

RESEARCH ARTICLE

Grizzly bear response to spatio-temporal variability in human recreational activity

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Funding information

International Bear Association; Parks
Canada; Alberta Conservation Association;
Mountain Equipment Co-op; Alberta
Environment and Parks; TD: Friends of
the Environment; Alberta Biodiversity
Monitoring Institute; Safari Club
International: Northern Alberta Chapter

Handling Editor: Sarah Durant

Abstract

1. Outdoor recreation on trail networks is a growing form of disturbance for wildlife. However, few studies have examined behavioural responses by large carnivores to motorised and non-motorised recreational activity — a knowledge gap that has implications for the success of human access management aimed at improving habitat quality for wildlife.
2. We used an integrated step selection analysis of grizzly bear (*Ursus arctos*) radio-telemetry data and a spatio-temporal model of motorised and non-motorised human recreational activity to examine how human recreational activity on trails affects both habitat selection and movement behaviour of individual bears. Grizzly bears were captured and radiocollared in the west-central Alberta Rocky Mountains and Foothills, and trail cameras were deployed on trails to obtain data on human recreational activity.
3. We found that models including data on recreational activity outperformed trail-proximity models when interactions with movement covariates were included. Responses were highly variable among individuals and across classes: males, females, and females with cubs.
4. Male and solitary female grizzly bears increased avoidance of trails with a high probability of motorised activity as well as displaying increased movement rates in response to motorised recreation. Females with cubs did not increase avoidance, however they had the largest response in terms of higher movement rates. In contrast, for all classes, selection for proximity to trail increased when probability of non-motorised activity was high, and the effect on movement was dampened relative to the motorised response.
5. *Synthesis and applications.* By combining selection and movement into a unified modelling framework, we show that bears alter selection and movement behaviour in response to trails and recreation, and that such responses are determined by the type of recreational activity. Reduced selection and increased movement in proximity to motorised trails could affect bears' ability to exploit foraging opportunities in these areas. Future access management actions for grizzly bear recovery should consider frequency and type of linear feature use by humans rather than solely relying on thresholds relating to feature densities.

KEYWORDS

grizzly bear, habitat selection, human activity, iSSA, linear disturbance, movement ecology, recreation, trails

1 | INTRODUCTION

Linear disturbance networks of roads and trails and their associated use by humans are known to affect wildlife (Fahrig & Rytwinski, 2009; McKenzie, Merrill, Spiteri, & Lewis, 2012). Many species are negatively affected by these features directly through mortality (Beebee, 2013) and through increased stress as a response to linear features and associated activity (Creel et al., 2002). Responses can be either physiological via increased cortisol or other related stress hormones (Creel et al., 2002; Wasser, Keim, Taper, & Lele, 2011) or via avoidance behaviour (Jaeger et al., 2005) whereby animals perceive human activity as a form of risk (Frid & Dill, 2002). Both elevated stress and risk avoidance can be costly for individual animals and potentially could influence an individual's fitness through changes in survival and reproduction (Creel & Christianson, 2008; Creel, Christianson, Liley, & Winnie, 2007).

Due to challenges in effectively documenting both the spatial and temporal variation in human use activity, particularly in inaccessible or remote areas (Ladle, Avgar, Wheatley, & Boyce, 2017; Northrup et al., 2012), most current literature documenting risk effects associated with road and trail networks treat linear features as a temporally static disturbance (Boulanger & Stenhouse, 2014; Prokopenko, Boyce, & Avgar, 2017). However, rather than the presence of the linear feature itself, human activity along the feature is a prominent driver of animal avoidance behaviour, such as road traffic (Northrup et al., 2012; Scrafford, Avgar, Heeres, & Boyce, 2018). Incorporating measures of variability in this activity over space and time increases one's ability to accurately identify animal responses to human disturbance. Even when comprehensive data are collected (e.g., Ladle et al., 2017), analytical techniques require much development to understand this potential variable "landscape of fear" (Ciuti et al., 2012; Laundré, Hernández, & Altendorf, 2001) and strengthen current knowledge that recreation use of trails can have negative consequences for wildlife (Hammit, Cole, & Monz, 2015; Monz, Pickering, & Hadwen, 2013; Naylor, Wisdom, & Anthony, 2009).

Telemetry data can be used to document animal distributions using models of space use with environmental variables to infer resource selection (Manly, McDonald, Thomas, McDonald, & Erickson, 2007). Resource selection functions (RSFs) compare a set of used resource units (relocation data) to a set of available (random) resource units (Manly et al. 2007; Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006). With improved GPS and radiotelemetry technology, relocation data are rapidly becoming more refined, dramatically improving our ability to approximate the true path taken by animals through the landscape (Thurfjell, Ciuti, & Boyce, 2014). Better characterisation of animal movements has advanced our understanding

of movement ecology by linking movement mechanisms to the observed movement pattern (Avgar, Mosser, Brown, & Fryxell, 2013; Avgar et al., 2015; Kays, Crofoot, Jetz, & Wikelski, 2015), offering a more detailed and accurate representation of how animals perceive and respond to external stimuli such as human activity.

Step selection functions (SSFs) in particular afford the advantage of relocations being temporally defined, thus allowing inclusion of fine-scale, temporally dynamic variables (Fortin et al., 2005; Thurfjell et al., 2014). This allows us to investigate movement behaviour, which may be an additional response to risks such as road traffic or human recreational activity (Avgar, Potts, Lewis, & Boyce, 2016; Avgar et al., 2013; Kays et al., 2015). Thus, wildlife behavioural responses to perceived risks can take place through a combination of changes in both movement and habitat selection (Abrahms et al., 2015).

