when close to trails (mean β =0.0056, 0.0028: 0.01; Fig. 3.5a). Male bears showed a similar switch in their movement response to trails with non-motorised recreation (mean β =0.0033, 0.025: 0.975 quantiles =-0.00024: 0.0081; Fig. 3.5c). No change in female movement response to trail proximity as a function of the probability of recreation was found (Fig. 3.5b, d).

3.4 Discussion

Using integrated step selection analysis (iSSA), I modelled habitat selection by grizzly bears using a mechanistic movement-model framework (Avgar et al. 2016). Grizzly bears selected trails, except where recreational activity was high. Male grizzly bears changed movement patterns, switching from slower movements when recreation was absent, to faster movements when activity was high. Our results demonstrate how grizzly bears alter multiple behaviours in response to recreational activity (Abrahms et al. 2015).

Our approach has led to an unbiased look at how grizzly bears select habitat relative to human recreational activity, whilst simultaneously investigating responses in movement. Current plans to recover grizzly bear populations in North America focus on reducing linear disturbance density to minimize bear mortality, specifically keeping open-road densities below a threshold of 0.6 km/km^2 (Mace et al. 1996, Alberta Grizzly Bear Recovery Team 2008). I found that, when examining changes in behaviour and habitat selection relative to linear disturbances, both feature density and the magnitude of activity need to be considered. The inclusion of motorised and/or non-motorised activity alongside distance to nearest trail improved our ability to explain habitat selection and movement in grizzly bears. Previous efforts to include measures of human activity have shown similar improvements in grizzly bear habitat selection models (Northrup et al. 2012a), highlighting the importance of incorporating the magnitude of human-use of a linear feature, and not just its presence. Tantamount to these findings, our results showed that grizzly bears alter not only habitat selection in response to trails and recreational activity, but they also alter movement behaviour through complex relationships and interactions with other site factors. This emphasizes how habitat selection analysis that ignore movement behaviour can miss important behavioural changes relating to movement patterns (Ordiz et al. 2013, Abrahms et al. 2015).

Human disturbance is known to have contrasting effects on different species in terms of habitat selection, with responses by grizzly bears being particularly complex (McLellan and Shackleton 1988, Rode et al. 2006, Boulanger and Stenhouse 2014, Elfström et al. 2014, Sahlén et al. 2015). Both male and female bears selected for areas closer to trails when recreational activity was absent, but showed no preference for trails when and where recreational use was high. Traffic volume alters grizzly bear responses to roads (Roever et al. 2010, Northrup et al. 2012a), switching from selection of low-use to avoidance of medium and high-use roads (Northrup et al. 2012a). The lack of avoidance of trails could be due to the unpredictability of recreational trail-use relative to traffic volume. Male grizzly bears reduced their movement rates when close to trails. This implies that bears are not specifically using trails to move faster, as has been seen in wolves (Dickie et al. 2016). Instead, bears are likely using linear disturbances for foraging opportunities (Roever et al. 2010), which would decrease their average movement speed. Grizzly bears often are attracted to open areas, such as linear-features and forest cutblocks (Nielsen et al. 2004a), because the lack of canopy cover allows growth of nutrient-rich foods (Nielsen et al. 2004b, 2010, Lamb et al. 2017). Male movement behaviours change when motorised activity is high; bears increase their movement speed at times of high recreational activity, likely diminishing their ability to exploit the nutrient-rich foods close to or on trails due to increased displacement (Ciuti et al. 2012b). Further work quantifying food quality found on and close to trails will inform us of the potential nutritional effect this loss of foraging opportunities has for bears. Additionally, identifying physiological responses in terms of stress, as seen in wolf (*Canis* lupus) responses to winter recreation (Creel et al. 2002), coupled with altered movement behaviour would help infer whether recreational activity on trails is detrimental to survival and reproduction (French et al. 2011). Such evidence would help to inform wildlife managers of the importance that access management can play in grizzly bear recovery.

I emphasise the high level of individual variability, resulting in large confidence intervals surrounding a number of coefficient estimates. Variation among individuals may be a consequence of age, social dominance, reproductive status, genotype or habituation, which can result in different trade-offs between perceived risks (Gomes and Sarrazin 2016). For example, intra-species dynamics, such as male competition, or sexual segregation (Smulders et al. 2012, Steyaert et al. 2016), can influence how an individual perceives trails and recreation relative to other dangers on the landscape (Berger 2007). Studies have shown that male bears are more wary of human activity (Rode et al. 2006, Steyaert et al. 2016), and this might help to explain why I see a consistent movement response to motorised recreation by males, but not females. Females, particularly females with cubs, can select for areas with human activity as a refuge from males and the threat of sexually-selected infanticide (Rode et al. 2006, Steyaert et al. 2016). However, I would have expected selection for high-use trails, if this was the case, which I did not.

Model uncertainly due to estimation or measurement error increases variability around coefficient estimates, and in more serious cases, can lead to biased results (Van Niel and Austin 2007, Frair et al. 2010). Error propagation associated with applying model outputs as data, as well as other sources of error such as GPS location error (Cagnacci et al. 2010) and error propagation in landscape variables (Hines et al. 2005, Van Niel and Austin 2007), are likely to increase the statistical power required to detect significant relationships. However, I did not believe that our estimates of recreational activity and food distribution bias our inference, as both approaches involved model validation methods quantifying prediction error (Nielsen et al. 2010, Ladle et al. 2017), which increased my confidence when applying the predicted values as covariates.

Conclusions

High motorised and non-motorised recreational activity quashed male grizzly bear selection for trails. By incorporating movement within the analysis, I showed that bears change their movement behaviour surrounding trails when motorised activity was high. I found substantial variation in both habitat selection and movement responses among bears. Further analyses might examine functional responses relating to habitat selection, and how behavioural plasticity might play a role (Leclerc et al. 2015). Linking avoidance behaviour with changes in habitat quality, both through selection and movement, will give insights into more direct fitness consequences through changes in food availability. Further information is required to determine if recreational activity is reducing survival or reproduction. Incorporating details relating to movement behaviour show that, although bears are not avoiding high-activity trails, they no longer select trails when and where activity is high. Coupled with increased displacement, these responses could have a number of negative consequences to bears, including reduced foraging opportunities, higher energy expenditure and higher stress hormone levels.

Our research shows the importance of including measures of recreational activity to better assess the effects of linear features on wildlife. Advances in remote-data-collection technology, such as trail cameras allows for increased availability of such data (Burton et al. 2015), make it easier to produce spatiotemporal layers of human activity (Ladle et al. 2017). I show that solely relying on linear-feature mapping, and not including measures of human activity or bear movement can result in poor inferences when assessing effects of recreation on bear behaviour. Future approaches should aim to incorporate both selection and movement in analyses, improving our understanding of grizzly bear responses to external stressors.

Table 3.1. Grizzly bears monitored between 2011 and 2015. Sample size represents the number of steps located within the study area and outside of the denning period (April 14 – September 30). Individual bear-years with less than 168 steps were not included in the analysis.

ID	Sex	Sample size	Year	Sample size by year
G004	F	5781	2011	2634
			2012	3055
			2013	92
G016	F	8435	2011	2487
			2012	2592
			2013	3356
G023	F	1278	2011	1278
G037		5245	2011	2704
			2015	2541
G111	F	8493	2011	785
			2012	3181
			2013	3360
			2014	1167
G118	F	1772	2011	1772
G119	F	6245	2011	2169
			2013	3443
			2014	633
G120	M	5394	2012	33
			2013	2153
			2015	3208
G126	F	1068	2013	1068
G127	M	1496	2013	1496
G129	M	841	2014	841
G131	F	3380	2014	2370
			2015	1010
G132	F	2059	2014	2059
G156	M	624	2015	624
G157	M	3132	2015	3132
G160	M	3048	2015	3048

Table 3.2. Description of variables used in iSSA, including units, any transformation that was applied and the source of the original variable.

Variable	Units	Transformation	Source
lnDroad	Metres	Natural log distance from nearest road	Foothills
lnDtrail	Metres	Max distance to trail – natural log (dtrail)	Foothills
lnDstream	Metres	Natural log distance from nearest stream or river	Foothills
lnSlength	Metres	Natural log step length (based on one hour fix rate)	NA
Motorised	NA	Logit transformed probability of motorised activity – min value	Ladle et al. (2016)
Non_motorised	NA	Logit transformed probability of non-motorised activity – min value	Ladle et al. (2016)
TRI	NA	Terrain Ruggedness Index	(Riley et al. 1999) (DEM from Foothills)
Food quality	NA	Temporally weighted Food Quality index	(Munro et al. 2006, Nielsen et al. 2010)
edge_in	Metres	Distance to forest edge from inside forest cover	NA
edge_out	Metres	Distance to forest edge from outside forest cover	NA

Table 3.3. Set of candidate models that represent competing hypotheses relating to the effects of recreational activity on grizzly bear habitat selection and movement. See Table 3.2 for description of variables. Variables in bold represent variables included beyond the previous model.

Model name	Covariates
food quality	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream + lnDroad
dtrail	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream **+** lnDroad **+ lnDtrail**
complete	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream + lnDroad + lnDtrail + **I (lnDtrail * motorised) + I (lnDtrail * non-motorised)**
dtrail + movement	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream **+** lnDroad **+** lnDtrail + **I (LnSlength * lnDtrail)**
non-motorised + movement	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream + lnDroad + lnDtrail + I (lnDtrail * non-motorised) + **I (LnSlength * lnDtrail) + I (LnSlength * lnDtrail * non-motorised)**
motorised + movement	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream + lnDroad + lnDtrail + I (lnDtrail * motorised) + **I (LnSlength * lnDtrail) + I (LnSlength * lnDtrail * motorised)**
complete + movement	LnSlength + food quality + TRI + edge_in + edge_out + lnDstream + lnDroad + lnDtrail + I (lnDtrail * Motorised) + I (lnDtrail * Non-motorised) + **I (LnSlength * lnDtrail) + I (LnSlength * lnDtrail * Motorised) + I (LnSlength * lnDtrail * non-motorised)**

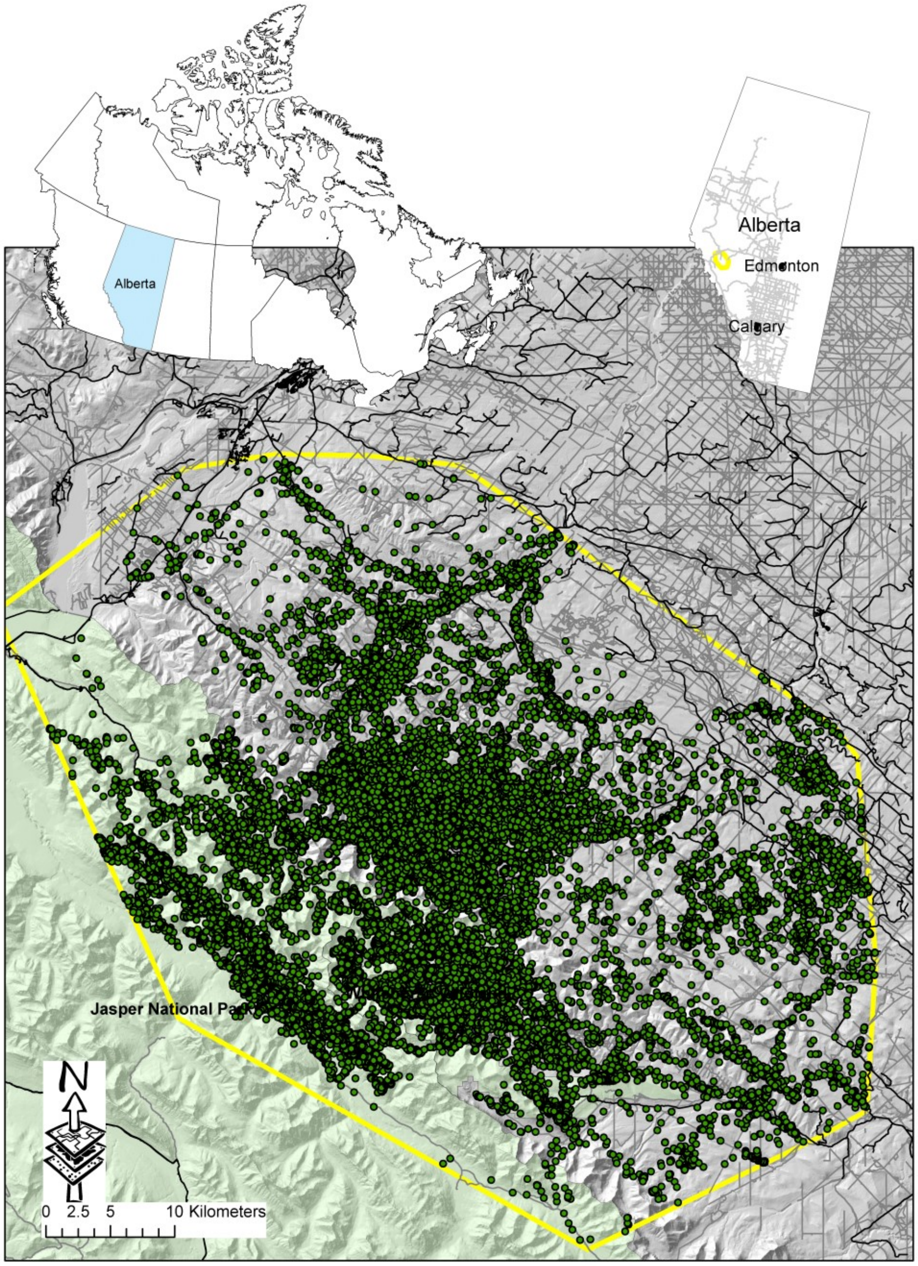


Fig. 3.1. Map of study area in West-central Alberta's Rocky Mountain slopes and foothills. including grizzly bear telemetry data collected between 2011 and 2015, road features (black) and trails (grey). Green shading represents protected areas. Yellow perimeter represents the study area, defined by the spatial extent of our trail camera locations (Ladle et al. 2016). Relocations outside of the perimeter were discarded from the analysis.