Such refined changes in habitat selection have been documented in grizzly bears (Brown & Kotler, 2004; Nielsen, Stenhouse, & Boyce, 2006), and habitats considered more risky have led to increased grizzly bear movement (Graham, Boulanger, Duval, & Stenhouse, 2010). Linear feature (roads, trails, seismic lines) networks influence grizzly bears by altering habitat availability and movement (Graham et al., 2010; Graves, Farley, & Servheen, 2006; Mace, Waller, Manley, Lyon, & Zuuring, 1996; Northrup et al., 2012; Roever, Boyce, & Stenhouse, 2010; Waller & Servheen, 2005). Analysis of autocorrelation patterns in grizzly bear step lengths has shown that bears in areas of high road density displayed both higher movement rates at night and disrupted movement patterns during the day (Boyce et al., 2010). Positive associations with linear features have been observed, including increased foraging opportunities adjacent to roadsides (Kite, Nelson, Stenhouse, & Darimont, 2016; Roever et al., 2010). Relatively little is known about grizzly bear responses to recreation (Fortin et al., 2016; Graves, 2002; Rode, Farley, & Robbins, 2006). However, the magnitude and type of activity are likely to influence the perception of linear disturbances by grizzly bears (Northrup et al., 2012).

To document how a species might alter movement and habitat selection in relation to linear disturbance and human activity, we investigated grizzly bear response to human recreational activity on a complex trail network using an integrated step selection analysis (iSSA; Avgar et al., 2016; Prokopenko et al., 2017; Scrafford et al., 2018) to account for the spatio-temporal variability in animal movement which historically has been left unaccounted. We formulated the following set of questions: (a) Do bears select trails (use/avoid more than random) and how does selection vary with different probabilities and forms of recreational activity? (b) Do bears change their movement rates in relation to trail proximity? (c) Does bear movement vary based on the probability and type of recreational activity along nearby trails?

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study in a 2,824 km² region of the eastern slopes and foothills of central Alberta's Rocky Mountains (Figure 1), located within Bear Management Unit 3 (Alberta Grizzly Bear Recovery Team, 2008). 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) as well as portions of Jasper National Park (JNP; no motorised activity or hunting), Whitehorse Wildland Park (WWP; no motorised activity, hunting is allowed), and reclaimed mine land (designated access routes, no hunting). Natural resource extraction is prevalent and diverse on public lands in the region, contributing to a high density of linear disturbance (seismic exploration cutlines, resource access roads, power lines,

pipelines) on the landscape, varying in density from 0 to 11.4 km/km², with a mean density across the study area of 1.17 km/km² (see Appendix S1, Supporting Information Figure S1).

2.2 | Grizzly bear movements

Between April 2011 and November 2015, we collected location data for grizzly bears residing in and around the study area using Global Positioning System (GPS) radiotelemetry 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 or aerial helicopter methods (Cattet, Caultkett, & Stenhouse, 2003). For this study, we included all locations inside the study area and between April 14 and September 30 (when information on bear foods was available). We identified consecutive locations (separated by 55–65 min) for each bear creating "steps" (Thurfjell et al., 2014), splitting data by bear, year, and removing partitioned datasets that had less than 2 weeks of data (336 steps). This resulted in a sample of 15 bears (5 males, 10 females) consisting of 26 bear-year datasets (Supporting Information Table S1).

2.3 | Recreational activity

We recorded hourly presence or absence of motorised and non-motorised recreational activity between May 2012 and November 2014, for a total of 240 trail locations, by placing infrared remotely triggered trail cameras (Reconyx LLP) on trails, defined to be anthropogenic linear features excluding active roads. We selected trail locations using a stratified random sampling design, varying locations based on land cover type, and monitored each for >20 days. For each hour of the day, we identified, if recreation had taken place, the type of recreation (OHV, truck, hiker, horse rider) and categorized it into motorised and non-motorised recreation. Using these data, we estimated the spatio-temporal variation in hourly probability of motorised and non-motorised occurrence using mixed-effect logistic regression, modelling temporal variation as a function of co-variables with the camera location as a random effect. The best linear unbiased predictors for each location were then spatially interpolated across the trail network, the final product being spatial maps of the probability of occurrence of motorised and non-motorised recreational activity that also varied in time (see Ladle et al., 2017 for full description of methods). Using AUC, we found no 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 (Supporting Information Table S2a,b), thus enabling us to extrapolate the probability of motorised and non-motorised occurrence for bear-years outside of those sampled. The probability of a motorised recreation event taking place per hour ranged from 0% to 36%, while the probability of a non-motorised recreation taking place per hour ranged