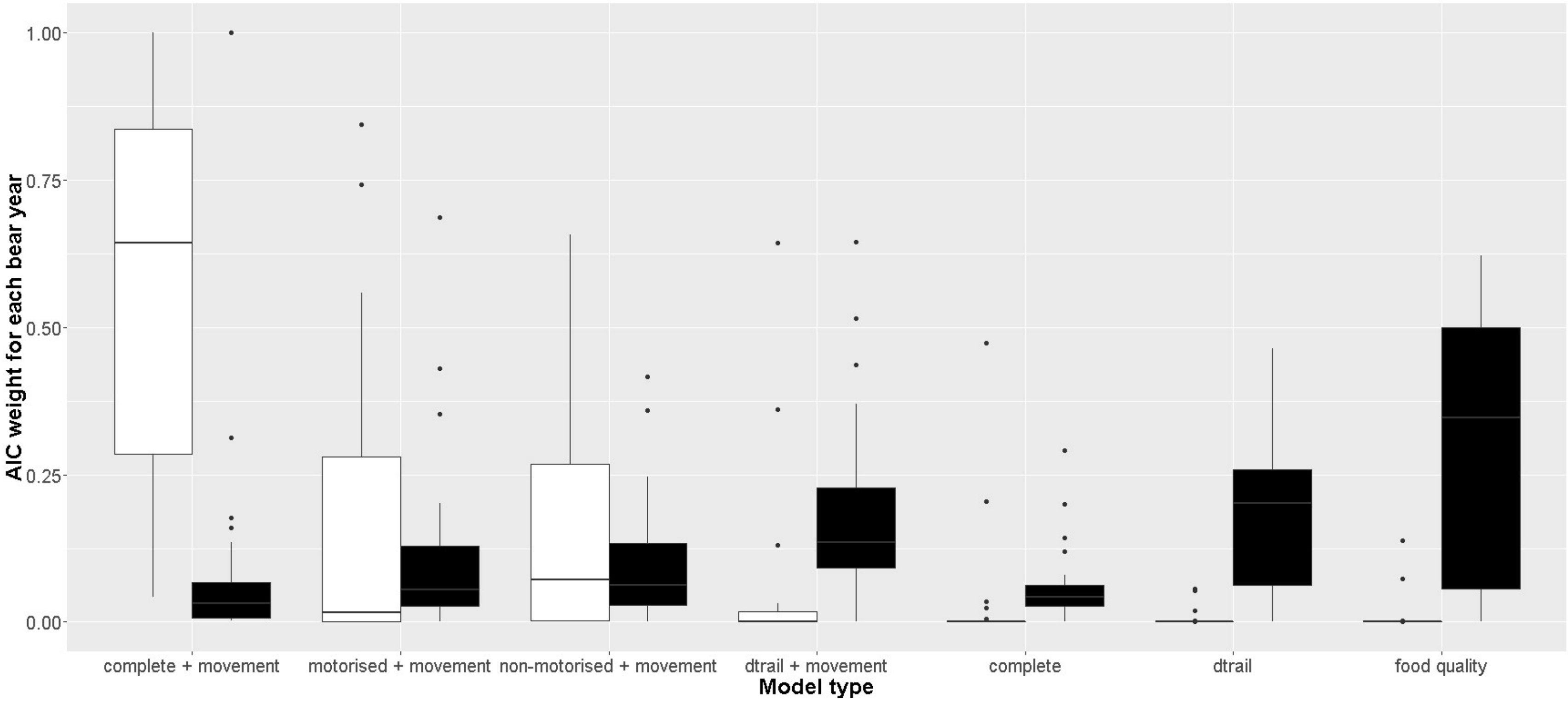


Fig. 3.2. Boxplot showing the AIC weight distribution for 27 individual bear-year models. Model type represents the different competing models described in detail in Table 3.3. White boxes represent daytime models, black boxes represent night time models. The central mark represents the median, and the tails represent the 2.5th (lower) and 97.5th (upper) percentiles.

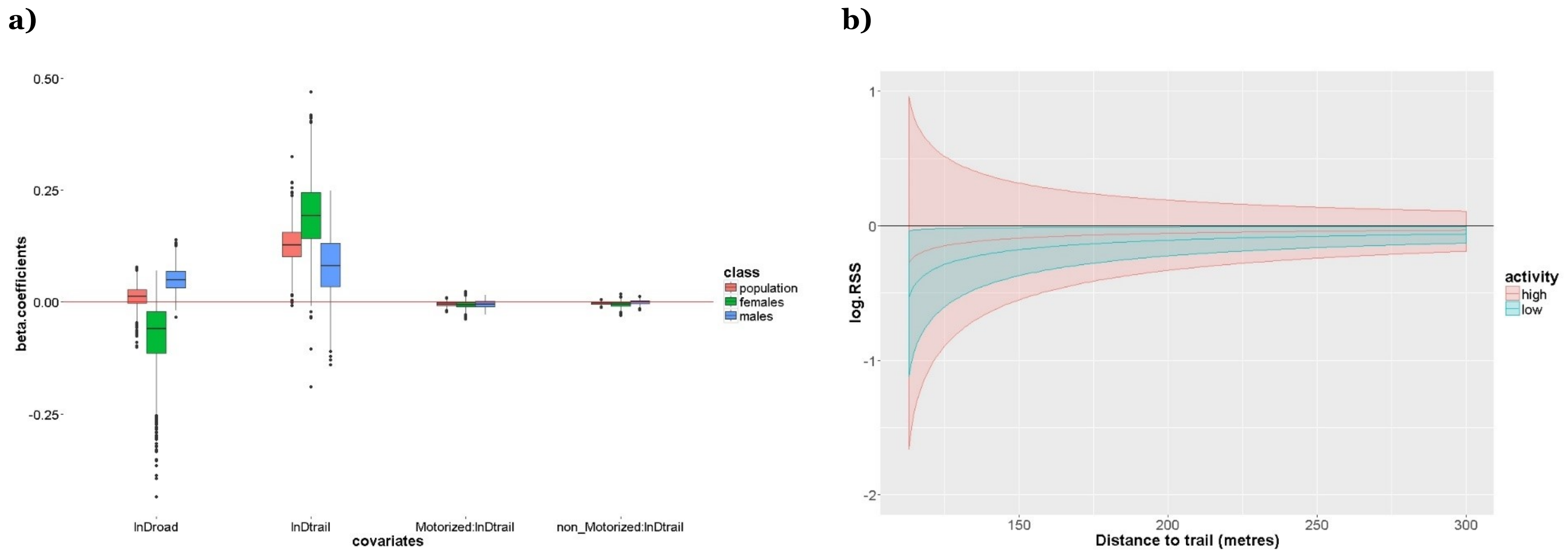


Fig. 3.3. Plots displaying habitat selection responses to trails and recreational activity. a) β coefficients and bootstrapped confidence intervals for grizzly bear habitat selection relating to human recreation, b) log- RSS and bootstrapped confidence intervals at the population level, where log – RSS represents the relative selection strength of moving away from the trail relative to towards as a function of absolute distance from trail. Colours represent this relationship at high (red) and low (blue) probabilities of motorised recreational activity. See Eq 1 for calculation**.**

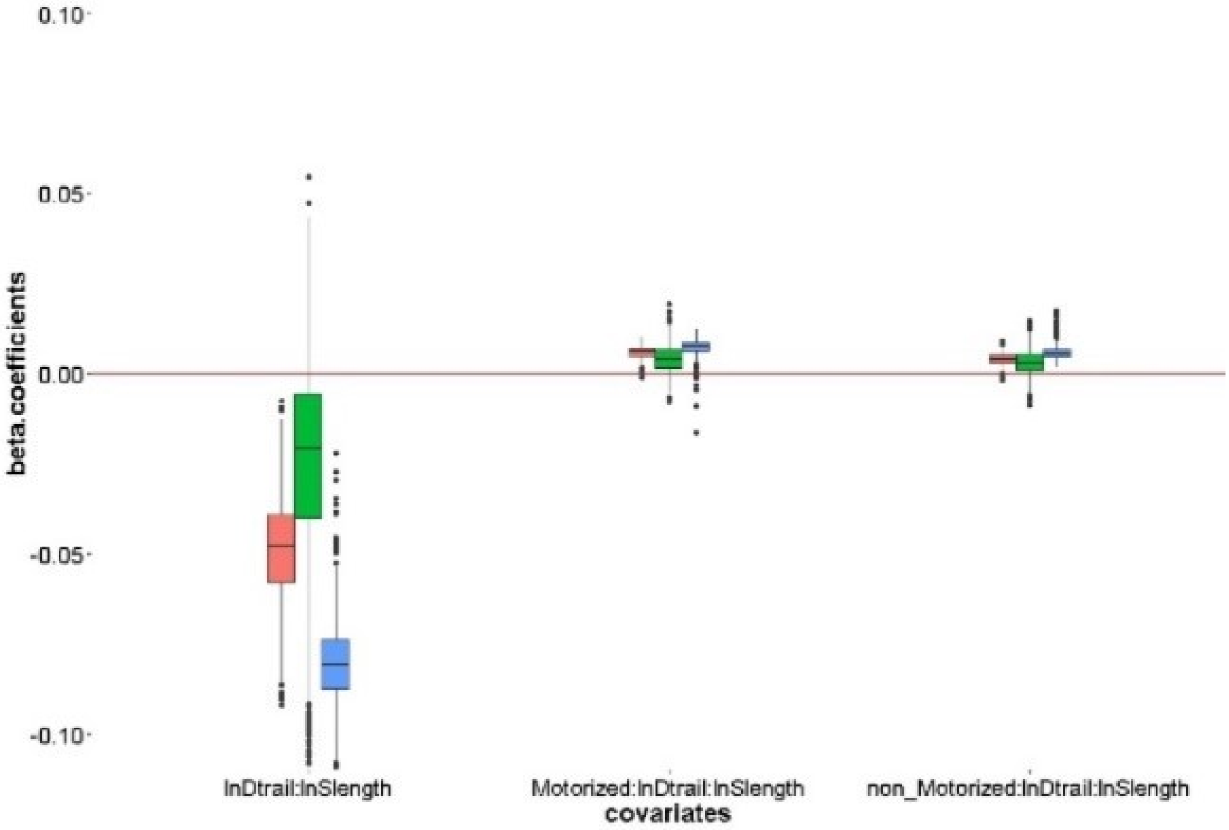


Fig. 3.4. Population level coefficient estimates and bootstrapped confidence intervals for movement behaviour by grizzly bears. The central mark represents the median, and the tails represent the 2.5th (lower) and 97.5th (upper) percentiles. Coefficients were treated as significant if the tails did not overlap zero (red line)

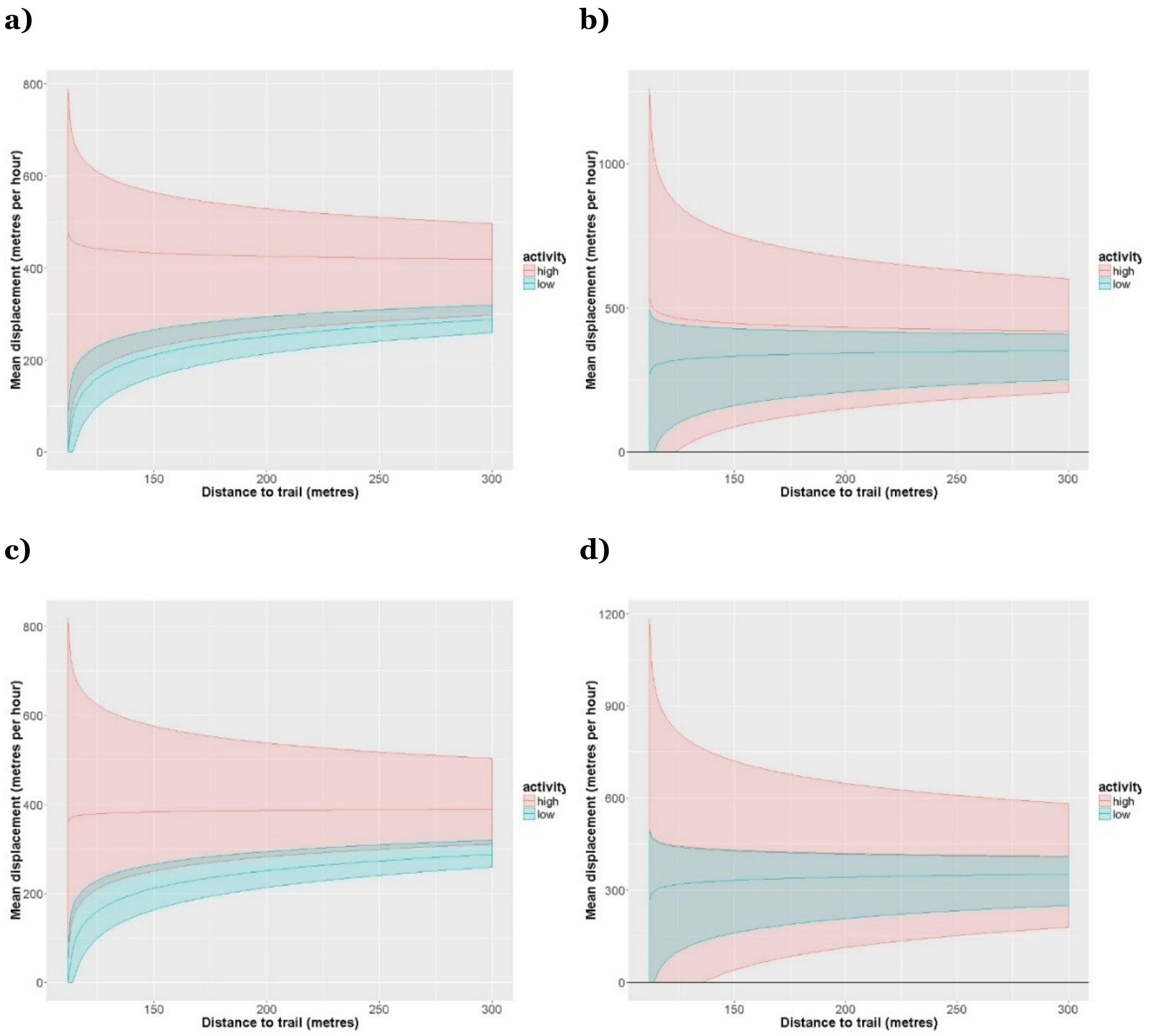


Fig. 3.5. a) the mean displacement rate for male grizzly bears in response to zero (blue) and high (red) motorised recreational activity, c) the mean displacement rate for female grizzly bears in response to zero (blue) and high (red) motorised recreational activity, d) the mean displacement rate for male grizzly bears in response to zero (blue) and high (red) non-motorised recreational activity and e) the mean displacement rate for female grizzly bears in response to zero (blue) and high (red) non-motorised recreational activity.

4 Significance of human recreational activity in shaping patterns of grizzly bear-black bear co-occurrence.

4.1 Introduction

Interspecific interactions play a fundamental role in shaping species' distributions and behaviour (Araújo and Luoto 2007), however incorporating such relationships into species distribution models can be logistically challenging and complex (MacKenzie et al. 2004). Interspecific competition can lead to resource partitioning that allows multiple species that are ecologically similar to coexist on the same landscape (Hutchinson 1965, Amarasekare 2002), resulting in sympatry with niche divergence (Rosenzweig 1991). These interactions can be altered by anthropogenic factors such as human activity (Carter et al. 2012), which has the potential to affect individual behaviour and habitat use. To understand species distributions and abundance it is important to incorporate such relationships, and factors that influence them (McLoughlin et al. 2010). Ignoring biotic interactions, between prey, competitors and predators, can lead to biased or inaccurate inferences regarding an animal's habitat selection or changes in behaviour (Rota et al. 2016).

Grizzly bears (*Ursus arctos)* and black bears (*U. americanus*) are sympatric across the majority of the grizzly bear range in North America, and inhabit similar niches in terms of food preference (Schwartz et al. 2010). Where these two species are sympatric, diet overlap is high; both are opportunistic omnivores (Mattson et al. 2005, Schwartz et al. 2014) that rely on berry crops to gain the necessary weight for denning (Holcroft and Herrero 1991, Munro et al. 2006). Reliance on the same food source leads to competition, and studies have shown that spatial displacement is common, such as black bears being displaced from salmon streams (Jacoby et al. 1999). Altered activity patterns also have been documented, with black bears switching daily activity patterns to reduce overlap with grizzly bears (Schwartz et al. 2010). Although displacement in these examples was due to competition for resources, there have been instances of intraguild predation, exacerbating black bear avoidance of grizzly bears (Schwartz et al. 2010). Conversely, there is little evidence that grizzly bears are negatively affected by black bear occurrence directly, however it is postulated that high black bear densities might result in reduced reproduction by grizzly bears through exploitation competition, despite grizzly bears being able to dominate high-quality foraging through resource defense competition and direct interference competition (Mattson et al. 2005, Apps et al. 2006).

Human recreational activity is an increasing issue for wildlife (Hammitt et al. 2015) and has the potential to affect ecological communities through redistribution and changes in activity patterns (Ordiz et al. 2014). Wildlife display differing responses to motorised and non-motorised activity (Gibeau et al. 2002, Whittington et al. 2005), which has in part led to restricted motorised recreation in many protected areas. The influence of recreational activity on bear habitat use and behaviour could be as important a factor as the interaction between grizzly and black bears, as shown in other species (Ciuti et al. 2012b). Many carnivore species that have few or no predators display negative responses to human disturbance (Frid and Dill 2002, Beale and Monaghan 2004). Perceived predation risk can have implications for individuals within a population, through spatial displacement (Rogala et al. 2011), temporal displacement (Carter et al. 2012), changes in movement behaviour (Northrup et al. 2012a) and increased stress responses (Creel et al. 2002). Varying responses to human activity due to different fear perceptions and costs associated with avoidance (Creel and Christianson 2008) has led to the ‘human shields’ hypothesis, by which animals use human activity to protect against predation (Berger 2007). Both grizzly bears and black bears are influenced by human activity, however this response varies between the two species. Black bears show increased activity near human developments (Schwartz et al. 2010). Grizzly bears in contrast avoid human infrastructure, such as high traffic-volume roads (Weaver et al. 1996, Roever et al. 2010) and alter their activity patterns to minimise temporal overlap (Northrup et al. 2012a).

Occupancy modelling is a statistical framework that allows researchers to investigate the relationship between the presence-absence of a species and associated habitat characteristics. Current methods for modelling occupancy were developed to account for imperfect detection (MacKenzie 2006). These models were originally designed for discrete, patch-based occupancy studies, such as territorial birds or amphibians in discrete ponds (MacKenzie et al. 2002). Although occupancy software also has been applied to free-ranging animals in continuous habitats (Burton et al. 2012, Carter et al. 2012), these applications are not dealing with strict “occupancy” at a site; rather instantaneous occurrence or habitat use of that site (Efford and Dawson 2012). Although occurrence informs us on species distribution across a landscape, and variables influencing this, we lose information by condensing count data to a binary response variable. However, these count data can be used as an informative measure of relative intensity of use, with a value of 1 as high use of a specific camera site. Thus, the “detection probability” in occupancy context is actually a metric of the intensity of use for applications to camera-trap data. In this context, intensity of use is a variable of interest, rather than a nuisance parameter (Cusack et al. 2016). Occurrence (ψ) is influenced by a populations distribution across the landscape, representing areas that are used versus areas that are never used. Measures of intensity of use (p), for trail camera data is primarily a consequence of variation in population density and individual movement patterns (Rowcliffe et al. 2008, Efford and Dawson 2012, Burton et al. 2015, Latif et al. 2016) rather than the ability to detect individuals at a given sample location as in occupancy studies (Burton et al. 2015). Both parameter estimates are effected by habitat variables and interspecific interactions with wildlife species and human activity, but infer different scales in terms of the response (Wiens et al. 1987). Further advances in occupancy modeling have included estimating the probabilities of co-occurrence between two or more species, and how the presence of a species might influence not just the probability of other species' occurrence, but also the detectability, or intensity of use in the present context, of other species' (MacKenzie et al. 2004). Such models have been applied to questions specific to community dynamics in sympatric owls (Bailey et al. 2009), Madagascan carnivores (Farris et al. 2015), rails (Richmond et al. 2010) and treefrogs (Waddle et al. 2010). More recently, multispecies models have been developed that allow comparison of occurrence for two or more interacting species (Rota et al. 2016), which opens up the ability to test hypotheses relating to community level spatial distribution and habitat use, whilst accounting for habitat preferences.

To evaluate the relative importance of interspecific interactions between two bear species; grizzly bear and black bear, and two types of human recreational activity; motorised and non-motorised, I placed camera traps on human-use trails within Jasper National Park and an adjoining area along the eastern Rocky Mountain foothills of

Alberta. I studied changes in occurrence and intensity of use using a suite of habitat variables, presence or absence of sympatric bear species, and presence or absence of recreational activities. In addition, I compared daily activity patterns between pairs of species' and recreational activities to answer the following questions: 1) To what degree do grizzly bears and black bears occur in different habitats? 2) Do I observe co-occurrence of grizzly and black bears on trails, or are they spatially and temporally separated? 3) How does motorised and non-motorised recreation influence trail use by and activity patterns of grizzly and black bears? and 4) Do I see different patterns of activity in the presence or absence of recreational activity and competing bear species?

4.2 Methods

Study area

The study was conducted in the central Alberta's Rocky Mountains and foothills (Fig. 4.1). The landscape consists of higher elevation, mountainous terrain in the west, and foothills at lower elevations to the east. Forest cover is prominent, and consisting of spruce (*Picea* spp.), fir (*Abies* spp.) lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). The study region includes Jasper National Park and Whitehorse Wildland Park, where motorised recreation is not allowed, and public lands with limited restrictions of recreational activity, where motorised recreation is prevalent (Ladle et al. 2016). Industrial activity, including oil and gas extraction, open-pit coal mining and timber extraction, are present within the public lands to the east, and have contributed to the high density of linear features.

Trail camera sampling

Trail camera data was used from a combination of two concurrent camera trap studies (see Ladle *et al.* 2016; Steenweg *et al.* 2016 for specific details on sampling design). In both studies, we placed cameras on anthropogenic trails using a systematic design, and deployed them more than one km from the nearest other camera locations. I used data collected between June 15 and August 25 2014, because these dates were outside of the black bear hunting season for the region (albertaregulations.ca). We set cameras (Reconyx Inc, Holmen, WI, USA) at 194 trail locations (Fig. 4.1) and monitored sites for > 20 days each. We set cameras to take pictures 24 hours a day at high sensitivity, and took a set of 3-5 pictures in rapid succession when triggered with no delay. At each location, we placed cameras at an angle from the trail approximately 1-3m from the trail to minimise the probability of missing fast-moving objects such as Off-Highway Vehicles' (OHV's). I classified images by date, time and species or recreation type. I classified bears as grizzly bears, black bears or unknown if I was unable to accurately identify species. If human recreation was present, I identified the type of recreation (truck, OHV, hiker, horse rider) and categorised the event as either motorised or non-motorised recreation.

Modelling framework

I adapted and applied a multispecies occupancy model (Rota et al. 2016) that expands MacKenzie et al.'s (2002) single-species model to two or more species by assuming a multivariate Bernoulli distribution (MVB). For example, when the number of species is 2

$$\boldsymbol{Z} \sim \mathrm{MVB}(\psi_{11}, \psi_{10}, \psi_{01}, \psi_{00}) \qquad \textbf{(1)}$$

where **Z** is a vector of 1's and 0's representing presence - absence of having been detected for each species, and ψ_{ij} is a combination of co-occurrences between species i and j. The log odds a species occurs at a site can be obtained from a corresponding probability mass function. These can then be modelled within a logistic regression framework as a function of covariates. In a two-species model the natural parameters for species 1, 2 and a combination of the two are;

$$f_1 = \log\left(\frac{\psi_{10}}{\psi_{00}}\right) = \boldsymbol{x'}_{\alpha}\boldsymbol{\alpha}$$

$$f_2 = \log\left(\frac{\psi_{01}}{\psi_{00}}\right) = \boldsymbol{x'}_{\beta}\boldsymbol{\beta} \qquad \mathbf{(2 - 4)}$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{01}\psi_{10}}\right) = \boldsymbol{x'}_{\gamma}\boldsymbol{\gamma}$$

Where $\boldsymbol{x_\alpha}$, $\boldsymbol{x_\beta}$, and $\boldsymbol{x_\gamma}$ are vectors of covariates that are predicted to explain species' occurrence, and $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$, and $\boldsymbol{\gamma}$, are vectors of respective slope parameters. The use of probability theory allows one to test a number of hypotheses on the relationship between interacting species. For example, one might hypothesise that two species occur independently, and their probability of occurrence is solely predicted by environmental variables. Here one would want to calculate the marginal probability of occurrence for each species;

$$P(z_1 = 1) = \psi_{11} + \psi_{10}$$

$$P(z_2 = 1) = \psi_{11} + \psi_{01} \qquad \mathbf{(5 - 6)}$$

where z_1 and z_2 are the presence of species 1 and species 2 respectively. In these cases, the parameter representing conditional probability based on the presence or absence of another species (f_{12}) is set to zero, inferring independence between species' occurrence.

Alternatively, one could hypothesise that there is pairwise dependence between the two species i.e. their probability of occurrence is correlated. In this scenario, one would be interested in the probability of occurrence of species 1, conditional upon the presence or absence of species 2, and vice versa;

$$P(z_1 = 1 \mid z_2 = 1) = \frac{\psi_{11}}{\psi_{11} + \psi_{01}} = logit^{-1}\,((\alpha_0 + \gamma_0) + \alpha_1 x)$$

$$P(z_1 = 1 \mid z_2 = 0) = \frac{\psi_{10}}{\psi_{10} + \psi_{00}} = logit^{-1}\,(\alpha_0 + \alpha_1 x) \qquad \textbf{(7 – 10)}$$

$$P(z_1 = 0 \mid z_2 = 1) = \frac{\psi_{01}}{\psi_{01} + \psi_{00}} = logit^{-1}\,(\beta_0 + \beta_1 x)$$

$$P(z_2 = 1 \mid z_1 = 1) = \frac{\psi_{11}}{\psi_{11} + \psi_{10}} = logit^{-1}\,((\beta_0 + \gamma_0) + \beta_1 x)$$

where γ_0 is an intercept modifier estimated as the effect of one species on the probability of occurrence of the other.

Lastly, one might predict that although two species may occur independently, one species may influence the intensity of use at a specific site, of another species. This can be incorporated within the model by estimating two parameters, one is the intensity of use given the presence of the other species e.g. $p\ (z_2 = 1)$, and in the absence e.g. $p\ (z_2 = 0)$.

Covariates

I first built a base model for both bear species that contained covariates known to influence bear habitat use. This inclusion allowed me to control for potential habitat and landscape variables outside of our species interactions which are the main interest and focus. Distance to road and distance to stream can both influence grizzly bear and black bear habitat use, and were included as natural log transformed variables (hereby *ln*DRoad and *ln*DStream). Elevation explains variation in bear distribution, with grizzly bears usually at higher elevations relative to black bears (Mowat et al. 2005, Apps et al. 2006). Lastly, I included Normalised Difference Vegetation Index (NDVI) for the buffered area around the camera location (500m) averaged across the sampling period. NDVI positively correlates with vegetation quality (Pettorelli et al. 2005) and forest cover and type (DeFries and Townshend 1994), and is therefore has been used as a predictor of bear habitat use (Baldwin and Bender 2010, Nielsen et al. 2010, Northrup et al. 2012a, Bourbonnais et al. 2013). I checked for collinearity between predictor covariates, and all correlation coefficients were below 0.7. As motorised recreation is not permitted in Jasper National Park, I included a protected-area variable influencing motorised and non-motorised occurrence and intensity of use. All covariates were extracted using ArcMap (ESRI, Redlands, CA, USA).

Interaction effects

Grizzly bears, black bears, motorised recreationists and non-motorised recreationists were included as individual "species" within the multi-species co-occurrence model. I collapsed our data into 4-day presence-absence sampling periods, to maintain moderate probabilities of detecting all species, improving model convergence

(Moreira-Arce et al. 2015, Steenweg et al. 2016b). Cameras with less than 4 surveys were removed, leaving 182 trail camera locations for analysis. I fit a set of candidate models to test a series of hypotheses. These models varied based on, a) co-occurrence of bears and recreation (independent versus conditional), b) co-occurrence between grizzly bear and black bear, c) the effect of recreation on bear intensity of use, and d) the effect of grizzly bear occurrence on black bear intensity of use.