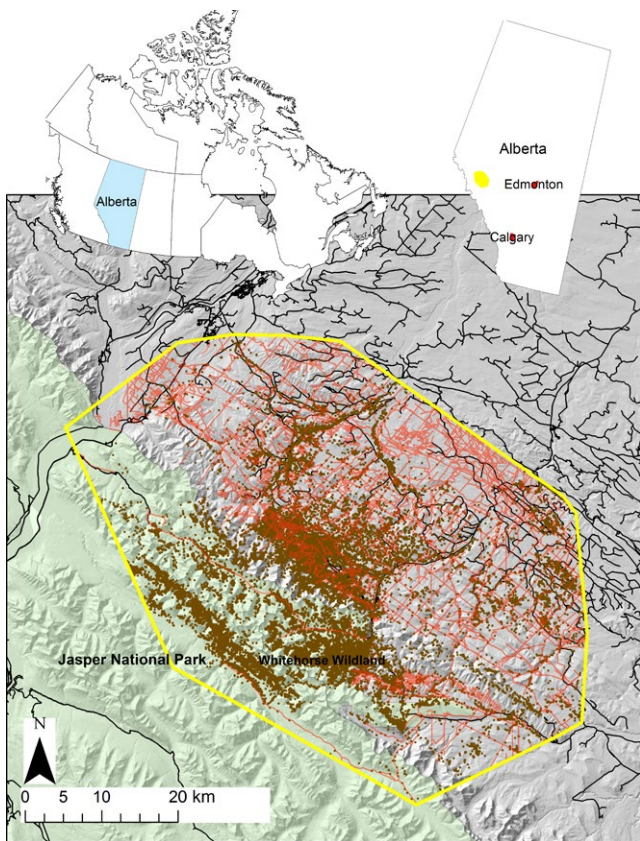


FIGURE 1 Map of study area including grizzly bear telemetry data (green points) over a digital elevation hillshade model with mapped linear disturbances (black = roads, blue = trails). Yellow perimeter represents the study area domain, defined by the spatial extent of our trail camera locations (Ladle et al., 2017). Points show the used locations for all bears between 2011 and 2015

from 0% to 40%. We transformed the probability of motorised and non-motorised occurrence (see Supporting Information Table S3 for full transformations). We checked for collinearity between the probability of motorised and non-motorised activity and found that it was minimal ($r = -0.03$).

2.4 | Habitat covariates

We used a spatio-temporal food-quality index that weighs different food types based on their biweekly diet consumption across the year (Nielsen, McDermid, Stenhouse, & Boyce, 2010; Appendix S4). In addition to food quality, distance to trail and associated probability of motorised and non-motorised recreational activity, we included covariates known to influence grizzly bear habitat selection (Nielsen, Boyce, Stenhouse, & Munro, 2002; Northrup et al., 2012). We used distance to road, distance to forest edge (both inside edge and outside edge; Northrup et al., 2012), distance to stream and terrain ruggedness (TRI; Riley, DeGloria, & Elliot, 1999).

We log transformed distance to trail, road, and streams. All variables (Supporting Information Table S3) were calculated using ArcMap (ESRI 2015) and the R statistical computing environment (R Core Team, 2014).

2.5 | Integrated Step Selection Analysis (iSSA)

An iSSA assumes that animal space use consists of two main components: a discrete-time movement kernel and a 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 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 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) and Scrafford et al. (2018) for a similar application.

We first characterised a tentative population-level probability distribution of step lengths using a gamma probability density function, where maximum likelihood estimates of the shape (b_1) and scale (b_2) parameters were obtained using nonlinear least squares from the MASS package in R (Venables & Ripley, 2002). We used all observed step lengths (across all bear-years) as the input ($b_1 = 0.492$, $b_2 = 588$). We shall refer to these observed values as the tentative shape and scale, which are confounded by the process of habitat selection. Once combined with the iSSA beta coefficient results, it allows us to estimate the selection-free step length distribution (see below and in Avgar et al., 2016). Next, we sampled a set of 10 random end points and associated steps and coupled them with each used location, their distance relative to the previous used location being sampled from the above step length distribution. Random

points were sampled under a uniform angular distribution. We extracted covariates (Supporting Information Table S3) for both the start and end points for each step (both used and random), based on their spatial and temporal positions. We modelled habitat selection and movement using conditional logistic regression in R (*clogit*; Therneau, 2015), with cluster (a group of one used step and its 10 associated random steps) ID as strata.

We included the natural logarithm of step length (hereafter *lnSlength*) as a covariate in each model to estimate the basal movement kernel when habitat selection had been included in the model; 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 we do here. Grizzly bears are known to alter their movement activity as well as alter their foraging patterns and response to roads as a function of time of day (Clevenger, Purroy, & Pelton, 1990; McLellan & McLellan, 2015; Munro, Nielsen, Price, Stenhouse, & Boyce, 2006; Northrup et al., 2012; Ordiz, Støen, Delibes, & Swenson, 2011). Based on this knowledge, we included a harmonic interaction term; $\sin\left(\frac{4*\pi*(\text{hour}-3)}{24}\right)$ which corresponds with peaks in activity during crepuscular hours.

2.6 | Model selection

We constructed two sets of candidate models representing alternative hypotheses. The first set did not include any movement-related covariates and can therefore be thought of as a traditional SSF (Table 1; Fortin et al., 2005), only accounting for changes in habitat selection. The second set incorporate movement covariates. Within each set, we begin with a null model that does not include trail or recreation effects (Table 1—*base model*). The remaining models become increasingly more complex by including distance to trail, and then interactions with probability of motorised and non-motorised occurrence, both in terms of habitat selection, and in the second set, movement (i.e., interacting with *lnSlength*). We based model selection (Burnham & Anderson, 2002) on individual grizzly bear-years. We calculated AIC weights for each of the competing models to identify changes in model parsimony through incorporating estimates of recreational activity and movement interactions. Lastly, we calculated mean AIC weight across bear-years for each model within each set. We used bear-year combinations because some bears were radiocollared for more than a single year and females reproductive class varied annually.

2.7 | Grizzly bear class responses to recreation

We classified individual bears as males, solitary females, and females with cubs. Females were categorised as either with cubs, solitary, or unknown based on field and capture observations from the year collared. We used a two-stage modelling approach to estimate class responses. First, we ran individual-level models and second, obtained coefficient values for the class response post hoc (Fieberg,

Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010; Prokopenko et al., 2017). To avoid pseudoreplication due to variation in sampling intensity of different bears, we bootstrapped coefficients by subsampling beta coefficients for each bear, not bear-year combination, x times, where $x = 2 \times$ number of individual bear-years in each class, and a mean coefficient was calculated. This approach ensured each bear had an equal probability of being included within the bootstrap sample. This was repeated 2,000 times for each beta coefficient, to obtain class-level median and associated confidence interval estimates (based on the 2.5th and 97.5th quantiles). Females where reproductive class could not be determined for that year (unknowns) were not included in the second stage of analysis.

2.8 | Relative selection strength and movement rate estimation

To identify changes in movement rates as a function of covariates, used the below equation:

$$\text{Selection-free movement rate} \left(\frac{\text{metres}}{\text{hour}} \right) = b_2 * [b_1 + \beta_{\ln \text{Length}} + (\beta_{(1...n)} * x_{(1...n)})]$$

where b_1 and b_2 are the tentative gamma shape and scale, respectively, $\beta_{\ln \text{Length}}$ is the estimated coefficient for $\ln \text{Length}$, and $\beta_{(1...n)}$ are the estimated coefficients for the interactions between covariates $x_{(1...n)}$ and $\ln \text{Length}$.

We calculated the $\ln$ -Relative Selection Strength ($\ln$ -RSS) using calculations outlined in Avgar, Lele, Keim, and Boyce (2017). For example, the $\ln$ -RSS as a function of $\ln$ distance to trail and high and low probability of motorised recreational occurrence is given by:

$$\ln\text{-RSS} = \ln \left\{ \left(\frac{h_{i(x_1)}}{h_{i(x_2)} - \Delta h_i} \right)^{[\beta_j + \beta_{ij} h_j(x_1)]} \right\}$$

where $h_{i(x_1)}$ is the value of distance to trail at location x_1 , Δh_i is the change in distance to trail between location x_1 and location x_2 , in this case the mean grizzly bear step length, β_j is the beta coefficient for $\ln$ distance to trail, β_{ij} is the beta coefficient for the interaction between $\ln$ distance to trail and probability of motorised activity, and $h_j(x_1)$ is the probability of motorised activity at location x_1 .

Lastly, as part of the second stage of the analysis, we calculated class-level changes in mean movement rate and $\ln$ -RSS using the same bootstrapping method used to obtain beta coefficient estimates.

TABLE 1 Sets of candidate models that represent competing hypotheses relating to the effects of recreational activity on grizzly bear habitat selection and movement. Bold text represents additional covariates relative to the base model. See Supporting Information Table S3 for description of variables

Model set	Model name	Covariates
Selection only	Base	food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$
	Trail	food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail}$ + $\ln \text{Dtrail:sin(hour)}$
	Motorised	food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail}$ + $\ln \text{Dtrail:sin(hour)}$ + $\ln \text{Dtrail: motorised_start}$
	Non-motorised	food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail}$ + $\ln \text{Dtrail:sin(hour)}$ + $\ln \text{Dtrail: non-motorised_start}$
	Complete	food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail}$ + $\ln \text{Dtrail:sin(hour)}$ + $\ln \text{Dtrail_start: motorised}$ + $\ln \text{Dtrail_start: non-motorised_start}$
Selection and movement	Base	$\ln \text{Slength}$ + $\ln \text{Slength:sin(hour)}$ + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$
	Trail	$\ln \text{Slength}$ + $\ln \text{Slength:sin(hour)}$ + food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail}$ + $\ln \text{Dtrail:sin(hour)}$ + $\ln \text{Slength: } \ln \text{Dtrail_start}$
	Motorised	$\ln \text{Slength}$ + $\ln \text{Slength:sin(hour)}$ + food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail: motorised_start}$ + $\ln \text{Slength: } \ln \text{Dtrail_start}$ + $\ln \text{Slength: motorised_start}$ + $\ln \text{Slength: } \ln \text{Dtrail_start: motorised_start}$
	Non-motorised	$\ln \text{Slength}$ + $\ln \text{Slength:sin(hour)}$ + food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail: non-motorised}$ + $\ln \text{Slength: } \ln \text{Dtrail_start}$ + $\ln \text{Slength: non-motorised_start}$ + $\ln \text{Slength: } \ln \text{Dtrail_start: non-motorised_start}$
	Complete	$\ln \text{Slength}$ + $\ln \text{Slength:sin(hour)}$ + food quality + food quality:sin(hour) + TRI + edge_in + edge_out + $\ln \text{Dstream}$ + $\ln \text{Droad}$ + $\ln \text{Droad:sin(hour)}$ + $\ln \text{Dtrail: motorised_start}$ + $\ln \text{Dtrail: non-motorised_start}$ + $\ln \text{Slength: } \ln \text{Dtrail_start}$ + $\ln \text{Slength: motorised_start}$ + $\ln \text{Slength: non-motorised_start}$ + $\ln \text{Slength: } \ln \text{Dtrail_start: motorised_start}$ + $\ln \text{Slength: } \ln \text{Dtrail_start: non-motorised_start}$

3 | RESULTS

3.1 | Model selection

Habitat selection-only models were included in our first model set. AIC weight for the complete model and models including interactions with probability of motorised and non-motorised occurrence did not increase model support relative to the base model (Figure 2a). When accounting for movement behaviour (second model set), models including probability of motorised and non-motorised recreational activity increased model support relative to the distance to trail model, with the complete model calculated to have the highest average AIC weight across all individual bear-year models (Figure 2b). Therefore, for the second stage of the analysis, we used the complete movement model.