I fit 48 models in Stan v. 2.8.0 via the Rstan (Stan Development Team, 2016) package in R (R Core Team 2014). Logistic prior distributions were used for all parameters (Rota et al. 2016). I ran 3 chains each consisting of 2,000 iterations (1,000 burn-in with 1,000 sampled) and ensured model convergence by calculating Brooks-Gelman-Rubin convergence diagnostic and checking that Rhat was close to 1 (Gelman et al. 2014). Candidate models were ranked using Watanabe-Akaike Information Criterion (WAIC), which is the optimum method for contrasting fully Bayesian models (Gelman et al. 2014).

Daily activity patterns

To investigate activity pattern overlap between grizzly bears, black bears and recreational activity, the timestamps of all independent events were used to build probability density functions across the 24-hour period for each species. I then used these distributions to estimate the coefficient of overlapping (Δ; Ridout & Linkie 2009) for each pairwise relationship. To further assess the influence of interspecific interactions on daily activity patterns, I compared activity patterns for a species at a set of sites where the competing species was present versus sites where the competing species was absent. I used a non-parametric calculation for Δ, due to small sample sizes in some circumstances (< 75;

Meredith & Ridout 2016). Confidence intervals were calculated using a bootstrap method following Meredith and Ridout, 2016. Analyses were done using the package 'overlap' (Ridout and Linkie 2009, Meredith and Ridout 2016). I predicted a high coefficient of overlapping between grizzly bears and black bears due to their similar behaviour patterns. However, I expected differences to coincide with times when recreational activity is high, with grizzly bears showing a lower amount of temporal overlap in activity than black bears.

4.3 Results

Between June 15 and August 25 2014, cameras were active for 10,514 days across 182 sites. I captured 235 grizzly bear and 235 black bear black bear observations. Of the 182 monitored sites included in the analysis, grizzly bears were photographed at 84 locations (naïve occurrence: 0.46) and black bears were photographed at 74 locations (naïve occurrence: 0.40). Grizzly bears and black bears co-occurred at 34 sites. There were 2,893 motorised recreation observations, at 73 locations (naïve occurrence: 0.40) while non-motorised recreation was more than double that of motorised, with 6,213 observations at 90 locations (naïve occurrence: 0.50). Motorised activity co-occurred more with black bears (37) than grizzly bears (27), however the inverse was true for non-motorised activity (40 black to 48 grizzly).

Model selection

The top model had a WAIC weight of 0.88 (Table 4.1). This model extended upon the base model by incorporating pairwise dependence in occurrence between bear species. Intensity of use by grizzly bears was influenced by the presence of recreational activity whereas the intensity of use by black was affected by grizzly bear presence and recreation. The global model was ranked second with a WAIC weight of 0.11 (Table 4.1). This model extended upon the top model by including co-occurrence between bear species' and both forms of recreational activity.

Covariates and occurrence

I examined the direction and significance of all posterior occurrence probability distributions for landscape variables obtained from the top model (Table 4.1). Grizzly bear occurrence increased as distance to road increased, while black bears did not show a strong relationship (Fig. 4.2a). Both species occurred closer to streams, as expected (Fig. 4.2b), with no significant difference between their responses. Black bears displayed high probabilities of occurrence in low elevation areas, however this probability of occurrence decreased as elevation increased beyond 1500m (Fig. 4.2c). Grizzly bears did not display a strong response to elevation, but had a much higher probability of occurrence at higher elevations (1500m – 2000m) than black bears. Grizzly bears and black bears showed inverse responses to NDVI, however the influence on probability of occurrence was small and not significantly different between the two species (Fig. 4.2d). Occurrence of motorised activity was far lower and non-motorised activity was significantly higher in protected areas. A similar pattern was observed in the intensity of use: intensity of trail use by non-motorised recreationists was much higher at sites inside protected areas.

Co-occurrence between species and recreational activity

Grizzly bears and black bears showed strong negative covariance in their occurrence, as predicted (f_{12}= -0.53). Interestingly, at trail locations where they co-occurred, intensity of use by black bears was significantly higher than at sites where grizzly bears were absent (*p* ($z = 1$) = 0.088, *p* ($z = 0$) = 0.001). I found evidence of pairwise interactions between bears and recreation, as shown by model selection results, however this evidence was weak as it did not significantly improve WAIC vales beyond a similar model with no recreational impacts on bear occurrence (Table 4.1). The effect of motorised activity on the intensity of use by bears was more prominent, with grizzly bears displaying reductions in intensity of use when at a site where motorised recreation was present. Conversely, the intensity of use of black bears increased in the presence of non-motorised recreation (Fig. 4.3).

Activity pattern responses

Daily activity patterns of grizzly bears and black bears overlapped substantially ($\Delta_1 = 0.8$) Grizzly bears displayed a dip in activity on trails around mid-afternoon, whereas black bears had a constant level of activity throughout early to late afternoon. Black bears showed higher overlap with recreational activity than grizzly bears (Fig. 4.4), resulting from higher levels of activity during the afternoon. Although the point estimate inferred reduced activity overlap between black bears and grizzly bears at sites where grizzly bears were present relative to sites where they were not, confidence intervals overlapped (Table 4.3). A similar pattern was observed between grizzly bears and recreation (Table 4.3), however this difference also was not significant.

4.4 Discussion

Species occurrence is determined by biotic interactions, through competition and predation, and abiotic interactions, through landscape characteristics and habitat suitability. Novel statistical methods allow multi-species occurrence to be modelled as a function of both habitat variables and conditional upon other species' presence (Rota et al. 2016). Results from our trail camera survey show that grizzly bears and black bears vary in their occurrence along trails based on landscape variables. Grizzly bears were less likely to occur close to roads; a similar response to road proximity was missing for black bears, they showed a slight increase in use of areas closer to roads. Such a result corroborates studies emphasising a disparate response to human activity between the two bear species (Kasworm and Manley 1990, Elfström et al. 2014). Bears also were shown to use different elevations, grizzly bears occurring at higher elevations than black bears. Grizzly bears are able to exploit vegetation growing at higher alpine and sub-alpine elevations such as roots of sweet vetch (Munro et al. 2006). Higher elevations also have lower levels of human activity relative to the foothills regions, which contain a higher density of linear features, industrial activity and motorised recreation (Ladle et al. 2016). Lastly, grizzly bears and black bears showed no significant difference in occurrence relative to NDVI, inferring an absence of competitive exclusion of black bears by grizzly bears from high quality habitat (Mattson 1990). The lack of a significant difference between the two species in their response to NDVI might be explained by the fact that NDVI is a poor metric for bear food quality, and is confounded by forest cover which has a high NDVI index, yet is not high food quality for bears. The use of presence-absence models (Munro et al. 2006, Nielsen et al. 2010) for bear foods may be a method for identifying grizzly and black bear use of habitats with different food quality.

Inclusion of pairwise dependence between grizzly bear and black bear occurrence within our top model suggests that the presence of one species affects the presence of the other. The model identified a strong negative correlation between grizzly bear and black bear co-occurrence, and this result supports research that suggests spatial segregation of the two species (Holm et al. 1999), at least within the scale of our study design. Interestingly, intensity of use by black bears was significantly higher at locations where they co-occurred with grizzly bears. Detection probability in the traditional sense (MacKenzie et al. 2002), when adapted for studies of free-moving animals in continuous habitats, can be influenced not only by nuisance "detection" variables, but also two metrics of interest: movement rates and abundance (Efford and Dawson 2012). Our result imply that black bears are found in higher abundance when co-occurring with grizzly bears, or that they are increasing their movement on trails when co-occurring with grizzly bears, which increases their probability of being detected. The latter explanation is more likely because increased rates of displacement are common responses to predators or perceived risks (Ciuti et al. 2012; Sahlén et al. 2015). For example, black bears increase their movement rates and home range size when sympatric with grizzly bears (Holm et al. 1999). Our inability to identify individuals from trail camera photos made it difficult to distinguish bear abundance and individual movement behaviour. Alternate studies that use non-invasive genetic sampling (see Morehouse & Boyce 2016) might be able to inform us on whether this increase in intensity of use is due to a higher number of black bears, or increased movements on trails.

Our main interest was whether grizzly bears and black bears avoid areas where recreational activity is present, the answer to which was not clear. Our results support work that stated grizzly bear avoidance of roads (Kasworm and Manley 1990), however I did not find a similar response for black bears. This differential response might benefit black bears relative to grizzly bears, as black bears can exploit areas closer to roads due to their higher tolerance of human activity (Mattson 1990). Contrary to our predictions, model results showed that interspecific interactions had a greater impact on species occurrence than the effects of human recreational activity. Although there was no pattern in co-occurrence between either species and recreation, I did find reduced intensity of use by grizzly bears when motorised activity was present. This result implies that, instead of completely avoiding trails with motorised use, grizzly bears are either found in lower abundance, or they are less active on the trails. Avoidance of trails by wildlife has been documented previously (Kasworm and Manley 1990), especially for trails used by humans (Carter et al. 2012). The increase in intensity of use on trails with non-motorised activity was surprising, however likely due to a combination of reduced fear response to non-motorised activity, as well as non-motorised recreation correlating with more rugged topography (i.e. in Jasper National Park), where trails are the most efficient means of navigating those areas for both people and wildlife (Rogala et al. 2011, Dickie et al. 2016).

The small effect of recreation on the occurrence of both species of bear at camera locations does not mean that bears are not responding at all to recreation, because I saw significant changes in the intensity of use as a function of motorised and non-motorised activity. Another way in which wildlife are able to alter their behaviour in response to competition and disturbance is by changing their daily activity patterns. Our results indicate that black bear activity on trails overlapped to a greater extent with recreation than grizzly bears, that displayed more crepuscular behaviour and less activity on trails during the afternoon. Small sample sizes likely influenced the ability to detect significant differences in activity patterns between sites that co-occurred with recreation and ones that did not. Grizzly bears did appear to show altered activity patterns when recreation was present relative to absent, signaling a change in behaviour aimed at reducing overlap with peak times of recreational activity, as seen in other studies (Schwartz et al. 2010, Northrup et al. 2012a).

Conclusions

Many management-based decisions are made at the single-species level, without regard for competing species that share the same landscape. This approach, although analytically far more accessible through software such as Presence (Hines 2006) and the unmarked R package (Fiske and Chandler 2011), can result in decisions with less-than-optimal outcomes for the species being managed. Multi-species occurrence models are a step forward and a tool that can be used by managers to more fully understand the system they aim to manage. Grizzly bear-black bear interactions are not generally discussed when investigating bear conservation, yet I show here that the interactions between species have stronger influence on bear habitat use than human recreational activity. Our finding that both bear species show no significant relationship in occurrence with recreational activity, but instead alter the frequency of trail use, is important and can be used to inform management policy relating to recreational access. Avoidance of trails might affect grizzly bears' ability to forage, especially if times of high recreational activity coincide with late summer and fall, when bears require high energy intake to prepare for denning. Differential response by grizzly bears and black bears to human disturbances could have implications for population demographics through risk effects (Creel and Christianson 2008) Additionally, it may be beneficial to investigate how altering daily activity patterns affects bear fitness, as such a response is likely when disturbances are temporally predictable but spatially less consistent. Lastly, future studies interested in animal habitat use should attempt to integrate spatial habitat segregation, species interactions, and the effects of human disturbance simultaneously when assessing habitat quality and making management decisions.

Table 4.1. Table displaying coefficient estimates and confidence limits for the top multi-species occurrence model. Psi represents grizzly bear and black bear occurrence (on the logit scale) and p represents the intensity of use (on the logit scale). Estimates where the confidence limits overlapped zero were defined as insignificant.

		Grizzly						**Black**					
	parameter	**psi**	upper	lower	**p**	upper	lower	**psi**	upper	lower	**p**	upper	lower
	intercept	**0.61**	2.64	-1.32	**-2.09**	-1.67	-2.50	**2.40**	5.01	0.02	**-6.81**	-5.39	-8.68
Habitat	lndroad	**0.29**	0.50	0.09	-	-	-	**-0.14**	0.13	-0.40	-	-	-
	lndstream	**-0.14**	0.16	-0.44	-	-	-	**0.23**	0.67	-0.19	-	-	-
	elevation	**-0.27**	0.27	-0.80	-	-	-	**-1.76**	-0.97	-2.77	-	-	-
	NDVI	**0.11**	0.55	-0.35	-	-	-	**-0.12**	0.45	-0.71	-	-	-
Interaction	grizzly	-	-	-	-	-	-	**-2.63**	-1.30	-4.21	**4.47**	6.38	3.14
	motorised	-	-	-	**-0.67**	-0.28	-1.08				**-0.65**	-0.06	-1.26
	non-motorised	-	-	-	**0.49**	0.94	0.05				**0.82**	1.45	0.22

Table 4.2. Coefficient of overlap (Δ) with lower and upper confidence limits of grizzly bears and black bears with opposing bear species and recreational activity (motorised and non-motorised combined). Data were collected between June 15 and August 25 2014. Results were estimated using frequency of trail camera events per hour for each species and a combination of both recreation categories. Total number of events contributing to each Δ estimate are displayed in the n columns.