3.2 | Grizzly bear class responses

Beta coefficient estimates obtained from individual bear-year models can be found in Supporting Information Table S5, which included seven male bear-years, nine solitary female bear-years, and nine female with cubs bear-years. Bootstrapped class-level estimates can be found in Table 2 and Supporting Information Figure S5.

3.3 | Response to trails and motorised recreation

Males and solitary females displayed weak to no avoidance for areas closer to trails, as confidence bounds for the beta coefficient estimate overlapped zero (Figure S5). Avoidance increased when the corresponding trail was associated with a high probability of motorised occurrence (Figure 3a,c). Females with cubs avoided trails, irrespective of associated motorised activity (Figure 3e).

We characterised the relationship between grizzly bear movement, distance to trail, and recreational activity in terms of: (a) changes in movement rate as a function of the probability of recreational activity on the nearest trail and (b) the effect of recreational activity on the relationship between movement rate and distance to trail. Irrespective of class and proximity to trail, grizzly bears increased their movement rates when the nearest trail had a high probability of motorised activity. This relationship was strongest for females with cubs, who displayed a threefold increase in movement rate (Figure 3f) when nearby motorised recreation was high relative to low. Bears tended to increase their movement rates when closer to trails, however this relationship varied based on class and recreational activity. Males increased their mean movement rate when the probability of motorised recreation was low, however this relationship flattened out when probability of motorised recreation was high (Figure 3b). Solitary females did not alter their movement rates relative to distance from trail, and this relationship was not influenced by motorised activity (Figure 3d). Females with cubs further increased their mean movement rate as proximity to high motorised activity trails decreased (Figure 3f).

3.4 | Response to trails and non-motorised recreation

We found a large difference in selection and movement rate estimates between trails with high motorised and non-motorised recreational activity. Rather than avoid non-motorised trails, male and solitary female bears increased selection of trails when the probability of non-motorised activity was high relative to low (Figure 4a,c). As with motorised recreation, most bears increased their movement rates when in the vicinity of trails with high non-motorised activity, however this increase was considerably lower. Only male bears displayed a sharp increase in movement as proximity to high non-motorised trails decreased (Figure 4b). Solitary females and females with cubs showed close-to-zero difference in movement rates when on high with respect to low non-motorised use trails (Figure 4d,f).

4 | DISCUSSION

We used iSSA, to model habitat selection by grizzly bears within a mechanistic movement-model framework (Avgar et al., 2016). Models that included probability of motorised and non-motorised activity as well as interaction terms characterising changes in movement behaviour improved model support. Emphasising how ignoring movement behaviour and instead focusing solely on habitat selection misses important behavioural changes relating to movement patterns (Abrahms et al., 2015; Ordiz et al., 2013).

Grizzly bears displayed highly variable responses to linear features and associated types and probabilities of recreational activity. Responses to human disturbance are complex (Elfström, Zedrosser, Støen, & Swenson, 2014; Rode et al., 2006; Sahlén, Ordiz, Swenson, & Støen, 2015), varying based on the gender and reproductive status of the individual. Previous work assessing the effects of outdoor recreation on brown bears has identified negative impacts associated with hiking, fishing, camping, and bear viewing (Fortin et al., 2016); however, the literature is sparse regarding the effects of motorised recreation (see Graves, 2002). We believe that this study is the first to document the separate effects of motorised and non-motorised recreation on grizzly bear habitat selection and movement. Our finding that grizzly bears' relationship with trails relies heavily on the type and probability of recreational activity is novel. Occurrence analyses using only trail camera data similarly found that black and grizzly bears showed reduced intensity of use trails with high motorised activity, yet increased their use of trails where non-motorised activity occurred (Ladle, Steenweg, Shepherd, & Boyce, 2018). This contrast in grizzly bear responses to two different forms of recreation is challenging to explain with the current data. However, it is likely due to a combination of a diminished fear response to non-motorised recreation coupled with factors that correlate with different forms of recreation. These include non-motorised recreation tending to occur in more rugged topography, thereby forcing wildlife such as bears onto trails, and higher quality food resources often coinciding with linear features such as trails (Finnegan, MacNearney, & Pigeon, 2018).

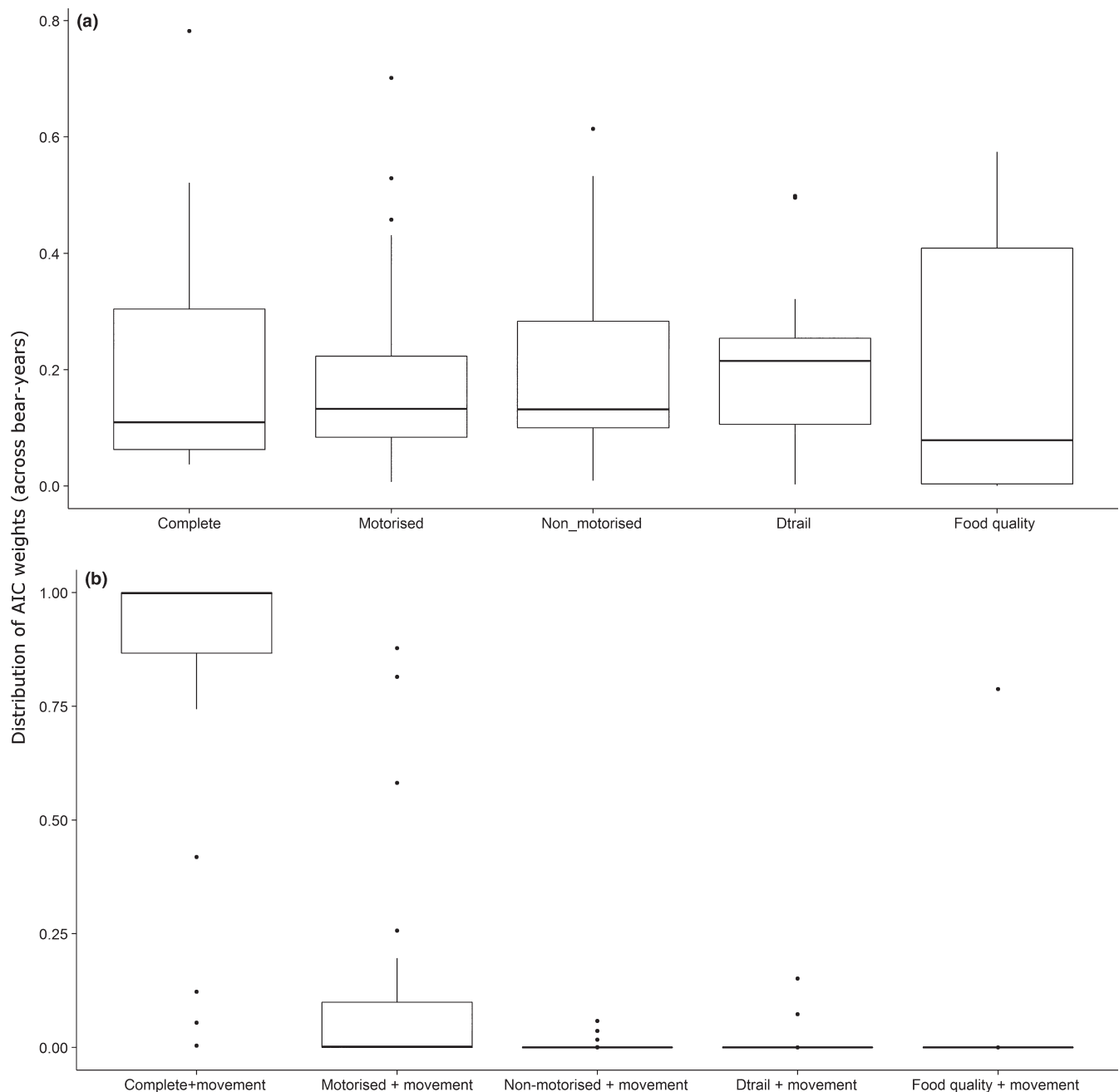


FIGURE 2 Boxplot showing the AIC weight distribution for models (Table 1) across all bear-years. (a) Model set without movement interaction coefficients (selection only), (b) Model set containing movement interaction terms (selection and movement). The central mark represents the median AIC weight across all bear-years, and the tails represent the 2.5th (lower) and 97.5th (upper) percentiles

The finding that our study bears did not show the same movement response to non-motorised activity as they did to motorised recreation further supports the hypothesis that they may elicit less extreme behavioural changes brought on by risk perceptions (Frid & Dill, 2002). Traffic volume alters grizzly bear responses to roads (Northrup et al., 2012; Roever et al., 2010), switching from selection of low-use roads to avoidance of medium- and high-use roads (Northrup et al., 2012). The absence of overall avoidance of high motorised recreation trails by females with cubs and the high variation in how individual mothers responses could be due to the unpredictability of

recreational trail use relative to more consistent and therefore predictable forms of human activity such as vehicle traffic. Rather than avoiding areas close to trails in response to recreation, it may be that mothers choose alternative avoidance behaviours such as drastically increasing their movement rates as we found here. The lack of “hiding” behaviour characterised by shorter movements when encountering human disturbances (Cristescu, Stenhouse, & Boyce, 2016) could be another symptom of the unpredictability of recreational use of trails. Habituation based on exposure of stimuli to bears is a further complication (Gunther & Biel, 1999; Jope, 1985), especially given that

TABLE 2 Coefficient estimates from the top movement model for grizzly bear movement (SL) and selection responses to roads, trails, and associated probability of motorised and non-motorised activity on trails, separated by grizzly bear class upper and lower values represent the 95% confidence (2.5th and 97.5th quantiles). Bold values represent estimates where confidence bounds did not overlap zero