	Bear								Recreation							
	Present	lower	upper	n	Absent	lower	upper	n	Present	lower	upper	n	Absent	lower	upper	n
Grizzly	**0.87**	0.78	0.94	93	**0.84**	0.76	0.91	140	**0.41**	0.27	0.54	26	**0.52**	0.4	0.64	47
Black	**0.81**	0.72	0.89	97	**0.88**	0.84	0.94	144	**0.68**	0.58	0.78	74	**0.6**	0.48	0.71	47

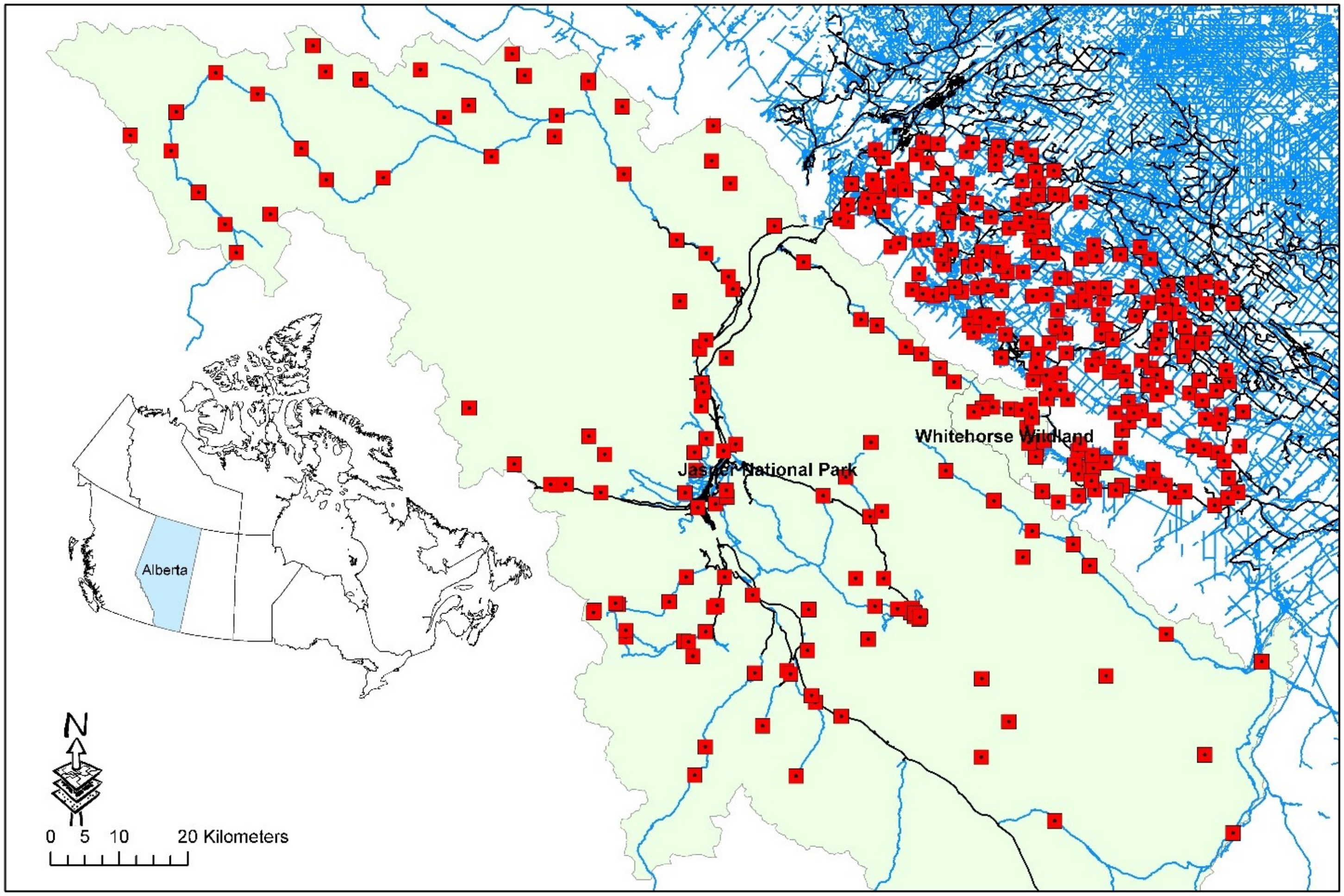


Fig. 4.1. Map of study area in West-central Alberta's Rocky Mountains and foothills, displaying all 194 camera locations that were active between June 15 and August 25 2014. Red squares represent camera locations. Roads (black) and trails (blue) are displayed, and green shading represents protected areas, including Jasper National Park and Whitehorse Wildland Park.

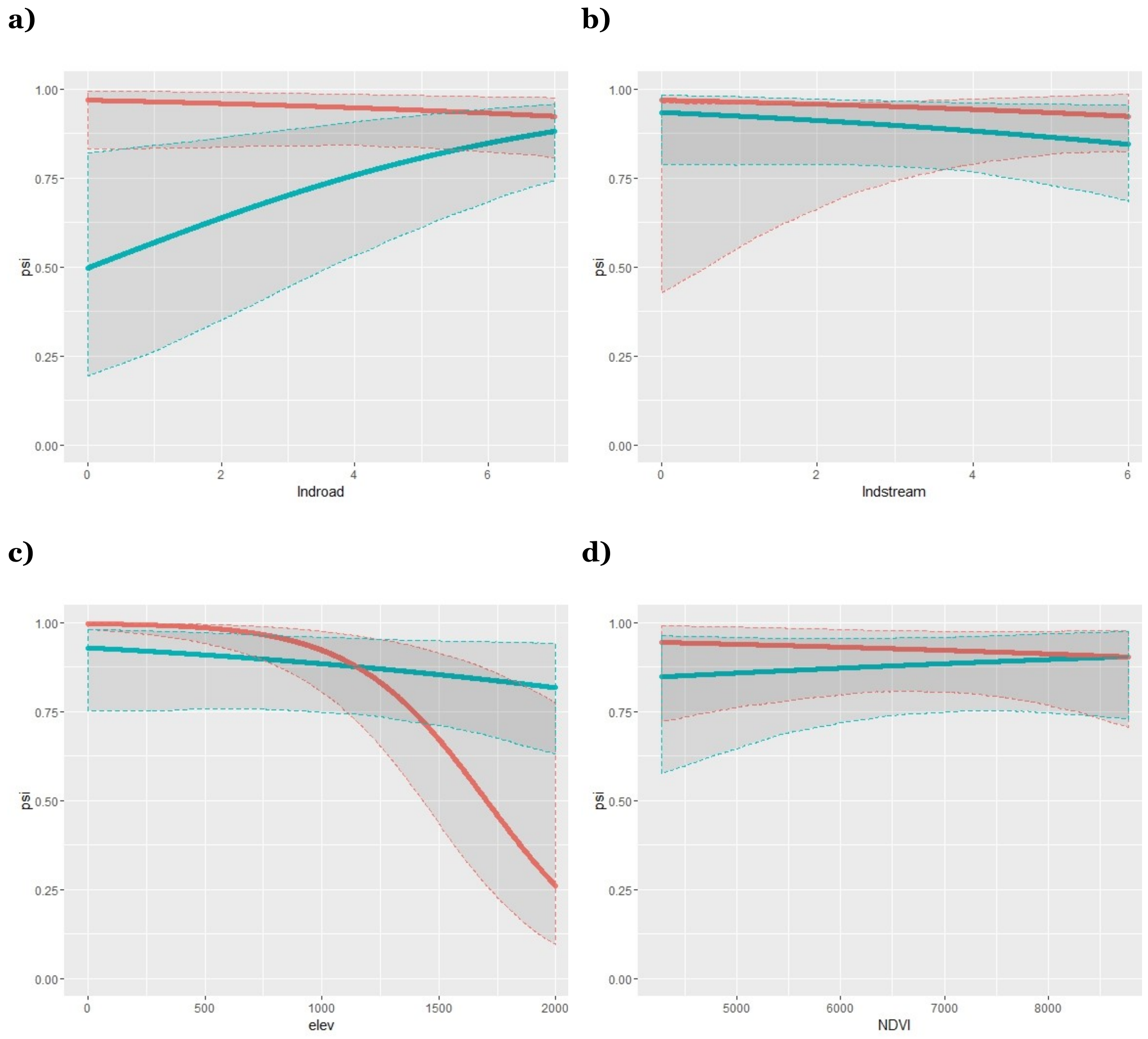


Fig. 4.2. Occurrence plots from West-central Alberta's Rocky Mountains and foothills for grizzly bears (blue) and black bears (red) for a) *ln*DRoad, b) *ln*DStream, c) elevation and d) NDVI. Shaded areas represent the 95% credible intervals. Variables that are not included in the plot were set to their observed mean value.

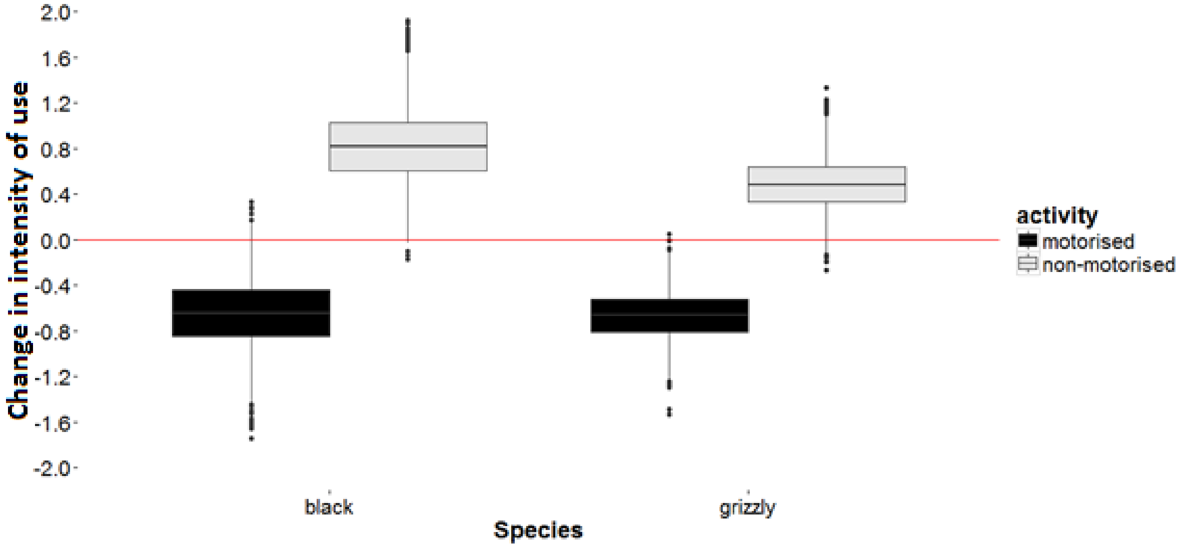


Fig. 4.3. Boxplots displaying the change in intensity of use by grizzly bears and black bears due to the presence of motorised (black) and non-motorised (grey) recreation (on the logit scale). The central mark represents the median, and the tails represent the 95% confidence intervals. Results were treated as non-significant if confidence intervals overlapped zero (red line).

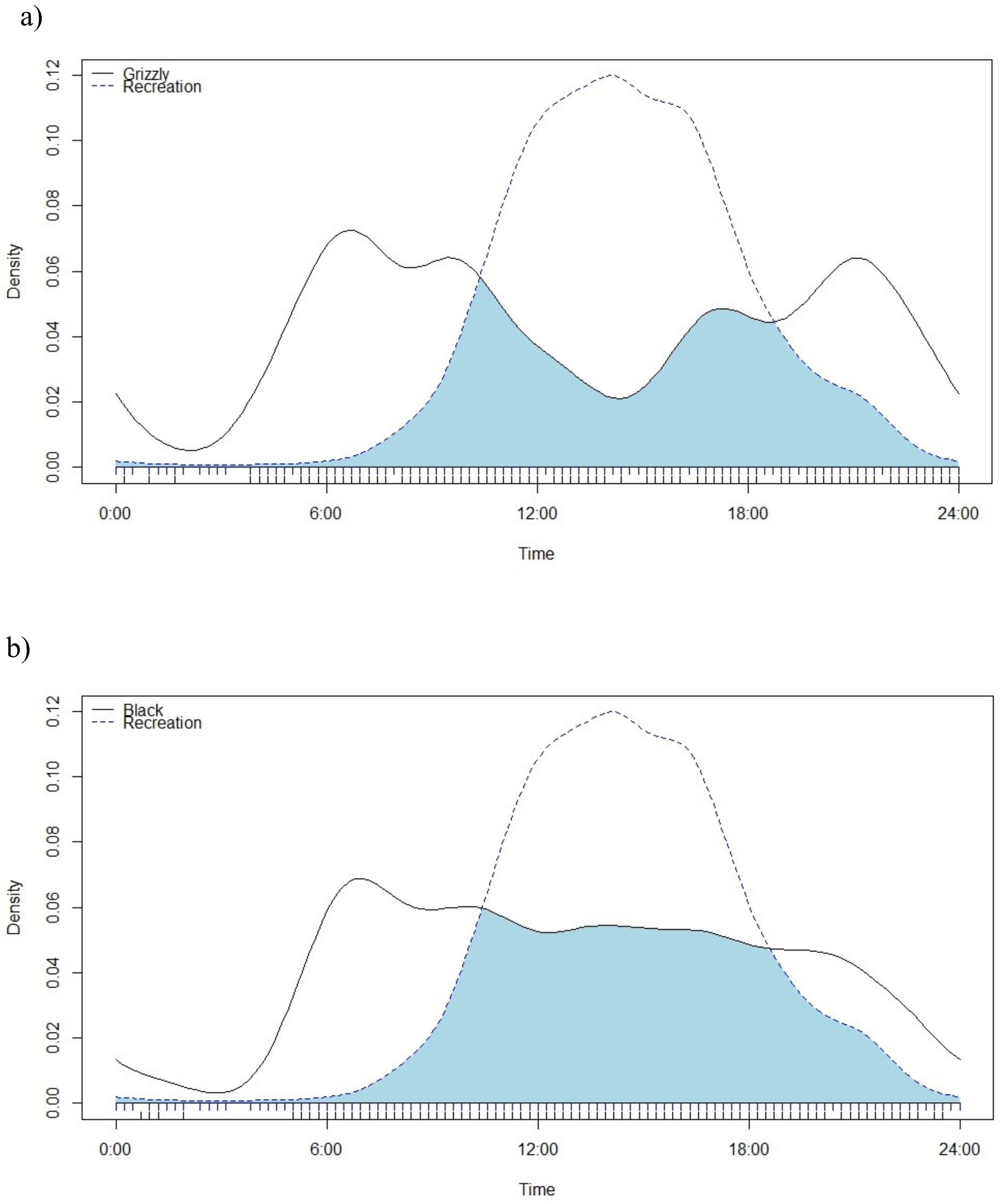


Fig. 4.4. Activity overlap plots for a) recreation (blue dash) and grizzly bears (black) and b) recreation (blue dash) and black bears (black) from West-central Alberta. Blue shading represents where bear species and recreational activity temporally overlapped in terms of activity. Activity patterns are kernel densities estimated using detection events on trail cameras (shown by dashed lines at base of each plot).