Covariate	Males			Solitary females			Females with cubs		
	Median	Lower	Upper	Median	Lower	Upper	Median	Lower	Upper
<i>lnDroad</i>	-0.062	-0.070	-0.034	0.032	-0.040	0.088	0.361	0.156	0.765
<i>lnDtrail</i>	0.005	-0.104	0.166	-0.123	-0.296	0.075	0.146	-0.012	0.413
Motorised	0.024	0.018	0.026	0.030	0.016	0.047	0.002	-0.022	0.034
Non-motorised	-0.032	-0.037	-0.023	-0.015	-0.031	-0.013	-0.022	-0.027	-0.002
<i>lnSlength</i>	-0.445	-0.879	-0.325	-0.201	-0.554	-0.003	-0.336	-0.755	-0.253
<i>lnSlength: lnDtrail</i>	-0.029	-0.063	0.017	-0.085	-0.097	-0.058	-0.035	-0.074	-0.006
<i>lnSlength: motor</i>	0.013	-0.013	0.049	0.068	0.006	0.106	0.108	0.028	0.140
<i>lnSlength: non-motor</i>	0.065	0.024	0.101	-0.003	-0.023	0.011	-0.011	-0.063	0.018
<i>lnSlength: lnDtrail: motor</i>	0.003	0.001	0.011	-0.001	-0.006	0.008	-0.002	-0.019	0.012
<i>lnSlength: lnDtrail: non-motor</i>	-0.006	-0.011	-0.001	0.006	0.003	0.011	0.003	-0.001	0.012

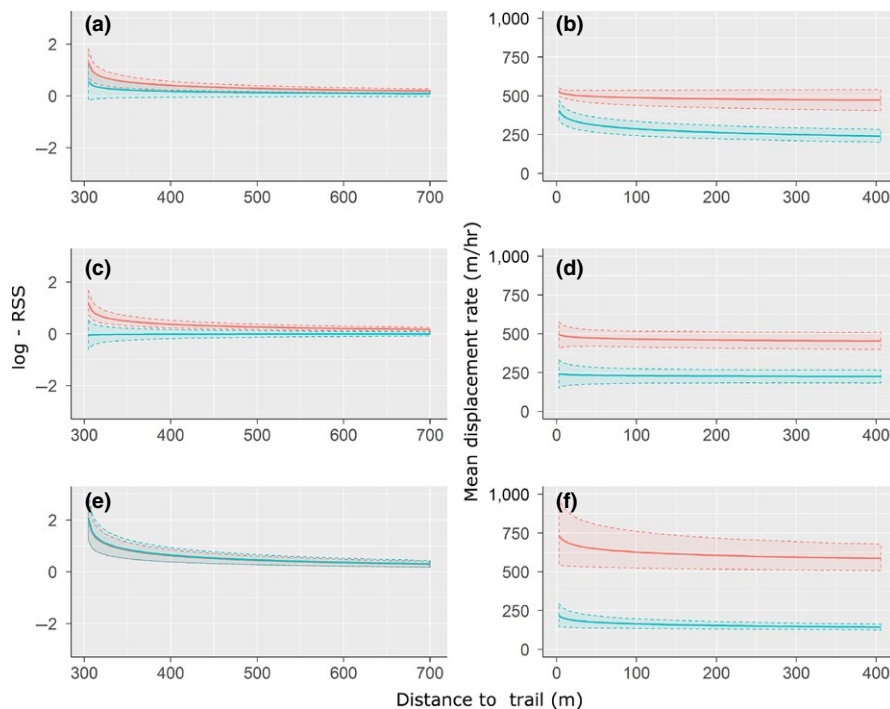


FIGURE 3 *ln*-RSS and mean movement rate (metres/hour) for males (a, b), solitary females (c, d), and females with cubs (e, f) for high (95th percentile of available values; red) and low (5th percentile of available values; blue) probability of motorised recreational activity. Positive *ln*-RSS values represent relative selection for location $h_{i(x_1)}$ relative to $h_{i(x_1)} - \Delta h_i$ (avoidance of trails) while negative values represent relative selection for $h_{i(x_1)} - \Delta h_i$ (selection for trails)

our sampling spanned protected (low motorised, high non-motorised) and public (high, motorised, low non-motorised) land. Further understanding will require greater temporal resolution of both bear movement and the timing and location of human disturbances (Ordiz et al., 2013). In terms of the effects of such behavioural responses on grizzly bear physiology and population demographics, both avoidance and increased movement rates likely diminish their ability to exploit nutrient-rich foods close to or on trails due to increased vigilance and displacement (Ciuti et al., 2012). Additional information quantifying bear foods found on trails will highlight the potential nutritional effect this loss of foraging opportunities might have for grizzly bears.

Identifying physiological responses related to survival and reproduction such as stress (French, González-Suárez, Young, Durham, & Gerber, 2011) as seen in grizzly bears as a response to road disturbance (Bourbonnais, Nelson, Cattet, Darimont, & Stenhouse, 2013) and wolf responses to winter recreation (Creel et al., 2002), would help to inform wildlife managers of the importance that access management can play in grizzly bear recovery (Lamb et al., 2018).