5 Using camera-based spatial mark-resight models to estimate density of a rare, unmarked large mammal.

5.1 Introduction

Explaining the abundance and distribution of animals defines the science of ecology (Andrewartha and Birch 1954). To understand how species are influenced by their environment, other species, and human disturbance, scientists require accurate methods for quantifying changes in the number and spatial distribution of animals over time. Population monitoring can be challenging for species the most in need; for example, large carnivores. These wide-ranging and elusive species are difficult to detect (Steenweg et al. 2016b), and at the same time are seeing declines that outpace other species (Ripple et al. 2014) due to historic and current persecution, brought about by human-wildlife conflict and exploitation. Problems with detection result in the need for huge survey effort to obtain accurate and precise estimates of population size, inflating costs. As a result, surveys tend to be infrequent which can be insufficient for making sound management decisions (Rout et al. 2009, Boyce et al. 2012).

The need for less expensive methods of collecting and analysing data on large carnivore populations is pressing. Reducing costs allows for either more continuous monitoring, giving wildlife managers the ability to respond to changes in species abundance and distribution in real time i.e. active adaptive management (Rout et al. 2009), or more funds for direct management actions to increase population recovery. The ability to quantify the distribution and abundance of cryptic carnivores at a lower financial burden has been revolutionised with the introduction of remotely-triggered trail cameras (O'Connell et al. 2010). The application of camera data to traditional mark-recapture has been successful for a number of rare species that had previously little demographic information, such as tigers (*Panthera tigris*; Karanth and Nichols 1998), leopards (*Panthera pardus*; Grey et al. 2013), jaguars (*Panthera onca*; Silver et al. 2004), and bobcats (*Lynx rufus*; Heilbrun et al. 2003). One thing all these animals have in common is that they are felids with unique coat markings that allow them to be identified to the individual level. Unfortunately, many species of interest are lacking means of individual identification, and therefore identity is unknown. In other circumstances, problems occur when only a portion of the population can be classified as "marked", and in these cases, we apply mark-resight models (Miller et al. 1997, McClintock and White 2009). Models for a fully unmarked population use information within spatial autocorrelation of counts between sampling sites to estimate the density of home range centres (Chandler et al. 2013), as well as methods that incorporate detection count and movement metrics within a gas diffusion model (Rowcliffe et al. 2008). However these method are thought to be biased (Rovero and Marshall 2009, Chandler et al. 2013), and have not had extensive testing with actual data.

The grizzly bear (*Ursus arctos*) is one such species where traditional capture-recapture methods are not an option when using cameras. Individual identification of grizzly bears is near impossible due to a lack of distinct marks and fluctuations in body size and hair colour across a single year (Sawaya et al. 2014). Current methods for density estimation rely on non-invasive genetic sampling (Woods et al. 1999). These methods most commonly use either lured corrals surrounded by barbed wire (Kendall et al. 2009) or barbed wire attached to natural rub objects (Stetz et al. 2010, Morehouse and Boyce 2016) to collect hair samples from which nuclear DNA is extracted and the individual bear identified. These methods are expensive and require substantial man power; they do, however, produce reliable and precise estimates of density, especially when incorporated in a spatial framework (Borchers, David & Efford 2008, Royle et al. 2014). In Alberta, Canada, the grizzly bear shares much of its distribution with agriculture, resource extraction, and outdoor recreation (Nielsen et al. 2006, Northrup et al. 2012b, Ladle et al. 2016, Morehouse and Boyce 2016). A previous estimate of abundance for Alberta placed the number of bears at 691 individuals in 2008 (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010), which led to a moratorium on hunting and listing as a threatened species provincially. Although the provincial grizzly bear recovery plan recommends that population units be reassessed every five years (Alberta Sustainable Resource Development 2008), high costs have prevented repeated surveys from occurring. Only recently have population estimates in some bear management areas (BMAs) been updated (Stenhouse et al.2015, Morehouse and Boyce 2016) and both of these estimates indicated local population increases.

Low-cost, accurate, and precise methods that allow for more frequent sampling are desirable. Abundance estimates derived from camera data from an unmarked or partially marked population could be promising if estimates were comparable to the current, more expensive, DNA capture-recapture methods. There have been few attempts at applying camera traps to estimate grizzly bear populations (Higgs et al. 2013, Whittington et al. *in review*), and to date there has not been a concurrent comparison of density and abundance estimates between the two methods for the same population.

In this paper, I compared two methods for estimating grizzly bear abundance: 1) spatial capture-recapture (Borchers, David & Efford 2008, Royle et al. 2014) using DNA hair-snag data and 2) spatial mark-resight (Sollmann, Gardner, Chandler, et al. 2013; Royle et al. 2014; Whittington et al., *in review*) using a combination of camera data and radiotelemetry data. I compared the efficacy of spatial mark-resight methods using telemetry and cameras relative to DNA-based spatial mark-recapture using concurrent grizzly bear datasets collected in the same region of the west-central Alberta Rocky Mountain and foothills.

5.2 Methods

Study area

My study was conducted in the eastern slopes and foothills of central Alberta's Rocky Mountains (Fig. 5.1). Forests dominated the vegetation, and consisted of spruce (*Picea* spp.), fir (*Abies* spp.) and lodgepole pine (*Pinus contorta*), with an increase in mixed forest including aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) farther east and at lower elevations. The region hosts a number of large mammal species, including elk (*Cervus canadensis*), moose (*Alces alces*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). Members of the carnivore guild include grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), cougar (*Puma concolor*), wolf (*Canis lupus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), wolverine (*Gulo* gulo) and lynx (*Lynx canadensis*). Previous estimates from 2004 put the grizzly bear density at approximately 4.79 bears per 1000km^2 (CI = 4.10 – 6.28; Boulanger et al. 2004), placing this population at low density relative to the remaining provincial grizzly bear range (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). The 2014 estimate for the BMA 3 core region, of which my study area is a small subset, estimated the density of bears to be 11.12 (CI: 8.28 – 14.92) bears per 1000km^2 (Stenhouse et al. 2015).

DNA hair snag data collection

DNA data were collected in 2014 for the study area using hair snag bait stations. Between June 9th and August 7th, hair stations were set up at 71 locations (8 rub trees, 63 baited corral sites), spread over a 20-km^2 grid (Fig. 5.1). Site location within cells was replicated from previous studies to improve comparison across monitoring events (Boulanger et al. 2004, Rovang et al. 2015). Each location was sampled for four sessions, each lasting 14 days. Hair samples were sent to Wildlife Genetics International, Nelson, B.C., for genetic analysis; species, sex, and individual identification were determined via the extraction of nuclear DNA from the hair follicle following established protocol (Paetkau 2003, 2004). Full methods can be found in Stenhouse et al. (2015).

Telemetry data collection

Between 2012 and 2014, grizzly bears were captured across the study area using a combination of aerial darting and culvert trapping. A total of 11 individual bears were captured (7 female, 4 male), and radiocollars were attached and treated as a ‘mark’. Although I aimed to conform to the assumption of random marking of individuals across the study area , an assumption implicit within spatial mark-resight models (Royle et al. 2014), due to uneven success between aerial darting (confined to western portion of study area) and culvert trapping (eastern portion of study area), detection probability probably varies between marked and unmarked populations. Relocations were recorded every hour. Previously collared bears from 2010 and 2011 that still had attached, non-functioning collars, also were included as ‘marked’ individuals (N = 3, all female) for the first two years of the analysis. This led to a total of 14 marked individuals that were exposed to our camera trap grid. Telemetry relocations were rarified to one relocation per week to allow for temporal and spatial independence.

Camera trap survey

From 2012-2014, 239 trail cameras (Reconyx, Holmen, WI) were deployed on human-use trails across the study area. The number of locations sampled varied among years (2012 = 129 camera locations, 2013 = 178 camera locations, 2014 = 131 camera locations), as did sampling intensity (Ladle et al. 2016). Sampling locations were selected using a systematic sampling design where I aimed to maintain three cameras per 50 km^2. Cameras were set a minimum of 1 km apart to avoid clustering. Camera sampling was conducted from April 15th to October 31st, and all images of grizzly bears were documented. Photographs of bears were treated as independent events if more than 5 minutes apart. Dependent offspring were not included in the analysis; therefore, the estimate is of independent grizzly bears. Marked bears were identified by cross-referencing time, date and location of the image with telemetry data. For photographs that could not be linked to a functioning collar, I used process of elimination based on bears with non-functioning collars that overlapped the camera location, type of collar (Telemetry Solutions, Concord, CA, USA; Followit, Lindesburg, Sweden) and known retrieved collars. Photos were classified as ‘unknown’ where individual identification was still ambiguous.

Spatial Capture-Recapture model

I used the standard SCR model outlined in Royle et al. (2014) for analysis of the DNA data. Spatially-explicit capture-recapture models (Borchers et al. 2008, Royle et al. 2014) estimate density of bears within a spatially-explicit context using encounter history data to estimate the abundance and geographic location of individual home-range centres across the area of interest. Encounter histories; the probability of individual i being detected at trap j during occasion k, were modelled using a binomial distribution and a half-normal detection function (Borchers, David & Efford 2008). The detection function consists of two estimated parameters; g_0 is the probability of detecting an individual given the trap is located at its home range centre, and σ, which is a spatial scale parameter that correlates with home range size. The distribution and abundance of home range centres are estimated within a point process, where N home range centres are distributed across an area of state space (S) following a uniform distribution. The state space should be chosen so that it is large enough that an individual with a home-range centre on the boundary has a zero probability of being encountered (Borchers, David & Efford 2008). To estimate N, I use data augmentation (Royle et al. 2007) to augment the dataset with an additional set of hypothetical individuals with zero encounter histories i.e. unobserved individuals, and modeled as the sum of a latent state variable, z_i, which is an identically and independently distributed (iid) Bernouilli variable. Individuals are included in the population ($z = 1$) or discarded ($z = 0$). The set of observed and unobserved individuals (M) should be set large enough to not truncate estimates of N (Sollmann et al. 2013a, Whittington and Sawaya 2015).

Spatial Mark-Resight model

I used a spatial mark-resight model (SMR; Royle et al. 2014) with telemetry data for marked individuals (Sollmann et al. 2013a ; Sollmann et al. 2013b; Whittington et al. *in review*). Traditional mark-resight models involve an initial capture period (in this present context collaring of a random subset of grizzly bears), and then a concurrent number of resight occasions (camera trap surveys). SMR models consist of a similar hierarchical model structure as outlined above for SCR models. The fundamental difference is that *N* contains encounter histories for marked individuals (10-day sampling occasions), and also spatially correlated counts of unmarked individuals that are used to update latent encounter histories of unknown individuals in a Bayesian framework (Whittington et al.*in review*; Sollmann et al.2013) using data augmentation (Royle et al. 2007). A key assumption of all mark-resight models is that marked and unmarked individuals have an equal probability of being resighted. Although this often holds when marks are natural marks randomly identified across the population, manual marking of animals tends to overlap with the resight trap grid, and this results in violation of this assumption (Royle et al. 2014). By applying an inhomogenous point process based on the distribution of marked individuals, it is possible to relax this assumption (Whittington et al.*in review*). If marked individuals have relocation information (e.g. if the mark is a radiocollar), this can be used to alter the intensity of the point process for marked and unmarked individuals, where thinning rate at location s is: $\lambda(s) = 1 - \prod_{j=1}^{J}(1 - \lambda^{M}(\mathbf{s}, \boldsymbol{x}_{j}^{\boldsymbol{M}})$, where λ^{M} is the encounter probability given the home range centre is at location s and $\boldsymbol{s}, \boldsymbol{x}_{j}^{\boldsymbol{M}}$ is the distance between location s and the home-range centre of marked individual *j*. The inhomogenous point process is then estimated for marked as $\mu(s)\,\lambda(s)$ and unmarked as $\mu(s)\,(1 - \lambda(s))$. Home range centres were estimated using the centroid of the home-range minimum convex polygon (MCP). Telemetry data from marked individuals is also incorporated within the data model to estimate values for σ. Due to the number of telemetry relocations, these data offered more insights regarding animal movements than solely resightings of marked individuals at camera sites (Sollmann et al. 2013a).

Application to grizzly bear data

For both models, I allowed the detection model to vary by sex. Due to the length of the session period for the SMR method, I included two parameters that allowed g_0 to vary based on occasion (quadratic function), as I predicted detection would be highest in the summer months when the bears are most active (Whittington et al. *in review*). Telemetry data were combined with the SMR data to estimate joint-likelihoods. All analyses were run in R (R core team, 2014). The SCR model was run using Rjags (Plummer 2013) and the SMR model was run using Metropolis-within-Gibbs MCMC from Whittington et al., *in review*. I ran three chains, each consisting of 50,000 iterations with a 5,000 burn-in. Coefficient of Variation (CV) was used to compare precision of the two methods.

5.3 Results

Spatial Capture-Recapture

In 2014, 92 detections of 48 grizzly bears were collected over the 72 trap locations. Grizzly bears were detected at 40.9% of trap locations. Number of individual bears detected at each site varied from one to ten bears (mean = 2.66, SE = 0.43). Male bears were detected more frequently than females (males = 57, females = 35). Encounter probability varied between males and females (Fig. 5.2a); males had a lower encounter probability at their home range centre (g_0: mean = 0.084, CI = 0.049 – 0.130; Table 5.1), and had the larger detection zones (σ = 7.15, 5.86 – 8.91). Females had smaller detection zones (σ = 4,21, 3.30 – 5.51) and likely due to this fact, had a higher encounter probability at their home range centre (g_0 = 0.16, 0.067 – 0.30).

Spatial Mark-Resight model

Over the period of the camera surveys, I documented 619 detections of grizzly bears. Grizzly bears were detected at least once at 60.3% of all trail locations across all years. Of the 619 events, 47 photographic events were resight events of collared individuals (2012 = 8, 2013 = 25, 2014 = 14) of 14 bears, which ranged from 1 to 12 resightings per bear. I was able to identify 25 events using relocation information from functioning collars. However, the remaining 22 events were of bears with non-functioning collars, of which I was able to identify 16 events to the individual level by process of elimination. There were six images where individual identification of the bear was not possible, due to multiple bears having overlapping home ranges and still wearing non-functioning collars. Encounter probability also varied in our SMR model (Fig. 5.2b) in a similar manner to the SCR model; males had a lower encounter probability at their home range centre (g_0 = 0.019, 0.014 – 0.028), and had the larger detection zones (σ = 11.72, 10,78 – 12.77). Sigma estimates representing detection zones of females were (σ = 5.35, 5.12 – 5.59) and females also had a higher encounter probability at their home range centre (g_0 = 0.034, 0.023 – 0.045). Encounter probability also varied across sampling occasion (Fig. 5.2c). Male bears had lower baseline encounter probabilities later in the year, while female encounter probability gradually increased, but with a high degree of error.

Accuracy and precision

Because DNA mark-recapture is currently considered to be the most reliable method for estimating abundance of grizzly bears, I took the SCR results as "truth" and compared the SMR results to the SCR results to evaluate performance in terms of accuracy and precision. The SCR method using DNA estimated the density of bears for the state space (Fig. 5.1) to be 14.89 (CI: 11.22 – 20.35; Fig. 5.3) grizzly bears per 1000 km^2. The SMR result was slightly higher at 16.03 (CI: 11.59 – 21.87; Fig. 5.3), however confidence bounds overlapped with the SCR result. In addition, I was able to obtain, using the SMR method, estimates for years 2012 and 2013, of 13.22 (CI: 9.07 – 18.34; Fig. 5.3) and 14.46 (CI: 10.38 – 19.35; Fig. 5.3) bears per 1000 km^2, respectively. Coefficients of variation (CV) were similar for both models (CV_{SCR} = 6.45%, CV_{SMR} = 5.55%).

5.4 Discussion

In this study, I had opportunity to compare two methods for estimating abundance and density of elusive large carnivores; 1) spatial capture-recapture using hair DNA samples, and 2) spatial mark-resight using a combination of radiocollaring and trail camera resightings. Estimates of grizzly bear density in the study region using the two methods were similar. Recent advances allow the relaxation of the assumption of random distribution of marked individuals across the state space (Whittington et al., *in review);* a problem that leads to biased estimates using SMR. When physical capture-recapture data are available for the marked individuals, the capture-recapture information aids in identifying the distribution of marked individuals within the state-space, thereby allowing varying spatial distributions for marked and unmarked individuals to be incorporated with the point process (Whittington et al., *in review*). The key advantage of SMR using camera data is that it requires a small subset of marked individuals with the majority of information coming from the camera trap information. Requiring detailed capture-recapture information to parameterise the point process increases the invasiveness of the method as well as financial costs. Regular checking of traps also is difficult when dealing with more rugged and inaccessible terrain, where aerial darting is the only feasible option for radiocollaring/marking animals. Additionally, these methods do not apply when bears are captured using non-trap methods such as aerial darting, as in this study. By incorporating location data for the marked individuals to modify the point process, I managed to reduce negative bias commonly associated with SMR methods when animals are physically marked (Royle et al. 2014). I show that it is possible to use telemetry data rather than capture-recapture information to inform this process, however further simulation testing should be done to check Confidence Interval Coverage (CIC) and potential presence of other biases.

Both methods yielded estimates with levels of precision in line with other grizzly bear density estimates (Whittington and Sawaya 2015, Morehouse and Boyce 2016), as shown by their respective CVs of 6.45% (SCR) and 5.55% (SMR). Both models estimated higher baseline encounter probabilities for females relative to males, and the inverse was true for estimates of sigma. These results align with previous estimates of detection and home-range sizes for male and females bears (Whittington and Sawaya 2015, Morehouse and Boyce 2016). Increased accuracy and precision of density estimates is directly linked with higher probability of detecting the species (Lukacs and Burnham 2005). Encounter probabilities were considerably lower for the SMR model than for SCR, likely inflating error around the estimates of abundance and density (Boulanger et al. 2002). Cameras placed on trails, have higher probability of detecting most large carnivores than cameras placed at random within forest vegetation (Burton et al. 2015). Cameras placed at rub trees and other natural attractants, or the addition of bait, will increase detection probability further. These are ways in which one can improve precision of our estimates without the need for necessarily inflating cost and effort. However, the use of any feature or attractant beyond random sampling brings with it potential biases (Harmsen et al. 2010, Morehouse and Boyce 2016). Trails may inflate our number of detections through repeated movement patterns of animals within their home ranges (Rowcliffe et al. 2008, Cusack et al. 2015) Rub tree use by bears is a social behaviour, and sex and social dominance influence the probability of an individual rubbing (Morehouse and Boyce 2016). The use of scent lure may be beneficial for detecting specific species, however lure use may result in biases attributable to drawing additional individuals into the study area. Such potential biases should always be acknowledged, and taken into consideration when stating conclusions.

I obtained our estimate with a relatively low proportion of the population marked (< 10%). Increasing the number of initial marked animals is another way of increasing the precision of estimates, however grizzly bear capture is not only invasive, but increases financial costs. Quantifying the relationship between the number of marked animals and the accuracy and precision of estimates will help reduce unnecessary costs associated with animal captures. Ear tags rather than radiocollaring may offer a more cost-efficient alternative, but would require supplementary capture-recapture information to inform the marking process (Whittington et al.*in review*) and still requires physical capture of the animal. For this reason, SCR methods that use non-invasive techniques for identifying individuals should still be prioritized when the only metric of interest is density. Movement (Kays et al. 2015) and habitat selection analyses (Cagnacci et al. 2010) often require animal relocation data; similarly, studies quantifying survival also can benefit from radiocollar data (Pollock et al. 1989). In such circumstances, deploying trail cameras allows for efficient estimation of additional population-level information such as density.

Our finding that current SMR methods result in similar density estimates to concurrent SCR estimates is encouraging, however, the availability of a feasible solution to long-term grizzly bear monitoring is still in question. Precision and accuracy are clearly strongly desired attributes to any monitoring scheme. However, limited resources demand that we consider more cost-efficient alternatives that may require sacrificing rigor, in exchange for more frequent monitoring. Increasing temporal resolution of monitoring is important for vulnerable species such as grizzly bears because it improves managers ability to engage in active adaptive management (Walters and Hilborn 1978, Whittington and Sawaya 2015). In addition, at such a financial cost, it raises the question of whether it is worthwhile to invest so heavily in monitoring (McDonald-Madden et al. 2010), relative to investing those funds in direct management and conservation actions instead (Nichols and Williams 2006, Possingham et al. 2012). Despite this delisting of threatened species require the implementation of post-delisting regulatory mechanisms, which includes monitoring (e.g. in the United States; U.S. Senate Committee on Environment & Public Works 1973).

Alternative solutions to the two methods discussed above are available and should be considered when discussing long-term monitoring options. Use of indices or proxies offers alternative, less expensive options, but come with their own assumptions e.g.

constant and direct relationship between the index and abundance (Pollock et al. 2002). Initial investment in monitoring also is required for calibration (Stephens et al. 2015). Alternative methods of obtaining DNA samples, e.g. using natural rub objects rather than artificial bait sites, is a more cost efficient approach that has had wide success with grizzly bears (Kendall et al. 2009, Morehouse and Boyce 2016), and refining sample protocols using resource selection functions can lead to more effective use of limited resources (Allen et al. 2008).

Table 5.1. Results for SCR model. Density (D) is in individuals per 1000km^2. N is for the total number of individuals estimated with their home range centres within the state space (10,074 km^2). I used a bivariate half-normal detection function, and the encounter model (both g_0 and sigma) were allowed to vary by sex. Confidence intervals were treated as the 2.5% and 97.5% quantiles.

Parameter	Mean	SD	2.50%	97.50%
D	15.02	2.35	10.91	20.02
N	283.43	44.3	206	378
g_0.male	0.08	0.02	0.05	0.13
g_0.female	0.16	0.06	0.07	0.3
sigma.male	7.13	0.76	5.84	8.8
sigma.female	4.17	0.56	3.28	5.44

Table 5.2. Results from SMR model with telemetry data for 2014. Density (D) is in individuals per 1000km^2. N is for the total number of individuals estimated with their home range centres within the state space (9,922 km^2). I used a bivariate half-normal detection function, and g_0 was allowed to vary by survey and sex, and sigma was allowed to vary by sex. Confidence intervals were treated as the 2.5% and 97.5% quantiles.

Parameter	Mean	SD	2.50%	97.50%
D	16.32	2.62	11.69	21.87
N	162	26	116	217
g0.male	0.019	0.0038	0.014	0.028
g0.female	0.034	0.0059	0.023	0.045
survey.male	-0.056	0.025	-0.11	-0.014
survey2.male	-0.013	0.0037	-0.021	-0.0065
survey.female	0.058	0.046	-0.023	0.15
survey2.female	-0.002	0.0048	-0.012	0.0069
sigma.male	11.72	0.52	10.78	12.77
sigma.female	5.35	0.12	5.12	5.59

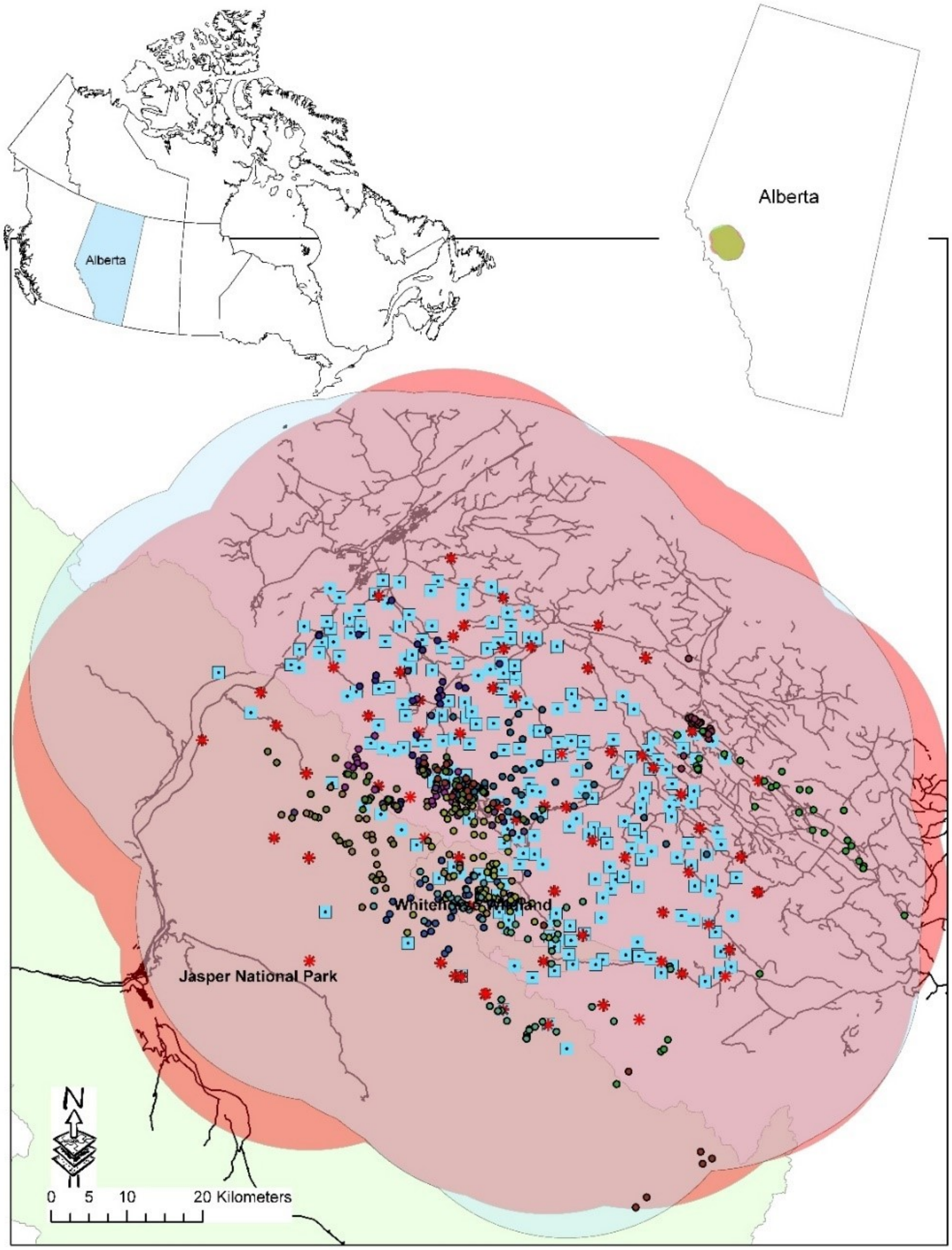
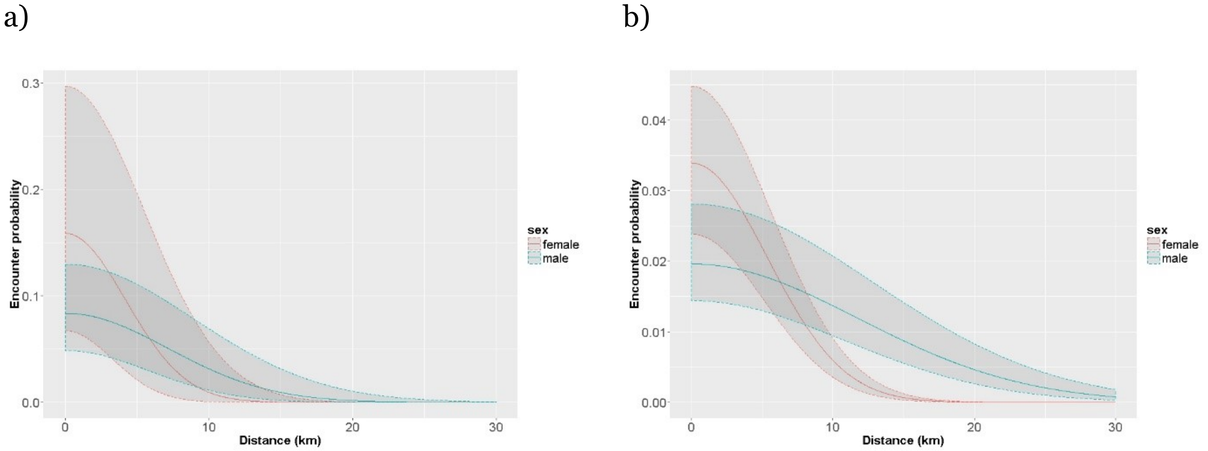


Fig. 5.1. Locations of camera locations (blue square) and hair snag locations (red stars). Buffers represent the state space (*S*) for SCR analysis (red) and SMR analysis (blue). *S* was defined as 25km buffers around outer perimeter of both traps and cameras. GPS locations are weekly relocations for each of the 'marked' bears with radiocollar data (*N* = 14).