We showed that some variation among individuals was a consequence of reproductive status, which can result in different trade-offs between perceived risks (Gomes & Sarrazin, 2016). For example, intra-species dynamics, such as male competition, or sexual segregation can influence

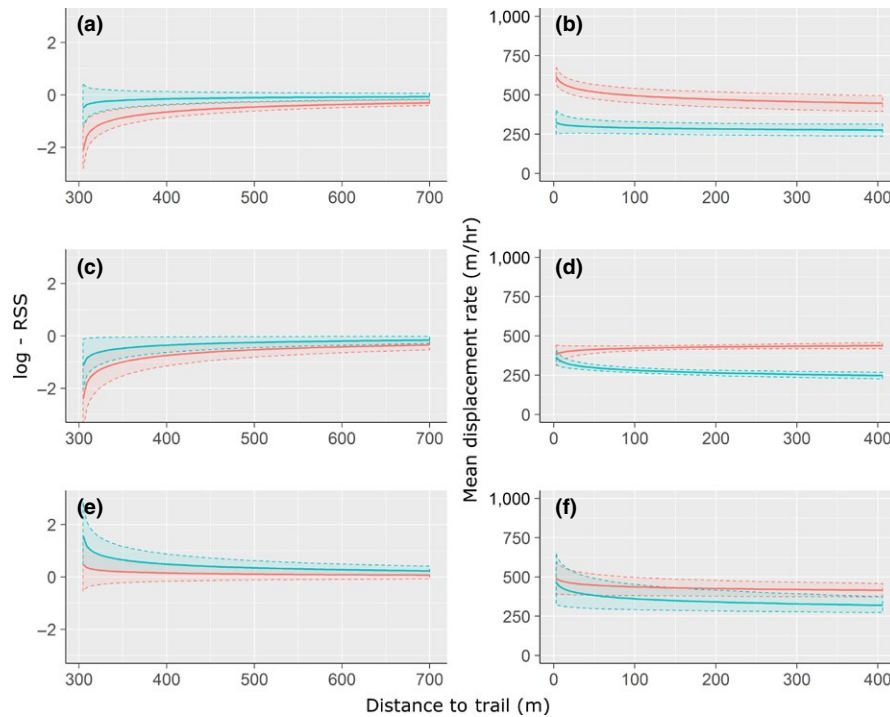


FIGURE 4 $\ln$ -RSS and mean movement rate (metres/hour) for males (a, b), solitary females (c, d), and females with cubs (e, f) for high (95th percentile of available values; red) and low (5th percentile of available values; blue) probability of non-motorised recreational activity. Positive $\ln$ -RSS values represent relative selection for location $h_{i(x_1)}$ relative to $h_{i(x_1)} - \Delta h_i$ (avoidance of trails) while negative values represent relative selection for $h_{i(x_1)} - \Delta h_i$ relative to $h_{i(x_1)}$ (selection for trails)

how an individual perceives trails and recreation relative to other dangers on the landscape (Berger, 2007). Previous studies have shown that male bears are more wary of human activity (Rode et al., 2006; Steyaert et al., 2016), however our results did not support this conclusion. We want to emphasise the high variability between individuals within each reproductive status, resulting in large confidence intervals and leading to multiple coefficient estimates overlapping zero. Further analyses that incorporate a greater number of individuals might examine functional responses relating to habitat selection and movement, and how variable exposure to human disturbance, learning (Morehouse, Graves, Mickle, & Boyce, 2016; Nielsen, Shafer, Boyce, & Stenhouse, 2013), and behavioural plasticity contribute to individual variation (Leclerc et al., 2015).

5 | CONCLUSIONS

Including measures of spatio-temporally variable human use and animal movement data can improve inference when assessing effects of human recreation on behaviour. Describing the landscape as static summary attributes hides important aspects of animal responses, thereby potentially masking conservation alternatives. Although we show that grizzly bears respond to more than just the presence of trails, additional information on recreational use of trails is expensive and time-consuming to collect. Further methods that model potential activity based on landscape variables, such as trail vegetation and industrial footprint (see Hornseth et al. 2018), could allow expansion of current recovery plan targets that

rely primarily on road densities. Our observed responses by grizzly bears to recreational activity suggest that management actions to restrict human access, specifically for motorised recreation, could benefit grizzly bears; although further information is required to determine if human-recreational activity is ultimately reducing grizzly bear survival or reproduction (Lamb et al., 2018). Linear features are associated with increased bear foods (Finnegan et al., 2018; Roever et al., 2010) and lack of selection for, and reduced intensity of use by bears of trails with motorised recreational activity could result in reduced foraging opportunities and possible exploitation by the more tolerant black bears (Ladle, Steenweg, et al., 2018). Controlling recreational access, particularly motorised activity, in areas with high-quality bear foods would be an important step in dampening potential negative consequences of human recreation, and continued monitoring of type and frequency of recreational access by both park and public land managers is required to fully understand the long-term influences of access management actions.

ACKNOWLEDGEMENTS

We thank funding agencies that contributed to the work: Alberta Biodiversity Monitoring Institute, Alberta Conservation Association, Alberta Environment and Parks, International Bear Association, Mountain Equipment Coop, Parks Canada, Safari Club International: Northern Alberta Chapter, T.D.: Friends of the Environment. G.B.S. and A.L. thank Terry Larsen, Terry Winkler, John Saunders, and Bernie Goski for their field support.

AUTHORS' CONTRIBUTIONS

A.L., T.A., M.W., and M.S.B. conceived the ideas and designed the methodology; A.L., G.B.S., and S.E.N. collected the data; A.L. and T.A. analysed the data; A.L. led the writing of the manuscript; and all authors contributed to revisions of drafts and gave final approval of the manuscript for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.nq68420> (Ladle et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Ladle A, Avgar T, Wheatley M, Stenhouse GB, Nielsen SE, Boyce MS. Grizzly bear response to spatio-temporal variability in human recreational activity. *J Appl Ecol*. 2018;00:1–12. <https://doi.org/10.1111/1365-2664.13277>