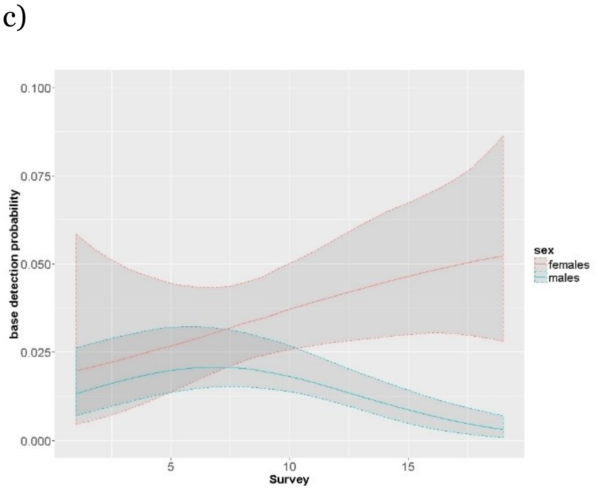


Fig. 5.2. Detection probability curves for a) SCR model as a function of distance, b) SMR model as a function of distance and c) SMR model for baseline detection probability as a function of survey (14-day intervals from April 15 – October 31st).

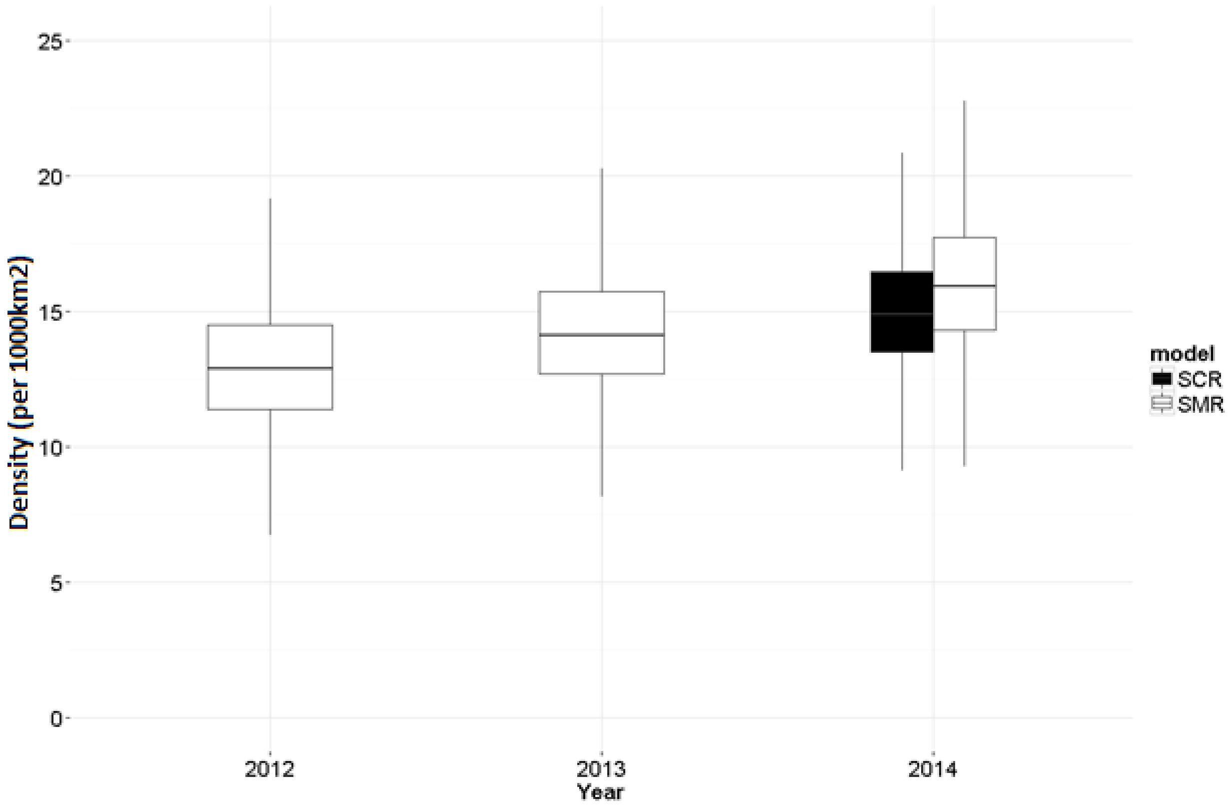


Fig. 5.3. Density estimates for West-central Alberta's Rocky Mountains and foothills grizzly bear population, (bears per 1000km^2) using spatial capture-recapture (SCR) and spatial mark-resight (SMR) methods. The central mark represents the median, and the tails represent the 95% confidence intervals. SCR result for 2014 is shown in black, and SMR results for 2012-2014 are shown in white.

6 General conclusions

Outdoor recreation is an activity enjoyed by people from all backgrounds. Clear benefits are associated with outdoor recreation: non-consumptive recreation benefits wildlife conservation through direct financial contributions (Green and Higginbottom 2000) and changing attitudes to wildlife (Duffus and Dearden 1990). Access management is therefore a controversial area of wildlife management (Knight and Gutzwiller 1995). Coupled with human population growth, unrestricted recreation should be taken seriously as a threat to habitat security (Knight and Gutzwiller 1995). Identifying the repercussions of increasing outdoor recreation on our surrounding ecosystems can help inform decisions relating to habitat conservation and management (Hammitt et al. 2015).

Motorised and non-motorised recreation are forms of human activity that have received relatively little attention regarding effects on wildlife (Taylor and Knight 2003). Formulating access management decisions is difficult due to the high variation in responses to recreation across species (Monz et al. 2013). The lack of a consensus on the effects of recreational activity on wildlife dilutes the argument for access restrictions further. Identifying the effect that recreation has on flagship species such as grizzly bears, may therefore prove useful. The main objectives of my thesis included developing techniques to quantify recreational activity across a landscape, and incorporating this information into novel methods for investigating behavioural responses at the single species and multispecies level. Lastly, I evaluate alternative methods for monitoring grizzly bear population density, in terms of accuracy and precision.

In Chapter 2, I proposed a model that improves our ability to quantify intensity of recreational use across a complex trail network. Camera traps are a useful tool for obtaining data on the intensity of recreational activity at different locations across a trail network. The number of cameras available defines the amount of data that can be collected, and a trade-off exists between maximizing spatial and temporal coverage (O'Connell et al. 2010). Rotating cameras between multiple sample locations is a common practice (Burton et al. 2012), but introduces temporal bias in sampling. By taking the initial step to model temporal variation in the intensity of use, and including location as a mixed-effect, I was able to estimate relative spatial variation at sites in the absence of temporal variation in sampling. Using Ordinary Kriging to interpolate to non-sampled locations across the trail network, I produced maps of the probability of non-motorised and motorised recreation that varied in both time and space. Application to grizzly bear habitat selection revealed that the model incorporating recreational activity outperformed models relying solely on distance to linear feature.

The increase over the past decade in the use of trail cameras in ecological research gives opportunity to accurately quantify human activity across scales relevant to large mammal conservation (Burton et al. 2015). Parks Canada has been implementing camera trap surveys for a number of years as part of their ongoing wildlife management research and to maintain information on visitor frequency and spatial distribution (Steenweg et al. 2016b). Application of my model will improve their ability to test hypotheses relating to the effect of hikers and other forms of non-consumptive recreation on wildlife. In addition, further monitoring is required outside of protected areas, as grizzly bear distributions are not constrained by park boundaries. Understanding the effects of access management actions of grizzly bear population recovery will require data encompassing grizzly bears located within all land use types.

Quantifying spatio-temporal variation in the intensity of use of the landscape by recreationists was an essential first step to understanding grizzly bear responses to recreation. In Chapter 3, I incorporated probability of motorised and non-motorised recreation to test alternative hypotheses focusing on how grizzly bears alter their habitat selection and movement in response to proximity to trails and associated recreational activity. Firstly, I revealed that habitat selection models were improved by including information on movement and recreational activity. When available, such as in radiotelementry studies, models should include movement metrics in conjunction with habitat covariates, and effort should be made to distinguish linear-features based on the associated intensity of human activity (Northrup et al. 2012a).

The direction of responses to trails and recreation varied between sexes. Trails with no recreational activity were selected for by both male and female grizzly bears. This significant selection disappeared however when probability of recreation was high. Contrary to expectations, grizzly bears reduced their movement speed as a function of trail proximity, implying they were using trails more for foraging (Stewart et al. 2013) than to facilitate faster movement, e.g., in wolves (Latham et al. 2011, Dickie et al. 2016). The switch to faster movement rates by males when and where motorised recreation was high is indicative of a fear response (Frid and Dill 2002), increasing movement as a potential avoidance strategy (Ciuti et al. 2012b). I emphasise the variation in individual bear responses to trails and recreation (Nielsen et al. 2002). This result emphasises the challenges facing wildlife managers who are required to manage areas at the ecosystem level (Simberloff 1998), because variation in responses to disturbance are not restricted to between species, but individual-based modeling highlights the amount of variation within a single species. Future directions of research should aim to investigate why such variation across individuals exists (Dingemanse et al. 2010, Grimm and Railsback 2013). I predict variation among individual behaviours is tied with cumulative exposure to motorised and non-motorised recreation across an animals' lifetime, as well as the more long-term consequences of natural selection on genotypes associated with avoidance behaviour. Identifying whether animals display a physiological response, e.g., increased stress (Creel et al. 2002) alongside behavioural changes, will aid in determining the potential fitness consequences for grizzly bears.

The multispecies model framework applied in Chapter 4 gave me the ability to test hypotheses at the community level. As predicted, grizzly bears and black bears displayed different responses to motorised and non-motorised recreation, suggesting contrasting perceptions of recreational activity as risk (Frid and Dill 2002, Schwartz et al. 2010). Black bears used areas where recreation was present more so than grizzly bears, and overlapped more with recreation relative to temporal activity patterns. Interestingly, both species responded to the presence of recreation by reducing their intensity of use of those areas, rather than avoiding the areas altogether (Northrup et al. 2012a). In addition, we documented this response only when motorised activity was present, revealing contrasting responses by bears to the type of recreational activity. Treating detection probability as a nuisance parameter rather than redefining it as a measure of intensity of use and instead focusing solely on changes in occurrence can result in misleading inference.

Chapters 3 and 4 give insight into how grizzly bears alter movement, habitat selection and use relative to human recreational activity. The ability for grizzly bears to change their behaviour in response to stressors, and the associated consequences of such changes can have a fundamental influence on population dynamics (Gomes and Sarrazin 2016). In Chapter 5, I address challenges faced by wildlife managers in monitoring changes in population density of grizzly bears. I estimated grizzly bear density for my study area using a combination of radiotelemetry data and trail camera data in a Spatial Mark-Resight model (Sollmann et al. 2013a, 2013b, Royle et al. 2014), and compared this result to concurrent estimates obtained using DNA data and a Spatial Capture-Recapture model (Royle et al. 2014, Whittington and Sawaya 2015). I demonstrate an alternative method of estimating density that can be applied with little additional cost in regions where animals are naturally marked, or where artificial marks such as radiotelemetry collars and ear tags are present. My results suggest reliable estimates also can be obtained using SMR as long as differences in detecting marked and unmarked individuals is accounted for, through incorporating location information for marked animals (Whittington et al.*in review*). Simulating distributions of marked versus unmarked animals and incorporating varying magnitudes of location information will increase understanding of model sensitivity in terms of accuracy and precision. In the present example, we treated our estimates using SCR models as truth: however, this method is susceptible to its own biases. Testing such methods in animal populations where census data means true density is known, is the best way forward (Rowcliffe et al. 2008).

Management applications

A method to estimate spatio-temporal variation in recreational activity is an important tool for wildlife managers. My first chapter offers a powerful approach to analyzing trail camera data on recreational activity, and the prospective map products can be used directly to coordinate access enforcement where it is effective and needed. When coupled with information on animal distribution, it is possible to identify times and areas where the potential for conflict is exacerbated, and if required, introduce access restrictions to mitigate negative effects for both wildlife and recreationists. Responses by grizzly bears to recreational activity suggest that access restrictions could benefit the species. Reduced movement rates by grizzly bears when close to trails infers use of trails for foraging, and lack of selection for and reducing intensity of use of trails with recreational activity may result in reduced foraging opportunities and exploitation by the more-tolerant black bears. Controlling access in areas with high-quality bear foods would be an important step in dampening potential negative consequences of human recreation.

Lastly, I showed that spatial mark-resight models can be a useful method for estimating grizzly bear densities, and should be added to the toolkit available to wildlife managers. Trail cameras are a useful, widely applied data collection tool (Burton et al. 2015, Steenweg et al. 2016a), with data currently being collected across a large amount of the Canadian Rocky Mountains. My analysis shows that even with just a small proportion of the grizzly bear population radiocollared, it is possible to estimate grizzly bear density to a similar degree of precision as traditional capture-recapture methods. Given the additional, multi-species information that comes with trail cameras, and the movement data that can be used to ask questions relating to movement behaviour and fine-scale habitat selection, I believe spatial mark-resight methods should be incorporated into population monitoring of grizzly bears in Alberta.

My dissertation research has revealed how grizzly bears alter their movement and habitat selection behaviour as a function of trails and recreational activity. Future management objectives should focus on continued, directed, hypothesis-driven monitoring of both behavioural and demographic responses to experimentally manipulated recreational disturbance in an adaptive management framework (Walters and Hilborn 1978, Nichols and Williams 2006). Consolidating monitoring actions alongside active adaptive management is the most efficient path forward, and will inform researchers to a greater extent than the sum of two parts (Nichols and Williams 2006, McDonald-Madden et al. 2010). As human population growth continues, and we see continued resistance to change from a political perspective; we will require sound, experimental research and monitoring on restricted budgets to ensure a solid science basis for management decision making.

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